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Original paper

The Main Patterns of the Black Sea Ecosystem Long-Term Changes

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Abstract

This study examines long-term changes in the Black Sea ecosystem, including the warming of its waters amid anthropogenic pollution and eutrophication. The aim of the study is to describe structural shifts in water masses and biotopes, as well as to assess alterations in key ecosystem components. Through the analysis of multi-year hydrological datasets, mathematical modelling, and hydrobiological studies, it has been demonstrated that a comprehensive understanding of the Black Sea's ecosystem changes requires consideration not only of climate warming, anthropogenic pollution, and eutrophication but also of chorological changes in water mass structure and associated biotopes. Ongoing deoxygenation is reducing the habitat layer for cold-water species, while warming has already caused the disappearance of the cold intermediate layer – with which these species are associated – dissolving it into surrounding waters at temperatures around 9 °C. Further warming of surface waters may lead to the degradation of cold-water species assemblages that form the trophic foundation of the Black Sea's current ecosystem. A significant transformation is expected due to the increasing dominance of warm-water and eurythermic species.

Keywords: Black Sea, ecosystem, climate change, deoxygenation, water masses, biotopes

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Основные закономерности многолетних изменений экосистемы Черного моря

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Аннотация
Анализируются многолетние изменения экосистемы Черного моря, выражающиеся, кроме прочего, в потеплении вод на фоне антропогенного загрязнения и эвтрофикации. Цель работы заключается в описании структурных изменений водных масс, биотопов, а также в оценке изменений ключевых компонентов экосистемы. На основе анализа многолетних массивов данных о гидрологии, математического моделирования и гидробиологических исследований показано, что для полного понимания изменений экосистемы Черного моря необходимо учитывать не только потепление климата, антропогенное загрязнение и эвтрофикацию, но и хорические изменения структуры водных масс и связанных с ними биотопов. Продолжающаяся деоксигенация сокращает слой обитания холодноводных видов, а потепление уже привело к тому, что холодный промежуточный слой, с которым эти виды ассоциированы, исчез и растворился в окружающих водах при температуре около 9 °C. Дальнейшее потепление поверхностных вод может привести к деградации комплекса холодноводных видов, создающих трофическую основу современной экосистемы Черного моря. Следует ожидать ее существенной трансформации вследствие увеличения роли тепловодных и эвритермных видов.

Ключевые слова: Черное море, экосистема, изменения климата, деоксигенация, водные массы, биотопы

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Introduction

Around 130 years ago, N. I. Andrusov [1)] was the first to demonstrate that the Black Sea (BS) was a two-layered system consisting of a thin (80–200 m) “living” oxygen layer and a hydrogen sulphide zone. Until the end of the 20th century, it was believed that a layer of co-existing oxygen and hydrogen sulphide waters, or a C-layer, existed between these two layers. The first publications about the absence of this layer were met with scepticism [1]. However, new techniques introduced at the end of the 20th century revealed that ideas about the C-layer were

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1) Andrusov, N.I., 1890. [Preliminary Report on Participation in a Black Sea Deep-Water Expedition]. *Izvestiya Russkogo Geografocheskogo Obshchestva*, 26(5), pp. 398–409 (in Russian).

erroneous [1–3]. A water mass measuring between 30 and 50 m deep composed of transformed Mediterranean water (O_2 < 10 μM, H_2S < 3 μM), or the Suboxic Layer (SOL), was found to exist between the oxygen zone and the hydrogen sulphide layer [1, 2]. The position of this layer within the water column is determined by the intensity of vertical water exchange and the concentration of dissolved organic matter. The Danube, Dnieper and Don rivers experienced a tenfold increase in nutrient inputs between the 1960s and 1990s, leading to anthropogenic eutrophication and the formation of large amounts of sinking organic matter [2]. The vertical water exchange did not provide sufficient aeration to compensate for the aeration needed to oxidise the large amount of organic matter, and the oxygen layer of the sea began to "shrink" [2, 4]. The depth to which oxygen penetrated the upper boundary of the SOL decreased from 130 m in 1955 to 90 m in 2013 [5]. Although eutrophication of the sea decreased by the beginning of the 21st century [6], deoxygenation of the depths continued due to the increase in surface water temperature [7].

Consequently, there have been significant changes in the composition of biotopes in the BS deep-water zone in recent years, which have had a considerable impact on the living conditions of plankton and fish. It is important to recognise that understanding the contemporary shifts within the BS ecosystem necessitates a comprehensive approach encompassing not only the impact of climate change, anthropogenic pollution and eutrophication but also the substantial alterations in the hydrological-hydrochemical and chorological characteristics of water masses and biotopes. (Chorological changes of water masses (from Greek *chora* – "place") are observed when a water mass changes its spatial position and acquires different ecological properties under the influence of a different combination of external factors in a new location [8].)

