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Ocean Science Discussions

Annual cycle of sound-scattering mesoplankton in the oxycline and hypoxic zone in the northeastern Black Sea

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Abstract. To investigate the annual cycle of sound-scattering layers in the Black Sea, a moored profiler equipped with an acoustic Doppler current meter, a conductivity-temperature-depth probe, and fast sensors for dissolved oxygen [O2] was employed. Approximately 13,350 multiparameter profiles from the near-surface layer down to the near-bottom layer were obtained at intervals of 1-2 h from 2013-2020. The acoustic system allowed for observations of ultrasound backscattering at 3 angles at 2 MHz frequency. Combinations of the volume strength data of the 3 acoustic beams (directional acoustic backscatter ratios, *R*) were found to be a useful tool for visualizing acoustic backscatter patterns associated with mesoplankton in the oxycline and hypoxic zone. The time series of *R* as a function of [O2] at depths where [O2] < 200 μM were analyzed to determine the annual cycle of sound-scattering mesoplankton aggregations. It was shown that from spring to early autumn, there are two sound-scattering maxima corresponding to the daytime aggregations of diel-vertical-migrating specimens usually at [O2] = 20-60 μM and the persistent layer of diapausing specimens at [O2] < 10 μM. During the rest of autumn until early winter, there is usually no persistent deep sound-scattering layer, while the maximum corresponding to the daytime mesoplankton aggregations shifted deeper to [O2] = 10-30 μM. During the rest of winter, the acoustic backscatter is basically uniform throughout the water column. The *R* graphs also indicate that the mesoplankton specimens tended to be oriented vertically in the lower part of the oxycline and hypoxic zone.

1 Introduction

The vertical stratification of the marine environment in the Black Sea creates unique conditions for the formation of layers that scatter sound. The data obtained by a short (up to 10 days) experimental deployment of a moored automatic mobile profiler equipped with an ultrasound probe operating at a frequency of 2 MHz and a dissolved oxygen sensor allowed Ostrovskii and Zatsepin (2011) to define the main sound-scattering zones as follows:

- in the lower hydrogen sulfide zone (usually deeper than 140-160 m), sound is scattered by deposited detritus and mineral particles, whose fluxes vary temporally while being rather homogeneous at different depths,

- above the hydrogen sulfide zone in the suboxic layer (where the dissolved oxygen [O2] < 10 μM) and above that, in the oxycline (where [O2] increases from 10 μM to 280-300 μM with decreasing depth), the sound scattering occurs from both suspended particles and mesoplankton with characteristic sizes from 200 microns to 20 mm,

- above the oxycline in the oxygen-rich euphotic zone, phytoplankton become an additional sound-scattering agent along with settling particles and living animals.

Copepod and chaetognatha aggregations result in sound-scattering layers (SSLs). The SSLs vary on temporal scales that match the physiological and behavioral cycles of mesoplankton. In particular, diel vertical migration was observed using ship echo sounding at frequencies of 120 - 200 kHz (Erkan, Gucu, 1998; Svetlichny et al., 2000; Mutlu, 2003, 2005, 2006, 2007; Stefanova, Marinova, 2015). The diurnal dynamics of *Calanus euxinus* were documented from ship-borne echograms by Svetlichny et al. (2000) and Mutlu (2003). For example, the average speed of copepod descent and ascent was estimated to be 1.6-2.8 cm s^{-1} and 0.9-1.1 cm s^{-1}, respectively (Svetlichny et al., 2000). The 24-h rhythm in the SSL was a prominent feature of the 2 MHz acoustic sensing data obtained by a moored profiler station (Ostrovskii and Zatsepin, 2011). An analysis of both echograms and Juday net haul samples showed that in the northeastern Black Sea, the SSLs at 2 MHz are associated with the zooplankton species *Calanus euxinus* and *Pseudocalanus elongates* (Arashkevich et al., 2014).

It should be noted that the diel migration of copepods in the Black Sea was described by marine biologists (Vinogradov et al. 1985; Flint 1989) long before bioacoustic studies. It was discovered that their diurnal rhythms adjust to external cues, including light, temperature and oxygen stratification. At night, species of *Calanus euxinus* and *Pseudocalanus elongates* rise into the warm higher-oxygen upper layer of the sea that is rich in phytoplankton, and in the morning, they descend into the deeper cold hypoxic zone with a density σ_Θ = 15.4-15.7 kg m^{-3} and an oxygen concentration of 0.35-1.15 mg l^{-1}. Additionally, the time *Calanus euxinus* spends on vertical migration in its daily cycle depends on the amount of oxygen dissolved in the seawater (Arashkevich et al., 1998). Copepods gather below the oxycline, where the oxygen content is in the range of 15-25 µM (Vinogradov et al. 1985; Flint 1989), i.e., in the deeper part of the hypoxic zone ([O2] < 63 µM (Middelburg and Levin, 2009)), where the low oxygen conditions affect the Black Sea biota (Jessen et al., 2017). This location of copepod clustering was explained by the fact that hypoxia may provide a metabolic advantage (Svetlichny et al., 2000). These and other studies contributed to the development of an optimal behavioral strategy model (Morozov et al., 2019) for structured communities of organisms of two mesoplankton species, *Calanus euxinus* and *Pseudocalanus elongates*, which are dominant in the northeastern part of the Black Sea. In the model, the diel vertical migrations were considered in connection with several biogenic and abiogenic factors, including the influence of anoxia. Model calculations were compared with daily zooplankton sampling data at a few stations in March-July, September-October, and December. According to that study, the relatively shallow (70-80 m) depth to which the zooplankton migrate in December and March increases to 150 m from April to September. The specific objective of this study is the annual cycle of the mesoplankton SSLs across the oxygen gradient from the subsurface oxygenated water to the deep anoxic zone in relation to thermohaline stratification. This observational study was made possible by the use of a moored Aqualog profiler equipped with an ultrasound probe, a conductivity-temperature-depth (CTD) probe, and a fast oxygen sensor. The advantage of this approach is that it provides frequent year-round measurements (with an interval of up to 1 h) of collocated vertical profiles of sound scattering, temperature, salinity, and oxygen concentration in the water column from the near-surface to the bottom layer with a high vertical resolution (up to 20 cm). This helps to fill in the gaps due to insufficient sampling at night and

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resolves difficulties with sampling at precise depths, thereby providing the information needed to locate the displacements of the mesoplankton aggregations.

This article addresses observations of the SSL based on the moored profiler data that were obtained on the upper continental slope in the northeastern Black Sea from 2013-2020. Analysis of the annual cycle of sound scattering on mesoplankton in the oxycline and hypoxic zone allows us to better understand the limiting role of hypoxia in daily migration and interseasonal variability in deep-sea mesoplankton aggregations. To distinguish the SSLs against the background patterns of vertical flow of settling particles and to study the orientation of zooplankton spices, we propose a simple method for the processing of ultrasound sensing data at three angles. This acoustic 3-beam geometry may therefore substantially reduce the development and deployment costs associated with underwater acoustic scattering apparatuses, thereby providing a partial pragmatic solution for the quest towards the multiple-angle scatter measurements suggested by models (Stanton, Chu, 2000; Roberts and Jaffe, 2007) and laboratory experiments (Roberts and Jaffe, 2008). It should be noted that since the late 1990s, researchers' efforts have been focused on creating multichannel instruments to measure acoustic backscatter (volume scattering strength) at several frequencies, such as the Tracor Acoustic Profiling System operating at the six frequencies of 265, 420, 710, 1100, 1850, and 3000 kHz (Smeti et al., 2015). Measurements at different frequencies allow one to get an idea of the size composition of the scatterers, since different frequencies bounce off objects of different sizes. Bio-Optical Multi-frequency Acoustical and Physical Environmental Recorder (BIOMAPER) is one of the most advanced among such devices (Wiebe et al., 2002). As this instrument is towed through the water, five sonar units transmit sound waves upwards at 43, 120, 200, 420 and 1,000 kHz. Another five units transmit downwards at the same frequencies. Multichannel instruments in conjunction with video cameras are fairly expensive systems that are used for the identification of mesoplankton in its natural habitat. Plausibly, a multichannel 3-angle system featuring several relatively cheap short-range 3-beam acoustic units each operating at an individual frequency when installed on a vertically profiling carrier would be a very effective tool for studying the composition and behavior of zooplankton aggregations.

2 Measurements

This study is based on the comparative analysis of the amplitude of sound backscattering data at a frequency of 2 MHz and oxygen concentration data in seawater obtained in the northeastern Black Sea using a moored Aqualog automatic mobile profiler (Fig. 1) (Ostrovskii and Zatsepin, 2011; Ostrovsky et al., 2013; Ostrovskii, Zatsepin, 2016). To obtain the depth profiles of the volume backscattering strength in the northeastern Black Sea, the Aqualog profiler was equipped with a Nortek Aquadopp acoustic Doppler current meter (https://www.nortekgroup.com/assets/documents/ComprehensiveManual_Oct2017_compressed.pdf).

