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Expansion of gelatinous macrozooplankton in the open Black Sea off Crimea under the weather events of recent years

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Abstract

Species composition, abundance, and distribution of gelatinous macroplankton in coastal and deep-sea areas of the Black Sea in November 2017 are discussed. Despite the fact that species composition of gelatinous macroplankton (medusa *Aurelia aurita*, ctenophores *Mnemiopsis leidyi*, *Pleurobrachia pileus,* and *Beroe ovata*) in 2017 did not differ from that in 2016, structural changes occured. In autumn 2017 *A. aurita* and *B. ovata* biomass was higher than in 2016 whereas the inverse difference was observed in their abundance values. Namely, *A. aurita* biomass was on average 514 g m^{-2} and 634 g m^{-2} in the outer shelf and deep-sea areas, respectively. Both parameters of *M. leidyi* and *P. pileus* declined in 2017 compared to the previous year. In addition, the share of large-sized individuals increased in 2017, while that of small-sized animals decreased, in comparison with 2016. The number of small individuals increased in *P. pileus* and decreased in *M. leidyi*, although their biomass before the seasonal appearance of *B. ovata* in plankton was close to that in 2016. The unprecedented increase in the medusae biomass in November 2017 could not be explained only by the competition with planktivorous ctenophores and may indicate alternative drivers controlling population dynamics of *A. aurita* in the Black Sea. A negative correlation was depicted between the Danube discharge in February-March and the rate of somatic growth of *A. aurita.*

Keywords: Black Sea; *Aurelia aurita*; ctenophores; hydroclimatic effect; inter-annual biomass dynamics.

Introduction

Predatory gelatinous macrozooplankton is an extremely important component of the marine pelagic ecosystems, where abnormal aggregations of gelatinous organisms can be both a cause and consequence of significant changes in food web structure (Vinogradov *et al*., 1999; Purcell 2005; Purcell *et al*., 2007). Under the conditions of jellyfish expansion, such ecosystems tend to be simplified and evolved towards increased dependence upon dominant gelatinous species which are the main consumers of plankton (Parsons & Lalli*,* 2002; Richardson *et al*., 2009; Robinson *et al*., 2014). Therefore, monitoring of these processes is essential for understanding the principal vectors of the modern development of marine pelagic communities.

Previous studies were focused on the dynamics of abundance (Vinogradov *et al*., 1995; 1999; Kideys & Romanova, 2001; Anninsky *et al*., 2013), distribution patterns (Mutlu, 2001; 2009), and interpopulation relations (Kideys, 2002) in the community of gelatinous macroplankton of the Black Sea. However, the causes of interannual changes to its populations remain unclear. In the absence of regular observations that take into account spatial and seasonal changes in plankton, it is practically impossible to unambiguously associate structural changes in this community with interpopulation relationships, climate change, fishing, and eutrophication (Oguz *et al*., 2006; Llope *et al*., 2011; Shiganova *et al*., 2019; Vereshchaka *et al*., 2019).

Additional data on the current state of populations of gelatinous macroplankton in the Black Sea are necessary not only for assessing the ecological effect of these populations but also to identify possible drivers of ecosystem changes. The latter is especially important because of the strong predatory and indirect impact of gelatinous species on plankton (Finenko *et al*., 2006; 2015; 2018; Shiganova *et al*., 2019), continued warming in the Black Sea region (Vostokov *et al*., 2019), an increase in the temperature of the cold intermediate layer (CIL), a decrease in the oxygen concentration at these depths, and changes in the biogenic regime of the upper epipelagic zone (Vidnichuk & Konovalov, 2021).

The goals of the present research (based mainly on the data collected in the 98th cruise of the RV 'Professor Vodyanitsky') were: 1) to study the current state of the mass populations of medusae and ctenophores in the Black Sea (distribution, abundance, and biomass); 2) to estimate the possible predatory impact of gelatinous predators on zooplankton of shelf and deep-sea regions; and 3) to expand the time series evaluating interannual changes in the structure of the gelatinous community in terms of possible climate changes and corresponding variations of environmental conditions. Due to the significant increase in the biomass of *A. aurita* in recent years (Anninsky *et al.*, 2019), the interannual changes in the rate of somatic growth of this species were also considered.

Materials and Methods

Field observations were conducted in the shelf and open Black Sea areas southwest of Crimea (43.57-45.12° N and 31.28-36.45° E, respectively) during the period from 15 to 27 November 2017 (Fig. 1). The study area covers the regions with different hydrological regimes, which restrict the distribution of zooplankton up to a depth of 120-200 m, depending on the type of surface water circulation. In the autumn months, two cyclonic gyres of equal intensity and quasi-stationary anticyclonic eddies with minimal seasonal activity are usually distinguished (Ivanov & Belokopytov, 2011). The main elements of the vertical thermal structure of the active layer of the sea during this seasonal period are considered to be: the upper quasi-homogeneous layer (usually up to a depth of 30 m), the seasonal thermocline (30-40 m), and the cold intermediate layer (CIL) with a temperature minimum at the depth of 40-70 m. The lower boundary of the oxygen zone of the sea corresponds to the isopycnic horizon with $\sigma_t = 16.2$.

Gelatinous zooplankton samples were collected in 2 replicates at 56 stations (including 36 stations in the deep epipelagic zone) using the Bogorov-Rass net (mouth diameter 80 cm, mesh size 300 µm). Vertical net hauls from the bottom to the sea surface in the shelf area and from the lower border of the oxygen zone (σ_t of 16.2 according to the Sea-Bird 911plus CTD) in the deep regions were performed. Immediately after the collection and prior to the fixation, all macroplanktonic organisms were identified and measured to the nearest millimetre, paying special attention to the diameter of medusae (distance between the opposite ropalia) and oral-aboral length of ctenophores. The jellyfish biomass was calculated from the length-weight relationships obtained in previous studies (Table 1). In order to account for the early life stages of ctenophores (< 5 mm) and *A. aurita* ephyrae, all zooplankton samples were fixed in a 4% borate-buffered formaldehyde solution and examined under a microscope in the laboratory.

The rates of somatic growth of jellyfish in 1999–2015 were estimated according to the data of long-term monitoring at the outer shelf of the Sevastopol Bay (Finenko *et al.*, 2015; Anninsky *et al.*, 2020b). The corresponding data for 2016 and 2017 were obtained from the results of research during the 89th (October) and 98th (November)

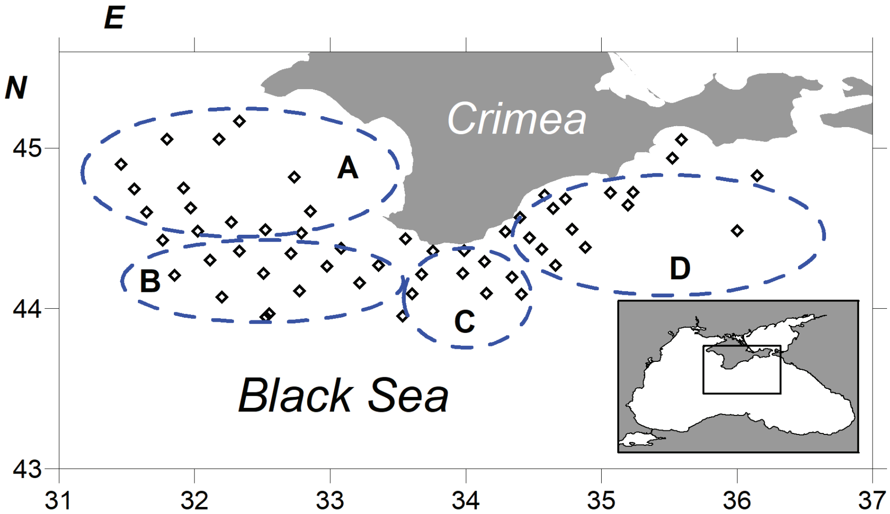

Fig. 1: A schematic map of sampling stations during the 98th cruise of the RV ‘Professor Vodyanitsky’ in the central deep-water areas of the Black Sea and adjacent regions in November 2017. The highlighted areas correspond to different zones of the Black Sea surface circulation: (A) the Sevastopol eddy; (B) north periphery of western cyclonic gyre; (C) the Rim Current convergence zone; and (D) the north-west periphery of eastern cyclonic gyre and region of the Crimean eddy.