The existing hydrological-hydrochemical understanding of the structure of surface water masses in the BS deep waters can be described as follows:

1. Upper Black Sea Water Mass (UBSWM): T > 20°C, S = 18.0…18.4 PSU, σ_t < 14 [2), 3)].
2. Cold Intermediate Layer (CIL): T < 8°C, S = 18.0…19.0 PSU, σ_t = 14.0…14.8 [2), 3)].
3. Suboxic Layer (SOL): T > 8°C, σ_t = 15.8…16.2 [2, 3].
4. Intermediate Black Sea Water Mass (IBSWM): T > 8°C, S > 20 PSU, σ_t = 16.2…17.9 [2), 3)]. (The coastal and deep-water masses are not discussed in this paper as only the surface water of the deep-water zone is discussed.)

The biotope structure in the BS deep waters can be presented as follows:

1. Surface film biotope (aerocontour): community of aerobic organisms of the surface film – neuston. Composition – permanent or temporary inhabitants of 0–5 cm layer: bacteria and protozoa, phytoplankton, zooplankton, eggs and larvae of invertebrates and fish [9, 10].

[2)] Beznosov, V.N., 2000. [*Environmental Effect of Marine Destratification. Extended Abstract of DSc Thesis, Biological Sciences*]. Moscow: MSU, 42 p. (in Russian).

[3)] Belokopytov, V.N., 2017. [Climate Changes of the Black Sea Hydrological Regime. *DSc Thesis, Geographical Sciences*]. Sevastopol: MHI RAS, 377 p. (in Russian).

2. UBSWM biotope (aerobic zone): a community of aerobic organisms above a seasonal thermocline, epibiota. (We used the terms "epibiota" and "bathybiota" following T. S. Petipa [4)] who first described epi- and bathyplankton.) Composition – thermophilic and eurythermal species inhabiting the upper water mass: phytoplankton, epiplankton, macroplankton and the main mass of fish (*Engraulis encrasicolus* Linnaeus, 1758, etc.) [4)] [6, 11].

3. CIL biotope (aerobic zone): community of aerobic organisms under a seasonal thermocline, bathybiota [4)]. Composition: bathyplankton and cold-water fishes (*Sprattus sprattus* (Linnaeus, 1758), etc.), eurythermal plankton species [4), 5)] [11–14].

4. SOL biotope (anaerocontour): community of aerobic and anaerobic microorganisms of the Suboxic Layer. (The term "anaerocontour" was first introduced by V. V. Melnikov [14].) Composition: aerobic and anaerobic species of cyanobacteria, denitrifying bacteria, methanotrophs, methanogens, iron-reducing bacteria, manganese-reducing bacteria [14].

5. IBSWM biotope (anaerobic zone): community of anaerobic microorganisms of the hydrogen sulphide zone. Composition: thione bacteria (up to 40% of the biomass of all bacterioplankton), purple and fermenting bacteria, methanotrophs, methanogens, manganese-reducing bacteria, anammoxibacteria and various archaea [6)] [14]. The coastal and deep-water masses are not discussed because only the surface waters of the deep-water zone are discussed.

Recent studies indicate that the above-described ideas about the structure of water masses and biotopes no longer correspond to the real situation due to prolonged warming of surface waters [7)]. To date, deoxygenation has reduced deep-sea oxygen concentrations by 44% [5]. The CIL temperatures began to rise and by 2019 this water mass had disappeared [15]. Information about this catastrophic event for the BS ecosystem, of course, requires verification using different data series. Continued warming of surface waters could cause cascading changes throughout the BS ecosystem, since cold-water copepods form the bulk of the forage zooplankton that constitutes the main part of the diet of small plankton-feeding fish in the BS [12–16]. In addition, one of the fundamental questions remains unresolved as to how the reduction of the total oxygen layer thickness in the deep sea has affected chorological changes in the structure of pelagial habitats. The present study fills this gap to some extent.

The aim of the work is to analyse the basic processes of long-term changes in the BS ecosystem under the influence of warming, anthropogenic pollution,

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4) Petipa, T.S., 1967. [*Life Forms of Pelagic Copepods and the Structure of Trophic Levels in the Structure and Dynamics of Aquatic Communities and Populations*]. Kiev: Naukova Dumka, pp. 108–119 (in Russian).

5) Flint, M.V., 1989. Vertical Distribution of the mass Mesoplankton Species in Connection with the Oxygen Field Structure. In: M. E. Vinogradov and M. V. Flint, eds., 1989. [*Structure and Production Characteristics of Plankton Communities of the Black Sea*]. Moscow: Nauka, pp. 187–212 (in Russian).

6) Sorokin, Yu.I., 1982. [*Black Sea. Nature. Resources*]. Moscow: Nauka, 216 p. (in Russian).

7) Masevich, A.V., 2022. [*Oxygen Dynamics in the Main Pycnocline of the Black Sea. Extended Abstract of PhD Thesis. Geographical Sciences*]. Sevastopol: MHI RAS, 24 p. (in Russian).

eutrophication and changes in the structure of water masses and to assess changes in key ecosystem components.