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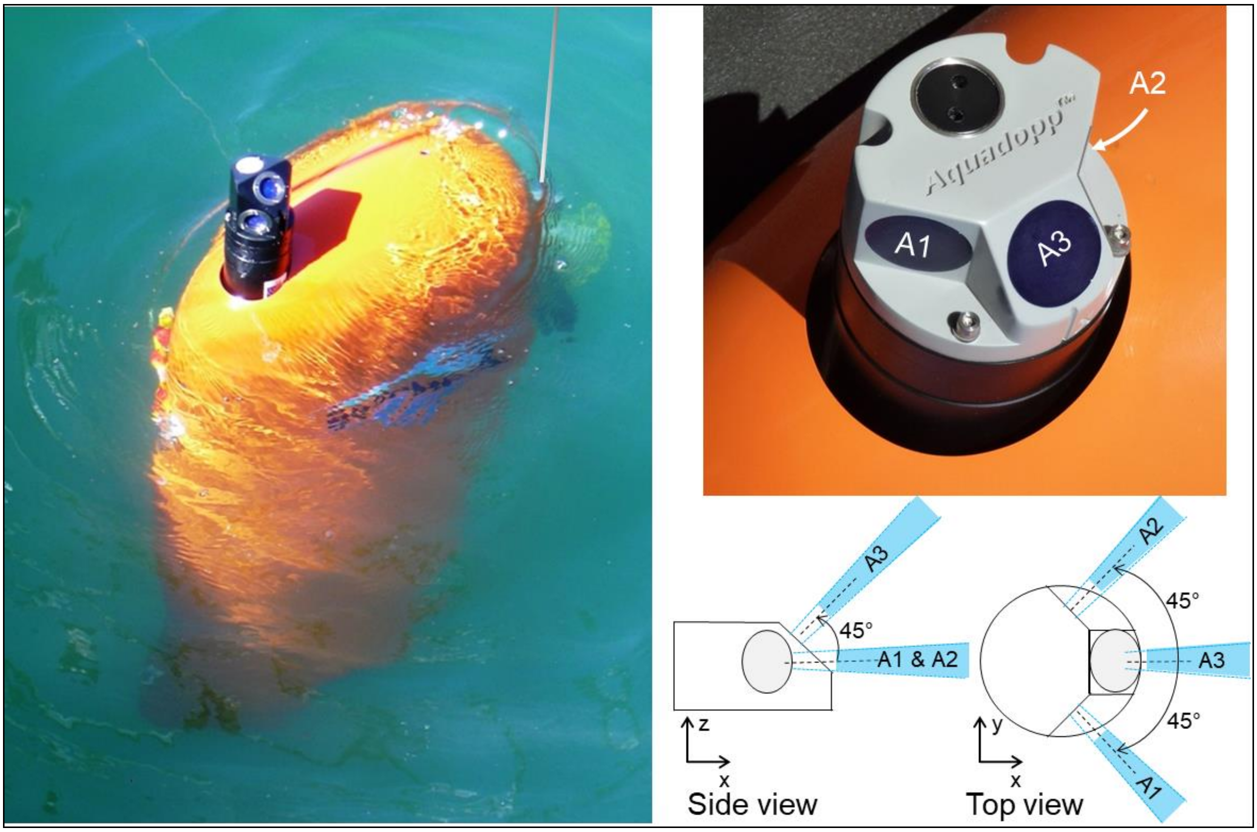

Figure 1: The moored Aqualog automatic mobile profiler with a deep-water Aquadopp acoustic Doppler current meter (left). Transducer head of the shallow-water Aquadopp acoustic Doppler current meter on the Aqualog profiler (right). Bottom right: the acoustic beams are shown in blue and are labeled A_1, A_2 and A_3.

The Aquadopp narrow-band instrument (https://support.nortekgroup.com/hc/en-us/articles/360029839331-The-Comprehensive-Manual-ADCP) emits short sound pulses (pings) at a constant frequency and receives reflected (echo) signals. Plankton and suspended matter, as well as air and gas bubbles, are the main scatterers of the sound. While sound pulses are scattered in all directions when they hit particles, a small fraction of the incident sound pulse intensity is reflected. The Aquadopp current meter employs a mono-static system in which 3 transducers are used to transmit and receive signals at an acoustic frequency of 2 MHz. Measurements are made in the 90 dB range with a resolution of 0.45 dB. In high-accuracy acoustic Doppler measurements, the acoustic beams are narrow and each has a cone angle of 1.7°. Three focused beams measure the scattering strength with high sampling rates in a small volume (referred to as a single point). Two-sided acoustic beams are directed horizontally with 90° spacing between the axes of the beams (Fig. 1). These beams measure the volume scattering strength at the level of the transducer. The third beam is inclined at an angle of 45° to the plane formed by the axes of the other two beams. The piezoelectric element of the transducer transmits sound waves when it vibrates. The vibration does not stop at once but is damped over time. The speed of sound in water and the damping time of the membrane vibration determine the dead zone. In our case, this distance along the acoustic beam is approximately 0.35 m from the piezoelectric

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element of the transducer to the measurement cell (in the form of a truncated cone). The sound pulses are scattered and reflected back to the transducer. In our case, the length of the cell along the axis of the acoustic beam is approximately 1.5 m. Therefore, the reflected sound pulse intensity obtained by the instrument is the weight average for the time during which the sound wave passes the distance of 1.85 m to the far boundary of the measurement cell plus 1.85 m on the way back. The received signal is processed in such a way that the greatest contribution to the average value is made by the scattering in the center of the measurement cell at a distance of approximately 1.1 m from the transducer. The device can transmit up to 23 sound pulses every 1 s. The average value of the volume scattering strength for sound pulses transmitted and received in 1 s is recorded in the device's memory.

The high frequency of 2 MHz allows observations of small-sized sound scatterers. Theoretically, a 2 MHz transducer is most sensitive to particles with a diameter of 0.23 mm (estimates for different frequencies for standard seawater are given, for example, in Hofmann, Peeters, (2013)). However, this is not entirely applicable to zooplankton due to the complex shape of these organisms, their structure, their lipid acid composition, and the presence of gases in their bodies (Lavery et al., 2007, Lawson et al., 2006). However, as a simplified model, zooplankton species are often considered cylinders, the scattering from which is defined as a function of the incident sound pressure, the acoustic wavelength, and the distance between the transmitter and the animal. An approximate formula for describing sound scattering from an elongated weakly scattering body of an animal also includes the angle of orientation of the body (Stanton et al., 1993). Unfortunately, the supplier of the Aquadopp instrument does not specify information about the acoustic power of its transducers. The Aquadopp measurement data for the volume scattering strength are presented in conventional units (counts). Without special calibration, it is not possible to determine the amount of falling sound pressure in water at a distance from the instrument transducer.

Since 2013, Aquadopp instruments with sideways-looking vertically mounted heads have been used on the Aqualog profiling carrier (Fig. 1). The carrier moves up or down at a speed of approximately 0.2 m s^{-1}, so the vertical resolution of the volume scattering strength data is 0.2 m. These data are averaged every 5 s, allowing for the detection of an SSL with a thickness on the order of $O(10^0)$ m.

In the context of this study, the ability to observe sound that has been reflected from zooplankton species at different angles is important. In the case of rounded particles, such as settling detritus, the volume scattering strength of the slanted beam A_3 and those of the horizontal beams A_1 or A_2 are approximately the same. If the elongated suspended particles are oriented vertically or inclined, the amplitude of A_3 will significantly differ from the amplitudes of A_1 and A_2. This was shown for copepods, based on both models of acoustic scattering at a frequency of 2 MHz (Stanton and Chu, 2000; Roberts and Jaffe, 2007) and laboratory experiments (Roberts and Jaffe, 2008).

Thus, by comparing the amplitudes A_1, A_2, and $A_{3,}$ one can judge the predominant orientation of species in zooplankton aggregations. It is assumed that aggregation's characteristic size is greater than the length of the acoustic measurement cell, that is, not less than ~2 m, and its lifetime is longer than 10 s. Therefore, during the Aqualog carrier movement at a speed of 0.2 m s^{-1}, the slanted and horizontal acoustic beams scan the same zooplankton aggregation.

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In addition to the Aquadopp instrument, a SeaBird 52MP CTD probe and Aanderaa 4330F and SBE 43F dissolved oxygen fast sensors were incorporated into the Aqualog profiler to monitor the hypoxic zone and the lower boundary of the aerobic zone (Ostrovskii, Zatsepin, 2016). The SeaBird 52MP CTD was specially designed for moored profiling application in which the instrument makes vertical profile measurements from a carrier that travels vertically beneath a subsurface floatation (https://www.seabird.com/moving-platform/sbe-52-mp-moored-profiler-ctd-optional-do-sensor/family?productCategoryId=54627473795). The CTD employed a pump that controls a flow at a constant speed through a single small diameter opening to ensure the minimizing of salinity spiking in the measurement data by the temperature and conductivity cell. On slow-moving Aqualog profiling carrier e.g., ~0.2 m s^{-1}, the CTD's sampling rate of once per second provided sufficient data to resolve ocean fine-scale thermohaline structure. The accuracy of the CTD probe is 0.002 °C for the temperature, ± 0.0003 S/m for the conductivity and ± 0.1% of full scale range for the pressure. The SeaBird 52MP CTD with SBE 43F was regularly calibrated at the facility of the Southern Branch of Shirshov Institute of Oceanology, Gelendzhik. The dissolved oxygen measurements by using the Aanderaa 4330F and SBE 43F sensors at the profiler were originally described in (Ostrovskii, Zatsepin, 2016) and later in the companion paper (Ostrovskii et al., 2018). The fast response sensing foils of the Aanderaa 4330F sensor were replaced by the new ones two times in past 4 years. The CTD and dissolved oxygen sensors were mounted at the leading edge of the Aqualog profiler pointing into horizontal oncoming flow while the hydrodynamic cowling (vertically-oriented, wing-like) helped to stabilize the profiler orientation with respect to the flow direction. Finally, it should be noted that the Black Sea environment is particularly suitable for the profiling measurements since there is no biological fouling on the sensors of the profiler, which is submerged into the hydrogen sulphide zone for ~10 min every 1-2 h.

