

UDC 574.5(262.5)

**STATE OF THE ICHTHYO-, MESO-, AND MACROPLANKTON COMPLEXES
OFF THE CRIMEAN PENINSULA (THE BLACK SEA)
IN CONNECTION WITH THE HYDROBIOLOGICAL REGIME FEATURES
IN OCTOBER 2016**

© 2023 T. N. Klimova¹, B. E. Anninsky¹, A. A. Subbotin¹, I. V. Vdodovich¹,
and P. S. Podrezova

¹A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS, Sevastopol, Russian Federation
E-mail: tnklim@mail.ru

Received by the Editor 14.07.2020; after reviewing 20.11.2020;
accepted for publication 16.02.2023; published online 31.05.2023.

The changes in the Black Sea hydrological regime recorded since 1990s have altered the state of epipelagic complexes of marine organisms, primarily the seasonal variability of their biological cycles. This largely affected the spawning phenology of natural fish populations, as well as ichthyoplankton species diversity and spatial distribution, and established trophic relationships within the plankton community. The interactions between links of the food chain in epipelagic complexes, as well as their seasonal and interannual variations, ultimately affect fish spawning efficiency, especially that of mass commercial species, and determine the replenishment of their new generations. To establish ichthyoplankton species composition, abundance, and spatial distribution, the study was carried out in shelf and open areas of the Black Sea (the Crimean coast) during the 89th cruise of the RV “Professor Vodyanitsky” (30 September – 19 October, 2016). Eggs and larvae of fish and the biomass of meso- and macroplankton were analyzed. Ichthyoplankton and macroplankton were sampled with Bogorov–Rass net (inlet area of 0.5 m²; mesh size of 300 μm) by vertical sampling technique. In the shelf areas, sampling was carried out from the bottom up to the surface, while in the deep-sea areas, from the lower boundary of the oxygen zone up to the surface. Ichthyoplankton was fixed with 4% neutralized formaldehyde and investigated under microscope to determine taxonomic composition and, if possible, to analyze contents of fish larvae intestines. Species composition and spatial distribution of ichthyo-, meso-, and macroplankton in October 2016 were studied, as well as the feeding of fish larvae of the Black Sea off the Crimean coast. The research covered the initial phase of the autumn hydrological season. In samples, eggs and larvae of 9 warm-water fish species and 6 temperate-water fish species were found. The mean abundance of eggs was 2.92 ind.·m⁻², and the mean abundance of larvae was 3.56 ind.·m⁻². The low percentage (30%) of dead eggs of the warm-water European anchovy *Engraulis encrasicolus* and the presence of its different-sized larvae evidenced the ongoing productive spawning. The zooplankton biomass increased from the shelf towards the deep-sea areas. Small plankton organisms prevailed in the shelf areas providing enough food for fish larvae to survive. Despite the significant biomass of gelatinous plankton feeders in October 2016, their effect on ichthyoplankton complexes of the Black Sea was apparently minor.

Keywords: ichthyoplankton, mesoplankton, gelatinous macroplankton, feeding of fish larvae, species diversity, spatial distribution, Black Sea

Climate change is one of the main factors affecting spawning phenology, spatial distribution, species structure, and trophic relationships in marine ecosystems [Richardson et al., 2009; Robinson et al., 2014; Turan et al., 2016; Vinogradov et al., 1999]. An increase in temperature in seas with a well-pronounced seasonality, *inter alia* in the Black Sea, led to an inversion of life cycles, a shift in the reproduction timing, and an expansion in the species diversity of hydrobionts at all trophic levels, from primary producers to predators [Auth et al., 2017; Fincham et al., 2013; McQueen, Marshall, 2017; Parsons, Lalli, 2002; Purcell et al., 2007]. The autumn hydrological season (October–November) is usually characterized by a restructuring of the surface current system from the summer type of circulation to the winter one; also, it is distinguished by maximum temporal gradients of the sea surface temperature [Artamonov et al., 2018; Troshchenko, Subbotin, 2018]. Interestingly, autumn ichthyoplankton can be formed by both warm-water and temperate-water fish species. In October, spawning of temperate-water fish begins (their eggs prevail in ichthyoplankton), and spawning of warm-water fish continues. However, small abundance of alive eggs and the absence of larvae of younger age groups indicate that the spawning is unproductive. In October, on a shelf and in deep-sea areas, eggs of temperate-water species *Sprattus sprattus* (Linnaeus, 1758) and *Merlangius merlangus* (Linnaeus, 1758) are common, as well as larvae of *Engraulis encrasicolus* (Linnaeus, 1758) of older age groups and juveniles of *Syngnathus schmidtii* Popov, 1928. Eggs, larvae, and juveniles of coastal species brought there by a current are found singly [Dekhnik, 1973; Dekhnik, Pavlovskaya, 1979; Gordina et al., 1991; Klimova et al., 2010].

For gelatinous macroplankton, the autumn hydrological season is important for several reasons. For the scyphomedusa *Aurelia aurita* (Linnaeus, 1758), it is a significant stage characterizing the success of spring generation; for *Mnemiopsis leidyi* A. Agassiz, 1865, it is the time of maximum elimination under the pressure of *Beroe ovata* Bruguière, 1789 [Finenko et al., 2003]. For many species of mesozooplankton, October is a period of active growth and reproduction against the backdrop of weakened predation by ctenophores. Although, with a decrease in *M. leidyi* abundance in a plankton community, a trend towards a rise in the trophic role of jellyfish was recorded; its predatory pressure on zooplankton in recent years usually does not reach a threshold critical for maintaining prey populations [Anninsky et al., 2016].

Unfortunately, the Black Sea ichthyoplankton in the shelf and open waters at the beginning of the autumn hydrological season was practically not analyzed due to its low abundance and species diversity [Dekhnik, Pavlovskaya, 1979; Klimova, Podrezova, 2018; Klimova et al., 2010, 2019]. The latest published data of ichthyo-, meso-, and macroplankton studies in the western sector of the Black Sea, including the area off the Crimean Peninsula, date back to October 2005 [Klimova et al., 2010]. Therefore, the results of complex plankton research carried out in October 2016 both in the shelf and deep-sea areas of the Black Sea off the Crimean Peninsula, from Cape Tarkhankut to the Kerch Strait, during the transition from the summer hydrological season to the autumn one are of particular interest.

The aim of the work is to analyze species composition, abundance, and spatial distribution of ichthyo-, meso-, and gelatinous macroplankton in October 2016 against the backdrop of climatic variability of the Black Sea hydrological regime.

MATERIAL AND METHODS

Plankton studies were carried out during the 89th cruise of the RV “Professor Vodyanitsky” (September 30 – October 19, 2016) in the shelf and deep-sea areas of the Black Sea off the Crimean Peninsula in the western (Cape Tarkhankut – the city of Alupka) and eastern sectors (Cape Meganom – the Kerch Strait) in the water area with coordinates from N43.22° to N45.15° and from E31.24° to E36.26° (Fig. 1).

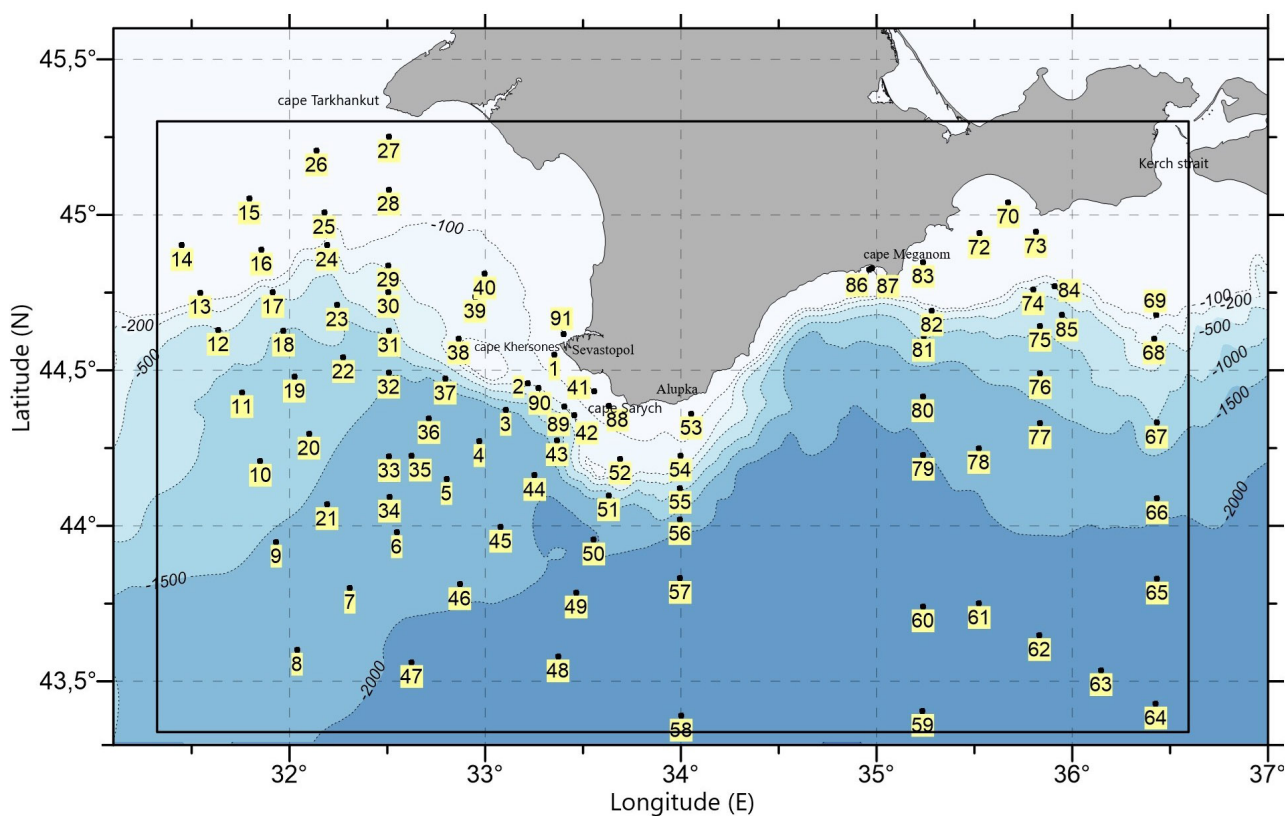


Fig. 1. Schematic map of sampling stations in the 89th cruise of the RV “Professor Vodyanitsky”