Materials and methods

The hydrodynamic analysis was derived from the NEMO ocean circulation model version 3.6 [8)]. This model was implemented in the BS region with a horizontal resolution of 0.037° × 0.028° and 31 irregularly spaced vertical levels. The online model is linked to the OceanVar assimilation scheme [17, 18]. The BS-REA includes observations of temperature/salinity (T/S) profiles derived *in situ* from SeaDataNet and CMEMS INS TAC, as well as sea level anomalies. A summary of all available observations from ships (SYNOP SHIP), bathythermographs (BATHY) and drifting buoys (DRIBU) as well as data sourced from the ECMWF operational archive is provided.

In this paper, we examined the spatial and temporal variations in the temperature of the CIL and its surrounding waters over the past 30 years. Long-period and spatial variations of sea surface temperature (SST) were calculated from daily satellite maps with a resolution of 0.05° × 0.05° covering a 40-year period from 1982 to 2021. All information was obtained from the Copernicus marine environmental monitoring service (https://www.copernicus.eu) [9)]. In addition, we used new data obtained during the recent large-scale expeditions of the Collective Use Center R/V *Professor Vodyanitsky* of the A. O. Kovalevsky Institute of Biology of the Southern Seas of RAS in 2017–2023 (using an Idronaut Ocean Seven 320Plus M CTD probe).

Materials from the BS western central part were used to investigate long-term changes in the vertical position of the SOL density boundaries. As the distribution of hydrochemical parameters in the deep sea has quasi-permanent isopycnic distributions, the assessment of long-term changes in the vertical position of the SOL boundaries was carried out on the conditional density scale. On average, these boundaries correspond to isopycnic surfaces: σ_t = 15.8 to upper boundary and σ_t = 16.2 to lower one [2, 3]. This approach solves two important methodological problems:

1) deficit of hydrochemical data: data on the hydrochemistry of the western deep-water zone are clearly insufficient to assess their long-term shifts (with almost an order of magnitude more hydrological stations);

2) influence of random factors on assessment accuracy: the use of density characteristics makes it possible to minimise the impact of random processes and obtain more reliable quantitative assessments of the evolution of the BS waters ecological structure.

[8)] Gurvan, M., Bourdalle-Badie, R., Bouttier, P.-A., Bricaud, C., Bruciaferri, D., Calvert, D., Chanut, J., Clementi, E., Coward, A. [et al.], 2016. *NEMO ocean engine*. France: IPSL, 412 p. (Note du Pôle de modélisation de l'Institut Pierre-Simon Laplace; No. 27). https://doi.org/10.5281/zenodo.3248739

[9)] SST_BS_SST_L4_REP_OBSERVATIONS_010_022 / E.U. Copernicus Marine Service Information (CMEMS). Marine Data Store (MDS). https://doi.org/10.48670/moi-00160

The western part of the sea was chosen because the seasonal dynamics of the isopycnic vertical position in this circulation is insignificant (~5 m) compared to the eastern circulation where it reaches 20 m. Considering that the interannual variability is also greater in the eastern circulation, density characteristics for determining long-term shifts in the western central part of the sea are more statistically reliable.

Data for calculations were collected in oceanographic cruises of research vessels of the USSR, Russia, Ukraine, Turkey, Bulgaria and Romania. Data sets from the databases of WOD18 [10)], SeaDataNet, Coriolis Ocean Dataset, Marine Hydrophysical Institute and Institute of Biology of the Southern Seas as well as from other sources were used for the reanalysis. The boundaries of the central and western high salinity zones are taken as follows: 42.5–43.5°N, 30–32.5°E. A total of 1453 hydrological stations were sampled by research vessels in 154 cruises and seven Argo buoys during the summer period from 1957 to 2021 (June–August). The highest annual number of observations dates back to the 1980s, when up to 120 were recorded in the summer. Recently, however, the number of summer observations in the western open Black Sea has not exceeded 20, similar to the situation in the 1960s. Data from each expedition were checked for reliability and obviously false values (outliers that did not correspond to similar features in the distribution of other environmental parameters) were rejected.

Based on this, the average conditional density profiles were calculated. Averaging was performed by the inverse distance method followed by additional smoothing by low-pass filtering. Vertical density profiles (EOS-80 formulas) were interpolated with 1 m depth resolution using the method described in [19], then a search for a given isopycnic level was performed based on minimum deviation. Quality control including filtration jumps and vertical density inversions is performed before isopycnic levels are calculated. Further time series of calculated isopycnic levels were filtered using the 3σ statistical criterion and then averaged over the summer periods of each year. The averaging procedure serves as a specific low-pass filter to reduce the intra-seasonal variability that is inherent in this layer due to the influence of mesoscale eddies. The vertical discretisation of the raw data has increased significantly since the 1990s so this part of the time series has more reliable values of isopycnic levels and exhibits less mesoscale "noise". The mesoscale variability estimated as standard deviations calculated over summer periods over the last 30 years is almost half the total interannual variability, which improves estimates of the current linear trend.

