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ABNORMAL DECREASE IN ABUNDANCE AND BIOMASS OF POPULATION OF *CALANUS EUXINUS* (COPEPODA) IN THE DEEP-SEA AREAS OF THE BLACK SEA IN AUTUMN 2019: WHAT IS HAPPENING WITH THE ECOSYSTEM?

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During plankton sampling in deep and shelf areas of the Black Sea off the Crimea in October 2019 (the 110th cruise of the RV “Professor Vodyanitsky”), the quantitative distribution, abundance, biomass, size and age structures, and lipid reserves of *Calanus euxinus* Hulsemann, 1991 population were studied. Zooplankton was sampled with the Bogorov–Rass net (inlet area of 0.5 m^2, and mesh size of 300 μm) by vertical net hauls from the bottom or the lower boundary of the oxygen zone to the sea surface. Size and age of *C. euxinus* were determined under a stereomicroscope in a laboratory. Lipid reserves in the population were estimated based on the specific oil sac volume at the late copepodite stages. As shown, in 2019, ongoing warming in the Sea of Azov–Black Sea region led to a decrease in *C. euxinus* abundance and biomass in deep-sea areas down to (5.3 ± 0.5) thousand $\text{ind.}\cdot m^{-2}$ and (3.7 ± 0.3) $g\cdot m^{-2}$, respectively, and also to changes in the population structure. Partly, these phenomena could be related to a weakening of winter convective mixing in the sea. Probably, a drop in river inflow after severe drought in 2018–2019 was even more important for *C. euxinus*, as it dramatically reduced the supply of nutrients to the sea. Due to a weak transfer of nitrates, phosphates, and especially silicates with the river flow, abundant phytoplankton (first of all, diatoms critically needing silicates) had insufficient mineral sources for its development in 2019 and, correspondingly, could not satisfy *C. euxinus* trophic requirements at the level of previous years. An increase in lipid content of V copepodites in autumn 2019 is explicable by an abnormally low density of *C. euxinus* population that year driven, apparently, by an extremely high biomass of planktivorous jellyfish, especially the medusa *Aurelia aurita* Linnaeus, 1757, in winter–spring 2017–2018.

Keywords: *Calanus euxinus*, abundance, biomass, lipid reserves, interannual dynamics, Black Sea

A copepod *Calanus euxinus* Hulsemann, 1991 is a key mesozooplankton species in the Black Sea constituting 60–75% of its total biomass, or 76–85% of crustacean plankton biomass in deep-sea areas [Anninsky, Timofte, 2009; Arashkevich et al., 2014; Zagorodnyaya et al., 2023]. This species is the largest Black Sea copepod: females can reach 4.5 mm in length, and males attain 3.4 mm [Sazhina, 1987]. *C. euxinus* features high wax content (up to 40% of its body volume) [Yuneva et al., 1999] accumulated primarily in late copepodites and adults within an oil sac. Because of these lipid reserves, some individuals can possess a reddish coloration. Due to its visibility, high nutritional value, and tendency to form localized aggregations, *C. euxinus* is critically important for the diet of small pelagic fish, particularly the cold-water Black Sea sprat *Sprattus sprattus phalericus* (Risso, 1827) which mostly consumes large cold-water zooplankton [Bayhan, Sever, 2015; Latun, 2014; Yuneva et al., 2016].

C. euxinus can produce up to eight generations annually [Sazhina, 1987] maintaining its biomass at relatively stable levels, with slight increases in spring and declines in winter [Vinogradov et al., 1999]. In the 1970–1980s, its biomass in open sea areas averaged 5–10 $g \cdot m^{-2}$. However, following the invasion of the lobate comb jelly *Mnemiopsis leidyi* (A. Agassiz, 1860), biomass of the copepod decreased to 1–3 $g \cdot m^{-2}$ in the Black Sea in 1991–1992 [Kovalev, 1996; Vinogradov et al., 1999]. By October 2005, *C. euxinus* biomass in the western deep-sea area had risen again to 6.2 $g \cdot m^{-2}$ [Anninsky, Timofte, 2009]. In the autumn of 2016 and 2017, at the sites to the south of the Crimea, it reached 7.1 and 7.3 $g \cdot m^{-2}$, respectively [Hubareva, Anninsky, 2022, 2024].

Significant interannual fluctuations in mesozooplankton abundance and biomass on the Black Sea shelf [Anninsky et al., 2020; Gubanova et al., 2022] evidence for the fact that populations of the copepod are not only vulnerable to planktivorous jellyfish invasions, but also dependent on hydrological regime shifts. Over the last decades, the annual mean surface temperature of the Black Sea was rising by 0.052 °C *per* year [Ginzburg et al., 2021]. Oxygen penetration depth in the sea decreased from 140 m in 1955 to 90 m in 2015, with total oxygen content declining by 44% [Capet et al., 2016]. Stagnation processes in the sea [Polonsky, Valle, 2020; Vidnichuk, Konovalov, 2021] disrupt vertical migrations and lipid formation in cold-water crustaceans, particularly *C. euxinus*, with its major population remaining constantly in diapause near the lower oxycline boundary [Vinogradov et al., 1992].

In 2019, an autumn study of *C. euxinus* abundance, biomass, distribution, size and age structures, and lipid reserves of the Black Sea population extended investigations carried out in 2016 and 2017 [Hubareva, Anninsky, 2022, 2024]. The survey was aimed at assessing the species response to regional climate warming and associated recent hydrological changes in the sea.

