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STATE OF POPULATION OF *CALANUS EUXINUS* (COPEPODA) IN THE OPEN PELAGIAL AND ON THE SHELF OF THE BLACK SEA NEAR CRIMEA IN AUTUMN 2016

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A copepod *Calanus euxinus* Hulsemann, 1991 is one of the most abundant mesozooplankton species constituting up to 60–80 % of planktonic crustacean biomass in the deeper Black Sea and being the main food component for small pelagic fish. Data on abundance, biomass, age structure, and lipid reserves of *C. euxinus* are required to estimate the state of its population in the open pelagial and on the shelf of the Black Sea. The data were obtained during the 89th cruise of the RV "Professor Vodyanitsky" (30.09.2016–09.10.2016) in the northwestern, central, and northeastern sea (62 stations). Zooplankton was sampled with a Bogorov–Rass net (mouth area of 0.5 m^2; mesh size of 300 μm) by vertical net hauls from the seabed to the surface on the shelf and from the lower border of the oxygen zone to the surface in the deep-sea area. The samples were fixed with 4 % formaldehyde; in the laboratory, the abundance and biomass of all copepodite stages of *C. euxinus* were determined. Wax ester content in the bodies of late copepodite stages and adult specimens was estimated based on the specific oil sac volume (% of the body volume). The relationship between the quantitative species distribution and the habitat depth and macroscale hydrological circulation was revealed. In the deep-sea area, the mean abundance and biomass of *C. euxinus* amounted to (8.3 ± 0.8) thousand ind.·m^{-2} and (7.1 ± 0.7) g·m^{-2}, respectively. On the outer shelf, the abundance and biomass of this species decreased twofold – down to (4.2 ± 1.4) thousand ind.·m^{-2} and (3.3 ± 1.2) g·m^{-2}, respectively. In the deep-sea area, copepodites V, females, and males constituted 91 % of the total abundance and 96 % of the total biomass of the population. On the outer shelf, the ratio of these developmental stages reduced to 67 % and 86 % of the total abundance and biomass, respectively. In the deeper pelagial, the specific oil sac volumes in copepodites V, females, and males [(17.1 ± 0.6), (11.2 ± 0.8), and (11.9 ± 0.5) %, respectively] were twice as high as in the same developmental stages from the outer shelf [(8.1 ± 0.8), (4.7 ± 0.8), and (6.0 ± 0.5) %, respectively] indicating a relation between lipid accumulation in this species and hypoxic conditions of the biotope. Relatively high values of the abundance, biomass, and wax ester content in *C. euxinus* indicate that the population returned to its previous state – the one observed *prior* to expansion of alien ctenophores in the late 1980s and recent climatic changes resulting in a warming of the Black Sea basin.

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

Calanus euxinus Hulsemann, 1991 is the most abundant representative of the Black Sea cold-water copepods; it forms 60–80 % of the biomass of planktonic crustaceans in open areas (Anninsky & Timofte, 2009 ; Yuneva et al., 1999) and is the key food source for small pelagic fish (Yuneva et al., 2016). For the Black Sea, the main patterns of the vertical distribution of the *C. euxinus* population are known since the early XX century (Nikinin, 1926), but many issues related to its annual renewal, spatial heterogeneity of the distribution in biotopes, and interannual biomass dynamics require further study.

Quantitative indicators of the state of the *C. euxinus* population in different Black Sea areas are considered in a number of works (Vinogradov et al., 1992 ; Zagorodnyaya et al., 2001 ; Svetlichny & Hubareva, 2011 ; Niermann et al., 1998). In 1980–1990, the biomass of this species in the central sea averaged 7–11 g·m^{-2} (Kovalev, 1996). However, the expansion of the ctenophore *Mnemiopsis leidyi* (A. Agassiz, 1860) in the late 1980s sharply reduced the *C. euxinus* biomass: in the central sea, it decreased to 0.5 and 1.1 g·m^{-2} in 1991 and 1992, respectively (Vinogradov et al., 1999); in the northern sea, it decreased to 4.3 g·m^{-2} in 1993 (Vinogradov et al., 1995). After the sea was invaded by the ctenophore *Beroe ovata* Bruguière, 1789 – the species feeding on planktivorous ctenophores alone – in the late 1990s, the trophic pressure on mesozooplankton by *M. leidyi* significantly decreased (Vinogradov et al., 1999). This resulted in the *C. euxinus* biomass recovery almost to the level of the 1980s (Anninsky & Timofte, 2009). It is unclear to what extent the population of this copepod could have been affected by the factors as follows: recent changes in the ecosystem associated with the effect of climate (Polonskii et al., 2013), phenological deviations in ecology, the reduction of a massive planktivore – the Black Sea sprat *Sprattus sprattus phalericus* (Risso, 1827) (Yuneva et al., 2016), gradual increase in the biomass of the scyphomedusa *Aurelia aurita* (Linnaeus, 1758) in the sea (Anninsky et al., 2019), and structural transformation of the entire community of planktonic gelatinous predators (Anninsky et al., 2020).