Predictive analyses were conducted using MS Excel forecasting functions using the AAA version of the exponential smoothing algorithm (ETS), which in Excel is based on the AAA (additive error, additive trend and additive seasonality)

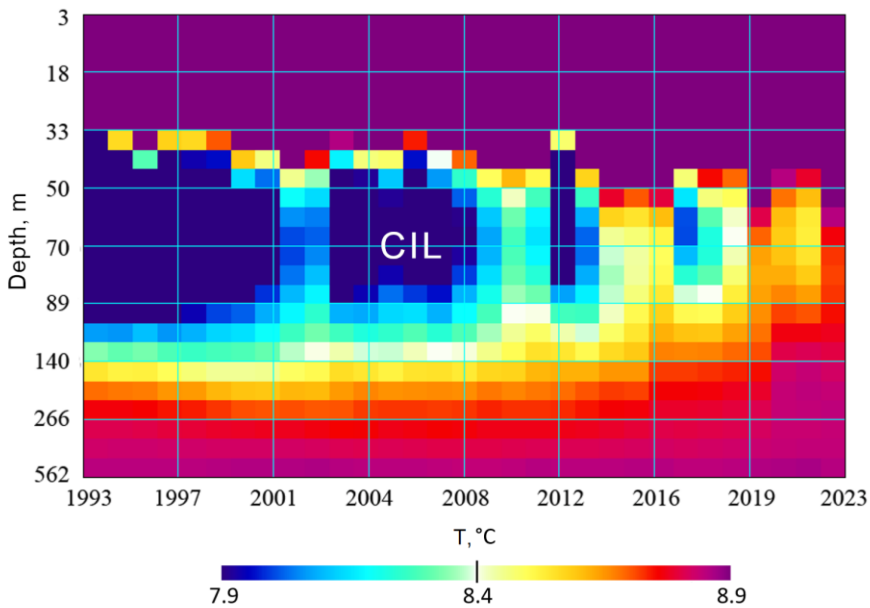
[10)] Mishonov, A.V., Boyer, T.P., Baranova, O.K., Bouchard, C.N., Cross, S., Garcia, H.E., Locarnini, R.A., Paver, C.R., Reagan, J.R. [et al.], 2024. *World Ocean Database 2023*. NOAA Atlas NESDIS 97, 207 p. Available at: https://www.ncei.noaa.gov/products/world-ocean-database [Accessed: 16 August 2024].

version of the exponential triple smoothing (ETS) algorithm which smooths out small deviations in past data trends by identifying patterns of seasonality and confidence intervals. This forecasting method is optimal for non-linear data models with seasonal or other recurring patterns.

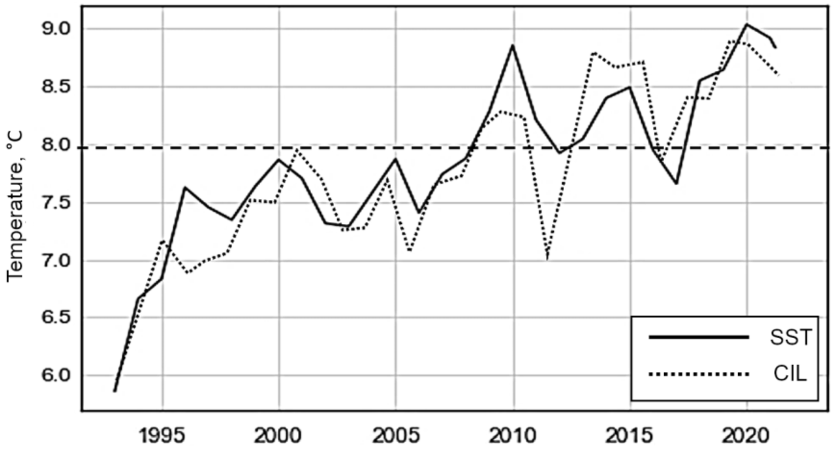
Results and discussion

Structural shifts in water masses

Fig. 1 presents averaged data on the long-term variability of the CIL vertical structure in the whole deep-sea zone from June to October in 1993–2023. The data reveal that in 2019, the upper and lower boundaries of the CIL merged at an average depth of about 70 m and this water mass, sustained the existence of the BS relict boreal species of forage zooplankton and planktivorous fish, had disappeared. This process did not occur overnight but as a result of a gradual warming of the CIL core over the last 20 years. The water renewal of its core decreased due to a succession of warm winters (Fig. 2) which recurring approximately every five years: in 1996, 2000, 2005, 2010, 2015, 2020 (based on the winters by SST calculated as the average for December–February). This is strongly evidenced by the high



F i g . 1 . Long-term variability of the cold intermediate layer (CIL)