MATERIAL AND METHODS

In autumn 2019 (7–21 October, the 110th cruise of the RV "Professor Vodyanitsky"), zooplankton was sampled in the Black Sea, at 69 stations covering deep-sea and shelf areas southwest, south, and southeast of the Crimea, in a sector from N43°02′ to N44°59′ and from E32°10′ to E38°40′ (Fig. 1). Three stations were situated in the inner shelf zone (depths < 50 m), and ten were located on the outer shelf (depths 50–200 m). Deep-sea stations were classified by their hydrological regime into cyclonic gyre cores, with an isopycnal depth ($\sigma_t = 16.2$) of < 125 m (18 stations); cyclonic peripheries, with a depth of 126–150 m (31 stations); and anticyclonic eddies, with a depth of > 150 m (7 stations) (Fig. 2).

Prior to plankton sampling, hydrological measurements were conducted at each station with a research tool Sea-Bird 911 plus CTD (the USA) to assess vertical profiles of temperature, salinity, and seawater conditional density (σ_t). Zooplankton was quantitatively sampled with a Bogorov–Rass net (inlet area of 0.5 m^2, mesh size of 300 μm) by total vertical hauls from the seabed or the lower boundary of the oxygen zone ($\sigma_t = 16.2$) to the sea surface. Samples containing *C. euxinus*, including copepodite developmental stages and adults, were preserved in a 4% borax-neutralized formalin solution. Subsequent laboratory processing involved examining the samples in a Bogorov chamber under a stereomicroscope to measure and identify *C. euxinus* developmental stages. Population structure was typically assessed by full examination of the entire sample. However, when late developmental stages were abundant, they were quantified *via* subsampling [Alexandrov et al., 2020]. Reserve lipid content in *C. euxinus* was evaluated based on oil sac volume in V copepodites, males, and females. Corresponding measurements were carried out for 20 ind. *per* certain developmental stage at each station.

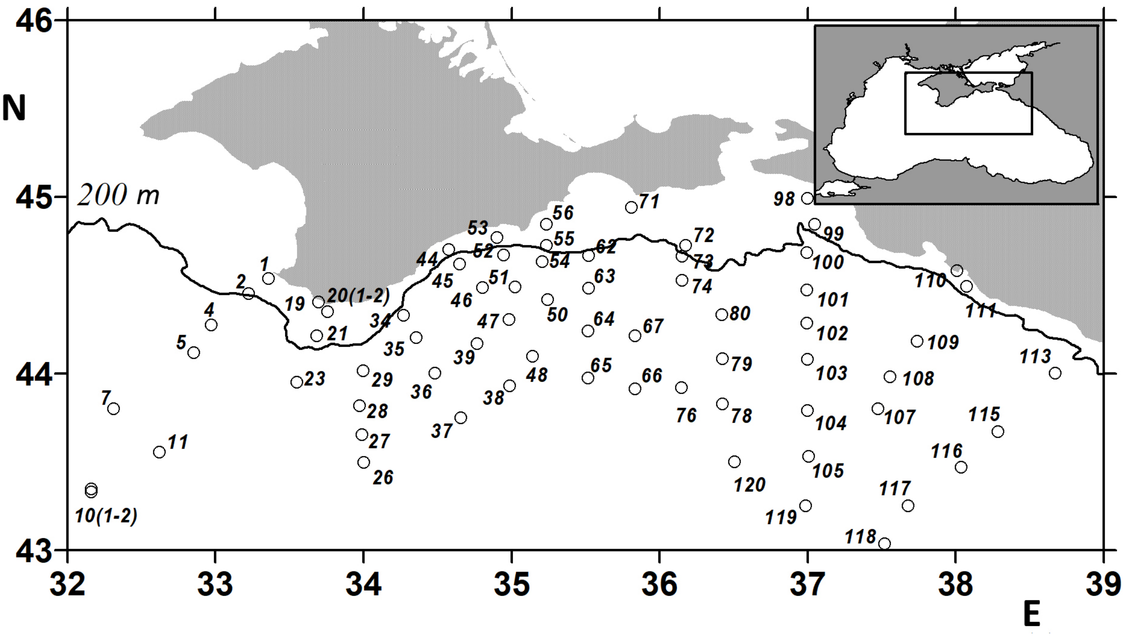

Fig. 1. The map of sampling survey (with station numbers identified) in the northwestern, central, and northeastern Black Sea during the 110th cruise of the RV "Professor Vodyanitsky" in October 2019. The line shows the 200-m isobath