For the *C. euxinus* population, an autumn hydrological season is a period characterizing the success of its spring generative renewal, effectiveness of survival and maturation of new generations in summer, and developmental degree of a new generation of spawners (autumn copepodites V, males, and females) for next spring. In autumn, the *C. euxinus* biomass is only slightly lower than its spring maximum values (Vinogradov et al., 1999).

The aim of this work is to assess the current state of the *C. euxinus* population in the open pelagial and on the shelf of the northeastern, central, and northwestern Black Sea. It is of great importance in connection with an annual renewal of the composition, abundance, and biomass of the population.

MATERIAL AND METHODS

Mesozooplankton, *inter alia* juvenile and adult specimens of *C. euxinus*, was sampled at 62 stations in the northeastern, central, and western Black Sea in the deeper epipelagial, on the outer shelf (depths 50–200 m), and on the inner shelf (depth < 50 m) during the 89th cruise of the RV "Professor Vodyanitsky" (30.09.2016–09.10.2016) (Fig. 1). Sampling was carried out with a Bogorov–Rass net (hereinafter BR net) (mouth area of 0.5 m^2; mesh size of 300 μm) by vertical net hauls from the seabed or the lower border of the oxygen zone (according to the CTD Sea-Bird 911plus, σ_t = 16.2) to the surface. To compare the catchability of all size–age stages of *C. euxinus*, parallel hauls were carried out with the BR net and the Juday net (mouth area of 0.1 m^2; mesh size of 112 μm) at two stations. Samples were fixed with 4 % formaldehyde; the composition and abundance of copepods were determined in the laboratory by examining zooplankton in a Bogorov chamber under a microscope. The individual wet weight of copepodites and mature *C. euxinus* (WW, mg) was calculated by the formula:

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

where l and d are the length and width of the cephalothorax, respectively, mm;

ρ is the mean body density, g·cm^{-3} (Svetlichny & Hubareva, 2011).