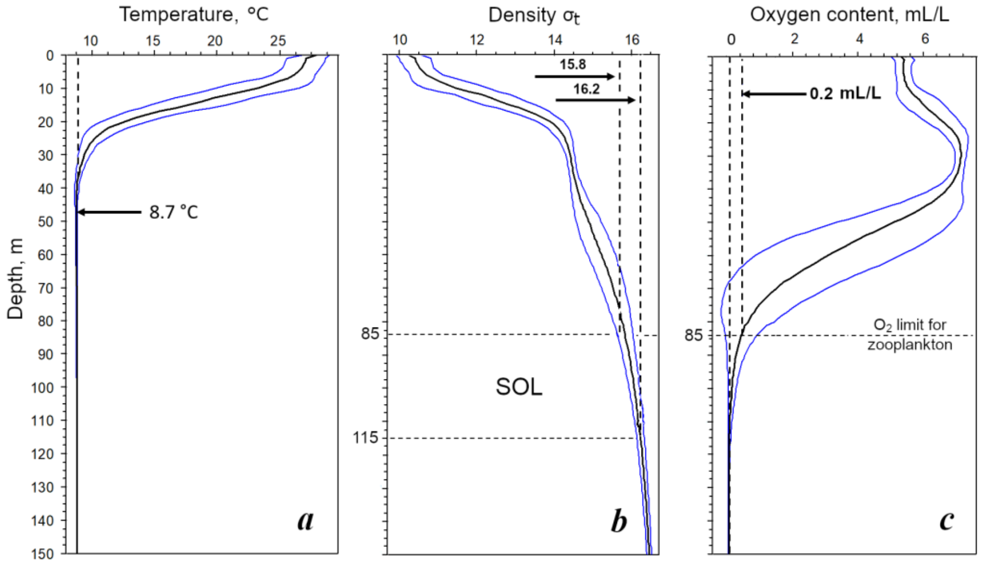


F i g . 2 . Average seasonal (winter) values of sea surface temperature, calculated as the average values for January, February and December, and the base value of the CIL in August for 1993–2022

rank Spearman correlation coefficient [20] between annual SST and CIL values, which is ~0.85 (Pearson correlation coefficient is ~0.89). The non-parametric rank correlation method is applied here because SST and CIL are not normally distributed according to the Shapiro–Wilk test [20]. The convergence of the upper and lower CIL boundaries has also led to an increase in the salinity of the surface layer. In 2023, at a depth of 50 m which usually corresponds to the position of the CIL core, salinity reached a maximum value of 19 PSU, which was previously observed only in the 60–70 m layer, i. e. at the average position of the lower boundary in summer.

Thus, a new stratification of water masses and associated biotopes had been emerged throughout the deep sea by 2021. Analysis of data from 84 hydrological profiles across the entire deep-water zone (0–150 m) revealed isothermia (~ 8.7 °C) under the thermocline at all depths up to the hydrogen sulphide zone (Fig. 3, *a*).

The distribution of water density characteristics in the same layer revealed the SOL and the associated anaerocontour biotope were located in the 85–115 m layer. Its upper boundary corresponded to the middle of the main pycnocline (σ_t = 15.8). The SOL average density boundaries are given in accordance with [2, 3]. Above it, the plankton and fish habitat was located in the oxygen zone (Fig. 3, *b*) in the 0–85 m layer (UBSWM and CIL). The maximum depth of zooplankton with a concentration [5)] of 10 μM, or 0.2 ml/L, coincided precisely with the upper boundary of the anaerocontour at the 85 m isobath (Fig. 3, *c*). At a depth of 115 m (with water density σ_t = 16.2), trace oxygen concentrations had disappeared completely and the chemocline layer began with a concentration of H_2S ~3 μM.