Ichthyo- and macroplankton, as well as large crustacean plankton (*Calanus euxinus* Hulse-mann, 1991) was sampled with an inverse conical Bogorov–Rass net (BR-80/113; inlet area of 0.5 m²; mesh size of 300 μm). Total mesozooplankton was sampled with a Juday net (inlet area of 0.1 m²; mesh size of 112 μm). Plankton was sampled by vertical hauls from the bottom to the sea surface in the shelf area and from the lower boundary of the oxygen zone ($\sigma_t = 16.2$, according to Sea-Bird 911plus CTD) to the sea surface in open waters.

With BR-80/113, sampling was carried out in one replication at 62 stations, including 39 stations in the deep-sea (> 200 m) epipelagic zone, 19 stations on the outer shelf (50–200 m), and 4 stations on the inner shelf (< 50 m). Large gelatinous macroplankton was filtered through a sieve with a 4-mm mesh from freshly taken samples and analyzed *in vivo* onboard the RV for taxonomic composition, abundance, oral-aboral body length of ctenophores, and umbrella diameter of jellyfish. The remaining plankton fraction, *inter alia* small (< 5 mm) gelatinous, meso-, and ichthyoplankton, was fixed and processed under stationary conditions. Species composition and abundance of early size–age stages of gelatinous, large copepods, and ichthyoplankton were determined under MBS-10 at a magnification of 8 × 2 and 8 × 4. The body weight of the organisms was calculated using known linear weight ratios [An-ninsky et al., 2013]. Fish eggs and larvae were identified according to [Dekhnik, 1973; D’Ancona, 1933; Russell, 1976].

Mesoplankton was sampled with a Juday net in duplicate on the outer shelf (sta. 1, N44.56°, E33.34°) and in the deep-sea areas (sta. 3, N44.37°, E33.07°), fixed, and identified under stationary conditions under a microscope (Fig. 1).

All plankton samples were fixed in 4% (v/v) formaldehyde buffered with borates.

The study of fish larvae feeding was carried out on a fixed material according to the technique of L. Duka and V. Sinyukova [1976]. Larvae were divided into size groups: *E. encrasicolus*, in accordance with [Dekhnik, 1960]; *S. schmidtii*, in accordance with [Gordina et al., 1991].

Using the formulas proposed by Yu. Odum [1986], diversity indices were calculated: species diversity [Shannon, Weaver, 1949], species richness [Simpson, 1949], dominance [Margalef, 1958], and evenness [Pielou, 1966].

To analyze the hydrological regime and the structure of surface currents, we used expeditionary data of vertical profiling with Sea-Bird 911plus CTD and data of acoustic Doppler current profiler ADCP 300 kHz WorkHouse [Artamonov et al., 2018]. Additionally, we used material of satellite observations of the sea surface temperature (hereinafter SST); maps of geostrophic and surface currents [Copernicus Marine Service, 2019; Marine Portal of the Marine Hydrophysical Institute, 2020; National Center for Environmental Information, 2018] for August–October 2016; and data of regular observations on water temperature and salinity in the coastal areas of Sevastopol and Karadag [Troshchenko, Subbotin, 2018; Troshchenko et al., 2019].

The relationship between the distribution of the studied plankton components and certain abiotic environmental factors (seawater temperature and salinity) was measured by ANOSIM in PAST 4.0 statistical program.

RESULTS

Features of the hydrological regime. The period of the survey (September 30 – October 19, 2016) corresponded to the initial phase of the autumn hydrological season. Intensive cooling of the sea upper layer with temperature gradients of more than 3–3.5 °C *per* month began in the third 10-day period of September and lasted until mid-December [Artamonov et al., 2018; Copernicus Marine Service, 2019; Marine Portal of the Marine Hydrophysical Institute, 2020; National Center for Environmental Information, 2018; Troshchenko, Subbotin, 2018; Troshchenko et al., 2019]. The autumn hydrological season is characterized by a restructuring of the surface current system from the summer type of circulation to the winter one. However, satellite observation data for the previous period and the time of the survey, geostrophic circulation calculations [Copernicus Marine Service, 2019; Marine Portal of the Marine Hydrophysical Institute, 2020; National Center for Environmental Information, 2018], and instrumental observations [Artamonov et al., 2018] indicate that the surface water circulation system in the study area in the first 10-day period of October 2016 corresponded to the summer one, with the preservation of its main features [Klimova et al., 2019]. Active meandering of the Rim Current jet along the continental slope contributed to the preservation of two quasi-stationary synoptic formations: the Sevastopol anticyclone (hereinafter SevAC) over the great topographic trough west of the Heracles Peninsula and the Crimean anticyclone (hereinafter CrAC) on the shelf south of the Feodosiya Gulf [Ivanov, Belokopytov, 2011]. To the south of the Rim Current area, in the western and eastern sectors of the survey, peripheral areas of western and eastern cores of the main cyclonic gyre (hereinafter MCG) with weak and unstable currents were traced (Fig. 2).

The general picture of the seasonal spatial distribution of the SST with a tendency to increase its values from the northwest (areas of the earliest and most intense SST decrease) to the east was disturbed by a strong storm on 9–10 October (Fig. 2). As a result, in the second 10-day period of October, background SST values throughout the study area decreased by 2–3 °C [Artamonov et al., 2018].

Thus, in the western sector, before the storm, the site of increased SST values (+21.0...+21.5 °C) corresponded to the SevAC zone; the site of minimum SST values (+19.0...+19.5 °C) was limited to a small shelf zone in the northwestern sea area [Artamonov et al., 2018] (Fig. 3).

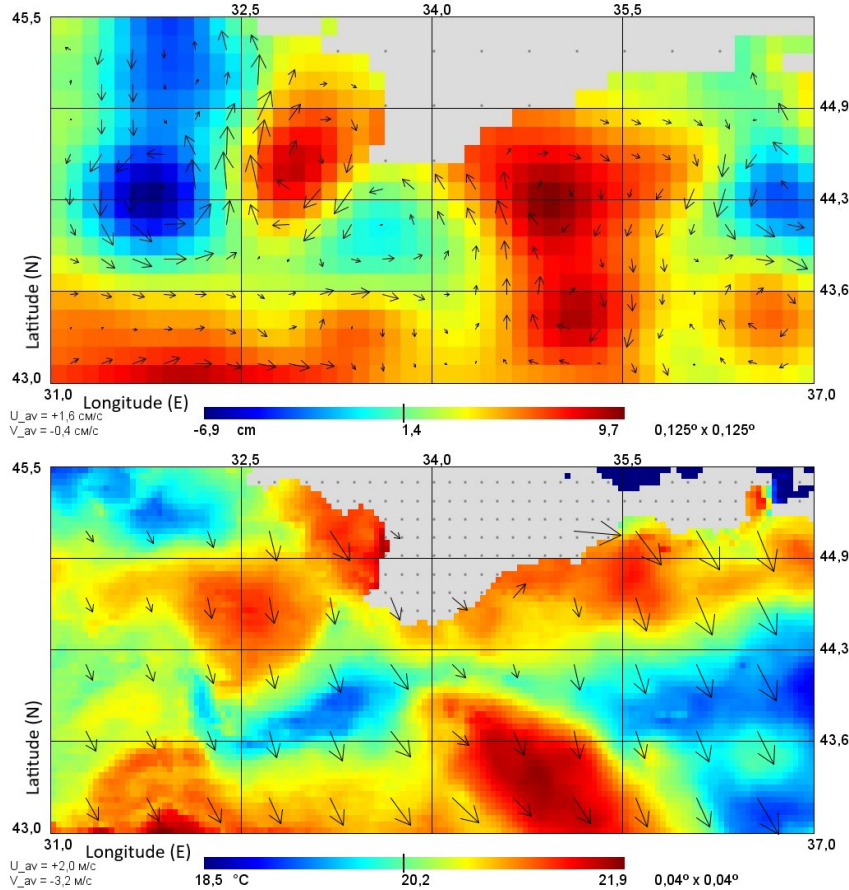


Fig. 2. Compositional maps of geostrophic currents (top) and sea surface temperature (bottom), 20–30 September, 2016 [Copernicus Marine Service, 2019; National Center for Environmental Information, 2018]

In the eastern sector of the survey, ichthyoplankton was sampled in the second 10-day period of October 2016. Background SST values dropped after the storm to +16...+16.5 °C. In the shelf area from Cape Sarych to Sevastopol, the values decreased to +17 °C (Fig. 4).