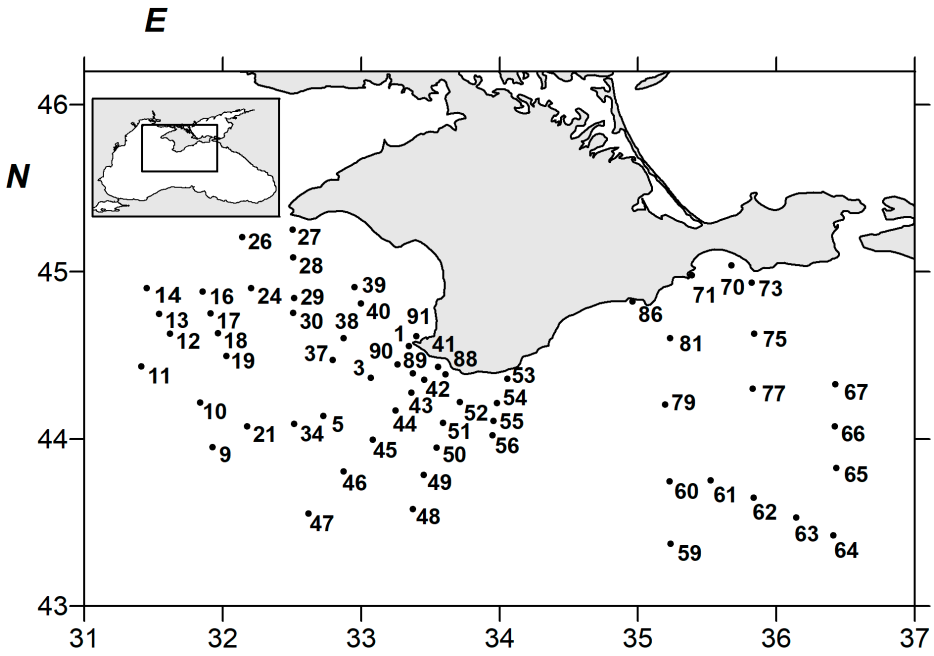

Fig. 1. Map of sampling survey (with station numbers identified) during the 89th cruise of the RV "Professor Vodyanitsky" in the Black Sea (September–October 2016)

The amount of reserve oil accumulated by the older stages of *C. euxinus* was estimated from the specific oil sac volume (Svetlichny & Hubareva, 2011). The oil sac volume (V_{sac}) was quantified according to the formula:

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

where l_{sac} and d_{sac} are the length and width of the oil sac, respectively, mm.

The body volume of copepodites, males, and females (V_b, mm^3) was calculated as follows:

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

where l_{pr} and d_{pr} are the length and width of the cephalothorax, respectively, mm;

k is the empirical coefficient equal to 0.64 for males and 0.58 for copepodites and females (Svetlichny et al., 2009).

The data were processed statistically using Grapher 3 and Surfer 8 software for Microsoft Windows. The means were compared applying the Student's *t*-test. Mean values are presented with the standard error.

RESULTS

The results of 10 parallel hauls with the BR net and the Juday net in different sea areas are supplemented by similar data from previous years (Anninsky & Timofte, 2009) and shown in Fig. 2. The analysis of the material indicates that two nets captured early and middle copepodite developmental stages (I–IV) of *C. euxinus* with almost the same efficiency, while the BR net turned out to be more effective in capturing copepodites V. This may be due to lower filtration resistance of the BR net, as well as lower probability of its avoidance by the older copepodite stages and adult copepods.

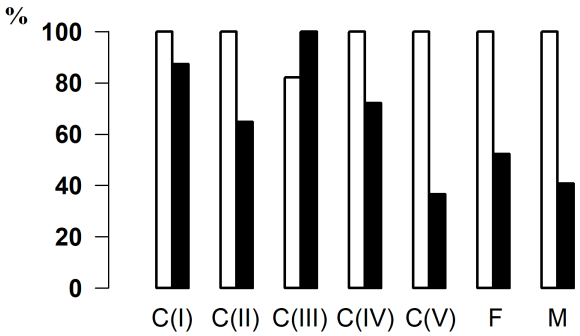

Fig. 2. Comparative catching efficiency for *Calanus euxinus* by the Juday net (black bars) and the Bogorov–Rass net (white bars) in 10 parallel vertical hauls in the Black Sea in September–October 2005 and 2016

The distribution of the *C. euxinus* abundance and biomass in September–October 2016 (Fig. 3) clearly shows a dependence on a macroscale hydrological circulation. The densest accumulations of individuals of this species (up to 21 thousand ind.·m^{-2} and 18.9 g·m^{-2} at stations 29, 63, and 79) were found on the periphery of the Eastern cyclonic gyre and in the core of the anticyclonic eddy west of Crimea (Sevastopol anticyclone). In the central Eastern gyre, there were fewer copepods. In the deep-sea area, the mean abundance and biomass of *C. euxinus* were (8.3 ± 0.8) thousand ind.·m^{-2} and (7.1 ± 0.7) g·m^{-2}, respectively. When moving from the open sea to the outer shelf, the abundance reliably decreased from (8.3 ± 0.8) to (4.2 ± 1.4) thousand ind.·m^{-2}, and the biomass reduced from (7.1 ± 0.7) to (3.3 ± 1.2) g·m^{-2}. On the inner shelf, due to single occurrence of the older copepodite stages, the abundance of *C. euxinus* amounted to only (0.10 ± 0.04) thousand ind.·m^{-2}, and the biomass was (0.09 ± 0.03) g·m^{-2}.