Table 1. Relationships between wet weight (WW, mg) and body size (D, L, mm) of four gelatinous macroplanktonic species of the Black Sea.

Species	Equation	Size range, mm	r^2	Reference
Aurelia aurita	$WW = 0.053\ D^{2.98}$	2-247	0.99	Anninsky, 2009
Beroe ovata	$WW = 0.85\ L^{2.47}$	10-120	0.92	Finenko *et al.*, 2006
Mnemiopsis leidyi	$WW = 1.31\ L^{2.49}$	5-70	0.98	Finenko *et al.*, 2006
Pleurobrachia pileus	$WW = 0.682\ L^{2.52}$	3-25	-	Mutlu & Bingel, 1999

autumn cruises of the RV ‘Professor Vodyanitsky’(Anninsky *et al*., 2019; present study). Samples of gelatinous macroplankton in both cruises were taken in the same areas by using the same technique. In all cases, calculations of the specific linear growth rate of medusa were carried out based on the assumption of the exponential growth for this generation (Zaika, 2002) and taking into account the possible period of mass appearance of ephyrae in the sea (middle of March). These data were used as an additional indicator of the jellyfish population state.

The composition of mesozooplankton items in the gastric cavity of the freshly collected medusa *Aurelia aurita* and ctenophore *Mnemiopsis leidyi* was identified under the microscope. In the calculations, the carbon equivalent of prey biomass consumed was assumed to be 0.076 mg C / mg wet weight of copepods (Arashkevich *et al*., 2014).

Interannual variations in sea surface temperature (SST) were estimated based on the electronic database (http://disc.sci.gsfc.nasa.gov/giovanni). Additional information on some external factors affecting the development of the zooplankton community in the Black Sea was compiled from the data on the long-term variability of these parameters. The available data set comprises long-term variations of: (i) Danube River discharge for the period of 2003-2014 (Pekárová *et al*., 2008; Dolinaj *et al*., 2019); (ii) oxygen content and temperature of the cold intermediate layer (below seasonal thermocline) in 2003-2019 (Vidnichuk & Konovalov, 2021); and (iii) suspended inorganic carbon concentration (PIC) as an indicator of coccolithophore bloom in the sea during 2003-2014 (Vostokov *et al*., 2019). Statistical evaluation of data was conducted using the software Grapher 3, Surfer 8, and PAST 4.06 (Hammer, 2019; available at https://folk.uio.no/ohammer/past/). Redundancy analysis (RDA) was applied to assess the relationships between the plankton community composition (Finenko *et al*., 2015), some functional features of gelatinous species, and environmental factors. Values presented in the figures and tables are means ± standard error. The comparison of the parameters was made using Student’s *t*-test.

Results and Discussion

In November 2017, the gelatinous zooplankton in the Black Sea predominantly consisted of a scyphomedusa *Aurelia aurita* (Linnaeus, 1758) and three species of ctenophores, *Mnemiopsis leidyi* (A. Agassiz, 1860), *Pleurobrachia pileus* (O.F. Muller, 1776), and *Beroe ovata* Bruguière, 1789, which usually co-exist in all studied regions (70% of samples). In addition to these species, in the coastal shelf area of the western Black Sea, the hydromedusa, *Clytia hemisphaerica* (Linnaeus, 1767), and separate unidentified hydroid polyps rarely occurred. A scyphozoan jellyfish, *Rhizostoma pulmo* (Macri, 1778), was observed from the board of the RV.

Individuals of *A. aurita* and *P. pileus* of all sizes and ages were found at all stations; their abundance was usually higher than that of *M. leidyi* and *B. ovata*, whereas *A. aurita* biomass was by far higher than that of all ctenophores and in all areas (Fig. 2). In some regions, the last two ctenophores were absent (*M. leidyi*) or represented as rare eggs and early larvae (*B. ovata*). The diameter of the medusa umbrella reached 190–195 mm in some cases but was usually close to 72 mm (mean geometric diameter). Mean geometric oral-aboral body length of *P. pileus*, *M. leidyi,* and *B. ovata* amounted to 6.3, 19.0, and 13.4 mm, respectively.

Due to the fact that sea surface temperature in No-

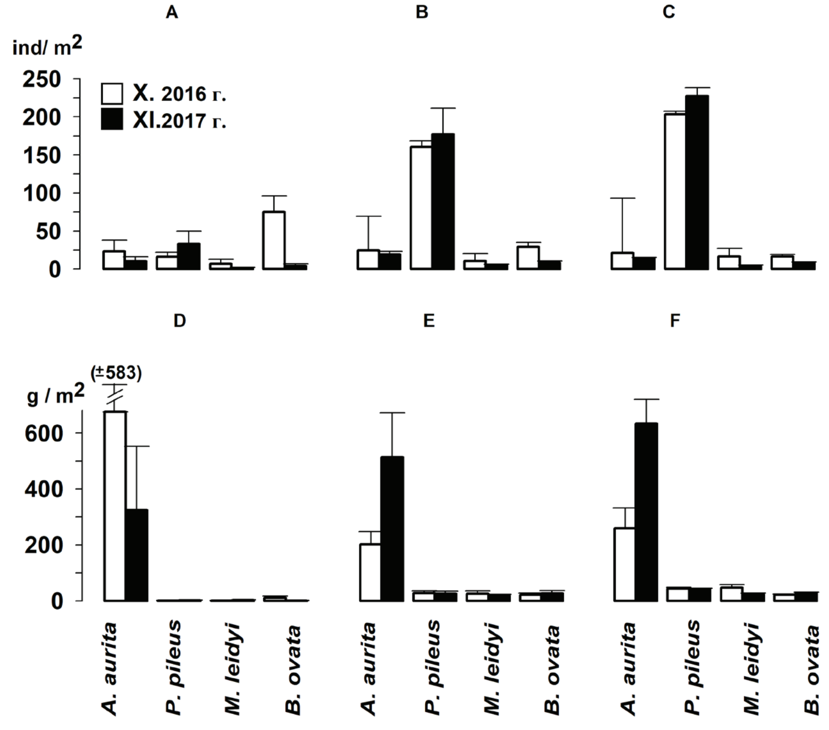

Fig. 2: Abundance (ind m^{-2}) (A–C) and biomass (g WW m^{-2}) (D–F) of gelatinous macroplankton in the regions of inner shelf (A, D), outer shelf (B, E), and deep-water zone (C, F) of the Black Sea in October 2016 and November 2017 (± SE).

vember 2017 (11.3–14.1 °C) was within the temperature tolerance range for all studied ctenophores, their regional distribution in that period was weakly regulated by the circulation of warm surface and cold deep-water masses set in motion by external climatic factors and meandering of the Rim Current (RC) (Fig. 3). Aggregations of *A. aurita* were observed mainly in the outer shelf zone near the extreme western tip of the Crimean coast (Cape Tarhancut), in the centres of the Sevastopol and Crimean anticyclonic eddies and also in the north eastern periphery zone of the western cyclonic gyre. Ctenophore *P. pileus,* usually living deeper than *A. aurita,* possessed