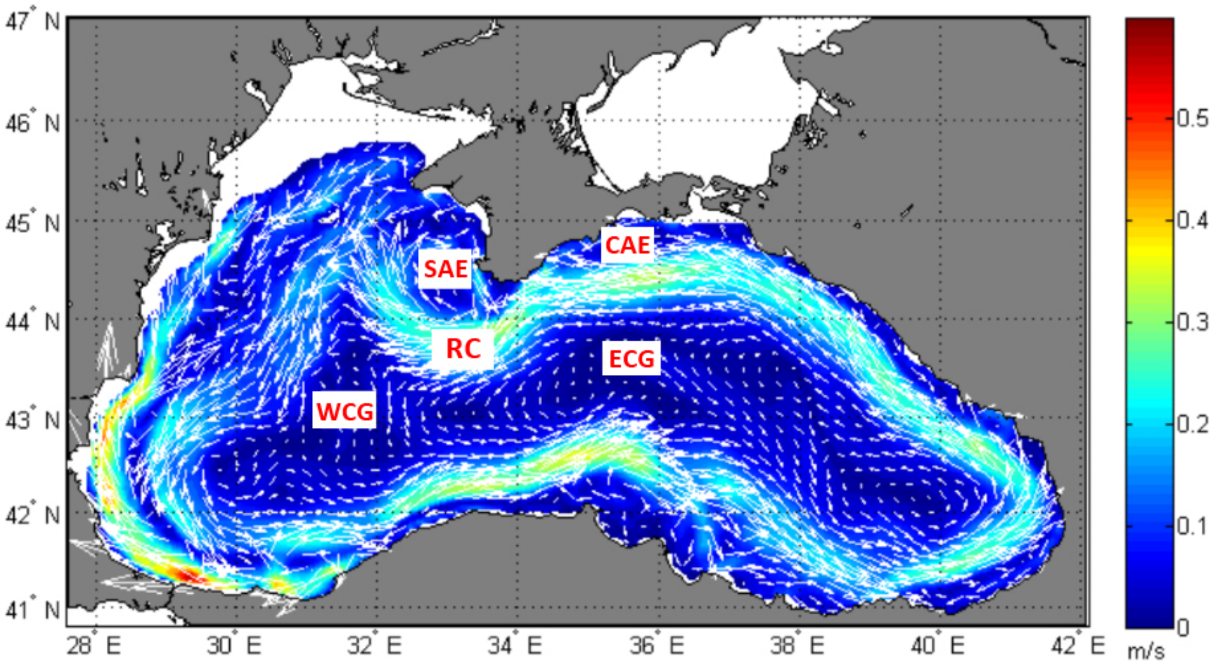

Fig. 2. Hydrodynamic activity in the Black Sea at a 30-m depth from 15 October to 15 November, 2019 (https://dekosim.ims.metu.edu.tr/BlackSeaModels/BlackSeaModels.shtml). RC, the Rim Current; WCG, the Western Cyclonic Gyre; ECG, the Eastern Cyclonic Gyre; SAE, the Sevastopol Anticyclonic Eddy; CAE, the Crimea Anticyclonic Eddy

The individual wet weight of copepodites and adult *C. euxinus* (WW, mg) was calculated by the formula:

$$WW = 0.58 \times l \times d^2 \times \rho \ ,$$

where l and d are prosome length and width, respectively, mm;

ρ is a mean body density, g·cm^{-3} [Svetlichny, Hubareva, 2014].

The body volume of copepodite stages, males, and females (V_b, mm^3) was determined using the formula:

$$V_b = k \times L_{pr} \times d_{pr}^2 \ ,$$

where L_{pr} and d_{pr} are prosome length and width, respectively, mm;

k is an empirical coefficient equal to 0.64 for males and 0.58 for copepodites and females [Svetlichny et al., 2009].

The oil sac volume (V_{sac}) was calculated as:

$$V_{sac} = \pi \times l_{sac} \times d_{sac}^2 / 6 \ ,$$

where l_{sac} and d_{sac} are oil sac length and width, respectively, mm [Svetlichny, Hubareva, 2011].

Data were processed in MS Office Excel 2010, Grapher 7, PAST 4.05 [Hammer et al., 2001], and Surfer. In all cases, means and corresponding values of a standard error (±*SE*) are provided. Differences between analyzed datasets were assessed using Student's *t*-test and non-parametric Mann–Whitney *U* test.

RESULTS

Hydrological conditions in the study area. Within the survey period, sea surface temperature ranged from +15.6 to +20.4 °C, with the mean of (+18.4 ± 0.1) °C. It was slightly lower in central deep-sea areas south of the Crimean Peninsula (Fig. 3).

In this area, the temperature field evidences for a significant upwelling of cold deep waters to the surface, and this is likely associated with hydrodynamic instability on the periphery of the Eastern Cyclonic Gyre. This was further supported by a concurrent increase in surface water salinity at the survey site. In the western study area, salinity varied within 18.28–18.62 psu, with the mean of (18.4 ± 0.02) psu. In the eastern study area, the range was wider, 17.37–19.36 psu, with the mean of (18.6 ± 0.1) psu. The lowest salinity values, 17.37–18.27 psu, were recorded at sta. 72 and 73 resulting from the inflow of freshened Sea of Azov water into the Kerch pre-strait.

The lower boundary of the upper quasi-homogeneous layer corresponding to the upper thermocline boundary was located at similar depths in the western and eastern deep-sea areas: at 11–36 m [the mean of (21.0 ± 1.0) m] and 14–34 m [the mean of (20.0 ± 1.4) m]. In both cases, the thermocline depth was mainly mediated by mesoscale water circulation. Thus, thermocline raises in cyclonic circulation zones (south of the Cape Chersonesus, sta. 23) and deepens within cores of anticyclonic eddies, with Sevastopol and Crimean anticyclones being especially notable.