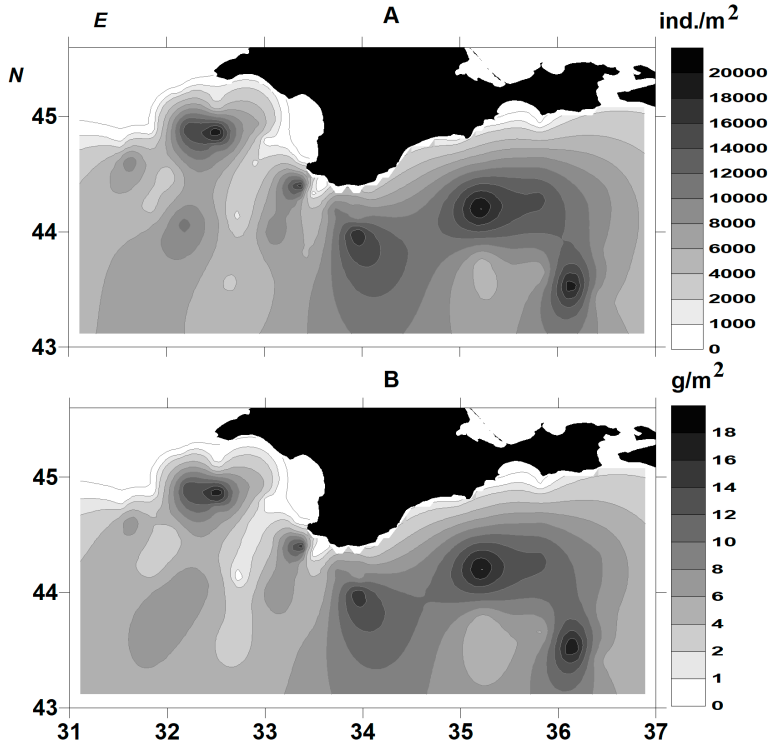

Fig. 3. *Calanus euxinus* abundance (A) and biomass (B) in the northeastern, central, and western Black Sea in September–October 2016

In the deep-sea area, with the lowering of the lower border of the oxygen zone (σ_t = 16.2) from 100–125 to 151–180 m, the *C. euxinus* abundance first increased ($p < 0.05$) from (7.3 ± 0.9) to (10.5 ± 1.1) thousand ind.·m^{-2} (with the depth reaching 126–150 m) and then decreased ($p > 0.05$) to (8.6 ± 2.1) thousand ind.·m^{-2} (with the lower border of the oxygen zone being at a depth of 151–180 m) (Fig. 4). The biomass varied in a similar way: the value first increased ($p < 0.05$) from (6.2 ± 0.8) to (9.02 ± 1.02) g·m^{-2} (at intermediate values of the lower border of the oxygen zone) and then decreased ($p > 0.05$) to (7.3 ± 1.9) g·m^{-2} (with the lowering of the lower border of the copepod biotope to 151–180 m). According to the data obtained, the *C. euxinus* abundance and biomass significantly increase ($p < 0.05$) in the direction from the central areas of cyclonic gyres to their borders. However, quantitative changes in the abundance and biomass of this species inhabiting cyclonic and anticyclonic circulation areas are generally insignificant.