Against the backdrop of seasonal cooling of the sea surface layer and intensification of wind-wave mixing, the thickness of the upper quasi-homogeneous layer increased everywhere compared to that of the summer period. The maximum values of the thicknesses of the upper quasi-homogeneous layer (up to 28–30 m) were registered in the SevAC and CrAC zones, while the minimum values (up to 12–16 m) were recorded in areas of water rise on the northern peripheries of the western and eastern cores of the MCG.

Over the entire study area, cold intermediate layer differed significantly from “classical” one [Ivanov, Belokopytov, 2011] in terms of the core temperatures. The range of its spatial temperature variability was 8.30–8.52 °C: up to 8.30–8.36 °C (minimum values), in the areas of water rise on the MCG periphery; up to 8.42–8.44 °C, in the SevAC; and up to 8.5–8.52 °C, in CrAC. The variability of the depth of the cold intermediate layer core also corresponded to the position of main circulation structures. The maximum depth (up to 85–90 m) was noted above the great topographic trough in the SevAC zone; the values up to 80 m were recorded in the CrAC zone; and the minimum depth was registered on the periphery of the western (up to 35–40 m) and eastern (up to 40–45 m) cores of the MCG.

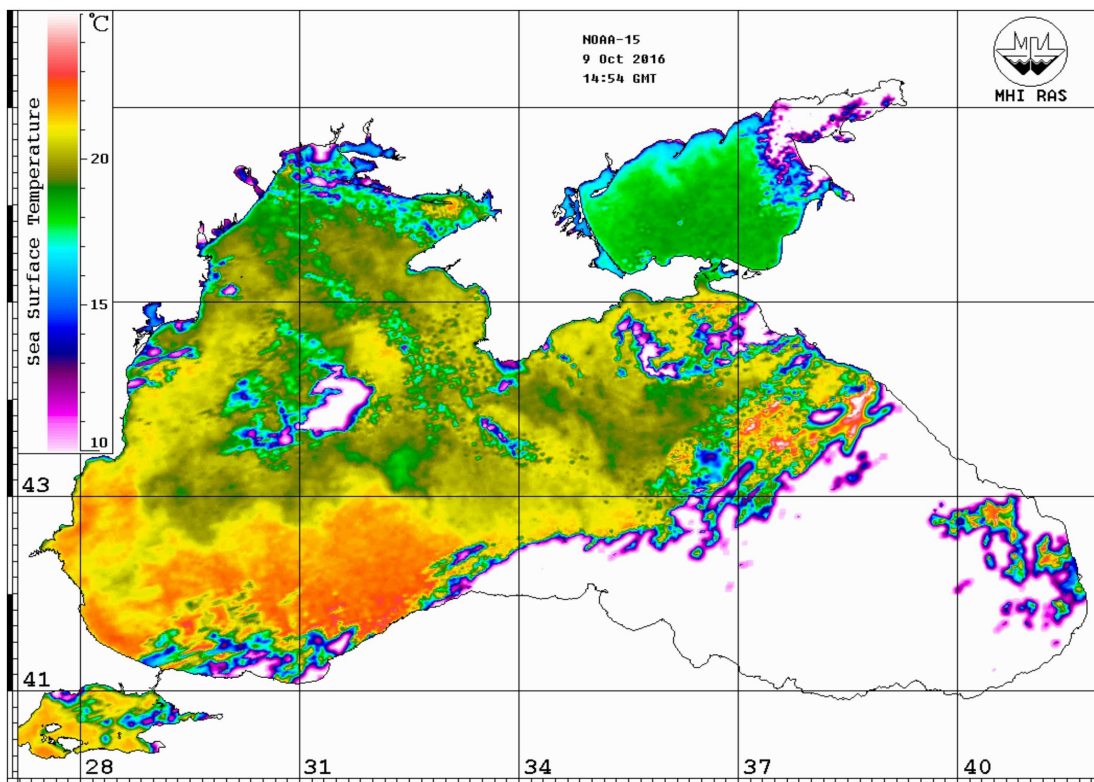


Fig. 3. Sea surface temperature according to NOAA-15 data (09.10.2016)

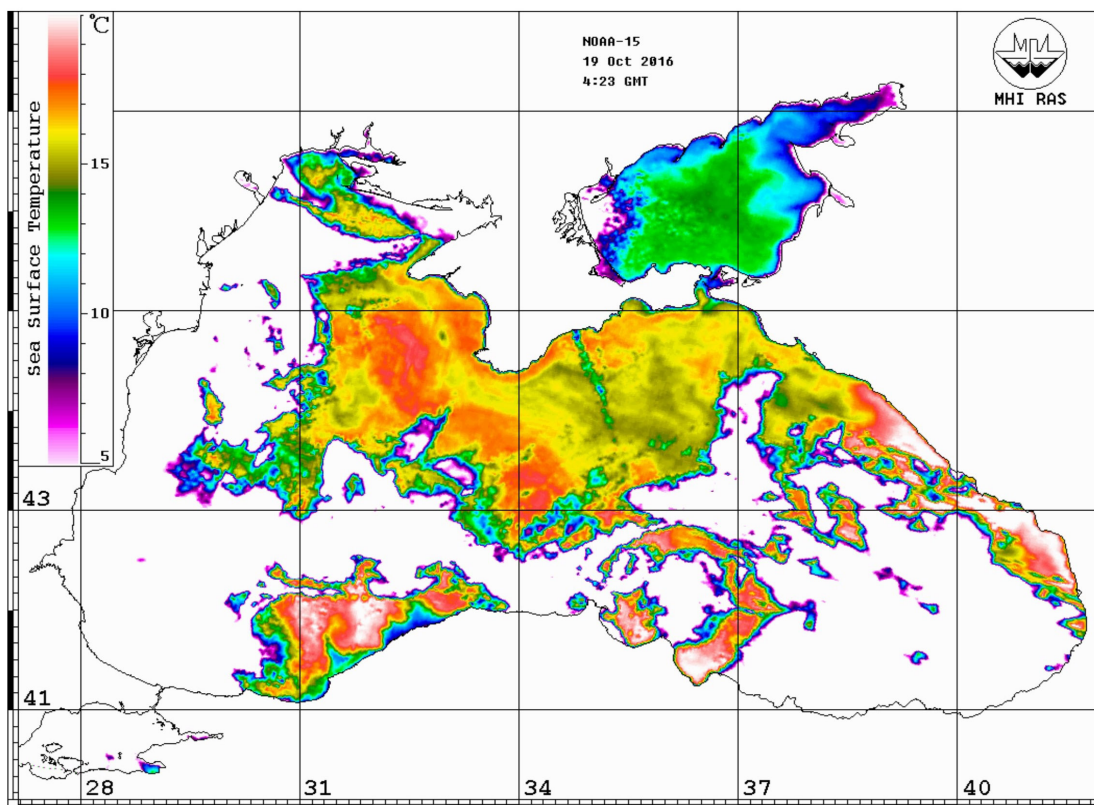


Fig. 4. Sea surface temperature according to NOAA-15 data (19.10.2016)

The spatial distribution of salinity of surface waters was determined by the proximity to the main sources of desalination, the direction of advection of desalinated waters, and the position of quasi-stationary dynamic formations. Low water salinity (< 18‰) was recorded in the SevAC and CrAC zones, where transformed desalinated waters from the northwestern sea area and from the Kerch Strait occurred. The most saline waters (18.45–18.50‰) corresponded to the peripheral areas of the MCG.

Ichthyoplankton. In ichthyoplankton, eggs and larvae of 15 fish species representing 9 families were identified (9 species of warm-water and 6 species of temperate-water fish). The mean abundance of eggs was 2.92, and larvae, 3.56 ind.·m⁻² (Table 1).

Table 1. Species composition and relative abundance (%) of fish eggs and larvae off the Crimean Peninsula in October 2016

Species	Eggs	Larvae
Family: Engraulidae		
<i>Engraulis encrasicolus</i> (Linnaeus, 1758)	27.0	39.4
Family: Clupeidae		
<i>Sprattus sprattus</i> (Linnaeus, 1758)	42.5	0.8
Family: Gadidae		
<i>Merlangius merlangus</i> Linnaeus, 1758	20.5	5.3
<i>Trisopterus luscus</i> (Linnaeus, 1758)	4.5	10.7
Gadidae sp.	–	3.6
Family: Lotidae		
<i>Gaidropsarus mediterraneus</i> (Linnaeus, 1758)	4.5	0.8
<i>Molva macrophthalma</i> (Rafinesque, 1810)	–	0.8
Family: Syngnathidae		
<i>Syngnathus schmidti</i> Popov, 1928	–	28.1
Family: Scorpaenidae		
<i>Scorpaena porcus</i> Linnaeus, 1758	–	0.8
Family: Gobiidae		
<i>Pomatoschistus marmoratus</i> (Risso, 1810)	–	0.8
<i>Pomatoschistus minutus</i> (Pallas, 1770)	–	3.7
<i>Pomatoschistus pictus</i> (Malm, 1865)	–	1.8
<i>Gobius</i> sp.	–	0.8
Family: Mugilidae		
<i>Mugil cephalus</i> Linnaeus, 1758	1.0	1.8
Family: Bothidae		
<i>Arnoglossus kessleri</i> Schmidt, 1915	–	0.8
Mean abundance in a catch, ind.·m ⁻²	2.92 ± 1.64	3.56 ± 1.63

In the western sector of the survey (Cape Tarkhankut – the city of Alupka), ichthyoplankton was sampled in the first 10-day period of October, when the surface water circulation system, as mentioned earlier, corresponded to the summer one, with the preservation of its main features. At seawater temperature reaching +19.0...+21.5 °C, eggs and larvae of 10 fish species were recorded; their mean abundance was 3.4 and 4.7 ind.·m⁻², respectively (Fig. 5).