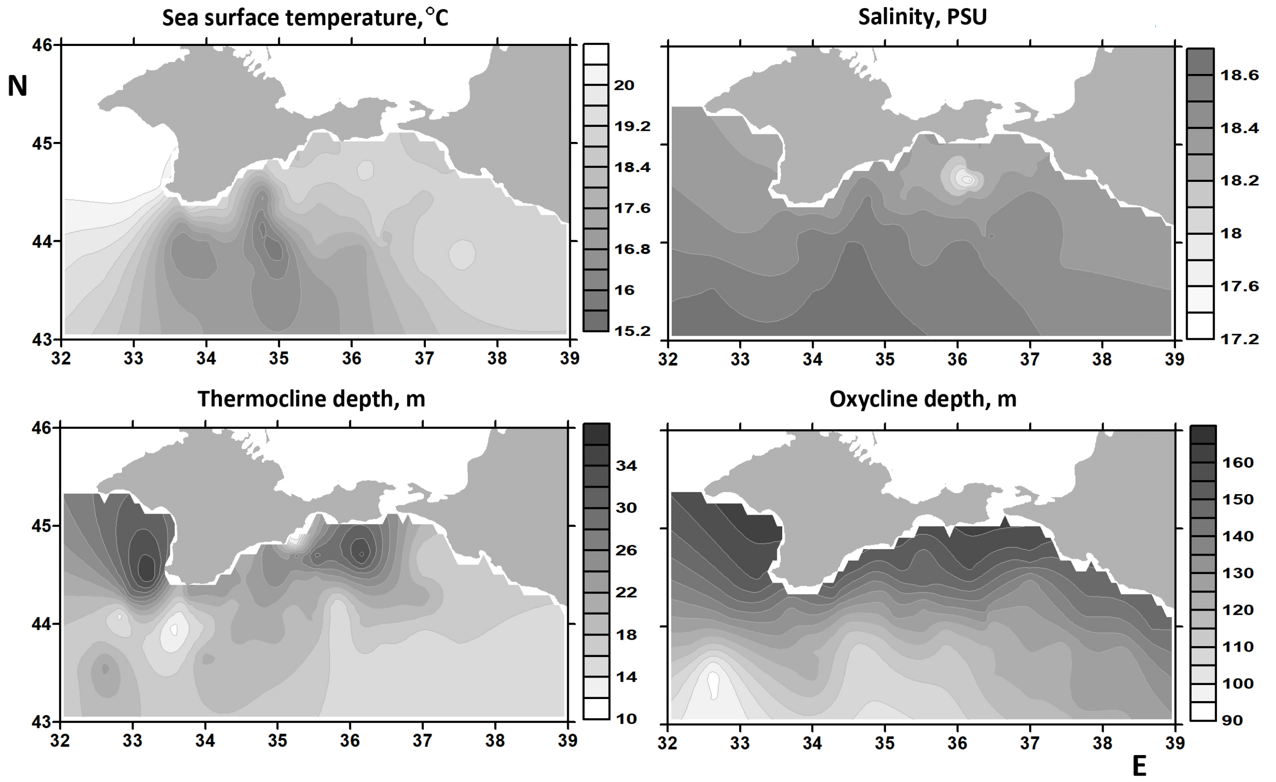

Fig. 3. Spatial distribution of temperature (°C) and salinity (psu) in the sea upper layer, as well as depths (m) of the upper boundary of the thermocline and the lower boundary of the oxygen zone in the Black Sea on 7–21 October, 2019

Quantitative distribution of *Calanus euxinus*. Its maximum abundance (21.2 thousand ind.$\cdot$m^{-2}) and biomass (15.3 g$\cdot$m^{-2}) in October 2019 (Fig. 4) were recorded in the cyclonic meander zone of the Rim Current identified by the relatively shallow thermocline depth and localized sea surface temperature decrease (sta. 23) (see Fig. 3). However, no statistically significant correlation was found between the species biomass and hydrodynamic phenomena in the deep-sea area, although its total abundance gradually rose with the deepening of the lower boundary of the oxygen zone (hereinafter LBOZ) ($r = 0.32$; $p < 0.05$). *C. euxinus* mean biomass slightly increased from central areas of cyclonic gyres [(3.2 ± 0.3) g$\cdot$m^{-2}] toward their peripheries [(4.2 ± 0.5) g$\cdot$m^{-2}], but decreased [(2.9 ± 0.4) g$\cdot$m^{-2}] with LBOZ deepening to 150–160 m. Abundance values followed this trend accounting for (3.7 ± 0.4), (6.2 ± 0.7), and (5.8 ± 1.1) thousand ind.$\cdot$m^{-2} (in the same sequence). A slight gain in the species abundance with LBOZ deepening was governed by higher abundance of early copepodite stages which develop in warmer waters displaced toward gyre peripheries by centrifugal currents.

In deep-sea areas, *C. euxinus* abundance and biomass were (5.3 ± 0.5) thousand ind.$\cdot$m^{-2} and (3.7 ± 0.3) g$\cdot$m^{-2}, respectively. On the outer shelf, the values decreased to (4.8 ± 1.1) thousand ind.$\cdot$m^{-2} and (1.5 ± 0.5) g$\cdot$m^{-2}. A significant (2.5-fold; $p < 0.001$) decline in biomass of this copepod reflects the dominance of early developmental stages in shallow waters. On the inner shelf, its abundance and biomass were even lower: (2.2 ± 1.5) thousand ind.$\cdot$m^{-2} and (0.3 ± 0.3) g$\cdot$m^{-2}, respectively.