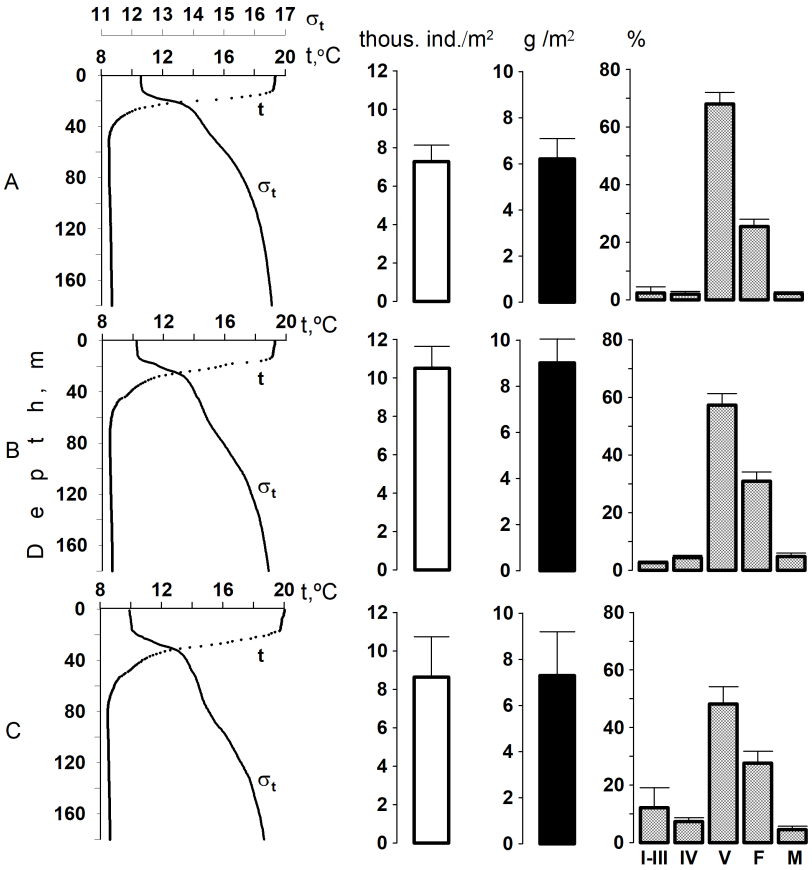

Fig. 4. Total abundance (thousand ind.·m^{-2}), biomass (g·m^{-2}), and age structure (% of total abundance) in the *Calanus euxinus* population in relation to seawater temperature (t, °C) and density (σ_t) in the upper epipelagial of the Black Sea (0–180 m). The lower border of the oxygen zone (σ_t = 16.2) is as follows: 100–125 m (A); 126–150 m (B); 151–180 m (C)

Specific changes in the structure of the *C. euxinus* population depending on the lower border of the oxygen zone indicate as follows: such variations in the abundance and biomass of crustaceans are caused by the redistribution of age stages with water masses of the surface epipelagial. Centrifugal flows in the area of cyclonic gyres displace to the periphery primarily copepodites I–IV inhabiting surface layers and adults. Copepodites V inhabiting a hypoxic biotope are affected to a lesser extent. In the area of anticyclonic eddies, on the contrary, centripetal flows can capture to a greater extent the younger copepodites inhabiting the near-surface water layer, as well as females and males. In this case, copepodites V either disperse or partially die. With the lowering of the lower border of the oxygen zone from 100–125 to 126–150 and 151–180 m, the ratio of copepodites I–III increased from (2.4 ± 1.9) to (2.6 ± 0.4) and (12.2 ± 6.8) %, respectively, and the ratio of copepodites IV

rose from (1.9 ± 0.9) to (4.3 ± 0.6) and (7.4 ± 1.2) %, respectively. With the lowering of the lower border of the oxygen zone, the ratio of copepodites V decreased from (67.9 ± 3.9) to (57.4 ± 3.7) and (48.2 ± 5.8) %, respectively; the ratio of adults remained almost at the same level – (25.5 ± 2.3), (30.9 ± 3.0), and (27.6 ± 4.0) % for females and (2.2 ± 0.4), (4.8 ± 1.0), and (4.6 ± 1.0) % for males.

The structure of the *C. euxinus* population changed similarly in the direction from the deep-sea area to the outer and inner shelf (Fig. 5). The total numerical prevalence of copepodites V [(58.0 ± 2.8) %] and females [(28.0 ± 1.8) %] in the open sea weakened on the shelf [36–40 % and 18–23 %, respectively], and the ratio of younger age stages, on the contrary, rose. On the shelf, it averaged 14–15 % for copepodites I–III and 24–25 % for copepodites IV. At the same time, no significant differences were found in the age structure of the *C. euxinus* populations from the outer and inner shelf.