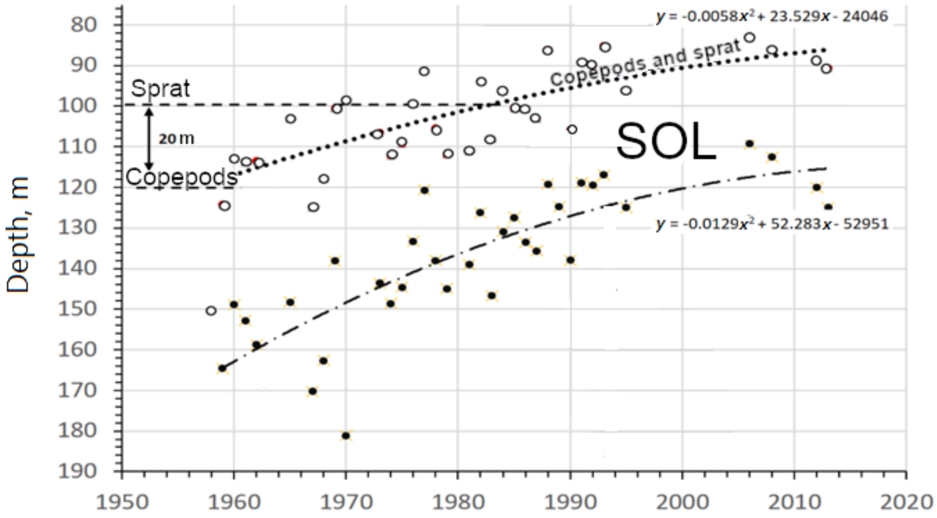


F i g . 3 . Average vertical profile of temperature (*a*), density anomaly (*b*) and oxygen content (*c*) in the 0–150 m layer in July and August 2021 in the central deep regions of the Black Sea, according to data from the 117th cruise of R/V *Professor Vodyanitsky*. Blue lines are SD, black lines are mean values

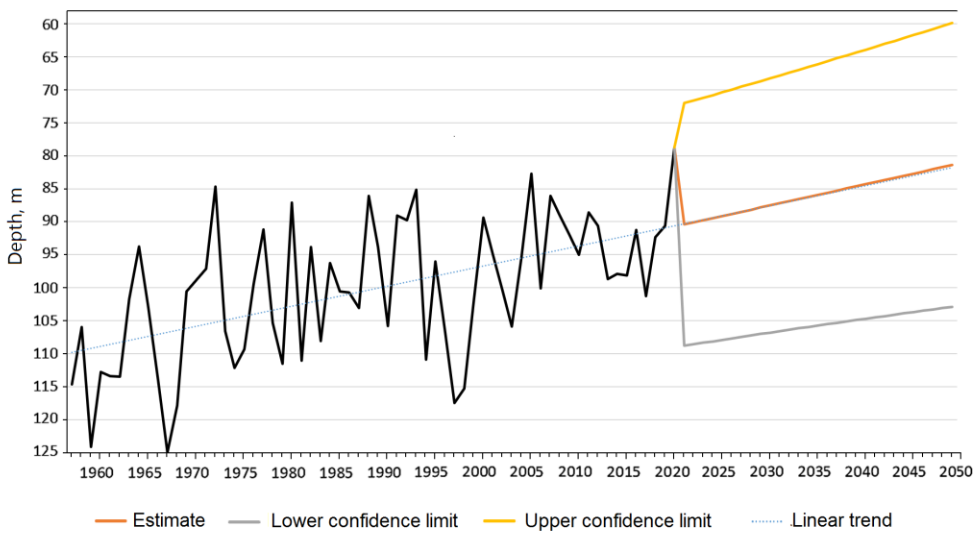
Structural shifts of biotopes

Fig. 3, *b* shows that the zone of daily accumulations of bathyplankton in 2021 aligned precisely with the upper boundary (at a depth of 85 m) of the biotope [12] of the anaerocontour. The study of the multiyear vertical dynamics of the vertical position of the anaerocontour from 1957 to 2021 was based on the fact that the average position of this contact zone corresponded to the upper boundary of the SOL at conditional density $\sigma_t = 15.8$ [2, 3].

The results of the study (Fig. 4) confirm that the upper boundary of this biotope ($\sigma_t = 15.8$) has moved 35 m closer to the surface over 60 years while its lower boundary ($\sigma_t = 16.2$) has risen from a depth of 165 to 115 m. This means that in 1983, the upper anaerocontour boundary (Fig. 4, white circles) rose to the isobath of 100 m which is the maximum depth of the Black Sea sprat *S. sprattus* habitat. Since then, deep accumulations of cold-water (forage) zooplankton concentrated near the upper anaerocontour boundary have appeared in the zone of accumulations of cold-water planktivorous fish. The lower anaerocontour boundary rise (Fig. 4, black circles) indicates that the chemocline, i. e. the hydrogen sulphide zone, has risen 50 m upwards.



F i g . 4 . Dynamics of the anaerocontour rise to the surface for 1957–2021, in summer in the western central deep-sea zone of the Black Sea: white circles are the upper anaerocontour boundary (σ_t = 15.8), black circles are the lower one (σ_t = 16.2). Average data by year: dotted line – upper contact zone; dashed-dotted line – lower contact zone; dashed lines – second-degree polynomial trends



F i g . 5 . Dynamics of the upper limit of the Suboxic Layer until 2050 (σ_t = 15.8) in the center of the western Black Sea (42.5–43.5° N, 30–32.5° E)

Knowledge of the dynamics and variability of SOL density boundaries makes it possible to calculate the approximate position of anaerocontour boundaries over the next 25 years. Analysis of hydrological data from the central part of the western cyclonic circulation for 1957–2021 has shown that the upper boundary of the anaerocontour defined by isopycnic σ_t = 15.8 (O_2 = 10 μM) was characterised by a steady tendency to rise to the surface (Fig. 5). In 1959, the average position of the upper boundary of the anaerocontour corresponded to a depth of 124 m. In 1982, this contact zone rose to a depth of 91 m, i. e. almost 33 m higher (compared to 1959), and at present, the upper SOL boundary in the center of the western circulation is located at a depth of 79 m, which is almost 50 m higher than the level observed in 1959. Calculations showed that the estimated shift of the upper SOL boundary could be a further 9 m by 2050 (Fig. 5, dashed line).