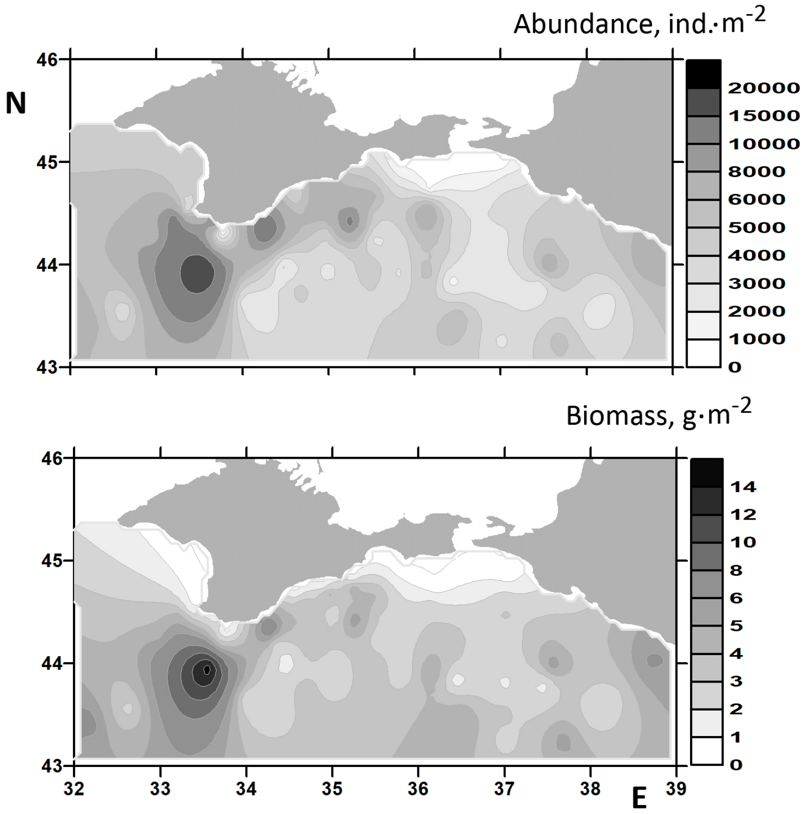

Fig. 4. Abundance and biomass of a copepod *Calanus euxinus* in the northwestern, central, and northeastern Black Sea in October 2019

Age structure of *Calanus euxinus* population. The population structure was mediated by features of hydrodynamic conditions (Fig. 5). In central cyclonic gyres, proportions of V copepodites [(49.5 ± 4.1) %] and females [(33.1 ± 3.2) %] were 1.5–2 times higher than in anticyclonic eddies [(31.4 ± 2.4) and (15.9 ± 4.5) %, respectively]. Proportions of I–III and IV copepodites increased inversely: from (6.2 ± 1.3) % and (2.2 ± 0.4) %, respectively, at LBOZ of 100–125 m to (35.3 ± 5.0) % and (10.5 ± 2.4) % at LBOZ of 150–160 m. The relative abundance of males varied between 6.7 and 10.5%.

On the outer shelf, the proportion of I–III copepodites increased to (64.8 ± 7.8) %, while proportions of V copepodites, females, and males dropped to (13.2 ± 3.1), (9.3 ± 4.0), and (2.8 ± 0.9) %, respectively. The numerical prevalence of early developmental stages in *C. euxinus* population became even more pronounced on the inner shelf: there, I–III copepodites constituted (89.0 ± 2.1) %, while V copepodites and adults occurred singly in autumn.

Lipid reserves of *Calanus euxinus* population. Late copepodite stages exhibited higher reserve lipid content in deep-sea areas, where the oil sac volume relative to body volume reached (24.0 ± 0.7) % in V copepodites, (7.0 ± 1.1) % in females, and (11.5 ± 0.5) % in males. Interestingly, in central cyclonic gyres, V copepodites, females, and males accumulated much more lipids than in peripheral areas [(25.7 ± 1.2), (9.7 ± 1.2), and (13.1 ± 0.8) %, respectively], though these differences were not statistically significant ($p > 0.05$). On the outer shelf, V copepodites stored half lipid reserves of those in open sea areas [(11.9 ± 1.7) %; $p < 0.001$]. However, the mean oil sac volume in females and males [(6.3 ± 0.8) and (8.0 ± 1.4) %, respectively] remained the same ($p > 0.05$).