The profiler mooring station was deployed approximately 4 nautical miles from the coast off the shelf break at the uppermost part of the continental slope at 44°29.3′N and 37°58.7′E (Fig. 2). From October 2013 to May 2020, 12 surveys, lasting from a few days to 3 months, were carried out using this profiler. During the surveys, the device automatically performed a profiling cycle every 1-2 h, descending to the near-bottom depth of 200-220 m and ascending to the upper layer while remaining submerged at a depth of 20-40 m. In total, more than 13,350 year-round (except March) multiparameter sets of vertical profiles were collected; however, the distribution throughout the year is uneven.

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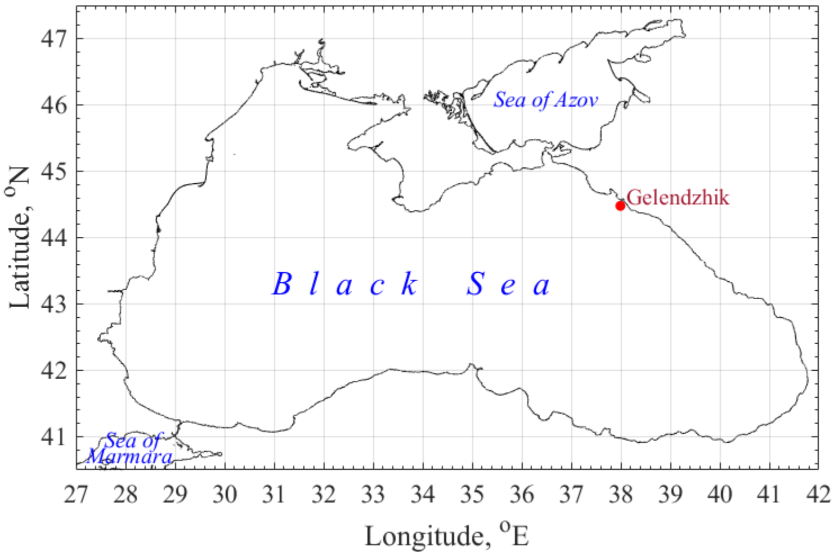

Figure 2: The Black Sea coastline (http://openstreetmapdata.com/data/coastlines). The observational site near Gelendzhik Bay is shown by a red dot. © OpenStreetMap contributors 2020. Distributed under a Creative Commons BY-SA License.

3 Results

3.1 Acoustic scattering by mesoplankton aggregations

The echograms based on the data from the horizontal-beam transducers A_1 and A_2 often reveal aggregations of zooplankton at depths of 80-120 m in the daytime (see example in Fig. 3). Clusters of mesoplankton begin to rise around sunset, concentrate at depths of 10-40 m at night, and migrate down before dawn. Thin, almost vertical lines on the echograms indicate acoustic traces of the migrating mesoplankton species. The echogram also shows patches that occupy the entire water column, from the upper to the lower measurement depth, penetrating into the hydrogen sulfide zone. Moreover, the slopes of these patches indicate that the latter signals propagate exclusively from top to bottom. These are fluxes of suspended matter and its components, which fall under their own weight (see, for example, Klyuvitkin et al., 2016). Acoustic scattering by clouds of particles falling from the upper layers of the water column can obscure zooplankton aggregations.

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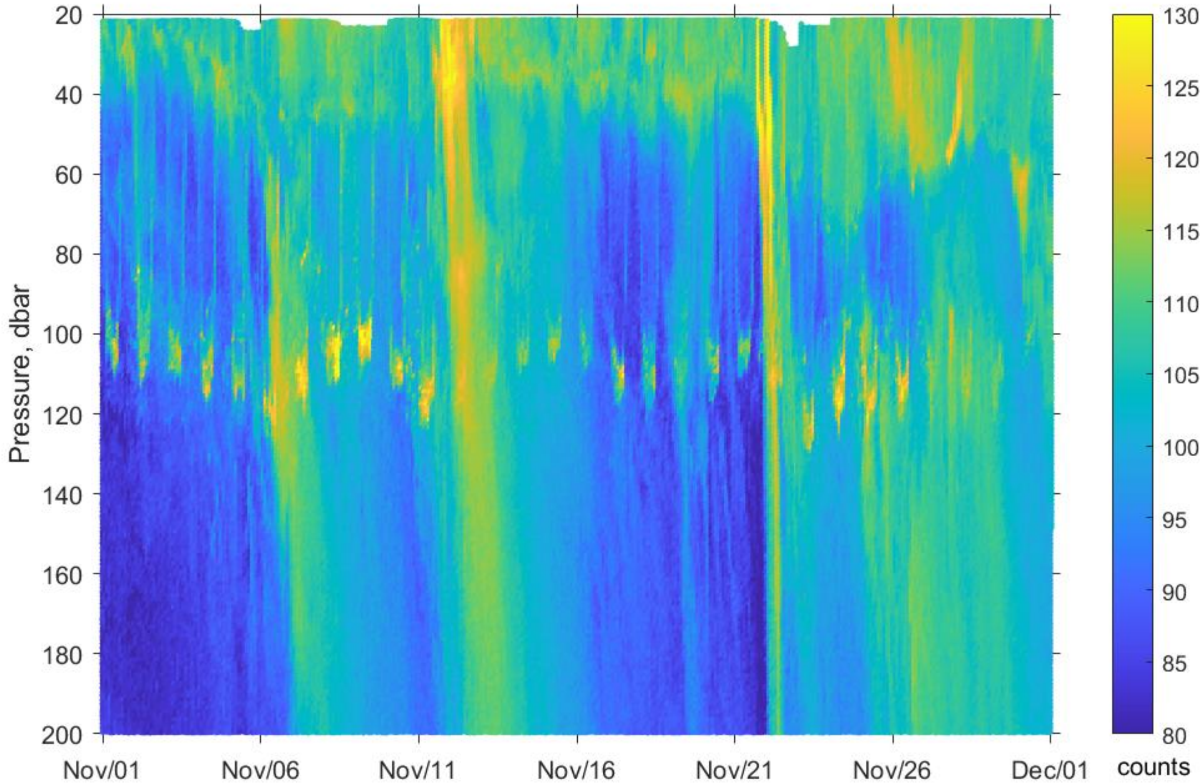

Figure 3: Example of the Aquadopp horizontal-beam (A_1 + A_2)/2 echogram showing acoustic backscatter intensity (counts) versus time and depth over the upper part of the continental slope near Gelendzhik Bay of the northeastern Black Sea in November 2019. The Aqualog profiler with the Aquadopp instrument performed ascending/descending cycles every 1-2 h depending on the time of day. The horizontal axis represents UTC time.

The ratio R is the average value of the volume scattering strength of the horizontal beams (A_1 + A_2)/2 to the volume scattering strength of the slanted beam A_3. It allows for drastic reduction of the noise associated with clouds of sinking particles (compare Fig. 3 with Fig. 4). This indicates that the suspended particles have an approximately equal area in the horizontal projection to the projection with a 45° angle of inclination. In some cases, for example, on November 12, 2019, this noise was so strong that it completely obscured the signal associated with the aggregation of mesoplankton in the 105-115 m layer. However, there were only a few such cases in November 2019. Usually at depths from 90 to 120 m during the daythe directional acoustic backscatter ratio R = 1.05-1.2, and at night R < 1.05. The zooplankton diel vertical migration trajectories in the R graph are very clear below 40 m (Fig. 4). The explanation of these phenomena could be that the scattering area of the elongated bodies of the zooplankton species is larger in the horizontal projection than in the inclined projection at an angle of 45°. Therefore, the orientation of the bodies of mesoplankton species appears to be mainly vertical during migration. At night, these specimens are randomly oriented in the upper layer, where $R \approx 1$.