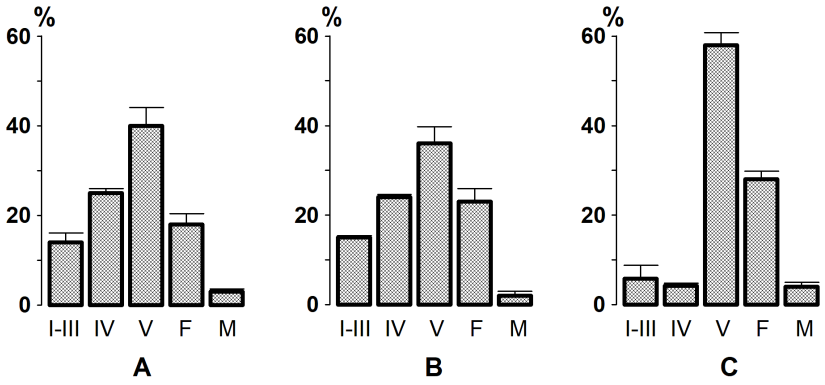

Fig. 5. Age structure of the *Calanus euxinus* population (% of total abundance) on the inner (A) and outer (B) shelf and in the deeper pelagial (C) of the Black Sea

The specific oil sac volume in copepodites V, females, and males of *C. euxinus* in the deep-sea area averaged (17.1 ± 0.6), (11.2 ± 0.8), and (11.9 ± 0.5) %, respectively (Fig. 6). On the outer shelf, the amount of wax esters accumulated by copepods decreased twofold– down to (8.1 ± 0.8) % of the body volume in copepodites V, (4.7 ± 0.8) % in females, and (6.0 ± 0.5) % in males.

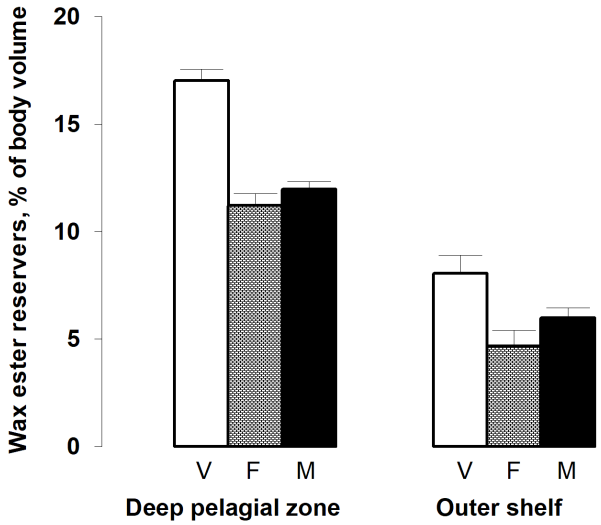

Fig. 6. Mean specific oil sac volume (% of the body volume) of *Calanus euxinus* in the deeper pelagial and on the outer shelf of the Black Sea in September–October 2016 (V denotes copepodites V; F, females; M, males)

DISCUSSION

Analysis of the quantitative characteristics of the state of the *C. euxinus* population in 2016, as well as similar data from previous years (Anninsky & Timofte, 2009 ; Arashkevich et al., 2002 ; Vinogradov et al., 1995 ; Zagorodnyaya et al., 2001 ; Kovalev, 1996 ; Svetlichny & Hubareva, 2014 ; Arashkevich et al., 2014 ; Vinogradov et al., 1999) did not allow revealing any interannual variability in the abundance and biomass for this species in the sea over the past decades. With the existing probability of such a dynamics, the range of interannual fluctuations in the copepod abundance and biomass (under predator pressure and effect of climatic factors) seemed to exceed significantly the possible limits of long-term changes in the population.