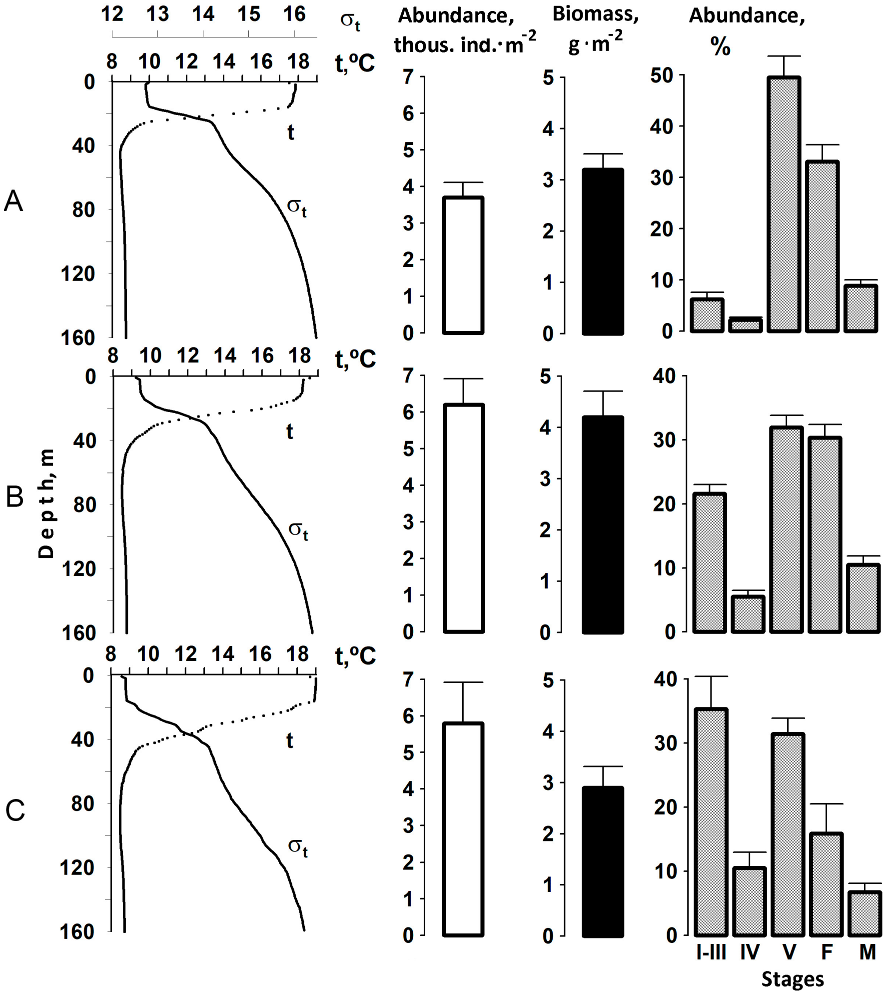

Fig. 5. Total abundance (thousand ind.·m^{-2}), biomass (g·m^{-2}), and age structure (% of total abundance) in *Calanus euxinus* population in relation to vertical profiles of seawater temperature (t, °C) and density (σ_t) in deep-sea areas of the Black Sea. The depth of the lower boundary of the oxygen zone (σ_t = 16.2): 100–125 m (A); 126–150 m (B); 151–160 m (C)

DISCUSSION

In deep-sea areas, *C. euxinus* biomass in October 2019 was nearly twice as low ($p < 0.001$) as during autumn of 2016 and 2017 [Hubareva, Anninsky, 2022, 2024]. Furthermore, it was significantly lower ($p < 0.05$) than biomass of this species in 2005 [Anninsky, Timofte, 2009], when mesozooplankton community seemed to be still recovering from the damage caused by the invader *M. leidyi*. Biomass of this copepod declined most sharply in central cyclonic circulation zones ($p < 0.001$) and on their peripheries ($p < 0.001$ in 2016; $p < 0.05$ in 2017). Even in areas of surface water downwelling, *C. euxinus* biomass was 2–2.5 times lower compared to that in 2016 and 2017, though high data variability in the first case precluded statistical significance ($p > 0.05$). On the outer shelf, a twofold biomass decline was also statistically unsignificant ($p > 0.05$).

In general, interannual changes in abundance of this copepod were similar to dynamics of its biomass. However, on the periphery of cyclonic gyres, in 2019, compared to 2016 and 2017, a decrease in *C. euxinus* abundance was 10–20% less intense than a decline in its biomass. In anticyclonic deep-sea areas, the difference reached 30–40%. This suggests that negative changes in the copepod population in 2019 had effect on the late developmental stages, that dominate in terms of contribution to biomass. At the same time, early copepodites which are more critical for abundance assessment, mostly preserved their stable level in plankton.

The analysis of *C. euxinus* population structure revealed that the proportion of I–III copepodites in deep-sea areas gradually increased: from 5.7% in 2016 to 17.6% in 2017 and 21.0% in 2019. This tendency was driven by a rise in their proportions in anticyclonic deep-sea areas, where these stages accounted for 12.2% of total abundance in 2016, 16.1% in 2017, and 35.3% in 2019. Concurrently, the proportion of V copepodites declined gradually from 48.2 and 35.7% in 2016 and 2017 to 31.4% in 2019. The same shifts were observed in females (from 27.7 and 25.3% to 15.9%).

Despite reduced abundance and biomass of V copepodites in 2019, their lipid reserves increased (Fig. 6). The oil sac volume in these copepodites rose compared to that in 2016–2017 under different hydrological regimes: in central cyclonic zones (from 16.6 and 17.2% to 23.7%), on gyre peripheries (from 16.6 and 18.7% to 24.4%), and in the zone of anticyclonic eddies (from 17.4 and 18.6% to 23.7%). No noticeable interannual changes were registered in *C. euxinus* female or male lipid reserves suggesting heterogeneity in their reproductive readiness. In contrast, much more elevated lipid reserves in V copepodites in 2019 seem to evidence for the proximity to final metamorphosis and their high reproductive potential upon maturation. Increased lipid reserves imply better feeding conditions in 2019 compared to those in 2016–2017 [Hubareva, Anninsky, 2022, 2024]. This appears to result from a more than twofold reduction in population size in 2019 compared to that in 2016–2019 and a corresponding weakening of intra-population competition for food.