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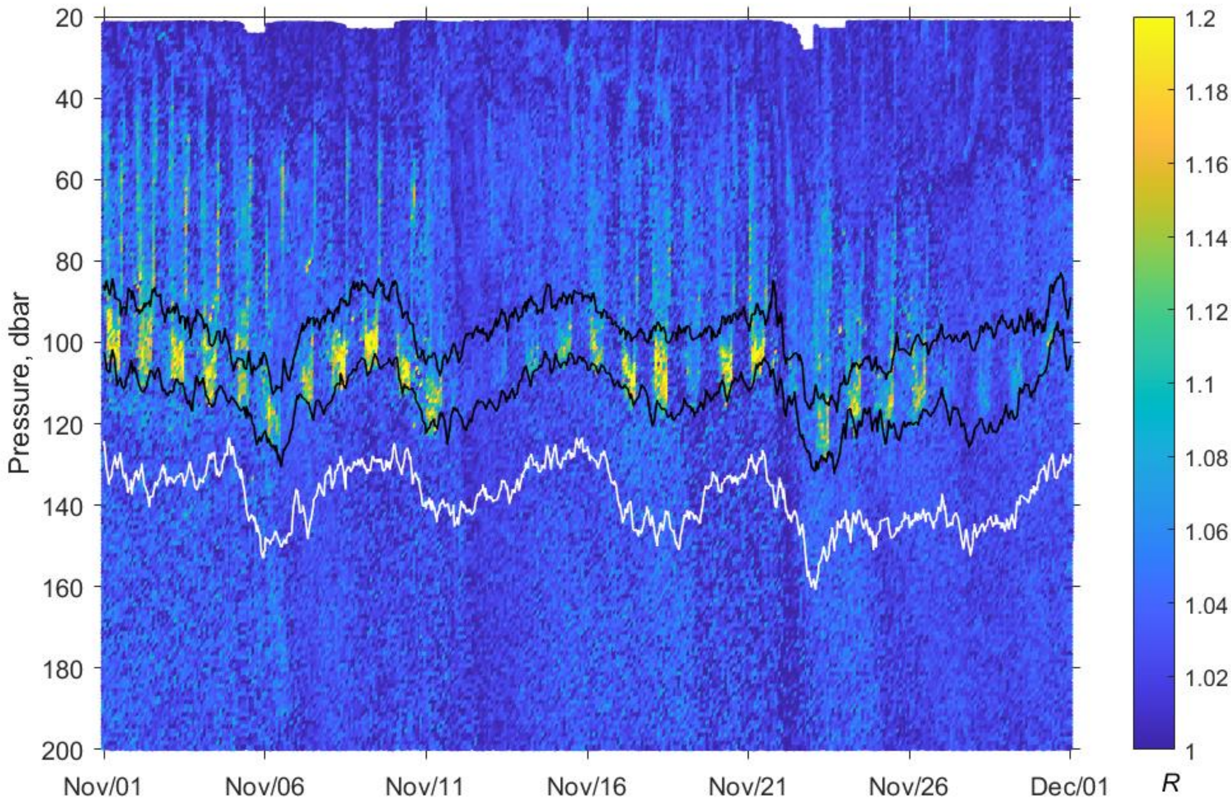

Figure 4: Time-depth graph of the directional acoustic backscatter ratio $R = (A_1 + A_2)/2A_3$ from the Aquadopp data during the same survey as that shown in Fig. 3. The upper and lower black lines are iso-oxylines of 50 and 10 µM, respectively. The white line indicates isopycnal $\sigma_\Theta = 15.9$ kg m^{-3}, which can be taken as a proxy for the boundary of the oxygen zone in the Black Sea (Glazer et al., 2006).

Certainly, dissolved oxygen is a major limiting factor for deep migrations of zooplankton in the Black Sea. Zooplankton aggregations in the hypoxic zone fluctuate along with vertical displacements of iso-oxylines (compare Figs. 4 and 5). It is noteworthy that in the Black Sea, the oxygen stratification strongly depends on the density stratification in the pycnocline (e.g., Konovalov et al., 2005) (Fig. 6).

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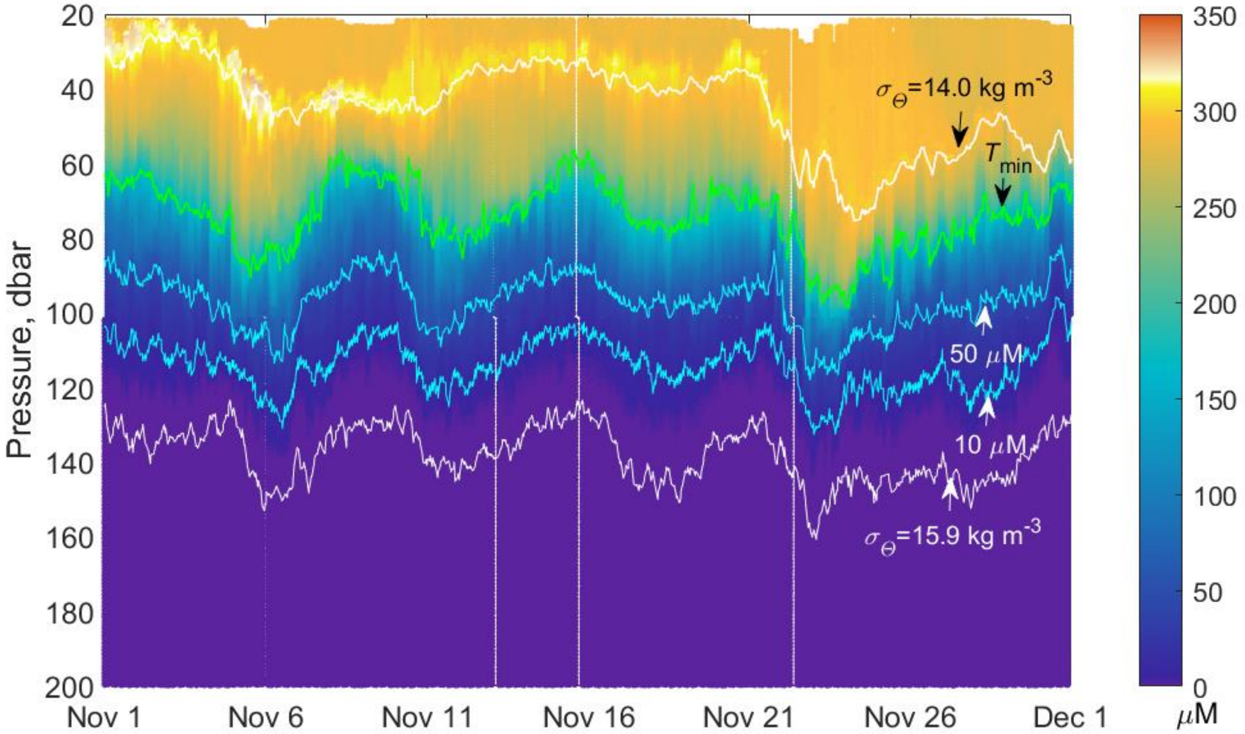

210 **Figure 5: Evolution of the dissolved oxygen at the profiler mooring site in November 2019 (the same period as in Fig. 3 and 4). The measurements were obtained using an SBE 43F sensor housed in the moored Aqualog profiler. The color lines indicate the following: the depths of the isopycnals σ_Θ = 14 and 15.9 kg m^{-3} (top and bottom white lines); the depth of the temperature minimum (green line); and [O2] = 50 and 10 µM (blue lines). The temperature minimum is always located in the cold intermediate layer that is colder than 8.5°C; at depths below 40 m, the temperature is usually 7-10°C (Ostrovskii, Zatsepin, 2016).**

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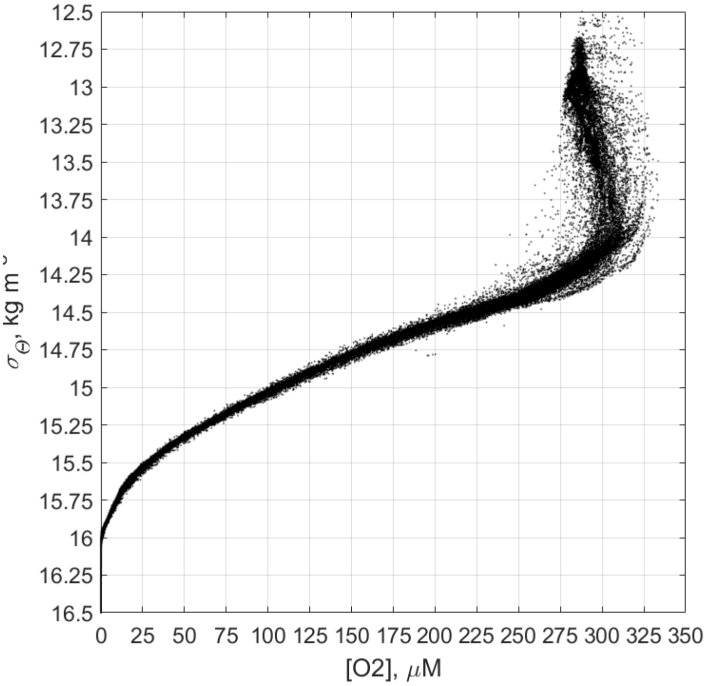

Figure 6: Diagram of the potential density versus dissolved oxygen, σ_Θ-[O2], plotted from the moored profiler data of November 2019. In this example, as well as for other observational periods, the dissolved oxygen deviates very little from isopycnal surfaces in the lower part of the oxycline where [O2] < 200 µM.

In addition to the diel vertical migrations, intraday vertical fluctuations of zooplankton occur with an inertial period that is approximately 17.3 h at the latitude of our observations (Fig. 7). However, unlike diel vertical migrations, which require a large amount of energy from zooplankton, movements with internal waves may not require additional energy. During their ~9 h stay at depth, the copepods spend only 5% of the energy lost in diel migrations (Svetlichny et al., 2000). It is unlikely that the copepods undertake much locomotor activity in the hypoxic zone within the range of σ_Θ = 15.3÷15.8 kg m^{-3}, where their motion should be slowed due to lack of oxygen. A more beneficial strategy would be to adjust their buoyancy to neutral. Having neutral buoyancy in the hypoxic zone, the copepods would not need to spend much additional energy floating up and down following crests and troughs of internal waves while avoiding entrainment into the suboxic layer.