Above the depths of more than 50 m, *S. sprattus* spawned; maximum abundance of its eggs, 22 ind.·m⁻², was recorded near the Cape Khersones above a depth of 92 m. In addition to *M. merlangus* (a common representative of the family Gadidae), eggs and larvae were found, which we identified

as *Trisopterus luscus* (Linnaeus, 1758) (Table 2). This cod species has been described for the North and Mediterranean Seas [Alonso-Fernández et al., 2010; D’Ancona, 1933; Russell, 1976]; there, its eggs and larvae are noted throughout the year with maximum abundance from October to May.

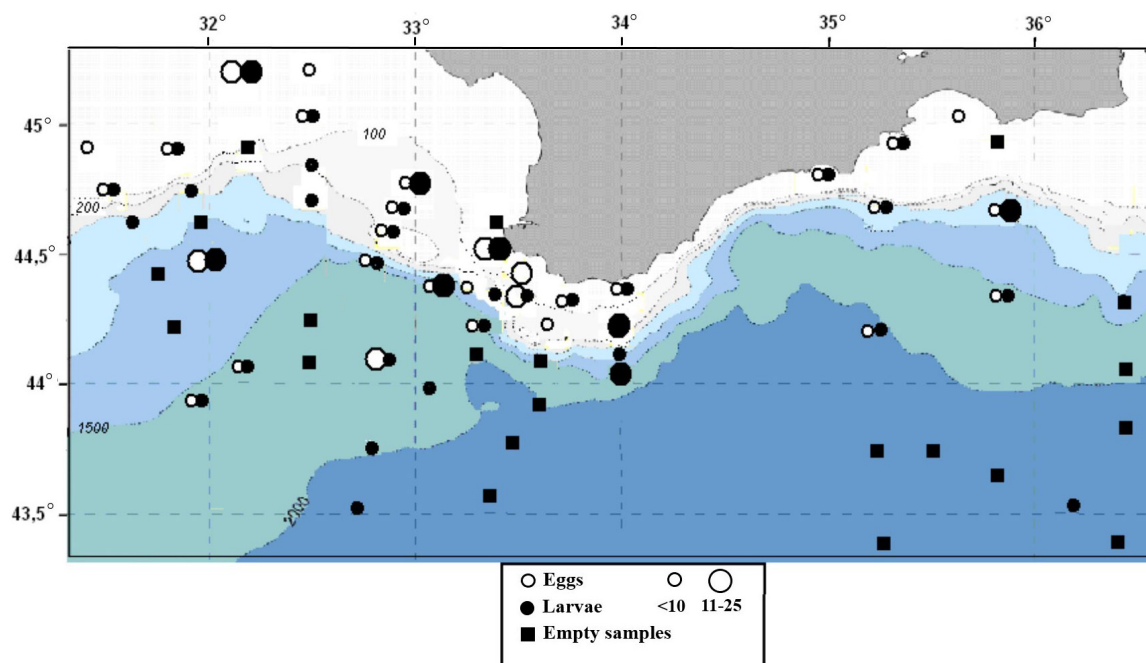


Fig. 5. Schematic map of ichthyoplankton distribution (ind. \cdot m $^{-2}$) in October 2016

Table 2. Ichthyoplankton species composition and mean abundance (ind. \cdot m $^{-2}$) in several areas of the Black Sea (2016)

Species	Cape Tarkhankut – the city of Alupka				Cape Meganom – the Kerch Strait	
	30.09–09.10		19.10		10.10–17.10	
	Eggs	Larvae	Eggs	Larvae	Eggs	Larvae
<i>Engraulis encrasicolus</i>	1.2	2.1	–	–	–	–
<i>Sprattus sprattus</i>	1.4	–	2.0	–	0.6	0.1
<i>Merlangius merlangus</i>	0.5	–	0.5	–	0.9	0.7
<i>Trisopterus luscus</i>	0.2	0.5	–	1.0	–	–
Gadidae sp.	–	0.2	–	–	–	–
<i>Gaidropsarus mediterraneus</i>	–	–	–	–	0.5	0.1
<i>Molva macrophthalma</i>	–	–	–	0.5	–	–
<i>Mugil cephalus</i>	0.1	0.1	–	–	–	0.1
<i>Syngnathus schmidti</i>	–	1.5	–	0.5	–	0.4
<i>Scorpaena porcus</i>	–	0.1	–	–	–	–
<i>Pomatoschistus marmoratus</i>	–	–	–	–	–	0.1
<i>Pomatoschistus minutus</i>	–	0.1	–	–	–	0.1
<i>Pomatoschistus pictus</i>	–	0.1	–	–	–	0.1
<i>Gobius</i> sp.	–	–	–	0.5	–	–
<i>Arnoglossus kessleri</i>	–	–	–	–	–	0.1
Mean abundance	3.4	4.7	2.5	2.5	2.0	1.8

Out of warm-water species, the European anchovy *E. encrasicolus* continued its spawning. It was productive, as evidenced by the presence in samples of live eggs at different stages of development and larvae on yolk, mixed, and external nutrition. The proportion of dead eggs in samples did not exceed 30%. Maximum abundance of the European anchovy eggs (18.0 ind. \cdot m⁻²) was registered on the Cape Kherstones traverse; of larvae (14 ind. \cdot m⁻²), at Cape Tarkhankut. In addition to the anchovy, samples contained larvae of gobies of the genus *Pomatoschistus* (*P. minutus* and *P. pictus*), flathead grey mullet *Mugil cephalus* Linnaeus, 1758, pelagic pipefish *S. schmidti*, and black scorpionfish *Scorpaena porcus* Linnaeus, 1758 (Table 2, Fig. 5).

In the second 10-day period of October, ichthyoplankton was sampled at 17 stations in the eastern sector of the survey (Cape Meganom – the Kerch Strait) after a sharp decrease in SST values (Fig. 5). There, eggs and larvae of 9 fish species were identified. The mean abundance of eggs was 2.0, and the mean abundance of larvae was 1.8 ind. \cdot m⁻² (Table 2). At coastal stations, in ichthyoplankton, in addition to eggs of the temperate-water *Gaidropsarus mediterraneus* (Linnaeus, 1758), larvae of warm-water species were registered – gobies of the genus *Pomatoschistus* and scaldback *Arnoglossus kessleri* Schmidt, 1915. At stations on the slope of depths, ichthyoplankton was mainly represented by eggs and larvae of fish species common for the winter spawning season – *M. merlangus*, *S. sprattus*, and *G. mediterraneus*. In ichthyoplankton, there were no European anchovy eggs and larvae. Out of warm-water species, single *S. schmidti* juveniles were caught, as well as larvae of gobies, which were probably brought there by the current along the eastern periphery of the CrAC due to increased northeast winds [Marine Portal of the Marine Hydrophysical Institute, 2020]. Above depths of more than 2,000 m, only at 1 out of 8 surveyed stations, *S. schmidti* larva was recorded.

At the end of the second 10-day period (on 19 October, 2016), 4 stations were surveyed from the city of Sevastopol to Cape Sarych in the depth range 73–314 m. There, in contrast to the SST in the first 10-day period of October, the SST no longer exceeded +17 °C. In ichthyoplankton, eggs and larvae of only 6 fish species were registered (with the mean abundance of ~ 2.5 ind. \cdot m⁻²) (Table 2). Out of warm-water species, single specimens of *Gobius* sp. larvae were found, and *S. schmidti* juveniles were noted. Temperate-water species were represented by eggs of *S. sprattus* and *M. merlangus*, as well as by larvae of Mediterranean predators that have recently invaded the Black Sea – *T. luscus* and *Molva macrophthalma* (the family Lotidae) [D'Ancona, 1933; Russell, 1976]. Those were caught above a depth of ~ 300 m seaward of the Laspi Bay (Table 2). In recent years, single larvae of these species are regularly recorded off the Crimean Peninsula from Cape Tarkhankut to the Kerch Strait [Klimova, Podrezova, 2018].

The nutrition of different-sized larvae of three fish species prevailing in ichthyoplankton was studied – two warm-water (*E. encrasicolus*, 21 specimens; *S. schmidti*, 22 specimens) and one temperate-water (*T. luscus*, 6 specimens) (Table 1).

The analysis of the size composition of *E. encrasicolus* larvae showed as follows: 9% were on yolk nutrition; 27%, on mixed; and 64%, on external. In *E. encrasicolus* larvae with a total length (TL) from 6.2 to 14.7 mm, which were on external nutrition, food objects in intestines were recorded mainly as an amorphous mass, and it could not be identified. Only two larvae had copepod nauplii, 0.15 to 0.2 mm in size, which retained chitinous membranes; in the intestine of a 14.7-mm larva, a copepodite *Acartia clausi* Giesbrecht, 1889 was identified (0.75 mm).

Juvenile stages of Copepoda (Calanoida) were predominantly found in intestines of the pelagic pipefish 13.2 to 87 mm in size. In certain cases, Cladocera and eggs of hydrobionts were noted. In the nutrition of *S. schmidti* of size group II, the proportion of small food items (up to 0.25 mm)

did not exceed 8%; in larvae of size group III, organisms 0.4–0.7 mm long prevailed in intestines. Pelagic *S. schmidtii* mostly consumes species predominating in plankton, and it is clear that the prevalence of larger food items in its intestines is related to their abundance in the sea.

In larvae, identified by us as *T. luscus*, with a length (TL) of 2.6–4.0 mm, there were juvenile stages of copepods (Calanidae and Oithonidae) ranging 0.175–0.375 mm – from 2 to 8 specimens *per* intestine.