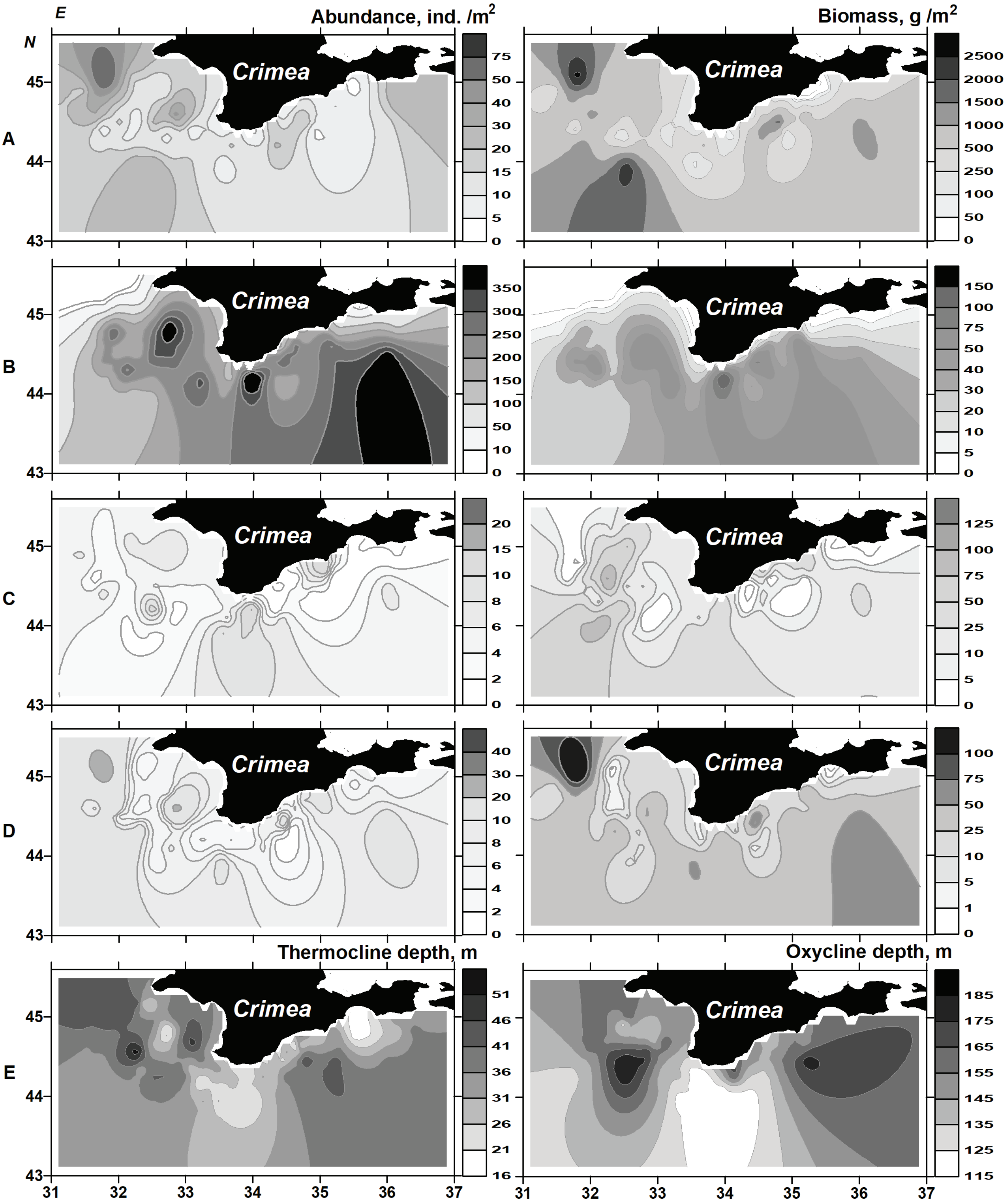

Fig. 3: Spatial distribution of abundance (left) and biomass (right) of gelatinous macroplankton (A–D) and some characteristics of hydrologic regime (E) in the central deep-water areas of the Black Sea and adjacent regions in November 2017. (A) *Aurelia aurita*; (B) *Pleurobrachia pileus*; (C) *Mnemiopsis leidyi*; (D) *Beroe ovata*; and (E) Deep horizons of the upper border of the thermocline and lower border of the oxygen zone (m).

maximum abundance (~ 540 ind./m^{-2}) and biomass (148 g m^{-2}) directly in the main centre of the eastern cyclonic gyre; however, this species, which generally prefers the deep-sea biotopes, was distributed quite uniformly. Only the aggregations of small individuals which did not contribute significantly to the total *P. pileus* biomass could be found in the regions of cyclonic gyres or their peripheries.

M. leidyi, which usually prefers warm surface biotopes (Mutlu, 1999; Vinogradov *et al*., 1999; Kideys & Romanova, 2001), was nearly absent in the centres of the Sevastopol and Crimean anticyclones, whilst *B. ovata* possessed maximum abundance and biomass in these zones. The apparent reason for this phenomenon is the predation of *B. ovata,* which strongly affected the abundance and biomass of *M. leidyi* in these regions due to high vulnerability of large chemically signalling individuals. In addition, epipelagic aggregations of *B. ovata* in late autumn could have formed under the influence of a new trophic vector, such as the increased availability of *P. pileus* for this predator. An increase in the biomass of *B. ovata* towards the open sea and an eastward-oriented aggregation of the same spatial configuration in distribution of this ctenophore and *P. pileus* confirm this assumption.

Development of populations of gelatinous macroplankton in all regions mainly depended upon the depth of pelagic biotopes due to relief of the bottom or lower boundary of the oxygen zone ($\sigma_t = 16.2$) (Table 2). The average biomass of every species increased towards the direction from the inner shelf to the deep regions; however, the abundance of the gelatinous organisms often changed in another way. Pronounced decrease in abundance ($p > 0.05$), accompanied by the increase in biomass of *A. aurita* in the deep regions, indicates the increase in body size of the species in the deep areas. In general, the biomass of medusa exceeded the biomass of ctenophores tenfold everywhere; however, *P. pileus* dominated in abundance in all areas, including the inner shelf (Fig. 2).

Two significant relationships ($p < 0.05$) for gelatinous zooplankton populations were revealed in the deep regions: 1) biomass increase of *A. aurita* from the periphery to the centers of anticyclonic eddies and 2) increase in abundance of *B. ovata* in the direction from the centres of cyclonic gyres to their peripheries and onwards to the centres of anticyclonic currents (Fig. 4). All other quantitative trends had lower degrees of significance ($p > 0.05$).

Individuals of each species were usually larger offshore than inshore. In particular, the umbrella diameter of the jellyfish in the areas of the inner shelf, outer shelf, and deep-sea zone averaged 41, 82, and 97 mm, respectively. Since the pre-wintering population of *A. aurita* is mainly represented by the generation that appears in plankton in February/March, the growth rate of this species can be estimated from the sizes of individuals in autumn months based on the exponential relationship between size and growth rate (Zaika, 2002). In 2017, the growth rate of *A. aurita* could reach 0.93% day^{-1} according to these calculations. In the same year and in the deep regions of the Black Sea, the abundance and biomass of *A. aurita* were one-third lower ($p < 0.05$) and 2.5-fold higher ($p < 0.01$), respectively, in comparison with the data obtained in October 2016 (See Fig. 2). Similar changes were recorded in the outer shelf area ($p < 0.1$). The data on *A. aurita* obtained for the inner shelf zone were unrepresentative.