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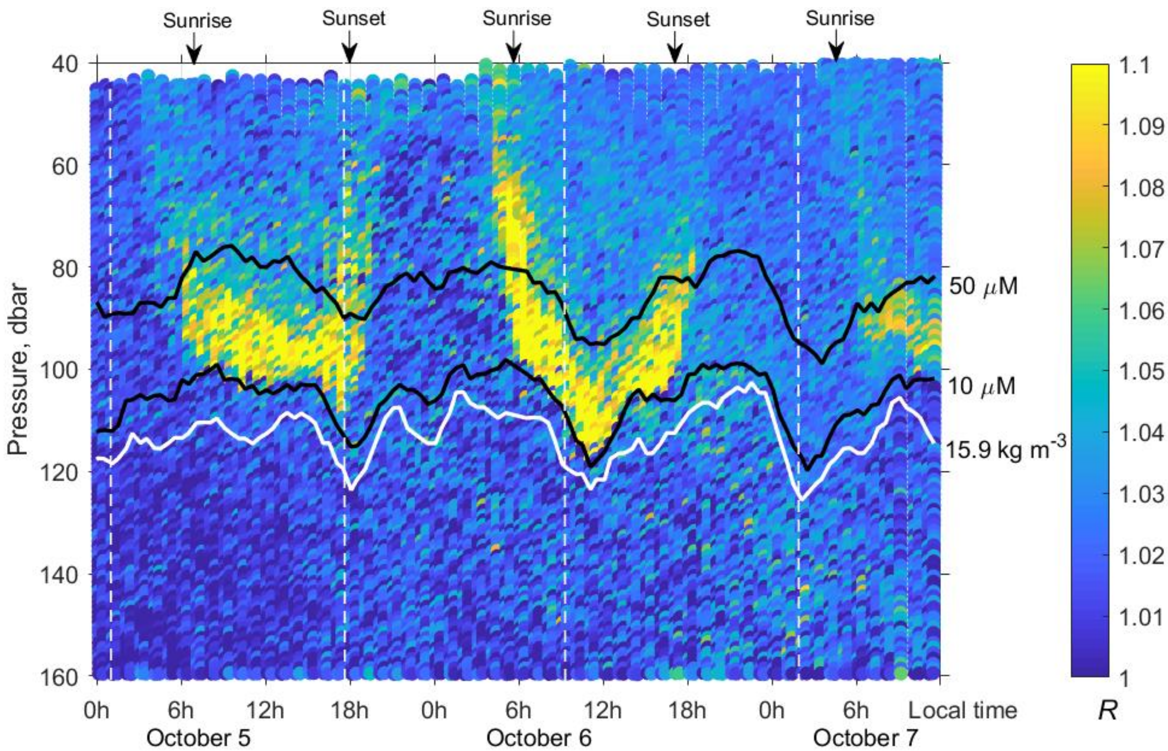

Figure 7: Daily fluctuations of deep mesoplankton aggregations in coherence with vertical displacements of isopycnals and iso-oxylines in October 2014. The displacements of isopycnals with amplitudes up to 20 m are mainly due to inertial waves. Vertical dotted white lines are drawn at a 17.3 h time interval, which is equal to the period of inertial oscillations at the latitude of the observation site. Vertical dotted white lines approximately coincide with troughs of the inertial waves.

Sound-scattering aggregations of mesoplankton oscillate up and down in coherence with isopycnals and iso-oxylines. This allows switching from the depth profiles of the directional acoustic backscatter ratio $R(z)$, where z is the depth, to the R([O2]) profiles to investigate the seasonal changes in R versus [O2]. The average monthly profiles of R([O2]) were constructed from $R(z)$ and [O2](z) data for every month when the data were available. Since the SSLs of deep zooplankton aggregations were observed only during the daytime, it is worth comparing the average R([O2]) profile with the profile of median values (Fig. 8). The average profile is sensitive to extremes in the data, while the median profile shows the most frequently observed R([O2]) value. For example, due to later sunrises and earlier sunsets in November, mesoplankton aggregate for shorter periods of time in the hypoxic layer than in the upper euphotic zone of the sea. Therefore, in the hypoxic zone, the median value of R([O2]) is significantly less than the average R([O2]) in the same range of values [O2]. The maximum value of $\langle R([O2])\rangle > 1.05$ was in the range of values [O2] = 12-25 μM in November 2019.

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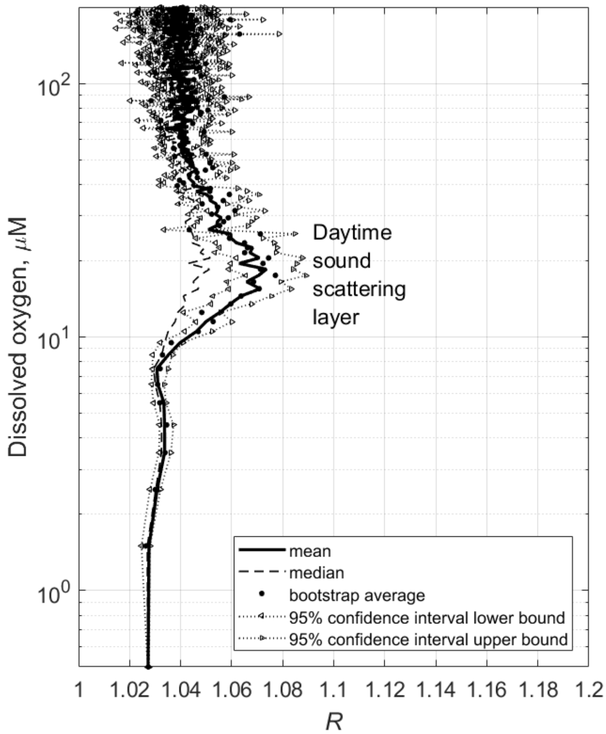

Figure 8: Profiles of the mean $\langle R([O2])\rangle$ (solid line), the median $R([O2])$ (dashed line), the bootstrap averages (black circles), and 95% confidence intervals for the bootstrap averages (triangles and dotted lines) in November 2019. The vertical axis ([O2]-axis) is on a log scale to reflect the lower parts of the profiles in more detail.

In the deep aggregations, the mesoplankton species, while being oriented vertically in general, may be tilted with respect to the vertical axis. The specimens are probably tilted randomly so that the broadside incident angles of the horizontal acoustic beams would dominate the acoustic backscattering data. Since the horizontal beams are orthogonal (Fig. 1), one can calculate the variance or the standard deviation of the ensemble of the ratio A_1/A_2 to check for the possibility of a tilt. There is a high probability that $\langle A_1/A_2\rangle = 1$ for the aggregations of tilted species, while the standard deviation should be significantly greater than 0. Such analysis shows that migrating species are mainly oriented vertically in the daytime deep SSLs so that r.m.s.(R) > 1.05 (Fig. 9).

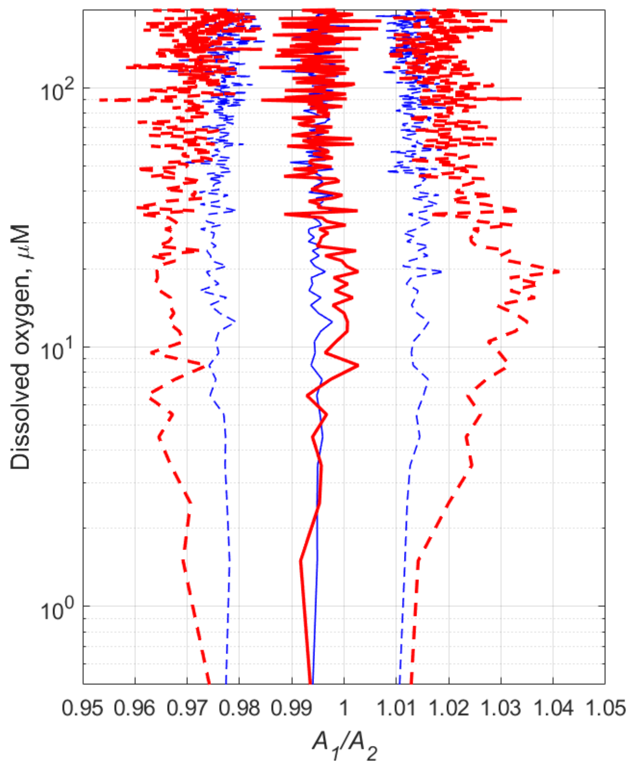

Figure 9: Monthly averages of the depth profiles of the acoustic backscattering amplitude ratio A_1/A_2 for the time series of the volume strength data with the maximum value of the monthly average R([O2]) > 1.05 (solid red line). Dashed red lines indicate the standard deviations. For comparison, the profiles A_1/A_2 for the time series of the volume strength data with the maximum value of the monthly average R([O2]) < 1.05 (solid blue line) and the corresponding standard deviations (dashed blue lines) are also shown.

According to our data, from spring to mid-autumn, another SSL appears below the maximum depths of diel vertical migration. This deepest and up to 10 m thick layer is observed around the clock. The persistent layer is caused by aggregations of diapausing zooplankton (Arashkevich et al., 2014). The diapause layer is usually located 5-20 m above the isopycnal surface of 15.9 kg m^{-3}. It is clearly distinguished by the value R > 1.05 (Fig. 10).