In general, during the study period (October 2016), low abundance of ichthyoplankton was observed, with a rather large number of species for open waters (15). For entire sample, the species richness index was 11.5. Due to a lack of pronounced prevalence in ichthyoplankton (dominance index was 0.2), we recorded rather high values of evenness index (0.7) and species diversity index (2.8) for the off-season [Odum, 1986; Pielou, 1966; Shannon, Weaver, 1949; Simpson, 1949].

Mesoplankton. Mesozooplankton was dominated by *A. clausi*, *C. euxinus*, *Paracalanus parvus* (Claus, 1863), *Penilia avirostris* Dana, 1849, and *Parasagitta setosa* (J. Müller, 1847), usually having a maximum or close to it biomass in autumn months. The only exception is *Pseudocalanus elongatus* (Brady, 1865): its biomass, as a rule, reaches the highest values in March–April. On the outer shelf and in the deep-sea areas, mesozooplankton composition differed somewhat. There was a regular increase in the proportion of cold-water species with distance from the coast. In descending order by biomass, on the outer shelf, the following species prevailed: *P. setosa* (20.4%), *P. parvus* (18.3%), *A. clausi* (12.2%), and *P. avirostris* (12.1%). At greater depths, the prevailing species were *C. euxinus* (32.1%), *P. elongatus* (21.5%), *P. parvus* (12.0%), and *P. setosa* (11.3%).

At 39 stations of the deep-sea epipelagic zone, the biomass of the dominant copepod *C. euxinus* varied depending on the position of the lower boundary of the oxygen zone ($\sigma_t = 16.2$). Specifically, with its shift from 100–125 to 126–150 m, the biomass of this crustacean increased from (6,200 ± 800) to (9,020 ± 1,020) mg·m⁻². In the deep-sea range of the lower boundary of the oxygen zone, 151–180 m, the value decreased to (7,300 ± 1,900) mg·m⁻². In total, the abundance and biomass of common and fodder (without *Noctiluca* species) zooplankton were twice as high in the open pelagic zone than on the shelf (Table 3).

Table 3. Mesozooplankton composition, abundance (ind.·m⁻²), and biomass (mg·m⁻²) on two stations of the Cape Khersones traverse (above the depth of 92 and 1,800 m) in October 2016

Species	Outer shelf (50–200 m)				Deep-sea areas (> 200 m)			
	ind.·m ⁻²	%	mg·m ⁻²	%	ind.·m ⁻²	%	mg·m ⁻²	%
Total mesozooplankton	332,153	–	7,570	–	569,524	–	14,840	–
Fodder mesozooplankton	315,599	–	6,700	–	552,134	–	13,950	–
Mesozooplankton < 0.5 mm	134,592	100	1,022	100	222,244	100	983	100
<i>Paracalanus parvus</i>	44,082	32.8	249	24.4	83,225	37.4	352	35.8
<i>Acartia</i> spp.	24,004	17.8	77	7.5	38,615	17.4	126	12.8
<i>Pseudocalanus elongatus</i>	4,885	3.6	22	2.2	23,174	10.4	109	11.1
<i>Centropages ponticus</i>	7,424	5.5	33	3.2	9,662	4.3	42	4.3
Copepoda nauplii	19,000	14.1	14	1.4	32,000	14.4	24	2.4
<i>Penilia avirostris</i> (< 0.5 mm)	2,315	1.7	23	2.3	625	0.3	6	0.1
<i>Oikopleura dioica</i>	14,250	10.6	377	36.8	3,750	1.7	108	11.0
Other organisms	18,632	13.8	227	22.2	31,193	14.0	200	20.3

This pattern was not observed for small fodder zooplankton (organisms < 0.5 mm), which is the main food of fish larvae. Its abundance on the outer shelf ($134,592 \text{ ind.}\cdot\text{m}^{-2}$) was inferior to the abundance in the deep-sea epipelagic zone ($222,244 \text{ ind.}\cdot\text{m}^{-2}$), but the opposite trend was noted for the values of the biomass of small organisms: $1,022 \text{ mg}\cdot\text{m}^{-2}$ on the shelf and $983 \text{ mg}\cdot\text{m}^{-2}$ at a deeper station. Out of small species and forms, copepodites *P. parvus* prevailed everywhere in terms of abundance (32.8 and 37.4%). In terms of biomass, *Oikopleura (Vexillaria) dioica* Fol, 1872 dominated on the outer shelf (36.8%), while *P. parvus* dominated in the deep-sea areas (35.8%).

In total, in the deep-sea areas, the biomass of copepods and, apparently, crustacean zooplankton was associated with the abundance and biomass of *Pleurobrachia pileus* (O. F. Müller, 1776) ($p < 0.01$), as well as with the abundance of *A. aurita* ($p < 0.05$).

Gelatinous macroplankton was mainly represented by the scyphomedusa *A. aurita* and three species of ctenophores (*M. leidy*, *P. pileus*, and *B. ovata*), occurring together in more than 90% of samples (Fig. 6).

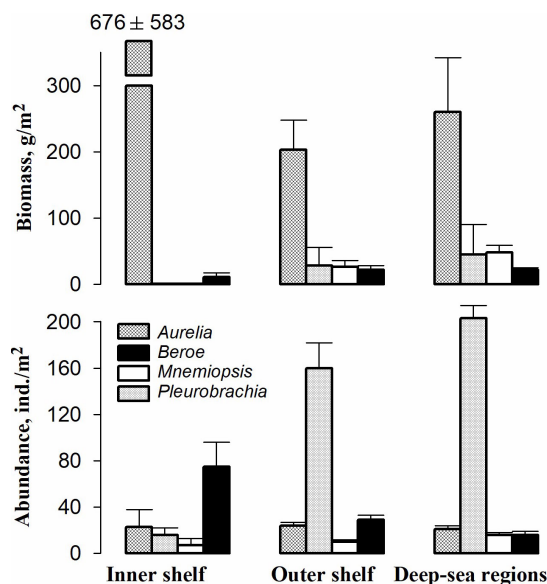


Fig. 6. Gelatinous macroplankton abundance ($\text{ind.}\cdot\text{m}^{-2}$) and biomass ($\text{g}\cdot\text{m}^{-2}$) in the central Black Sea in October 2016 (mean values \pm standard errors)

The mean biomass of *A. aurita* in areas with depths > 200 m was $203\text{--}260 \text{ g}\cdot\text{m}^{-2}$, and the abundance was $21\text{--}24 \text{ ind.}\cdot\text{m}^{-2}$. High biomass values were observed on the coastal shelf: $(676 + 583) \text{ g}\cdot\text{m}^{-2}$. The absence of significant differences in the biomass and abundance of the scyphomedusa in various areas of the epipelagic zone can be traced according to the geometric mean estimates ($79\text{--}157 \text{ g}\cdot\text{m}^{-2}$ and $10\text{--}21 \text{ ind.}\cdot\text{m}^{-2}$) and is confirmed statistically ($p > 0.05$). For this species, the maximum biomass ($2,611 \text{ g}\cdot\text{m}^{-2}$) and abundance ($92 \text{ ind.}\cdot\text{m}^{-2}$) were noted on the periphery of the eastern core of the MCG (sta. 79).

On the shelf and in the deep-sea areas, ctenophores *P. pileus* and *M. leidy* competing with the jellyfish had the same mean biomass, but *P. pileus* prevailed in terms of abundance and distribution. There were two areas of the largest accumulations of this ctenophore – the periphery of the eastern core of the MCG (up to $161 \text{ g}\cdot\text{m}^{-2}$ and $444 \text{ ind.}\cdot\text{m}^{-2}$) and border areas of the SevAC (up to $93 \text{ g}\cdot\text{m}^{-2}$ and $331 \text{ ind.}\cdot\text{m}^{-2}$).

M. leidy was found in macroplankton at 58 stations. In total, this ctenophore occurred more often and in higher abundance in the direction from the inner shelf towards the deep-sea epipelagic zone. Despite its local concentrations (up to 325 g·m⁻² at sta. 79), its biomass usually did not exceed 50 g·m⁻²; in open waters, the value averaged 26–48 g·m⁻². *M. leidy* abundance increased closer to the eastern sea area, where, in rare cases, the value reached 70 ind·m⁻² (sta. 63).

The third species, *B. ovata*, was found almost everywhere in the sea. Its mean biomass ranged 11–22 g·m⁻², and the values were higher in the same areas, as the biomass values for *M. leidy* ($p < 0.01$). *A. aurita* reached higher abundance there as well ($p < 0.05$). The abundance of ctenophores was maximum in the Feodosiya Gulf area (108–112 ind·m⁻²) and decreased with distance from the Crimean coast. These data give grounds to suggest that *B. ovata* population initially developed in the coastal zone, and its spreading to open waters occurred later.

The total abundance of ichthyoplankton, as well as fish eggs and larvae separately, was higher ($p < 0.05$) in areas with higher abundance of a ctenophore *B. ovata*. Moreover, the abundance of fish larvae turned out to be positively related to the abundance of the scyphomedusa *A. aurita* ($p < 0.05$) and, apparently, to the temperature of the sea upper layer ($p < 0.07$). The occurrence of particular ichthyoplankton representatives could be associated with various biotic and abiotic conditions. The abundance of *E. encrasicolus* eggs and larvae was related to the abundance of *B. ovata* alone ($p < 0.05$). The abundance of *S. schmidt* larvae and juveniles mainly correlated with the abundance and biomass of the copepod *C. euxinus* ($p < 0.05$), the biomass of all mesoplankton (taking that on average its value is 1.6 times higher than that of *C. euxinus* [Anninsky, Timofte, 2009]) ($p < 0.05$), and the abundance of the jellyfish *A. aurita* ($p < 0.05$). For eggs of *S. sprattus* and *M. merlangus*, no relationship with the habitat conditions of these species was found ($p > 0.05$).