Interannual changes of ctenophores abundance and biomass varied between species (Fig. 2). The mean number and biomass of *P. pileus* in 2017 were close to those in 2016. The abundance of *M. leidyi* in 2017 was significantly reduced in the outer shelf area ($p < 0.05$) and in deep regions ($p < 0.001$). The biomass turned out to be 2-fold lower (only in the deep regions) than that in 2016 ($p < 0.05$). In 2017 the mean number of *B. ovata* decreased in all areas ($p < 0.05$) compared to 2016; however, mean biomass (except three stations at the coastal shelf) increased by 23% (5 g m^{-2}) and by 27% (6 g m^{-2}) in the outer shelf and deep regions, respectively. It is not known whether the biomass of *M. leidyi* and *P. pileus* was low in winter-spring-summer 2017 or became low due to an intensification of predatory pressure by *B. ovata*. Since the biomass of *B. ovata* represents, to some extent, a part of assimilated biomass of other ctenophores, the possible consumption of these species by *B. ovata* can be evaluated. In ctenophores the food assimilation

Table 2. Abundance (ind m^{-2}) and biomass (g m^{-2}) of gelatinous macroplankton species in the central Black Sea in November 2017 (± SE). The mean geometric values are in the parentheses.

Species	**Inner shelf** < 50 m n = 3		**Outer shelf** 50 - 200 m n = 17		**Deep-sea regions** > 200 m n = 36	
	ind. m^{-2}	g m^{-2}	ind. m^{-2}	g m^{-2}	ind. m^{-2}	g m^{-2}
Aurelia aurita	10 ± 6 (7)	325 ± 228 (109)	19 ± 4 (14)	514 ± 159 (176)	14 ± 1 (12)	634 ± 87 (441)
Pleurobrachia pileus	33 ± 17 (22)	1.5 ± 0.95 (1.1)	177 ± 34 (135)	26 ± 9 (13)	227 ± 11 (220)	43 ± 3 (40)
Mnemiopsis leidyi	~1.3 (0.7)	~2.96 (1.2)	5 ± 1 (3.3)	19 ± 5 (9)	4 ± 1 (2.8)	23 ± 5 (9)
Beroe ovata	4 ± 2 (3.3)	~ 0.004 (0.003)	8 ± 2 (5.9)	27 ± 10 (15)	8 ± 1 (5.8)	28 ± 4 (18)

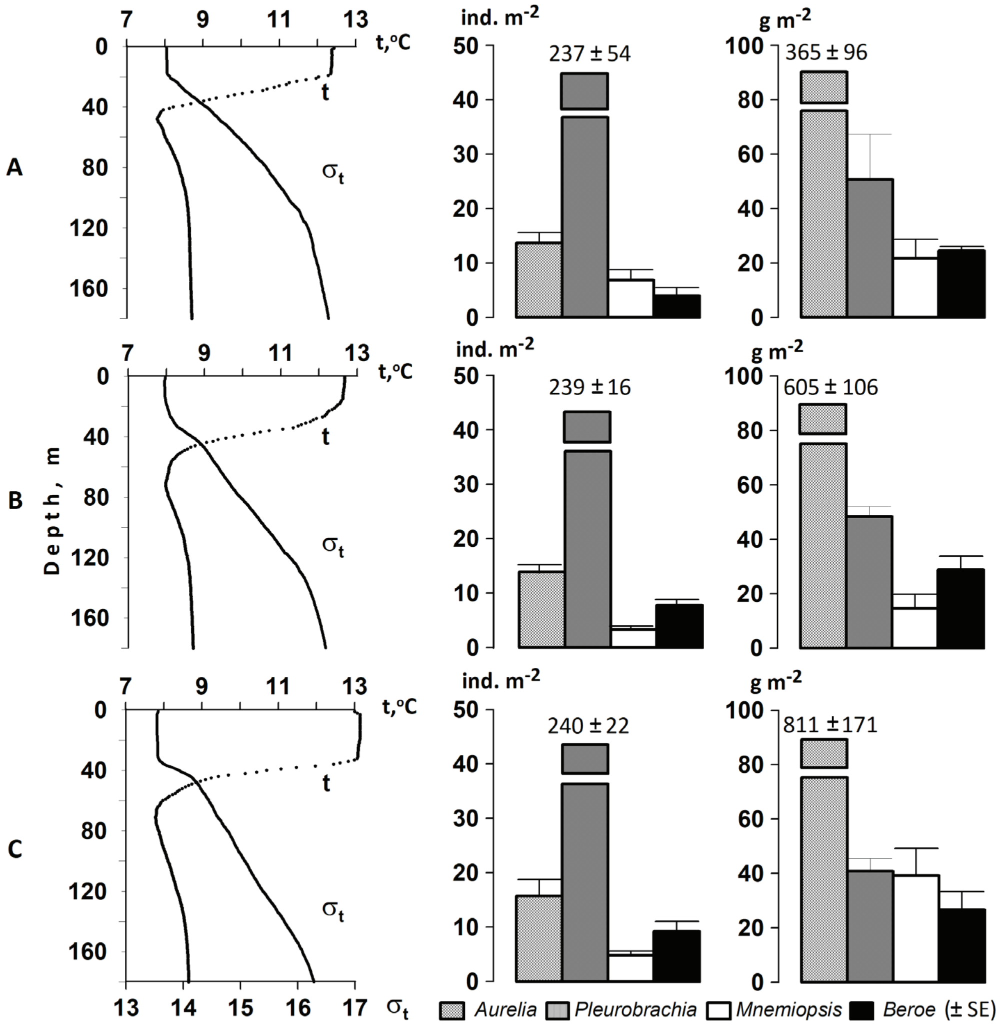

Fig. 4: Abundance (ind. m^{-2}) and biomass (g m^{-2}) of gelatinous macroplankton in the deep-water regions of the Black Sea with different vertical profiles of the temperature (t, °C) and relative density (σ_t) of seawater in November 2017. The depth of the lower boundary of the oxygen zone of the sea (σ_t = 16.2): (A, centre of the cyclonic gyre) 115–130 m; (B, periphery of the cyclonic gyre) 131–160 m; and (C, anticyclonic eddies) 161–185 m.

efficiency constitutes 80%, the growth efficiency (K_2) amounts to 30%, and the disproportion in organic matter content for *B. ovata* (B), *P. pileus* (P), and *M. leidyi* (M) is expressed as B:P:M = 2.5:2.2:1.1 mg g^{-1} of wet body weight (Anninsky *et al*., 2005). Therefore, an increase in *B. ovata* biomass by 1 g m^{-2} is equivalent to a decrease in *P. pileus* biomass by ~5 g m^{-2} and ~9 g m^{-2} in *M. leidyi*. Consequently, if in 2017 *B. ovata* fed exclusively on *M. leidyi*, the population of the latter should lose 45 g m^{-2} on the outer shelf and 54 g m^{-2} in deep-sea areas. The assumption that *B. ovata* partially feed on *P. pileus* may lead to the underestimation of *M. leidyi* biomass losses and, at the same time, indicate an increase in the initial biomass of *P. pileus*. Since both *P. pileus* and *M. leidyi* are the potential prey items of *B. ovata* (Mutlu, 2009), the share of every species in its ration can be determined only hypothetically. However, the results of our calculations for the deep-sea zone led to the conclusion that at least the total biomass of *M. leidyi* and *P. pileus* should be higher in 2017 (94 – 98 mg C_{org} m^{-2}) than in 2016 (80 mg C_{org} m^{-2}).