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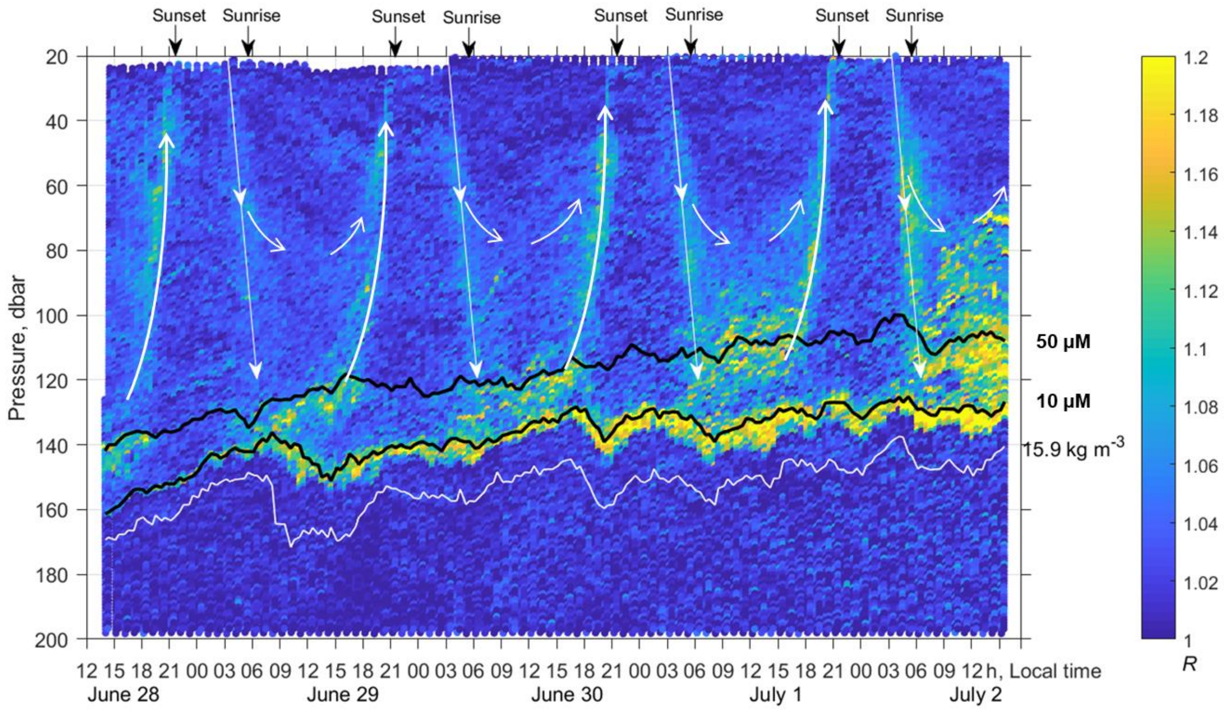

Figure 10: Sample plot of time-depth variation in *R* based on the measurements of sound backscattering in June-July 2014. Color lines show [O2] = 50 µM (upper black line); [O2] = 10 µM (lower black line); and σ_{Θ} = 15.9 kg m^{-3} (white line). There is a persistent SSL under the iso-oxyline [O2] = 10 µM. This SSL is due to the mesoplankton diapause (see Appendix to the article (Morozov et al., 2019)). Thin white arrows schematically show the diel migration of mesoplankton. The maximum depth of the diel vertical migration is 120-150 m, although some specimens dive to depths of only 80-100 m. The slope of the straight arrow pointing downwards corresponds to a diving speed of ~1.5 cm s^{-1}. The ascent is accelerated and reaches values of approximately 2.5 cm s^{-1} in the upper 60 m depth.

The persistent SSL caused by the diapausing mesoplankton appears on the spring and summer profiles of *R*([O2]) as the maximum in the layer where [O2] < 10 µM, i.e., in the suboxic layer (Fig. 11). This maximum is characterized by the median value of *R*([O2]), which does not differ much from the average $\langle R([O2])\rangle$. The orientation of the mesoplankton species in this layer is mostly vertical (Fig. 12) but tends to be slightly more tilted than in the daytime aggregations of migrating mesoplankton, as indicated by the A_1/A_2 ratio (Fig. 9).

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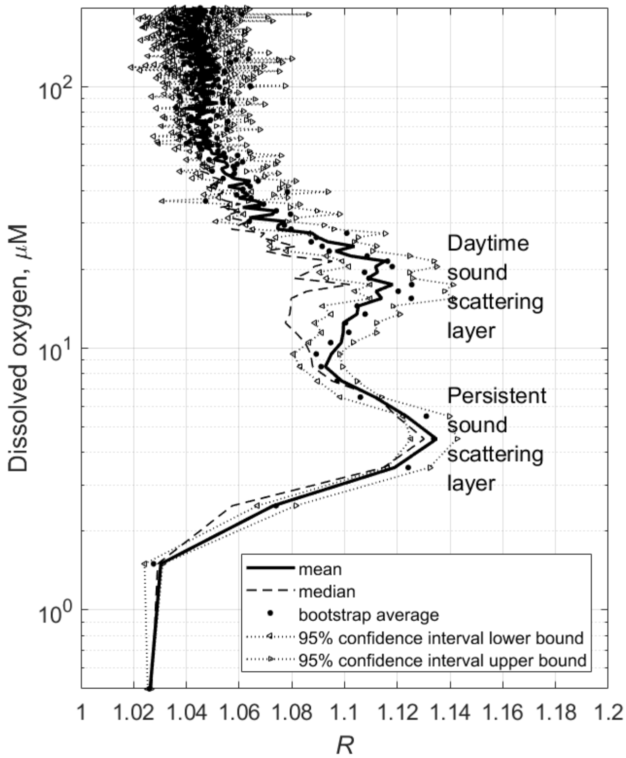

280 **Figure 11: The same as Fig. 8 but for August 2019.**

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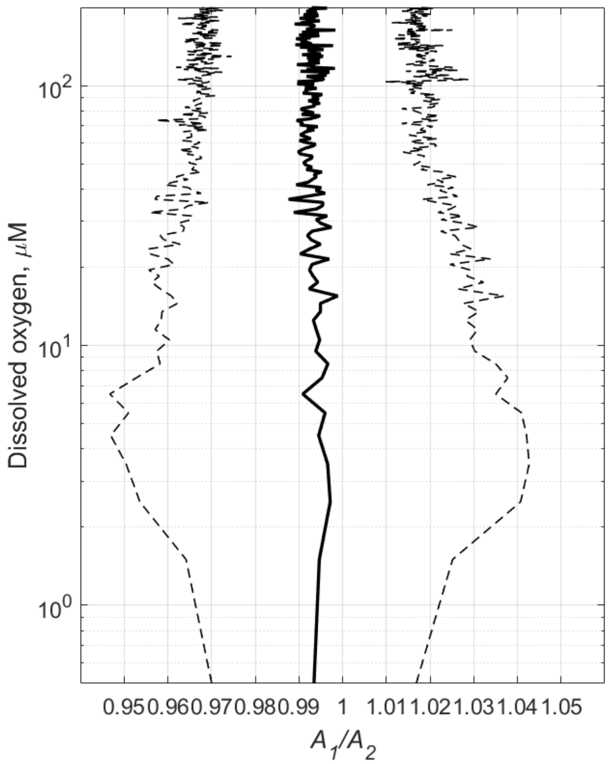

Figure 12: Monthly average profile of the acoustic backscatter amplitude ratio A_1/A_2 (solid line) for August 2019. Dashed lines indicate the standard deviations.

3.2 Seasonal variation in mesoplankton dynamics in relation to dissolved oxygen concentrations

The average monthly $\langle R([O2]) \rangle$ profiles show the annual cycle of mesoplankton distribution evolution (Fig. 13). The SSLs are barely discernible in January-February. Although we unfortunately do not have data for March, in April, two peaks appear in the $\langle R([O2]) \rangle$ profiles in the layers where the dissolved oxygen is 25-60 μM and 4-9 μM. These maxima correspond to the daytime mesoplankton aggregations and the diapause layer, respectively. The upper maximum of $\langle R([O2]) \rangle$, which corresponds to the daytime aggregations of mesoplankton, weakens in June-July. However, it becomes stronger again in August, when it can be as high as 1.11-1.12. This is the largest value for this maximum over the entire observation period. It is worth noting that at that time, the maximum shifts downward into the layer where [O2] is 10-25 μM. In May 2020, the lower maximum of diapause mesoplankton was strongest, reaching almost 1.2 at [O2] = 6-8 μM. In June – July, the diapause layer remains strong with $R > 1.1$ at [O2] = 4-9 μM. In August, the diapause mesoplankton layer shifts deeper in the lower part of the suboxic zone where [O2] = 3-7 μM. Both maxima become weaker in September. The daytime and persistent SSLs are coming closer in October while showing mixed behavior in terms of their location within the hypoxic zone depending on the year. In October 2014 as compared with October 2016, both layers where elevated so that the diapause layer rose to depths of [O2] = 8-20 μM, i.e., just below the layer of the daytime mesoplankton aggregations. In

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November, the diapause layer tends to disappear. In December 2014, the profile $\langle R([O2]) \rangle$ did not contain any maxima, and in December 2019, there was one peak between the 10 μM and 30 μM iso-oxylines.