Specifically, the mean biomass of the species in deep-sea central [(6.5 ± 1.1) g·m^{-2}] and north-eastern [(8.9 ± 1.3) g·m^{-2}] areas in 2016 was comparable with the corresponding data of 1999 [9.7 g·m^{-2}] (Arashkevich et al., 2002). In the western deep-sea, the *C. euxinus* biomass [(5.9 ± 1.2) g·m^{-2}] was the same [$p > 0.05$] as in October 2005 [(6.2 ± 1.1) g·m^{-2}] (Anninsky & Timofte, 2009). Interestingly, in October 2010, its biomass in these areas (2.8 g·m^{-2}) (Svetlichny & Hubareva, 2014) was at least two times lower than in 2005 and 2016. The mean *C. euxinus* abundance varied in the same way: the value reached (9.9 ± 1.8) thousand ind.·m^{-2} in 2005 (Anninsky & Timofte, 2009) and (7.3 ± 1.3) thousand ind.·m^{-2} in 2016, but decreased to 3.9 thousand ind.·m^{-2} in 2010 (Svetlichny & Hubareva, 2014). On the outer shelf of the central sea, the *C. euxinus* abundance in autumn 2016 [(4.3 ± 1.9) thousand ind.·m^{-2}] on average exceeded the corresponding value for October 2005 [(2.5 ± 0.49) thousand ind.·m^{-2}], but the difference was statistically insignificant [$p > 0.05$]. If such changes did occur in the copepod population, they could not be associated with the interannual dynamics of the biomass of gelatinous macroplankton in general or its representatives. Importantly, despite the fact that the biomass of *M. leidyi* decreased in the sea (from (76 ± 22) g·m^{-2} in 2005 to (48 ± 11) g·m^{-2} in 2016), the biomass of another planktivorous ctenophore – *Pleurobrachia pileus* (O. F. Müller, 1776) – increased over these years (from (22 ± 4) to (45 ± 4) g·m^{-2}, respectively). Moreover, during this period, the biomass of the jellyfish *A. aurita* increased as well, at least by 5 times – from (44 ± 15) to (260 ± 72) g·m^{-2} (Anninsky et al., 2019). Apparently, the annual reproduction of the *C. euxinus* population in the sea is affected not so much by predators as by climatic factors. Specifically, a relation was found between the *C. euxinus* biomass and an increase in water temperature in April ($r^2 = 0.61$; $p < 0.01$) and May ($r^2 = 0.51$; $p < 0.01$) (Anninsky et al., 2020). Importantly, the water temperature in April and May 2016 was on average 0.5 and 2.2 °C higher, respectively, than in the same months of 2005. Therefore, it is more likely that an increase in the copepod abundance and biomass also occurred between 2005 and 2016.

The total prevalence of copepodites V and adults in the deep-sea area for most of the year (Arashkevich et al., 2014 ; Besiktepe, 2001 ; Svetlichny et al., 2009) indicates that the deep-sea hypoxic biotope is important for the development of the *C. euxinus* population: in a certain way, it regulates the accumulation of lipids in the body of copepods (Isinibilir et al., 2009 ; Yuneva et al., 1999). In the deeper pelagial in 2016, the older copepodite stages of the species had significant reserves of wax esters required for the completion of metamorphosis, sexual maturation, and generative production. The decrease in content of reserve lipids in females, males, and copepodites V in the direction from the open sea to the outer and inner shelf reflects the general patterns of formation of oil reserves in the Black Sea population of *C. euxinus*. Daily vertical migrations of the older copepodite stages into deep hypoxic layers can significantly reduce energy expenditure and increase the efficiency

of lipid accumulation (Svetlichny et al., 2006). In the shallow water area in the absence of hypoxia, copepods accumulate fewer reserve lipids; however, due to higher temperature in the biotope, they can develop faster (Svetlichny & Hubareva, 2014).

The formation of oil reserves in *C. euxinus* begins at copepodite stages III and IV, when the mean oil sac volume does not exceed 1–2 % of the body volume. Then, it gradually increases and averages 16–17 % of the body volume in copepodites V (Svetlichny & Hubareva, 2011). In autumn 2016, the specific oil sac volume in copepodites V averaged (17.1 ± 0.6) %; at some deep-sea stations, it reached 20 % of the body volume. Such a high content of reserve lipids for *C. euxinus* is comparable with oil content recorded in April 2003 in the southwestern sea during the bloom of the alga *Proboscia alata* (Brightwell) Sundström, 1986 (16–22 %) (Svetlichny et al., 2009). Similar values of the specific oil sac volume in copepodites V [(16.1 ± 7.6) %] were obtained in October 2005 in the western sea (Svetlichny & Hubareva, 2014). Thus, both in terms of quantitative indicators and content of reserve lipid in the body of copepods, the *C. euxinus* population in the Black Sea in the autumn 2016 was in a more developed state than in the years of the pelagic ecosystem recovery (early 2000s), after the uncontrolled effect of *M. leidyi* at the late XX century.