Ctenophores, which possess a diverse food spectrum and produce large biomass, are the principal trophic competitors to *A. aurita* (together with small pelagic fish) in the Black Sea. Moreover, the competition between gelatinous predators is considered to be so strong that the expansion of one species may result in the depression of others (Vinogradov *et al*., 1999; Kideys, 2002). On the contrary, the Black Sea conditions in 2017 were favourable for the entire gelatinous community since they not only caused a strong increase in the biomass of *A. aurita*, but also contributed to an increase in the biomass of ctenophores (except for *P. pileus* and *M.leidyi* in deep regions). The size structure of gelatinous populations (except *P. pileus*) changed substantially as well: in 2017 the share of large-sized individuals increased, while that of small-sized animals decreased (Fig. 5). Though the predominance of *A. aurita* ephyrae with a diameter of about 5 mm in 2017 may be due to the later sampling dates, a phenomenon of synchronous decrease in the number of individuals of 10–50 mm and increase in the number of medusae of 70–170 mm can hardly be explained by time lag in sampling. Assuming that the umbrella diameter of *A. aurita* increases from 44 mm in October (mean geometric diameter in 2016) to 72 mm in November (mean geometric diameter in 2017), one can calculate the so-

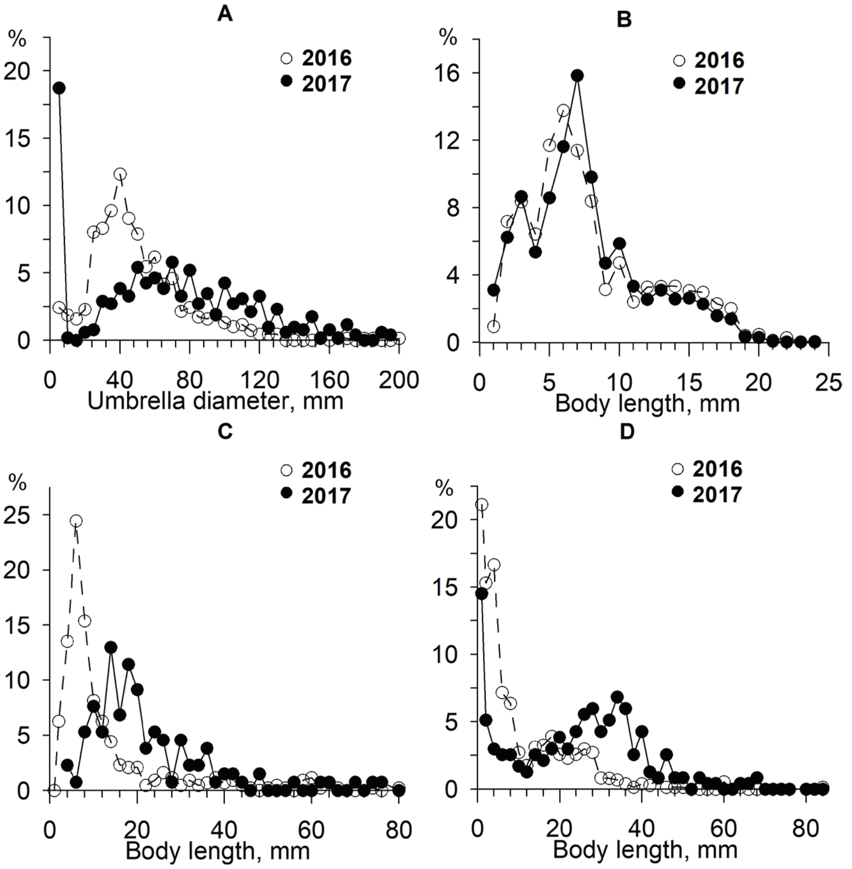

Fig. 5: Size structure of individuals in the populations of gelatinous macroplankton of the Black Sea in October 2016 and November 2017. (A) *Aurelia aurita*; (B) *Pleurobrachia pileus*; (C) *Mnemiopsis leidyi*; and (D) *Beroe ovata.*

matic growth rate of this species. For example, for *A. aurita* with the umbrella diameter of 57 mm (wet weight of 9.05 g ind^{-1}), the daily weight increase should reach 3.4% of body weight or about 450 µg of organic matter (235 µg C_{org}) (Anninsky, 2009). Correspondingly, the daily ration of medusa feeding on copepods should be within the limits of 10–13 mg ind.$^{-1}$ which is equivalent to the consumption of 13–17 large copepods (*Calanus euxinus* with the wet weight of 0.77 mg ind.$^{-1}$) or 300–400 middle-sized copepods (*Acartia clausi* with the wet weight of 0.03 mg ind.$^{-1}$) (Anninsky, 2009). Such high feeding rates were not detected for *A. aurita* in nature and under conditions of prolonged experiment (Anninsky *et al.*, 2020a). Therefore, in October 2017, the individuals of *A. aurita* should have been significantly larger than those in October 2016.

Similar interannual differences in the body size were observed in ctenophores *M. leidyi* and *B. ovata* (Fig. 5). In the population of *M. leidyi*, the modal size class of individuals shifted from 5-10 mm in 2016 to 10-20 mm in 2017. A pronounced shift of maximum abundance was also registered in the medium-sized *B. ovata*. Despite later sampling dates, when the size of individuals usually decreases due to lack of food (Anninsky et al., 2005), most of the ctenophores were significantly larger in 2017 (25–40 mm) than in 2016 (12–28 mm). This fully explains why, despite the significantly lower number of individuals in 2017, the biomass of *M. leidyi* in 2017 was comparable to that in 2016 (especially in the outer shelf), while the biomass of *B. ovata* exceeded the previous values. Interannual changes in the *P. pileus* population were the opposite, i.e. with the number of *P. pileus* being higher in 2017, the biomass of this species was lower. This could be due to the increased elimination of the last year's generation (12-24 mm individuals) in the late autumn of 2017 (Anninsky *et al.*, 2020b). Thus, the generative renewal of *P. pileus* population was more efficient in 2017 (higher abundance and lower biomass) than in 2016. This was not observed in the populations of *M. leidyi*, *B. ovata*, and *A. aurita*, where large sizes, high biomass, and lower numbers of individuals may indicate an increase in the rate of somatic growth. The growth rate of *A. aurita* in 2017 (0. 933 % day^{-1}) was higher than that in 2016 (0. 890 day^{-1}), but also lower than in 2003, 2006 and 2008 (Fig. 6).