DISCUSSION

Ichthyoplankton species composition, abundance, and spatial distribution in various areas of the Black Sea are mostly limited by the hydrological regime, primarily by water temperature as a factor determining the rhythm of biological processes; also, those are limited by the food supply and the impact of predators [Dekhnik, Pavlovskaya, 1979].

The period of plankton studies corresponded to the initial stage of the autumn hydrological season with a rather smooth decrease in the SST during the survey in the western sector in the first 10-day period of October 2016 and with a sharp drop in SST values in the eastern sector in the second 10-day period, after a strong storm.

In October, warm-water fish species usually complete their spawning, while temperate-water ones only begin to spawn. Therefore, ichthyoplankton, as a rule, is dominated by larvae of older age groups of warm-water fish and eggs of temperate-water fish [Dekhnik, 1973]. In the first 10-day period of October 2016, in the western sector of the survey, 10 species were identified in ichthyoplankton, and a relatively high mean abundance of fish eggs and larvae was observed. Out of larvae, the warm-water *E. encrasicolus* prevailed; in terms of abundance of eggs, temperate-water *S. sprattus* dominated. However, eggs of the European anchovy accounted for a rather significant proportion in samples, 35.3%. Moreover, in 2016, unlike the situation in previous years [Dekhnik, 1973; Klimova, Podrezova, 2018; Klimova et al., 2010], *E. encrasicolus* spawning was productive, as evidenced by the presence of larvae in samples (44.7% of the total abundance of all species) of all age groups. At the same time, eggs of 3 species and larvae of 2 species of temperate-water fish were recorded (see Table 2). On 1–14 October, 2005,

when the SST was on average 2 °C lower than in 2016, eggs and larvae of 11 fish species were found in ichthyoplankton [Klimova et al., 2010]. The mean abundance of eggs was twice as low as in 2016. Only common temperate-water species spawned: *S. sprattus*, *M. merlangus*, and *G. mediterraneus*. Spawning was productive for *M. merlangus* alone. Larvae of warm-water fish were represented by 8 species. *E. encrasicolus* completed its spawning; its larvae of older age groups prevailed in samples. This corresponded to the data of ichthyoplankton studies of the 1950s–1970s [Dekhnik, 1973].

A sharp change in the parameters of thermal stratification after the storm on 9–10 October, 2016, altered the structure of species composition of ichthyoplankton on the shelf of the southwestern Crimea (from Cape Sarych to the city of Sevastopol): the proportion of temperate-water fish increased. The abundance of ichthyoplankton species at the end of the second 10-day period of October has almost halved; the mean abundance of fish eggs and larvae did not exceed 2.5 ind.·m⁻² (Table 2). Eggs of temperate-water *S. sprattus* and *M. merlangus* were registered, but their spawning was unproductive. Samples contained only larvae of temperate-water invaders *T. luscus* and *M. macrophthalmia*. In catches, there were no *E. encrasicolus* eggs and larvae. Warm-water species were represented only by single larvae of gobies and *S. schmidtii* juveniles.

In the eastern sector of the survey, ichthyoplankton was sampled in the second 10-day period of October 2016. After the storm, background SST values dropped to +16...+16.5 °C. On the shelf and on the slope of the northeastern water area (from Cape Meganom to the Kerch Strait), eggs and larvae of 9 fish species were noted, and this is almost the same number of species as in the western sector of the survey before the storm. However, the absence of *E. encrasicolus* eggs and larvae in samples (those prevailed in samples of the western sector of the survey in the first 10-day period of October) led to a decrease in the mean abundance of eggs to 2.0 ind.·m⁻² and larvae to 1.8 ind.·m⁻² (see Table 2). Temperate-water species were represented by eggs and larvae of fish common to winter ichthyoplankton (*S. sprattus*, *M. merlangus*, and *G. mediterraneus*), while warm-water ones were represented only by single larvae of *Pomatoschistus* gobies and *A. kessleri*, as well as by *S. schmidtii* juveniles. Southward, at deep-sea stations, samples were practically empty (as mentioned earlier, at 8 surveyed stations, just 1 specimen of the pelagic pipefish was caught).

Both in October 2016 and October 2005, favorable conditions were observed for the survival of larvae of warm-water and temperate-water fish [Klimova et al., 2010]. Larvae on mixed and external nutrition with empty intestines were not found during the daytime. In October 2016, the food of *S. sprattus* larvae on external nutrition was mostly in the form of an amorphous mass; in the largest specimens, juvenile stages of copepods were identified. This corresponds to the data of [Duka, Sinyukova, 1976] on feeding habits and intestinal structure of larvae of this species. A detailed analysis of *S. schmidtii* feeding of various size groups is given based on material sampled in September 1987, when the SST was comparable to that in October 2016 [Gordina et al., 1991]. In larvae of size group III, both in September 1987 and October 2016, large food organisms (0.4–0.7 mm long) prevailed in intestines. In the feeding of *S. schmidtii* larvae of size group II, small food objects prevailed in September 1987; their proportion did not exceed 8% in October 2016. Previously, small *Oithona nana* Giesbrecht, 1893 accounted for 18–51% of the total abundance of consumed organisms in intestines of the pelagic pipefish of size group II [Gordina et al., 1991]. Currently, this species is not recorded in the Black Sea zooplankton.

High amount of food objects in intestines of fish larvae indicated a good food supply; this was confirmed by mesoplankton studies. In the initial phase of the autumn hydrological season in 2016, the sea cooling occurred more slowly than in 2005, and favorable temperature conditions for the development

of warm-water zooplankton were maintained for longer [Klimova et al., 2010]. Mostly due to the growth in populations of warm-water species (*P. parvus*, *Centropages ponticus* Karavaev, 1895, *P. avirostris*, etc.), in 2016, the abundance and biomass of fodder zooplankton, both on the outer shelf and in the deep-sea areas, reached the level of the upper limit of the corresponding data of 2005 [Klimova et al., 2010]. A small number of samples in 2016 does not allow us to estimate interannual differences in the abundance and biomass of small-sized zooplankton statistically. However, during this period, the abundance of food organisms < 0.5 mm in size increased by 4–6 times, and their biomass rose by 7–8 times. This is quite consistent with the trend towards a rise in the abundance of all crustacean plankton that has emerged in recent years [Anninsky et al., 2016]. An increase in its abundance and biomass indicates certain (possibly temporary) rise in trophicity of the Black Sea water, which is also confirmed by data on predatory jellyfish [Anninsky, Timofte, 2009]. In the deep-sea areas, the biomass of the jellyfish *A. aurita* was significantly higher in 2016 ($p < 0.01$) than in 2005. *P. pileus* biomass doubled over this period ($p < 0.001$). *M. leidyi* biomass ($\sim 250 \text{ g}\cdot\text{m}^{-2}$ prior to a seasonal outbreak of *B. ovata*) increased by 2–3 times. All this indicates that there were more gelatinous macroplankton in 2016. Potentially, it could have a stronger effect on entire mesozooplankton, including ichthyoplankton complexes, than in 2005. However, considering the abundance of mesozooplankton and that of fish eggs and larvae, the predatory pressure of gelatinous species did not cause significant damage to the populations of prey. Apparently, this is also indicated by the positive relationship between the total abundance of fish larvae and the abundance of *A. aurita*. Such a dependence, as well as a similar one (between the abundance of early age stages of the European anchovy and a ctenophore *B. ovata*), may indicate obvious trophic vectors of ichthyoplankton distribution in the sea. In the first case, such a vector could be the abundance of microplankton; in the second case, it could be greater development of small feeding zooplankton under a weak predatory pressure of plankton-feeding ctenophores. It is worth noting that *B. ovata* has a stronger effect on *M. leidyi* population than in previous years. It appears earlier in plankton and adapts more quickly to seasonal shredding of individuals in the prey population, forming its own, small-sized generation via larval reproduction [Finenko, Datzkyk, 2016]. Moreover, *B. ovata* penetrates the deep-sea epipelagic zone, where *M. leidyi* used to escaped complete grazing [Anninsky et al., 2013].

On the one hand, relatively high SST values in the first 10-day period of October 2016 contributed to the prolongation of spawning of the European anchovy and other warm-water fish species. On the other hand, those prevented full expansion of the sea surface layer in October by cold-loving gelatinous species (*A. aurita* and *P. pileus*), which prefer lower temperature [Anninsky, 2009]; this could lead to the displacement of both species into deeper horizons. High abundance of *A. aurita* and *P. pileus* intensified their competition and intraspecific food rivalry at these depths. Apparently, this caused a decrease in both mean umbrella diameter of jellyfish and growth rate of its generation. Specifically, in October 2016, the growth rate of *A. aurita* generation was one of the lowest over the past 15 years.

Conclusions:

1. In October 2016, against the backdrop of climate change, in the hydrological regime of the Black Sea, eggs and larvae of 15 species representing 9 families of both temperate-water and warm-water complexes were registered in shelf and deep-sea areas off the Crimean Peninsula. The mean abundance of eggs was 2.92, and larvae, 3.56 ind. $\cdot\text{m}^{-2}$. Relatively high indices of species diversity, a wide size range of larvae, and the presence of food organisms in their intestines indicated favorable conditions for ichthyoplankton survival during the study period.