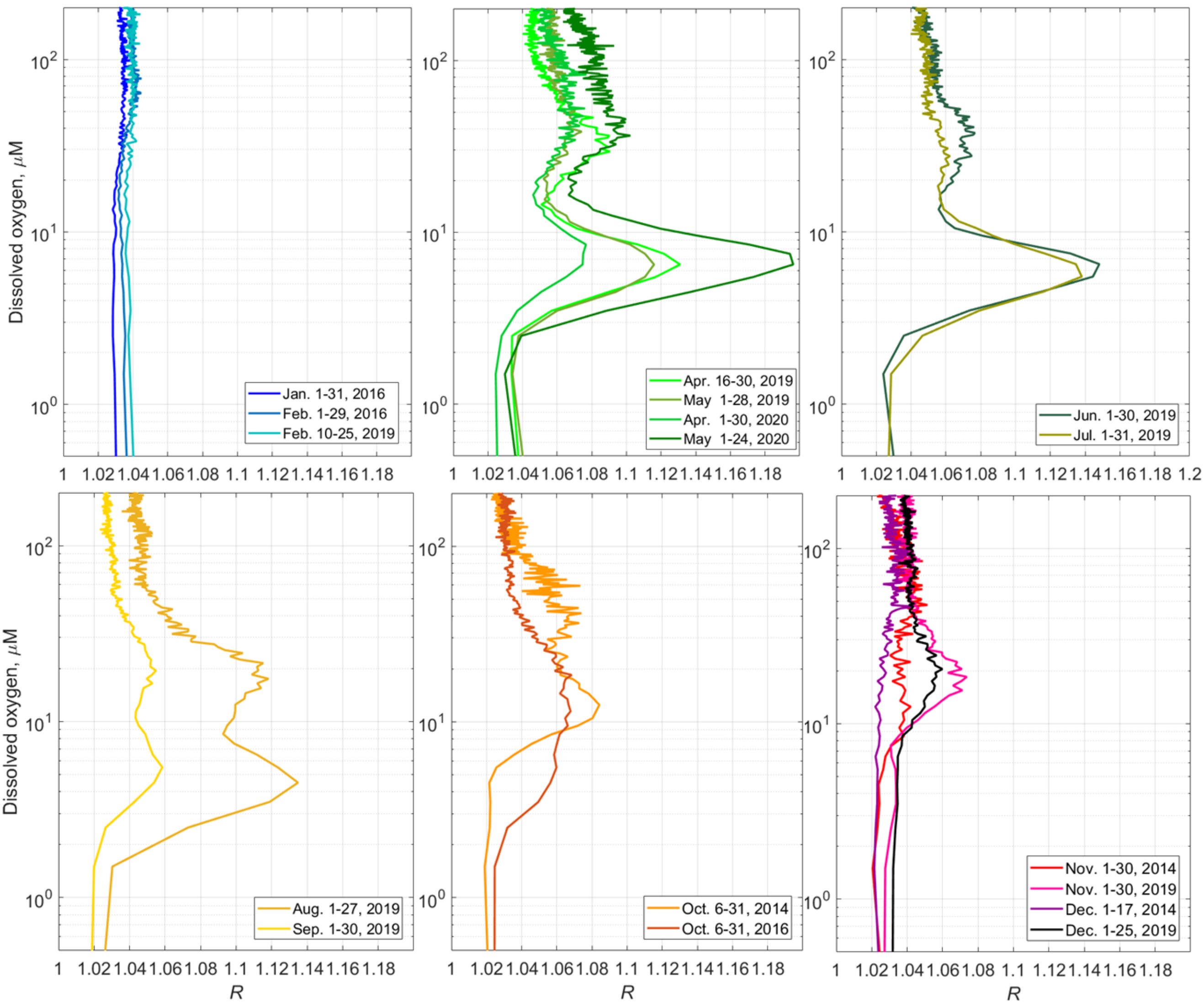

Figure 13: The monthly averaged profiles of $\langle R([O2]) \rangle$ over the upper part of the continental slope near Gelendzhik Bay of the northeastern Black Sea.

4 Discussion

Previously, acoustic measurements at a frequency of 2 MHz were not considered a tool for observations of acoustic scattering layers in the sea due to the limited range of soundings. However, with the advent of ocean profilers with acoustic Doppler current meters, such as the Nortek Aquadopp, it has become possible to obtain the depth profiles of the volume

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scattering strength at 2 MHz frequency in the entire water column and to study the diel vertical migration of zooplankton, such as those in the Black Sea (Ostrovskii, Zatsepin, 2011; Pezacki et al., 2017). The acoustic sounding data from this instrument have already been compared with samples of zooplankton near Gelendzhik Bay in the northeastern part of the Black Sea (Arashkevich et al., 2014). Juday net hauls over 24 h with 3 h sampling intervals targeted zooplankton aggregation layers that were identified in the in situ backscattering data. Analysis of the data obtained using Juday net hauls in June 2011 revealed that these zooplankton constituting the SSL in echograms at a frequency of 2 MHz are mainly *Calanus euxinus* and *Pseudocalanus elongates*, which have a characteristic size on the order of $O(1)$ mm (Arashkevich et al., 2014). The six layers that were sampled were the upper mixed layer, thermocline, two layers in the cold intermediate layer (CIL) (temperature less than 9°C), and two layers in the suboxic zone between the isopycnals σ_Θ 15.4 and 15.7 kg m^{-3} and between 15.7 and 15.9 kg m^{-3}. At that time, the upper mixed layer (temperature 24-25°C) was inhabited by thermophilic zooplankton (mainly cladocerans and the copepods *Acartia clausi*). The fluorescence peaked in the thermocline, which was permanently occupied by the heterotrophic dinoflagellates *Noctiluca scintillans* and the younger stages of the copepodites *Calanus euxinus* and *Pseudocalanus elongates*. The older stages of the latter two species performed diel vertical migrations and aggregated in the lower part of the CIL during the daytime and ascended to the thermocline at night (for details, see the supplement to the paper by Morozov et al., 2019). The lower boundary of their daytime aggregation coincided with an oxygen concentration of 30 μM (Arashkevich et al., 2014). The deepest layer of zooplankton aggregation was mainly formed by diapausing *Calanus euxinus* (CVs). Its thickness was 5-7 m, and below it was limited by σ_Θ = 15.9 kg m^{-3}. The oxygen concentration in this layer was 3-5 μM.

On the echograms, the mesoplankton SSLs stand out against the background of patches associated with suspended particles of $O(10^{-2})$ - $O(10^{-1})$ mm in size (Klyuvitkin et al., 2016). Some of these patches are due to the falling of clumped detritus from the surface sea, while others are caused by sinking lithogenic matter, mainly clay minerals with an admixture of silt-sized minerals.

Acoustic sounding of a mesoplankton SSL at two angles is made possible by using the side-looking head of the Nortek Aquadopp instrument. The combination of horizontal and tilted beam signals allows, on the one hand, eliminating the time variability associated with the patches of particles and equalizing the background scattering level of the echogram and, on the other hand, determining the preferred orientation of mesoplankton species migrating through the oxycline. Earlier, Stanton and Chu (2000) reproduced the influence of the orientation of a 3-mm calanoid copepod (modeled as a high-resolution approximation of an animal profile) on the acoustic target strength at 2 MHz with respect to an incident sonar beam. The reduction was found to be 5-15% when copepod orientation was shifted from 0° (broadside incidence) to 30-60°. Benfield et al. (2000) carried out field observations in the area of George Bank in the North Atlantic and showed that most *Calanus finmarchicus* (75%) in the depth range of 10-70 m were within ±30° of the prosome-up or prosome-down orientation. Benfield et al. (2000) suggested that one reason for the behavior underlying the head-up orientation pattern may lie in the predator avoidance strategy aimed at reducing the conspicuousness of *Calanus* when viewed from above. Such individuals would present a significantly reduced cross-sectional area to an echo-sounder's transducer with correspondingly

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diminished target strength. It was concluded that it is necessary to know how the orientation of individuals changes in aggregations with depth to correctly account for the biomass of mesozooplankton. Experiments using a multiple-angle acoustic receiver array on live copepods and mysids in a laboratory tank showed that it is possible to use the scattered acoustic signal to distinguish among zooplankton taxa (Roberts and Jaffe, 2008). Reflections in the frequency range from 1.5 to 2.5 MHz were recorded from untethered 1 – 4 mm calanoid copepods and 8 – 12 mm mysids over an angular range of 0–47°. That study demonstrated the utility of a multiple-angle acoustic array for zooplankton identification.