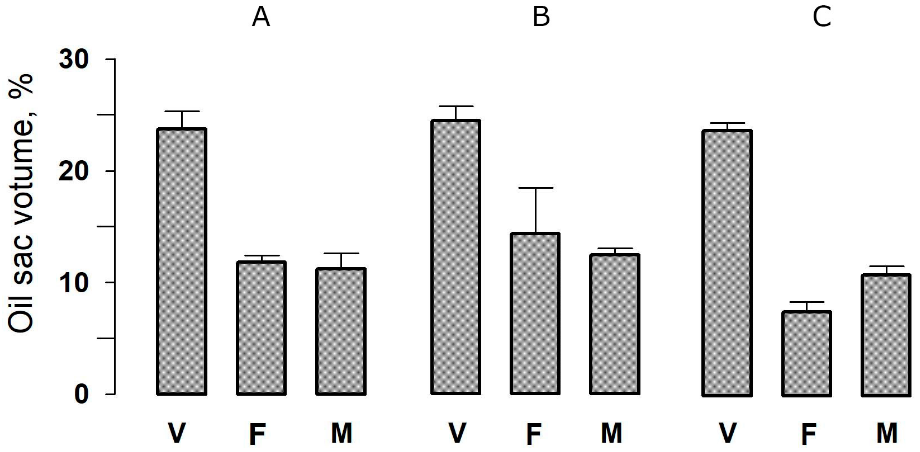

Fig. 6. Specific oil sac volume (% of body volume) in V copepodites (V), females (F), and males (M) of *Calanus euxinus* from the Black Sea areas with different depths of the lower boundary of the oxygen zone ($\sigma_t = 16.2$) in October 2019: 100–125 m (A); 126–150 m (B); 151–160 m (C)

Thus, the most distinctive features of *C. euxinus* population in 2019 are as follows:

1) a significant decline in abundance and biomass;
2) structural population shifts mainly mediated by a greater representation of juveniles and a decline in abundance of older age stages;
3) increased reserve lipid content in V copepodites.

The exact reasons of these changes remain unclear, the same as their temporal dynamics. However, several key factors undoubtedly affected both the Black Sea pelagic biota in general and *C. euxinus* population in particular in 2017–2019.

Within 2017–2019, the mean annual temperature in the Black Sea increased by approximately 2 °C. The winter of 2017/2018 was warmer than usual, while the winter of 2018/2019 was exceptionally warm, with air temperature 2.7 °C above the norm [Ginzburg et al., 2021]. This warming not only slowed the seasonal cooling of the sea surface, but also maintained temperature at least 1 °C higher in the core of the cold intermediate layer and within the main pycnocline zone. Convective mixing of water masses during winter significantly weakened, and this, combined with a rise in temperature, contributed to formation of stagnant conditions near LBOZ [Polonsky, Valle, 2020]. Oxygen content in the oxycline layer ($\sigma_t = 15.4$) halved, the upward transport of nitrates from the main pycnocline to the upper layers slowed, and the intensity of spring phytoplankton bloom declined [Vidnichuk, Konovalov, 2021]. The winter–spring phytoplankton peak which usually occurred in February has not been noted at all in recent years [Stelmakh et al., 2023] or was observed in coastal areas alone [Vostokov et al., 2019].

These hydrological shifts projected across the entire pelagic biota and inevitably affected *C. euxinus* population by narrowing boundaries of its oxygenated biotope and reducing the supply of nutrients to the zone of active photosynthesis. However, the effect of spring phytoplankton bloom on this copepod appears to be secondary due to the short duration of this process or the small size of algal cells proliferating during this period [Silkin et al., 2022] and possessing low nutritional value for large copepods [Amelina et al., 2017].

A positive correlation ($r = 0.81$; $p < 0.01$) was observed between *C. euxinus* biomass on the outer shelf of the Sevastopol Bay in 2003–2021 and the sea surface temperature in April and May [Anninsky et al., 2020]. It highlights strong dependence of *C. euxinus* population on regional climate features, particularly in winter and spring. The prevalence of cyclonic atmospheric circulation was characterized by early warming, increased precipitation, and elevated river inflow into the Black Sea [Oguz et al., 2006]; this contributed to greater productivity of the copepod population. This is likely driven by intensified spring flow from rivers, such as the Danube and Dnieper: those account for over 70% of total freshwater inflow to the Black Sea peaking in April and May [Ivanov, Belokopytov, 2011]. Strong floods enhance nutrient enrichment in the pelagic zone and thus form favorable trophic conditions for the copepod providing improved summer–autumn development of large diatoms and phytoplankton in general [Yunev et al., 2021]. Furthermore, chlorophyll *a* anomalies in the upper mixed layer correlate significantly with the Danube inflow across all the Black Sea regions [Nezlin, 2006].

For the Danube basin and the Sea of Azov–Black Sea region, 2018 was one of the driest years in a century [Ginzburg et al., 2021; Hänsel et al., 2022]. Apparently, river flow in 2019 (it was an almost equally low-water year) remained extremely weak [Chasovnikov, Borodulina, 2022]. Such a reduction in freshwater inflow severely limited the supply of nutrients to the sea. Accordingly, concentrations of nitrates, phosphates, and especially silicates in seawater in 2019 were the lowest during the period of observations, at least since 2009 [Chasovnikov, Borodulina, 2022; Orekhova, 2021]. The scarcity of silicates, a critical resource for diatoms, deprived phytoplankton communities of minerals needed for their growth. Consequently, phytoplankton failed to satisfy trophic requirements of *C. euxinus* and other copepods at levels noted in previous years [Datsyk et al., 2020].