The high growth rate of *A. aurita* in 2017*,* together with its high abundance and increased number of large individuals in the population (up to 195 mm in the umbrella diameter) (Fig. 5), should account for the observed significant increase in biomass, which in the open sea was higher in November 2017 than in October 2016. *A. aurita* biomass (in terms of the wet weight) was two-fold higher in 2017 than in 1978 and was close to *M. leidyi* biomass in 1994-1995 (Vinogradov *et al.*, 1999; Kideys & Romanova, 2001) (Fig. 7). Taking into account higher organic matter content in the body of medusa (1.5 mg g^{-1} of wet body weight, according to Anninsky, 2009 and Kogovšek *et al.*, 2014) in comparison to ctenophore (1.1 mg g^{-1} of wet body weight, according to Anninsky *et al.*, 2005), it is estimated that in 2017 the population of *A. au-*

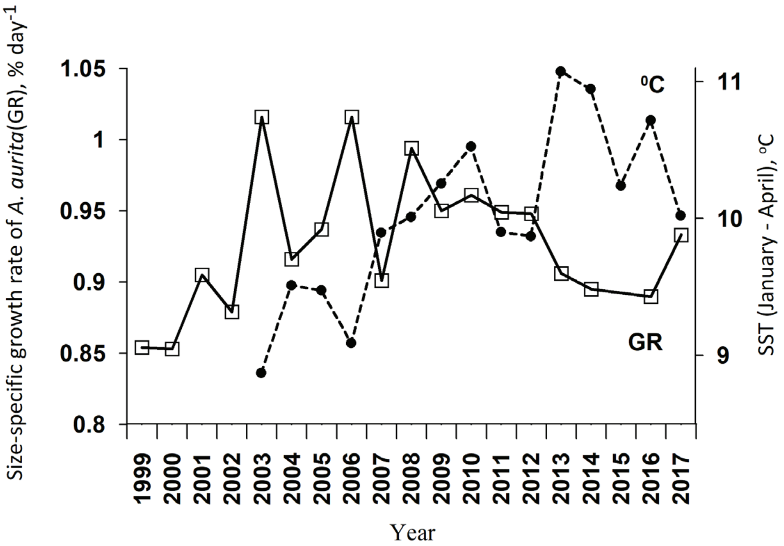

Fig. 6: Interannual dynamics of the specific linear growth rate of medusa *Aurelia aurita* (solid line) and the mean sea surface temperature (SST) for the period from January to April (dotted line) in the Black Sea. Data of 1999-2014 by: Data of the long-term monitoring at the outer shelf of Sevastopol Bay (Anninsky *et al*., 2020b); Data of 2016 by Anninsky *et al*., 2019: Data of the 89th cruise of the RV 'Professor Vodyanitsky' (Anninsky *et al*., 2019); Data of 2017: present study Data of the (98th cruise of the RV 'Professor Vodyanitsky').

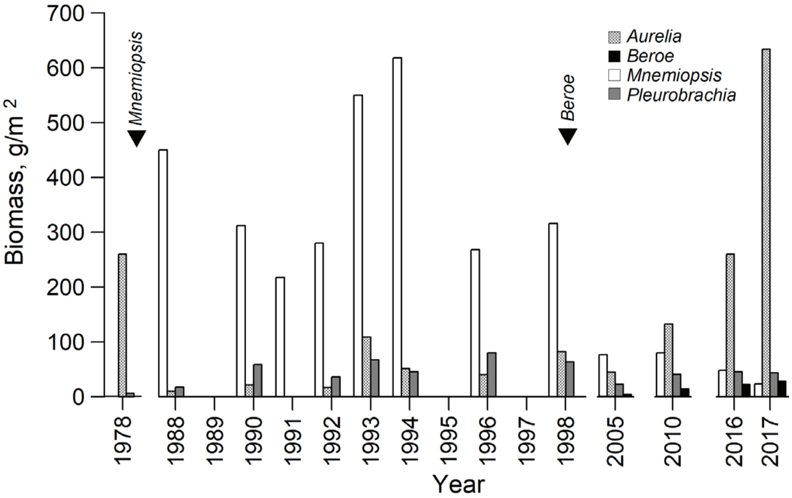

Fig. 7: Long-term dynamics of biomass of dominating gelatinous species in the central regions of the Black Sea (depths more than 200 m) in autumn 1978–2017 according to the data from the net tows. Data of 1978 and 1988 by Vinogradov *et al*. (1999). Data of 1990, 1994, 2005, 2010 by Anninsky *et al*. (2013). Data of 1991–1993 by Vinogradov *et al*. (1995). Data of 1996, 1998 by Kideys & Romanova (2001). Data of 2016 by Anninsky *et al*. (2019). Data of 2017: Present study. Vertical arrows indicate the years of penetration of invasive species (*M. leidyi* and *B. ovata*) into the Black Sea ecosystem.

rita accumulated 1.5-fold more organic matter than that of *M. leidyi* in 1994-1995 (during autumn biomass peak). Therefore, the potential predatory impact of *A. aurita* on planktonic communities in 2017 could have been stronger than that of *M. leidyi* during the years of expansion into the Black Sea. Although the respiration rate of medusa is close to its maximum at 20 ° C (224.6 μl O day^{-1} for 1 g WW individual) and should decrease to 116.4 μl O day^{-1} for 1 g WW individual at habitat temperature of 11 °C (Anninsky, 2009), the food requirements of *A. aurita* to compensate metabolic losses (Anninsky, 2020b), during November 2017 could reach ~245 mg zoopl. m^{-2} day^{-1} (~19 mg C_{org} day^{-1}) and ~280 mg zoopl. m^{-2} day^{-1} (~21 mg C_{org} day^{-1}) at the outer shelf and in the deep areas, respectively. It remains unclear to what extent these food requirements could be compensated by mesoplankton. Adults and copepodite stages of Copepoda (*A. clausi, Paracalanus parvus*, *Oithona davisae*, *Pseudocalanus elongatus, C. euxinus*), Appendicularia (*Oikopleura dioica*), Chaetognatha (*Parasagitta setosa*), Cladocera (*Penilia avirostris*) and Bivalvia veligers dominated among the most visible prey items of *A. aurita*. In addition to them, large singular cells of diatoms (*Coscinodiscus janishii* and some other species) were often observed in the food of *A. aurita* during 2017. The same mesozooplankton species were observed in the food of *M. leidyi* as well, but the algae cells and vegetative fragments were never found among them.

Significant interannual differences in the biomass, size, and growth rate of *A. aurita* cannot be explained only by the shift in the sampling dates from October in 2016 to November in 2017 and may indicate a change in the conditions of population development in these years. The reasons for the increase of *A. aurita* biomass in 2017 are not completely clear. It is unlikely that the quantitative growth of the mass populations of mesoplanktonic prey species may be the main cause of that phenomenon. In April-May and June-July 2017, in the open regions of the Black Sea, more than 50% of the total biomass of mesozooplankton was accounted for by the chaetognaths *P. setosa*, while copepods (especially *P. elongatus* and *C. euxinus*) dominated in abundance everywhere (93 – 96%). The total biomass of Copepoda in the deep-sea areas was close to 10.3 and 6.4 g m^{-2} (68.9 x 10^{-3} and 42.6 x 10^{-3} g m^{-3}) (Klimova *et al*., 2021), that remained within the pattern of the long-term (since 1970) interannual fluctuations in mesozooplankton biomass in the Black Sea (Arashkevich *et al*., 2014). In November 2017, the abundance and biomass values of copepods such as *C. euxinus* (9.9 ± 0.5 x 10^3. ind. m^{-2} and 7.3 ± 0.4 g m^{-2}), which typically forms more than 90% of the Copepoda biomass in the deep-sea part of the Black Sea (Arashkevich *et al*., 2014), were similar to those observed in 2016 (8.4 ± 0.8 x 10^3 ind. m^{-2} and 7.2 ± 0.7 g m^{-2}) (Hubareva & Anninsky, 2020). Moreover, in the studies on the Crimean shelf, no valid relationship was found between the rate of somatic growth or biomass of the jellyfish and the total number (or biomass) of fodder zooplankton or copepods only (Anninsky *et al*., 2020b).