2. Shifts in the abundance and species structure of ichthyoplankton were mediated by the characteristics of the hydrological regime during the research. In the first 10-day period of October (the initial phase of the autumn hydrological season, when the surface water circulation system in the study area was still consistent with the summer one, and the water temperature exceeded +21 °C), eggs and larvae of 10 fish species were noted in the western sector of the survey. Their mean abundance was 3.4 and 4.7 ind. \cdot m⁻², respectively. In the sea, productive spawning of the warm-water *Engraulis encrasicolus* still occurred, as evidenced by a low proportion of dead eggs (30%) and the presence of larvae of all age groups in samples – on yolk (9%), mixed (27%), and external (64%) nutrition. The spawning of temperate-water *Sprattus sprattus* and *Merlangius merlangus* was unproductive. Single larvae of two Gadidae species were recorded.

In the second 10-day period of October, with a sharp drop in the sea surface temperature to +16.5...+17 °C against the backdrop of increased wind-wave mixing, in the eastern sector of the survey, eggs and larvae of 9 more fish species were registered, but their mean abundance decreased to 2.0 and 1.8 ind. \cdot m⁻², respectively. Species structure was already typical for the autumn spawning season. In samples, there was no *E. encrasicolus*. Productive spawning of temperate-water *Gaidropsarus mediterraneus*, *S. sprattus*, and *M. merlangus* was noted. Warm-water species were represented only by larvae of older age groups.

At the end of the survey, on the shelf of the southwestern Crimea, from the city of Sevastopol to Cape Sarych, ichthyoplankton was represented only by 6 species: single specimens of warm-water larvae of *Gobius* sp. and *Syngnathus schmidtii*, eggs of temperate-water *S. sprattus* and *M. merlangus*, and larvae of Mediterranean invaders *Trisopterus luscus* and *Molva macrophthalma*.

3. Despite the fact that gelatinous predators were abundant in 2016, they did not cause significant damage to meso- and ichthyoplankton populations. In 2016, early appearance (in April) of a ctenophore *Beroe ovata* and its penetration into the deep-sea epipelagic zone weakened the predatory pressure of *Mnemiopsis leidyi* on zooplankton of the upper quasi-homogeneous layer, where eggs and larvae of most fish species develop. The relatively high sea surface temperature (more than +20 °C) prevented full expansion of this biotope by cold-loving gelatinous species (*Aurelia aurita* and *Pleurobrachia pileus*) and contributed to their displacement into deeper horizons, where their competition and intraspecific food rivalry intensified.

This work was carried out within the framework of IBSS state research assignment “Regularities of formation and anthropogenic transformation of biodiversity and biological resources of the Sea of Azov–Black Sea basin and other areas of the World Ocean” (No. 121030100028-0), “Investigation of mechanisms of controlling production processes in biotechnological complexes with the aim of developing scientific foundations for production of biologically active substances and technical products of marine genesis” (No. 121030300149-0), and “Functional, metabolic, and toxicological aspects of hydrobionts and their populations existence in biotopes with different physical and chemical regimes” (No. 121041400077-1). The research was carried out at the core facility RV “Professor Vodyanitsky” (IBSS).

Acknowledgement. The authors express their sincere gratitude to Yu. Zagorodnyaya, PhD, for her help in identifying food objects in intestines of fish larvae.

REFERENCES

1. Anninsky B. E., Timofte F. The distribution of zooplankton in the western Black Sea in October 2005. *Morskoj ekologicheskij zhurnal*, 2009, vol. 8, no. 1, pp. 17–31. (in Russ.). <https://repository.marine-research.ru/handle/299011/996>
2. Anninsky B. E., Finenko G. A., Datsyk N. A., Ignatyev S. M. Gelatinous macroplankton in the Black Sea in the autumn of 2010. *Okeanologiya*, 2013, vol. 53, no. 6, pp. 758–768. (in Russ.). <https://doi.org/10.7868/S0030157413060014>
3. Anninsky B. E., Finenko G. A., Datsyk N. A. The trophodynamic role of gelatinous predators in planktonic communities of the coastal regions of the Black Sea. In: *Morskie biologicheskie issledovaniya: dostizheniya i perspektivy* : v 3 t. : sb. materialov Vseros. nauch.-prakt. konf. s mezhdunar. uchastiem, priuroch. k 145-letiyu Sevastopol'skoi biologicheskoi stantsii, Sevastopol, 19–24 Sept., 2016. Sevastopol, 2016, vol. 2, pp. 221–224. (in Russ.). <https://repository.marine-research.ru/handle/299011/3169>
4. Artamonov Yu. V., Alekseev D. V., Skripaleva E. A., Shutov S. A., Deriushkin D. V., Zavyalov D. D., Kolmak R. V., Shapovalov R. O., Shapovalov Yu. I., Fedirko A. V., Shcherbachenko S. V. Peculiarities of seasonal and synoptic variability of water structure in the zone of the Rim Current at autumn and winter 2016. *Ekologicheskaya bezopasnost' pribrezhnoi i shel'fovoi zon morya*, 2018, no. 1, pp. 32–43. (in Russ.). <https://doi.org/10.22449/2413-5577-2018-1-32-43>
5. Gordina A. D., Oven L. S., Tkach A. V., Klimova T. N. Distribution, reproduction and feeding of the pelagic pipe-fish, *Syngnathus schmidtii*, in the Black Sea. *Voprosy ikhtiologii*, 1991, vol. 31, no. 1, pp. 107–114. (in Russ.)
6. Dekhnik T. V. Pokazateli eliminatsii v embrional'nyi i lichinochnyi periody razvitiya chernomorskoj khamsy. *Trudy Sevastopol'skoi biologicheskoi stantsii*, 1960, vol. 13, pp. 216–244. (in Russ.). <https://repository.marine-research.ru/handle/299011/5474>
7. Dekhnik T. V. *Ikhtioplankton Chernogo morya*. Kyiv : Naukova dumka, 1973, 235 p. (in Russ.). <https://repository.marine-research.ru/handle/299011/5654>
8. Dekhnik T. V., Pavlovskaya R. M. Zakonomernosti raspredeleniya, dinamiki chislennosti i vyzhivaniya ryb na rannikh etapakh ontogeneza. *Productivity of the Black Sea* / V. N. Greze (Ed.). Kyiv : Naukova dumka, 1979, pp. 268–272. (in Russ.). <https://repository.marine-research.ru/handle/299011/8059>
9. Duka L. A., Sinyukova V. I. *Rukovodstvo po izucheniyu pitaniya lichinok i mal'kov morskikh ryb v estestvennykh i eksperimental'nykh usloviyakh*. Kyiv : Naukova dumka, 1976, 134 p. (in Russ.). <https://repository.marine-research.ru/handle/299011/7900>
10. Ivanov V. A., Belokopytov V. N. *Oceanography of the Black Sea*. Sevastopol : EKOSI-Gidrofizika, 2011, 212 p. (in Russ.)
11. Klimova T. N., Vdodovich I. V., Anninskii B. E. Ichthyoplankton in the plankton community of the western sector of the Black Sea in October 2005. *Voprosy ikhtiologii*, 2010, vol. 50, no. 3, pp. 349–355. (in Russ.)
12. Klimova T. N., Subbotin A. A., Melnikov V. V., Serebrennikov A. N., Podrezova P. S. Spatial distribution of ichthyoplankton near the Crimean Peninsula in the summer spawning season 2013. *Morskoj biologicheskij zhurnal*, 2019, vol. 4, no. 1, pp. 63–80. (in Russ.). <https://doi.org/10.21072/mbj.2019.04.1.06>
13. *Marine Portal of the Marine Hydrophysical Institute* : site. (in Russ.). URL: http://dvs.net.ru/mp/index_ru.shtml [accessed: 16.06.2020].
14. Odum Yu. *Ekologiya* : in 2 vols / transl. from English / V. E. Sokolov (Ed.). Moscow : Mir, 1986, vol. 2, 376 p. (in Russ.)
15. Troshchenko O. A., Subbotin A. A. Abioticheskie faktory i usloviya obitaniya gidrobiontov pribrezhnoi zony Yugo-Vostochnogo Kryma. *Gidrologicheskie osobennosti*. In: *The Biology of the Black Sea Offshore Area at the South-Eastern Crimea*