How, then, can the high lipid content in V copepodites in 2019 be explained? One of the factors contributing to substantial lipid reserves in *C. euxinus* could be the sparsity of its population (and thus reduced intraspecific competition for food) under limited availability of small diatoms in the sea. It is also possible that gelatinous zooplankton and other planktivores played a certain role. In 2019, *M. leidyi* biomass increased to (144 ± 21) $g \cdot m^{-2}$, and *C. euxinus* occasionally dominated among preys of the lobate comb jelly in deep-sea areas [Anninsky et al., 2024]. However, even more pronounced effect on the copepod population may be related to the extremely high biomass of the common jellyfish *Aurelia aurita* Linnaeus, 1757 in autumn 2017: (514 ± 159) $g \cdot m^{-2}$ on the outer shelf and (634 ± 87) $g \cdot m^{-2}$ in deep-sea areas, that was threefold higher than the long-term mean over 2005–2019 [Anninsky et al., 2022]. The relatively high biomass of *C. euxinus* during autumn study in 2017 does not preclude a sharp decline later that year or in early 2018. Specifically, after the mass development of *M. leidyi* in 1988–1989, a decrease in the copepod biomass became evident only in 1991–1992 [Vinogradov et al., 1999]. The vertical distribution of *A. aurita* population overlapped more with *C. euxinus* populations, than it was typical for *M. leidyi*. Abundance of the copepod might have dropped due to intense predation by the common jellyfish on eggs, early developmental stages, and, in some cases, migrating V copepodites and adults. Apparently, the active accumulation of lipid reserves in *C. euxinus* was facilitated by its ability to feed on large-cell diatoms adapted to inhabit nutrient-poor waters [Stelmakh et al., 2023].

Conclusion. Ongoing warming in the Sea of Azov–Black Sea region led to large-scale transformations in the Black Sea pelagic zone in 2019 causing a sharp decline in abundance and biomass, as well as structural shifts in the population of the key mesozooplankton species, *Calanus euxinus*. While the most of the copepod annual cycle occurs at low temperature near the lower boundary of the oxygen zone, direct thermal effects on its population over the recent years have been minimal. However, even slight deviations in winter sea temperature from a norm significantly degraded the species habitat conditions in 2019. The weakening of winter convective water mixing exacerbated stagnation near the lower boundary of oxygen zone. Oxygen content in the oxycline layer decreased twofold, nitrate flux from the main pycnocline to the upper layers slowed, and the intensity of spring phytoplankton bloom declined. However, a drastic reduction in river inflow due to a severe drought of 2018–2019 was even more crucial for *C. euxinus*: it minimized allochthonous supply of nutrients to the sea. In 2019, content of nitrate, phosphate, and especially silicate was the lowest since at least 2009 due to reduced river inflow. Accordingly, abundant phytoplankton, particularly silicate-dependent diatoms, was deprived of mineral resources for its development in 2019 and failed to satisfy *C. euxinus* trophic requirements at the level of previous years, as well as those of copepods in general. Slightly elevated lipid reserves in V copepodites in 2019 might reflect the anomalous sparsity of *C. euxinus* population in that year, potentially driven by unprecedented high biomass of planktivorous jellyfish, especially *Aurelia aurita*, during winter and spring in 2017–2018.

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АНОМАЛЬНОЕ СОКРАЩЕНИЕ ЧИСЛЕННОСТИ И БИОМАССЫ ПОПУЛЯЦИИ КОПЕПОДЫ *CALANUS EUXINUS* В ГЛУБОКОВОДНЫХ РАЙОНАХ ЧЁРНОГО МОРЯ ОСЕНЬЮ 2019 Г.: ЧТО ПРОИСХОДИТ В МОРСКОЙ ЭКОСИСТЕМЕ?

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В ходе планктонных работ, проведённых в глубоководных районах Чёрного моря и на его шельфе у Крымского полуострова в октябре 2019 г. (110-й рейс НИС «Профессор Водяницкий»), исследовали количественное распределение, численность, биомассу, размерно-возрастную структуру и жировые резервы популяции копеподы *Calanus euxinus* Hulsemann, 1991. Пробы зоопланктона отбирали сетью Богорова — Расса (площадь входного отверстия 0,5 м^2, ячея 300 мкм) методом тотальных вертикальных ловов от дна или от нижней границы кислородной зоны до поверхности моря. Размеры и возраст *C. euxinus* определяли под микроскопом. Содержание запасных липидов в популяции оценивали по удельному объёму жировых мешков у рачков старших возрастных стадий. Установлено, что продолжающееся потепление в Азово-Черноморском регионе привело в 2019 г. к сокращению численности и биомассы *C. euxinus* в глубоководных районах до (5,3 ± 0,5) тыс. экз.·м$^{-2}$ и (3,7 ± 0,3) г·м$^{-2}$ соответственно, а также к изменениям в структуре популяции. Отчасти этому способствовало ослабление зимнего конвективного перемешивания водных масс. Вероятно, ещё более существенным для *C. euxinus* было то́, что из-за сильной засухи 2018–2019 гг. произошло резкое снижение паводкового стока рек, ограничившее до минимума поступление биогенных элементов в море. Вследствие слабого выноса с речным стоком нитратов, фосфатов и особенно силикатов массовый фитопланктон (прежде всего нуждающиеся в силикатах диатомовые водоросли) не имел в 2019 г. минеральных ресурсов для своего развития и, соответственно, не обеспечивал на уровне прежних лет трофические потребности *C. euxinus*. Некоторое повышение жирности V копеподитов осенью 2019 г. объяснимо аномальной разреженностью популяции *C. euxinus* в этом году, обусловленной, возможно, беспрецедентно высокой биомассой желетелых планктофагов и особенно медузы *Aurelia aurita* Linnaeus, 1757 в зимне-весенний период 2017–2018 гг.

Ключевые слова: *Calanus euxinus*, численность, биомасса, запасные липиды, межгодовая динамика, Чёрное море