Population dynamics of gelatinous macroplankton may be affected by numerous factors, i.e., annual temperature and other climatic conditions of the given region, volume and biogenic parameters of river discharge, and competitive and other trophic relations in the zooplankton community. Climatic characteristics in 2017 differed from those in 2016. In 2017, the Black Sea surface temperature was on average 0.43 °C lower than in 2016. The first part of 2017 (including summer) was colder whilst autumn was warmer. Within the studied area (44.4–45.5° N, 32.4–33.6° E), the seawater temperature was 0.72 °C and 1.19 °C lower in January–April and July–August, respectively, while in November the seawater temperature was 1.78 °C higher than in 2016. These temperature variations were advantageous for *A. aurita*, although they did not always directly affect the somatic growth of the jellyfish. Weaker warming-up of surface layers of the sea in July–August 2017 undoubtedly reduced the temperature isolation of this species, which rarely penetrates into the surface horizons at > 20 °C, and individuals found in warm waters in most cases are damaged specimens from the dying generation of the last year (Anninsky *et al*., 2020b). Near the thermocline, where the main part of *A. aurita* population usually aggregates in summer (Mutlu, 2001), the concentration of individuals has decreased, the competition for food with the cold-water ctenophore *P. pileus* (Mutlu & Bingel, 1999) has weakened; therefore, the trophic conditions for the existence of the jellyfish have improved. It is unlikely that this could have been influenced by *M. leidyi*, because the distribution of this species in the summer months is usually restricted to the upper mixed layer (Mutlu, 1999). Slow decrease in temperature in autumn is important for the continuation of the development of warm-water mesozooplankton (*P. avirostris* and other Cladocera, *O. davisae,* and other Copepoda, meroplankton) (Arashkevich *et al*., 2014), which is considered to be the substantial food source not only for *A. aurita* but also for other gelatinous predators (Finenko *et al*., 2006). However, due to the predatory impact of *B. ovata,* which significantly diminished the biomass of competitive ctenophores up to the end of autumn (Kideys & Romanova, 2001 Finenko *et al*., 2006), *A. aurita* was the species that gained advantage from this situation. The jellyfish population should develop successfully under the conditions of weak competition, a large amount of food (including mesozooplankton), and comfortable seawater temperature (10-14 °C in November 2017). However, the unusually strong increase (2.5-fold) in the biomass of *A. aurita* this year cannot be explained only by these circumstances. This is evidenced by the minor differences in the biomass of planktonic crustaceans in 2016-2017 (Hubareva & Anninsky, 2020). At the same time, the extremely high biomass of *P. setosa*, predator of microplankton (Casanova *et al*., 2012), in the spring and summer of 2017 (up to 20 g m^{-2}) (Klimova *et al*., 2021) probably indicates an atypically active growth of microplankton this year.

A positive effect of low temperatures on *A. aurita* growth has not been confirmed by its detailed physiological studies (Anninsky, 2009). Nevertheless, the data obtained in 2003–2017 showed that the somatic growth rate of *A. aurita* decreased after the rise in the sea surface temperature in January ($r = -0.62$; $p < 0.05$) and during the periods from January to April ($r = -0.68$; $p < 0.01$), January to May ($r = -0.62$; $p < 0.05$), January to June ($r = -0.59$; $p < 0.05$), and to a less extent, in August ($r = -0.54$; $p < 0.05$) (Fig. 6). As in the case of the biomass dynamics of the flagellate *Noctiluca scintillans*, and the chaetognath *P. setosa*, this occurs independently of planktonic crustaceans, which usually accumulate higher biomass in years with early seasonal warming of seawater (Anninsky *et al*., 2020b). Since a new generation of *A. aurita* usually appears in plankton in high abundance only at the end of March, the earlier increase in seawater temperature could not directly affect the somatic growth. This is also evidenced by the weakening of the temperature dependence of the jellyfish growth in the period from April to June ($r = -0.45$; $p > 0.05$). The interannual variability of somatic growth could be also due to other external factors responsible for the quality of seawater and the state of the ecosystem favourable for the *A. aurita* population: climate-dependent changes in the hydrological regime and biogenic balance of the upper epipelagic zone of the sea. This may be confirmed by the negative correlation between the rate of somatic growth of the jellyfish (Anninsky *et al*., 2020b) and the Danube discharge (Pekárová *et al*., 2008) in February ($r = -0.85$; $p < 0.01$), March ($r = -0.71$; $p < 0.05$), and during the period from February to March ($r = -0.82$; $p < 0.05$) (Fig. 8). Moreover, an analogous relationship between the biomass of *A. aurita* (Anninsky *et al*., 2020b) and the Danube discharge

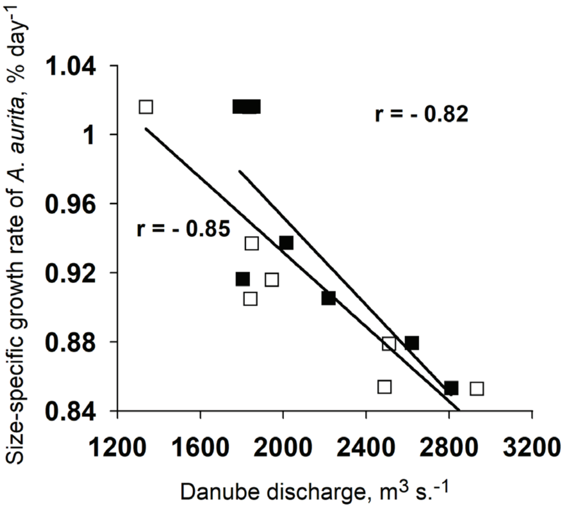

Fig. 8: Influence of the Danube discharge (near Bratislava) (data by Pekárová *et al*., 2008) in February (white squares) and during the period from February to March (black squares) on the size-specific growth rate (% day^{-1}) of *Aurelia aurita* in the Black Sea (Anninsky *et al*., 2020b).

in February–March ($r = -0.73$; $p < 0.05$) was revealed.

Since the Danube discharge is mainly regulated by precipitation, the conditions being favourable for *A. aurita* are formed under the influence of anticyclonic circulation, which bring the cold dry air from Arctic to the Black Sea basin during winter through spring. Unfavourable conditions are provoked by the Atlantic cyclones carrying the warm wet air with heavy rains, which intensify the terrigenous water flow, mixing, and circulating of seawater masses (Oguz *et al*., 2006). Due to high salinity tolerance of *A. aurita* in the range of 13–34 (Lucas, 2001), the negative effect of increased river flow on the population of this jellyfish could not be a result of a minor decrease in salinity (from 18) of the epipelagic layer in the spring months. It is more likely that this phenomenon is due to synchronous variations in the mixing of seawater and/or changes in the biogenic balance of the sea due to the river discharge before the spring development of autotrophs (Humborg *et al*., 1997). It follows from the data obtained in 1999–2006 (Oguz *et al*., 2008) that the biomass and abundance of *A. aurita* and the number of ephyrae tend to increase with the rise in the concentration of dissolved inorganic nitrogen in the sea surface layers ($r = 0.98$, $p < 0.01$; 0.85, $p < 0.05$; and 0.90, $p < 0.01$, respectively) (Anninsky *et al*., 2020b). However, the correlations between the biomass of *A. aurita* and silicate concentration in the seawater and between the somatic growth rate of medusa and silicate concentration ($r = -0.44$ and -0.64, respectively) are more likely ($p > 0.05$) negative. The relationship between the biomass and somatic growth rate of this species and phosphate concentration ($r = -0.66$ and -0.71, respectively) tends to be negative ($p > 0.05$) as well. Since both silicates and phosphates are transported to the marine ecosystem mainly from the terrigenous sources (Oguz *et al*., 2008), the concentrations of these substances in seawater should be higher at the strong flood. Therefore, the *A. aurita* population will develop more slowly at high initial concentrations of silicates and phosphates (which are necessary for growth of diatoms and, consequently, for planktonic crustaceans) than at low concentrations of these compounds and disproportionately high accumulation of dissolved inorganic nitrogen (DIN) in seawater. The increase in DIN concentration generally brings to the increase in numbers of bacteria, mixotrophic algae (Dinophyta, Haptophyta etc.), microzooplankton, fine filter-feeders, and top predators feeding on these organisms (Pomeroy *et al*., 2007; Amelina *et al*., 2017). Indirect evidence of a similar scenario of the pelagic ecosystem functioning in 2017 may be an extremely intensive summer bloom of coccolithophore *Emiliania huxleyi* (data from the 95th-97th cruises of the RV 'Professor Vodyanitsky'), high number of chaetognaths in the mesozooplankton, and pronounced domination of *A. aurita* among the gelatinous consumers (Klimova *et al*., 2021; Korchemkina & Mankovskaya, 2020). Moreover, the positive interannual relationship between the coccolithophorid biomass and the growth rate of *A. aurita* in the Black Sea ($r = 0.96$) is confirmed by the known data at a statistically significant level ($p < 0.05$) (Mikaelyan *et al*., 2011) . A similar relationship between coccolithophorid biomass and *M. leidyi* biomass in the summer months turned out to be positive as well ($r = 0.69$) (Vostokov *et al*., 2019). Probably, planktivorous ctenophores can also take advantage of this situation, consuming microplankton predominantly or using this food at temporary deficiency in mesoplanktonic prey. At the same time, the mass appearance of flagellates can be caused not only by the reaction of pelagic ecosystems to interannual changes in the biogenic and hydroclimatic regime of the sea, but partly by jellyfishes and ctenophores themselves, providing the nutrient release into the environment (Shiganova *et al*., 2019). The smaller prey size in a long-term perspective is able to affect the size structure of individuals in the predator populations (Daufresne *et al*., 2009).