Discussion

Trends in changes to the ecological properties of water masses

1. *UBSWM*. It has been established that at the end of the last century the winter SST in the deep-sea zone was about 5.8°C, now its average value has risen almost to 9°C (see Fig. 2). The SST growth rate in the BS is equal to about 0.6°C/10 years. This is consistent with the data of the authors of [21] that the SST increase in 1982 and 2020 was 0.40 ± 0.21 and 0.71 ± 0.19°C/10 years, respectively. Modelling [22] showed that from 1980–1999 to 2080–2099, the SST would increase by a further 3.7°C. According to our calculations, in recent years, the salinity in the UBSWM has started to increase: from 18.0–18.4 PSU [3)] [8] to 18.61–18.8 PSU.

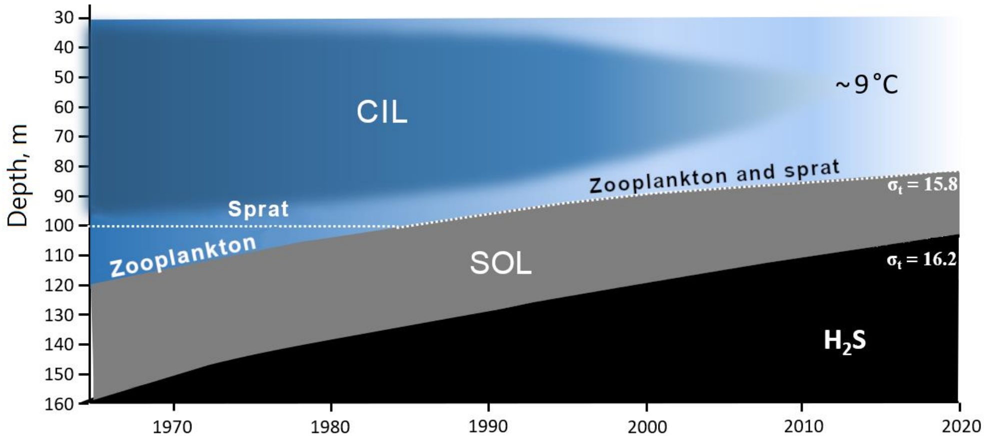
2. *CIL*. We confirm the information of E. V. Stanev et al. [15] that by 2019 warming caused the disappearance of the CIL. In the water layer between the middle of the seasonal thermocline and that of the pycnocline, main environmental parameters changed significantly (Figs. 1, 6). Between 1993 and 2023, temperature changed from 6.0–7.8 to 9°C, salinity – from 18.0–19.0 to 18.8–20.4 PSU and conditional density σt – from 14.0–14.8 to 14.3–15.8.

3. *SOL*. The rise of the Suboxic Layer to the surface has been a steady trend over the last 60 years (Figs. 4, 6). Its upper boundary (σ_t = 15.8) in the deep sea was at a depth of 115 m in 1957, rising to 85 m by 2021; its lower boundary (σ_t = 16.2) was at a depth of 165 m in 1957, rising to 115 m by 2021.

4. *IBSWM*. The upper boundary of this water mass is the chemocline, from which the hydrogen sulphide layer extends deep to the bottom. The results of the present work (Fig. 6) indicate that during 60 years, the hydrogen sulphide layer has risen approximately 50 m upwards.

Trends of major changes in the structure of biotopes

1. *Surface film biotope* (neuston [9]). Currently, the number of neuston copepods of the family Pontellidae has decreased by 50–70%. Their occurrence has decreased so much that they are listed in the Black Sea Red Book [10]. A further increase in SST by almost 4°C [22] by the end of this century can not only lead to a change in the taxonomic composition of traditional neuston species, but also affect the biology of merohyponeuston organisms.



F i g . 6 . Changes in the structure of water masses, biotopes and vertical distribution of zooplankton and fish aggregations at the lower boundary of the oxygen layer in the central deep waters of the Black Sea in 1960–2020 (day-time, in summer) in the 30–160 m layer

2. *UBSWM biotope* (epibiota). The bulk of works on anthropogenic and climatic changes in the BS ecosystem were published mainly on the basis of data on changes in the biota of this layer [6, 11, 23, 24]. Therefore, we will only note that under warming conditions over the last few decades, the UBSWM biota began to change significantly due to the appearance of warm-water species and their intentional or unintentional introduction. Now, more than 300 invasive species have been recorded in the BS, the appearance of which has accelerated, especially in recent years [25]. At first, 26 new invasive species were described [26], then their number increased to 59. By 2009, 156 non-indigenous species had been described, most of them from the Mediterranean [27]. In 2017, 261 invasive species were described [28].