- / N. S. Kostenko (Ed.). Simferopol : ARIAL, 2018, pp. 46–59. (in Russ.). <https://repository.marine-research.ru/handle/299011/5150>
16. Troshchenko O. A., Subbotin A. A., Eremin I. Yu. Variability of main limiting environmental factors in the process of bivalve mollusk cultivation at the mussel farm in Sevastopol. *Uchenye zapiski Krymskogo federal'nogo universiteta imeni V. I. Vernadskogo. Geografiya. Geologiya*, 2019, vol. 5 (71), no. 2, pp. 308–321. (in Russ.)
 17. Finenko G. A., Datzyk N. A. The reproductive features of ctenophore *Mnemiopsis leidyi* in inshore zone of the Black Sea. In: *Morskie biologicheskie issledovaniya: dostizheniya i perspektivy* : v 3 t. : sb. materialov Vseros. nauch.-prakt. konf. s mezhdunar. uchastiem, priuroch. k 145-letiyu Sevastopol'skoi biologicheskoi stantsii, Sevastopol, 19–24 Sept., 2016. Sevastopol, 2016, vol. 1, pp. 317–319. (in Russ.). <https://repository.marine-research.ru/handle/299011/3048>
 18. Alonso-Fernández A., Vergara A., Saborido-Rey F. Embryonic development and spawning pattern of *Trisopterus luscus* (Teleostei: Gadidae) under controlled conditions. *Journal of the Marine Biological Association of the United Kingdom*, 2010, vol. 91, spec. iss. 6, pp. 1281–1287. <https://doi.org/10.1017/S0025315410000147>
 19. Anninsky B. E. Organic composition and ecological energetics of the jellyfish *Aurelia aurita* L. (Cnidaria, Scyphozoa) under Black Sea conditions. In: *Trophic Relationships and Food Supply of Heterotrophic Animals in the Pelagic Ecosystem of the Black Sea* / G. E. Shulman, B. Öztürk, A. E. Kideys, G. A. Finenko, L. Bat (Eds). Istanbul, Turkey : Black Sea Commission Publications, 2009, pp. 99–160.
 20. Auth T. D., Daly E. A., Brodeur R. D., Fisher J. L. Phenological and distributional shifts in ichthyoplankton associated with recent warming in the northeast Pacific Ocean. *Global Change Biology*, 2017, vol. 24, iss. 1, pp. 259–272. <https://doi.org/10.1111/gcb.13872>
 21. *Copernicus Marine Service* : [site]. URL: <https://data.marine.copernicus.eu/products> [accessed: 02.11.2019].
 22. D'Ancona U. Order: Acanthini. Family 1: Gadidae. In: *Fauna and Flora of the Bay of Naples*. Monograph No. 38: Eggs, larvae and juvenile stages of Teleostei / S. Lo Bianco (Ed.). 1933, pt. II, pp. 188–261, plates XII–XV. (English transl. by Israel Program for Scientific Translations, 1969).
 23. Finenko G. A., Romanova Z. A., Abolmasova G. I., Anninsky B. E., Svetlichny L. S., Hubareva E. S., Bat L., Kideys A. E. Population dynamics, ingestion, growth and reproduction rates of the invader *Beroe ovata* and its impact on plankton community in Sevastopol Bay, the Black Sea. *Journal of Plankton Research*, 2003, vol. 25, iss. 5, pp. 539–549. <https://doi.org/10.1093/plankt/25.5.539>
 24. Fincham J. I., Rijnsdorp A. D., Engelhard G. H. Shifts in the timing of spawning in sole linked to warming sea temperatures. *Journal of Sea Research*, 2013, vol. 75, pp. 69–76. <https://doi.org/10.1016/j.seares.2012.07.004>
 25. Klimova T. N., Podrezova P. S. Seasonal distribution of the Black Sea ichthyoplankton near the Crimean Peninsula. *Regional Studies in Marine Science*, 2018, vol. 24, pp. 260–269. <https://doi.org/10.1016/j.rsma.2018.08.013>
 26. Margalef R. Information theory in ecology. *General Systems*, 1958, vol. 3, pp. 36–71.
 27. McQueen K., Marshall T. C. Shifts in spawning phenology of cod linked to rising sea temperatures. *ICES Journal of Marine Science*, 2017, vol. 74, iss. 6, pp. 1561–1573. <https://doi.org/10.1093/icesjms/fsx025>
 28. *National Center for Environmental Information* / National Oceanic and Atmospheric Administration (NOAA) : [site]. URL: <https://www.nodc.noaa.gov/SatelliteData/pathfinder4km> [accessed: 22.04.2018].
 29. Parsons T. R., Lalli C. M. Jellyfish population explosions: Revisiting a hypothesis of possible causes. *La Mer*, 2002, vol. 40, pp. 111–121. http://www.sfjo-lamer.org/la_mer/40-3/40-3-2.pdf
 30. Pielou E. C. Species-diversity and pattern-diversity in the study of ecological succession. *Journal of Theoretical Biology*, 1966, vol. 10, iss. 2, pp. 370–383. [https://doi.org/10.1016/0022-5193\(66\)90133-0](https://doi.org/10.1016/0022-5193(66)90133-0)

31. Purcell J. E., Uye S. I., Lo W. T. Anthropogenic causes of jellyfish blooms and direct consequences for humans: A review. *Marine Ecology Progress Series*, 2007, vol. 350, pp. 153–174. <https://doi.org/10.3354/meps07093>
32. Richardson A. J., Bakun A., Hays G. C., Gibbons M. J. The jellyfish joyride: Causes, consequences and management responses to more gelatinous future. *Trends in Ecology & Evolution*, 2009, vol. 24, iss. 6, pp. 312–322. <https://doi.org/10.1016/j.tree.2009.01.010>
33. Robinson K. L., Ruzicka J. J., Decker M. B., Brodeur R. D., Hernandez F. J., Quiñones J., Acha E. M., Uye S., Mianzan H., Graham W. M. Jellyfish, forage fish, and the world's major fisheries. *Oceanography*, 2014, vol. 27, no. 4, pp. 104–115. <https://doi.org/10.5670/oceanog.2014.90>
34. Russell F. S. *The Eggs and Planktonic Stages of British Marine Fishes*. London ; New York ; San Francisco : Academic Press, 1976, 524 p.
35. Shannon C. E., Weaver W. *The Mathematical Theory of Communication*. Urbana, IL : University of Illinois Press, 1949, 117 p.
36. Simpson E. H. Measurement of diversity. *Nature*, 1949, vol. 163, pp. 688. <https://doi.org/10.1038/163688a0>
37. Turan C., Erguden D., Gürlek M. Climate change and biodiversity effects in Turkish seas. *Natural and Engineering Sciences*, 2016, vol. 1, iss. 2, pp. 15–24. <http://dx.doi.org/10.28978/nesciences.286240>
38. Vinogradov M. E., Shushkina E. A., Mikaelyan A. S., Nezhlin N. P. Temporal (seasonal and interannual) changes of ecosystem of the open waters of the Black Sea. *Environmental Degradation of the Black Sea: Challenges and Remedies* / S. Beşiktepe, Ü. Ünlüata, A. S. Bologna (Eds). Dordrecht : Kluwer Acad. Publ., 1999, pp. 109–129. (NATO Science Series: 2. Environmental Security ; vol. 56).

**СОСТОЯНИЕ ИХТИО-, МЕЗО- И МАКРОПЛАНКТОННЫХ КОМПЛЕКСОВ
У КРЫМСКОГО ПОЛУОСТРОВА (ЧЁРНОЕ МОРЕ)
В СВЯЗИ С ОСОБЕННОСТЯМИ ГИДРОЛОГИЧЕСКОГО РЕЖИМА
В ОКТЯБРЕ 2016 Г.**

Т. Н. Климова¹, Б. Е. Аннинский¹, А. А. Субботин¹, И. В. Вдодович¹, П. С. Подрезова

¹ФГБУН ФИЦ «Институт биологии южных морей имени А. О. Ковалевского РАН»,
Севастополь, Российская Федерация
E-mail: tnklim@mail.ru

Климатические изменения в гидрологическом режиме Чёрного моря, отмечаемые с 1990-х гг., отразились на состоянии эпипелагических комплексов морских организмов, прежде всего на сезонной изменчивости их биологических циклов. Это оказало существенное влияние на фенологию нереста природных популяций рыб, видовое разнообразие и пространственное распределение ихтиопланктона, а также на устоявшиеся трофические взаимоотношения в планктонном сообществе. В конечном итоге характер взаимодействия между различными звеньями трофической цепи в эпипелагических комплексах, их сезонная и межгодовая изменчивость влияют на эффективность нереста рыб, прежде всего массовых промысловых видов, и в значительной степени определяют успех пополнения их будущих поколений. С целью изучения видового состава, численности и пространственного распределения ихтиопланктона в октябре 2016 г. (89-й рейс НИС «Профессор Водяницкий», 30 сентября — 19 октября) были проведены исследования в шельфовых и открытых водах Чёрного моря у Крымского полуострова, проанализированы не только икра и личинки рыб, но и биомасса мезо- и макропланктона. Пробы ихтио- и макропланктона отбирали сетью Богорова — Расса (площадь входного отверстия — 0,5 м²; ячей — 300 мкм) методом тотальных вертикальных ловов от дна до поверхности моря

в области шельфа и от нижней границы кислородной зоны до поверхности моря в глубоководной части. Ихтиопланктон фиксировали 4%-ным раствором формалина и анализировали позже под микроскопом, определяя таксономический состав организмов и по возможности — наличие и состав пищи в кишечниках личинок рыб. Проанализированы данные о видовом составе и пространственном распределении ихтио-, мезо- и макропланктона, а также о питании личинок рыб Чёрного моря у Крымского полуострова в октябре 2016 г. Период съёмки соответствовал начальной фазе осеннего гидрологического сезона. Ихтиопланктон был представлен икрой и личинками 9 видов тепловодных и 6 видов умеренноводных рыб. Средняя численность икры рыб составляла 2,92, а личинок — 3,56 экз.·м⁻². Низкая доля (30 %) мёртвой икры тепловодной хамсы *Engraulis encrasicolus*, а также наличие её разноразмерных личинок в море свидетельствовали о продолжении результативного нереста. Биомасса зоопланктона возрастала в направлении от шельфа к глубоководным районам. Мелкоразмерные фракции планктонных организмов преобладали на шельфе, обеспечивая здесь лучшие кормовые условия для выживания личинок рыб. Несмотря на значительную биомассу желтелых-планктофагов в октябре 2016 г., их влияние на ихтиопланктонные комплексы Чёрного моря, по-видимому, оставалось несущественным.

Ключевые слова: ихтиопланктон, мезопланктон, желтелый макропланктон, питание личинок рыб, видовое разнообразие, пространственное распределение, Чёрное море