Some of the possible drivers of interannual dynamics of biomass and growth rate of gelatinous species were detected by a multivariate analysis of the zooplankton complex at the outer shelf of the Sevastopol Bay in 2003–2017 (Finenko *et al*., 2015; Anninsky *et al*., 2020b). RDA

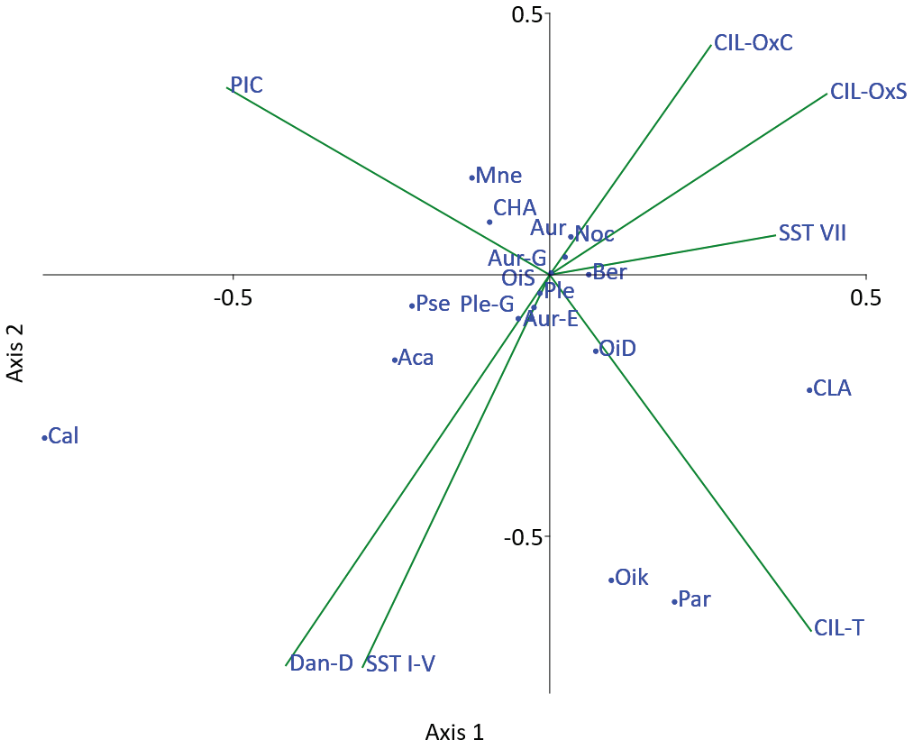

Fig. 9: Redundancy analysis (RDA) of biomass and some functional rates of gelatinous microzooplankton species with some environmental factors taken as explanatory variables (vectors). Biomass of species: Aur = *A. aurita*, Ber = *B. ovata*, Mne = *M. leidyi*, Ple = *P. pileus*, CHA = *P. setosa*, Noc = *N. scintillans*, Oik = *O. dioica*, CLA = Cladocera, Aca = *A. clausi*, Cal = *C. euxinus*, OiD = *O. davisae*, OiS = *O. similis*, Par = *P. parvus*, and Pse = *P. elongatus*. Functional rates of species: Aur-G = *A. aurita* growth rate, Ple-G = *P. pileus* growth rate, and Aur-E = *A. aurita* elimination rate. Explanatory variables: Dan-D = Danube River discharge; SST I-V = sea surface temperature in January-May; SST VII = sea surface temperature in July; CIL-T = cold intermediate layer temperature; CIL-OxS = oxygen saturation in the cold intermediate layer; CIL-OxC = oxygen concentration in the cold intermediate layer, and PIC = particulate inorganic carbon concentration (as an indicator of coccolitophore bloom).

analysis of 17 plankton characteristics in a system of 7 external factors showed that these factors reliably explain 64% of the total variability of the data (F = 1.78; permutation p, n = 999: < 0.04) (Fig. 9). The first two axes account for 46.8% of the total variation in zooplankton parameters. In the graphical distribution of the dominant species biomass (as well as some functional parameters of gelatinous species), two main vectors are distinguished along these axes and several secondary ones. An increase in discharge of the Danube River, coupled with SST in January–May and CIL temperature, is accompanied by an increase in the overall biomass of copepods, cladocerans and *O. dioica*, the growth rate of *P. pileus* and elimination rate of *A. aurita*. The reverse change in temperature and hydrological regimes leads to the population development of Chaetognatha and *N. scintillans,* and contributes to increased somatic growth of *A. aurita*.

Thus, studies of the gelatinous macroplankton of the Black Sea in 2017 showed that, despite the similarity in species composition of this community between 2017 and 2016, its structure underwent interannual changes caused by climatic and trophic factors, as well as interpopulation relations under changed conditions. In general, in 2017 the gelatinous populations responded in different ways to the changes in the Black Sea ecosystem state due to climatic or other factors. The climate systems seem to affect (through temperature, precipitation, and nutrients) the pelagic communities in such a way that either the main trophic chain (diatoms–zooplankton) predominantly operates by creating the favourable conditions for ctenophore populations, or the so-called ‘microbial loop’ (Pomeroy *et al*., 2007) is activated causing the improvement of biotic conditions for the jellyfish. According to the data obtained in 2017, the pelagic ecosystem functioned using the scenario favourable for *A. aurita,* which brought a dramatic increase of the medusa biomass. The growing predatory impact of all gelatinous macroplankton on the ecosystem as a whole and on the populations of planktonic crustaceans creates the basis for possible worsening of trophic conditions for planktivorous fish in the near future. At the same time, in comparison with planktivorous ctenophores, *A. aurita* due to its preference for low-temperature conditions in the sea and opportunistic feeding (from microorganisms to large crustaceans and fish larvae) did not affect significantly the structure of pelagic communities in previous years (Anninsky, 2009).

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