3. *CIL biotope* (bathybiota). An increase resulting in temperature values more than 8°C leads to serious disturbances in the spawning phenology of moderately cold-water fish species which start spawning in late September instead of December and finish in May. In recent years, the ontogenetic development cycle of the sprat *S. sprattus* from egg to hatching has almost halved (from seven to two to three days), and the average size of larvae at hatching and their transition to external feeding has decreased [29].

This is also obviously the case with other cold-water species. For example, it is known that the development time of *Calanus euxinus* Hulsemann, 1991 is up to 66 days (from egg to adult) at 8°C, whereas at 18°C this period is almost halved [30]. The compression of the habitat layer of this species due to deoxygenation of the depths has resulted in the disruption of trophic relationships. In 1960–1970s, the habitat (volume of the environment occupied by the population [30]) of *C. euxinus* in summer occupied the entire thickness of the CIL water mass to a depth of 130 m, where 10 µM isooxygene was located [5], while the habitat of the Black Sea sprat *S. sprattus* occupied only the upper CIL part to a depth of 100 m. The Black Sea sprat feeds on copepods only during the day, either in the zone where they migrate vertically or in the hypoxic zone where they gather near the upper boundary of the Suboxic Layer.

The deeper the copepods concentration layer at the lower boundary of the anaerocontour, the fewer fish are able to descend into it to feed [12]. In the 1960–1970s, the Black Sea sprat could intercept copepods only during their daily vertical migrations (Fig. 6). In recent years, the entire population of *C. euxinus* (including diapause individuals) throughout the deep-water zone of the BS is in the habitat layer of the Black Sea sprat. The merger of their habitats [11)] took place in 1985 (see Fig. 4), which could cause a tenfold increase in sprat stocks at its maximum fat content [31]. It was during these years that *C. euxinus* began to dominate the food boli of these fish. In the near future, due to the disappearance of the CIL, the amount of cold-water zooplankton in the central deep-water areas can decrease significantly because such species as *Oithona similis* Claus, 1866 and *Pseudocalanus elongatus* (Brady, 1865) prefer temperatures below 8°C [31].

4. *SOL biotope* (anaerocontour). Shifts in the position of vertical boundaries of this biotope are the main mediator of climatic changes in the BS ecosystem. The results of the present study show that during the last decades, the upper boundary of the anaerocontour with oxygen concentration of 0.2 ml/L and density σ_t = 15.8 has risen by almost 40 m (see Fig. 4). It is estimated that the habitat of plankton and fish can be reduced by a further 10 m in the deep sea by 2050 (see Fig. 5).

5. *IBSWM biotope*. In the next 25 years, further rise of the hydrogen sulphide zone to the surface by another 10 m can occur in the BS deep waters (see Fig. 5). In the long term, this could lead to the release of anaerobic waters to the surface, which could cause serious damage to the ecosystem, fisheries, recreational and bioclimatic resources of the Black Sea coast.

Conclusion

Thus, the results of the present study have shown statistically significant shifts in the structure of water masses and associated hydrobiont biotopes of the Black Sea pelagic zone over the last decades. Habitat conditions for cold-water species have become particularly complex in the CIL mixed with the surrounding warmer waters under the influence of warming. It is likely that this water mass can reappear under the influence of long-term hydrological cycles and cold-water organisms will not disappear. The variability of the intensity of atmospheric circulation

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[11)] Beklemishev, K.V., 1969. [*Ecology and Biogeography of the Pelagic Zone*]. Moscow: Nauka, 291 p. (in Russian).

over the North Atlantic, which affects the balance between the inflow of high-salinity water masses from the Mediterranean Sea (averaging ~170 km^3 per year) and river runoff into the sea (averaging ~370 km^3 per year), plays a huge role here. This balance depends on the difference in levels between the seas, on currents, including drift currents caused by wind action, and thus can also depend on atmospheric circulation and climate change. Accordingly, the SOL represented by transformed Mediterranean water is also related to climate change.

Changes in river runoff volumes are also one of the important consequences of climatic change that determine the intensity of renewal of the CIL waters. The number of baby fish, biomass and catches of the Black Sea sprat *S. sprattus* were found to be in direct dependence on the dynamics of the runoff volumes of the Danube and Dnieper rivers. Apparently, the increase in runoff leads to the removal of large volumes of dissolved organic matter (especially in the area of the north-western shelf), which ensures the development of phyto- and zooplankton. This can create favourable conditions for feeding young pelagic fish species or lead to hypereutrophication and extensive fish kill. It is shown that the increase in the BS water temperature is likely to have an unfavourable effect on the reproduction and catches of cold-water predators, including sprat, whiting, horse mackerel and bottom benthophagous species such as halibut and mullet. The paper describes the process of the warming-induced disappearance of the CIL, which is the habitat of the BS cold-water pelagic species. This process can serve as a precursor of large-scale ecological shifts in other regions of the World Ocean.

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