Conclusion. The data obtained indicate that spatial distribution of *Calanus euxinus* in the northeastern, central, and western Black Sea in September–October 2016 was heterogeneous and depended on the habitat depth and macroscale hydrological circulation. In the deep-sea area, the copepod abundance and biomass were almost twice as high as the values for this species on the outer shelf; this is due to peculiarities of the hydrodynamics of the Main Black Sea Current, cyclonic gyres, and anticyclonic eddies. In the *C. euxinus* population of the deeper pelagial, copepodites V prevailed; with females and males, those accounted for up to 91 % of the total abundance and 96 % of the total biomass of the species. On the outer and inner shelf, the ratio of the older copepodite stages naturally decreased. Copepodites V, females, and males inhabiting deep-sea area had two times more reserve lipids than the older copepodite stages on the shelf; this is due to specific patterns of lipid accumulation in this species. Relatively high values of the abundance, biomass, and wax ester content in *C. euxinus* indicate that the population returned to its previous state – the one observed *prior* to expansion of the alien ctenophores in the late 1980s and recent climatic changes resulting in a warming of the Black Sea basin.

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СОСТОЯНИЕ ПОПУЛЯЦИИ *CALANUS EUXINUS* (COPEPODA) В ОТКРЫТОЙ ПЕЛАГИАЛИ И ЗОНЕ КРЫМСКОГО ШЕЛЬФА ЧЁРНОГО МОРЯ ОСЕНЬЮ 2016 Г.

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Копепода *Calanus euxinus* Hulsemann, 1991 — один из наиболее массовых видов мезозоопланктона Чёрного моря, образующий в глубоководных районах 60–80 % биомассы планктонных ракообразных и составляющий здесь основу рациона мелких пелагических рыб. Данные о численности, биомассе, возрастной структуре и жировых запасах *C. euxinus* необходимы для оценки состояния его популяции в открытой пелагиали и шельфовой зоне Чёрного моря. С этой целью в 89-м рейсе НИС «Профессор Водяницкий» (30 сентября — 9 октября 2016 г.) проведены исследования в северо-западных, центральных и северо-восточных районах моря (62 станции). Пробы мезозоопланктона отбирали сетью Богорова — Расса (площадь входного отверстия — 0,5 м^2; ячея — 300 мкм) методом тотальных вертикальных ловов от дна до поверхности моря в области мелководного шельфа и от нижней границы кислородной зоны до поверхности моря в глубоководной части. Пробы фиксировали 4%-ным раствором формалина, численность и биомассу всех копеподитных стадий *C. euxinus* определяли в лабораторных условиях. Содержание восков в теле старших копеподитов и половозрелых особей *C. euxinus* оценивали по удельному объёму жирового мешка (относительно объёма тела). Выявлена зависимость количественного распределения вида от глубины биотопа и макромасштабной циркуляции водных масс в море.

В глубоководной части моря средняя численность *C. euxinus* составляла (8,3 ± 0,8) тыс. экз.·м$^{-2}$, биомасса — (7,1 ± 0,7) г·м$^{-2}$. На внешнем шельфе численность и биомасса вида снижались вдвое — до (4,2 ± 1,4) тыс. экз.·м$^{-2}$ и (3,3 ± 1,2) г·м$^{-2}$ соответственно. В глубоководных районах копеподиты V стадии вместе с самками и самцами составляли 91 % численности и 96 % биомассы популяции. На внешнем шельфе доля этих возрастных стадий сокращалась до 67 % численности и 86 % биомассы. В районах глубоководной пелагиали удельный объём жирового мешка у V копеподитов, самок и самцов [(17,1 ± 0,6), (11,2 ± 0,8) и (11,9 ± 0,5) % соответственно] был вдвое выше, чем у этих же возрастных стадий на внешнем шельфе [(8,1 ± 0,8), (4,7 ± 0,8) и (6,0 ± 0,5) % соответственно], что указывает на зависимость между накоплением липидных резервов у данного вида и гипоксическими условиями в биотопе. Сравнительно высокие величи́ны численности, биомассы и содержания восков у *C. euxinus* свидетельствуют о том, что его популяция практически вернулась к прежнему состоянию (наблюдавшемуся до экспансии гребневиков-вселенцев в конце 1980-х гг. и последних климатических изменений, которые привели к потеплению в бассейне Чёрного моря).

Ключевые слова: *Calanus euxinus*, численность, биомасса, резервные липиды, Чёрное море