In the Black Sea, females of the copepods *Calanus euxinus* and *Pseudocalanus elongatus* in developmental stages CVI, CV, and CIV migrate down to the deep 100-140 m layer (Morozov et al., 2019). According to Svetlichny et al. (2020), calanoid copepods have two swimming gaits as follows: i) cruise swimming that is propelled by the beating of the cephalic feeding appendages and ii) short-lasting jumps that are propelled by the power strokes of the four or five pairs of thoracic swimming legs. Considering the mechanical energy of the moving specimen, Svetlichny et al. (2020) arrived at the conclusion that larger copepods are cruise swimmers. Based on the argument that the density of the calanoid copepod body is higher than the density of water, downward movement should be faster than the sinking speed, and upward movement should be slower than the speed of sinking. Taking into account that the sinking speed of females of *Calanus helgolandicus* (*euxinus*) can reach 0.8 cm s^{-1} at a temperature of 20°C, Svetlichny et al. (2000) suggested that their maximum swimming speed could be 1.4 cm s^{-1} in the upward direction and 3 cm s^{-1} in the downward direction. In the case of our data, we have to take into account that the water temperature below 40 m is usually only 7-10°C, which should slow down the cruising speed. As emphasized by Svetlichny et al. (2020), the rate of planktonic crustaceans varies in proportion to the temperature coefficient Q_{10} = 2, i.e., a decrease by a factor of 2 when the temperature drops by 10°C. Therefore, the swimming speed of ascent could not be higher than 0.3 cm s^{-1} at temperatures as cold as 8-10°C. In fact, according to our observations and those of Mutlu (2003), the upward migration speed of a copepod species within the CIL is 2.3-2.5 cm s^{-1}. The uneven rate of vertical movement of zooplankton was pointed out by Mutlu (2003). According to his data, the swimming speed of *Calanus euxinus* during migration varied from a passive sinking speed of 0.57 cm s^{-1} within the suboxic zone to an active speed of 2–3 cm s^{-1} (upward) and to 2.7 cm s^{-1} (downward) through well-oxygenated water. Our data of acoustic sounding of mesozooplankton aggregations at a constant frequency of 2 MHz at 3 different angles indicated that the zooplankton was oriented vertically in the lower part of the descent and ascent trajectories. Since individuals migrate at significant speeds, they should certainly be driven by the beating of swimming legs (cephalic feeding appendages). Therefore, the species should progress head-down while migrating downward and head-up while migrating upward. This change in orientation would be easier if the center of gravity of the individual is shifted to the head during the descent and to the tail during the ascent. It is unlikely that this daily change in buoyancy is due to lipid metabolism because fatty acid accumulation processes are slower (see, for example, Helenius et al., 2019). Perhaps it is reasonable to assume that copepods descend with full guts and ascend with empty guts. In this way, their weight in the water is greater when moving down than when moving up. This could be the reason for the observed higher rate of vertical migration compared to the one predicted for cold intermediate water earlier (Svetlichny et al. 2020). Here, it should be noted that diel vertical migration can increase the vertical flow of

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carbon and thus contribute to the functioning of the biological pump in the ocean (Tutasi et al., 2020). The mesoplankton and micronekton that feed at the surface but metabolize and excrete at depth contribute to transport of organic matter; more quantitatively this contribution is estimated between around 10–50% of the local sinking flux of organic particles (Bianchi et al. (2019) and the references therein).

Our observations show that during the annual cycle, the daytime aggregations of vertically migrating mesoplankton are observed at different depths within the hypoxic zone: from April to July at [O2] = 25-60 μM and in August-December in the deeper layers of the sea at [O2] = 8-30 μM. This clarifies earlier observations (Svetlichny et al., 2000), which suggested that *Calanus euxinus* undergoes diel vertical migrations during summer stratification with an amplitude of approximately 117 m, from the oxygenated, warm (18°C) surface layer to the lower-temperature (~8°C in 1996 and 1997) hypoxic zone. According to our data, the temperature in the hypoxic zone in spring and summer can either be higher or lower than in the main oxycline depending on the severity of the previous winter. For example, in April 2019 and 2020, the water temperature in the zone of daytime aggregations of mesoplankton was 8.6-8.75°C (Fig. 14).

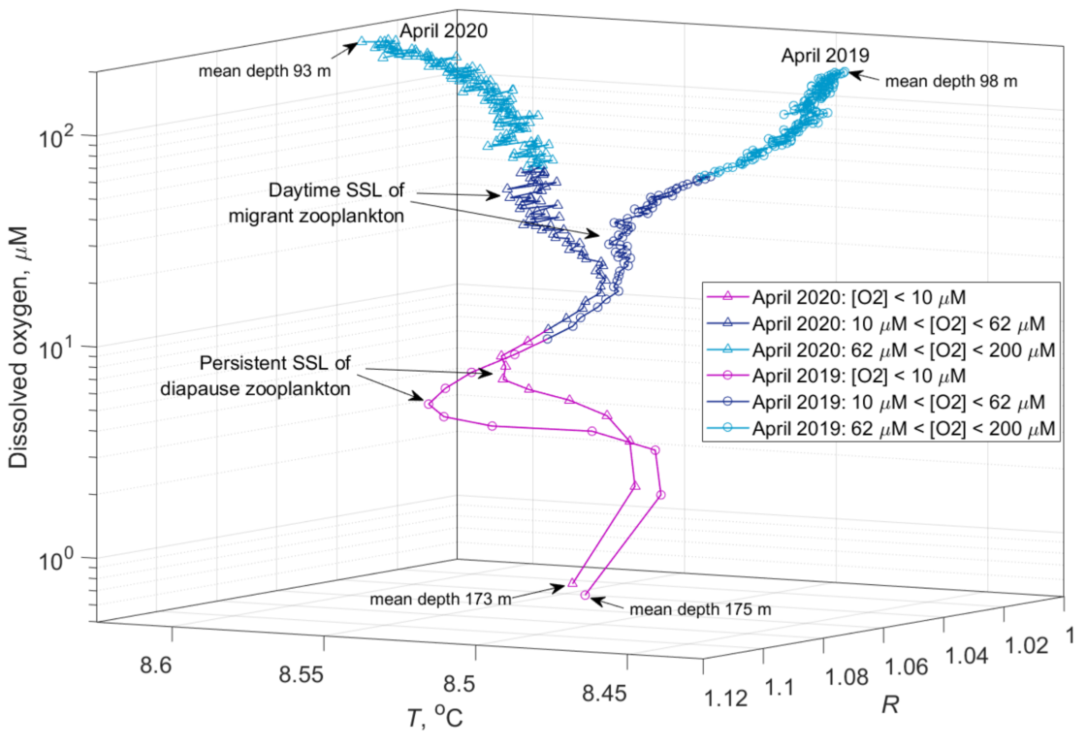

Figure 14: The monthly average *R* as a function of temperature *T* and dissolved oxygen [O2] for April 2019 and 2020. Note that for monthly average data in April 2019, the minimum temperature was 8.41°C at a depth of 75.9 m, while in April 2020, the minimum temperature was 8.68°C at 102.4 m.

From observations in the eastern tropical North Pacific, it is known that calanoid copepod species can change their vertical distributions and depth of maximum abundance in response to changes in the depth and intensity of the oxygen minimum zones and their oxycline inflection points (Wishner et al., 2020). Some species adjust their diel vertical migration, especially the nighttime upper depth. Some shift their depth of diapause. Compared with the open ocean conditions, there are only two migrating copepods in the Black Sea, and their diel vertical migration depths are rather shallow, less than 120 m (Morozov et al., 2020). In the winter, the Black Sea oxic zone is usually ventilated due to surface cooling, turbulent mixing, and deep convection (e.g., Ostrovskii et al., 2018). The vertical gradients of dissolved oxygen vary greatly in the winter. Oxygen stratification is sometimes characterized by the fall from approximately 300 to 10 μM across a 40 m thick layer (Ostrovskii et al., 2018). Such conditions would be a substantial barrier for the vertical migration of zooplankton. In our January-February data, zooplankton aggregations are hardly distinguishable in the sound scattering profiles in the lower part of the oxycline where [O2] < 200 μM. According to Morozov et al. (2020), the depth of diel vertical migration decreases in winter. More specifically, *Calanus euxinus* migrates down to 60-70 m in February-March, while *Pseudocalanus elongates* migrates down to only 40-50 m depth. Unfortunately, we do not have data for March. In April, the diel vertical migration of *Calanus euxinus* deepens to 120 m (Morozov et al., 2020). The profiler measurements indicate that the daytime SSL and the persistent SSL developed in April are associated with migrating and diapausing zooplankton, respectively (Fig. 13). Our observations are consistent with the hypothesis that hypoxia zone provide a refuge from large visual predators, which generally need higher oxygen concentrations (e.g., Bianchi et al., 2019). Remarkably, the diapause mesoplankton congregates at very lower oxygenated water in the suboxic zone that might be impenetrable for most predators. The sound scattering from diapausing aggregations of zooplankton is strong at oxygen levels of 4-8 μM in May-July (Fig. 13). In August-September, this SSL shifts to lowest oxygen levels of 3-6 μM where it gradually disappears by the end of October.

5 Conclusions

The analysis of the mesoplankton distribution versus the dissolved oxygen concentration is particularly important for the Black Sea because this basin has strong oxygen stratification. The oxygen stratification determines the depths of the mesoplankton aggregations. The latter results in SSLs in the echograms. By using the ultrasound device attached to an ocean profiler, it becomes possible to observe the temporal variability in different stages of the mesoplankton yearly life cycle. The surveys involving the moored profiler with the 2 MHz acoustic Doppler current velocity meter, the CTD probe, and the fast sensors for dissolved oxygen allow us to determine the annual cycle of the SSLs in the Black Sea. In such a way, the seasonal march of the daytime and diapause SSLs is described in great detail. It is important that in the Black Sea, the dissolved oxygen profile tightly hinges on the density stratification since both are basically due to vertical mixing processes (e.g., Ostrovskii et al., 2018). Hence, displacements of the SSLs with regard to the oxy-isolines are much smaller than those versus the depths.

Daytime aggregations of vertically migrating mesoplankton are observed within the hypoxic zone. In January-February, daytime accumulations of mesoplankton are poorly distinguished on echograms, and the monthly average profiles of the directional acoustic backscatter ratio $\langle R([O2]) \rangle$ do not contain maxima. From early spring to mid-summer in the

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daytime, the mesoplankton are aggregated in the layer where [O2] = 20-60 μM. At the end of summer until mid-autumn, the mesoplankton aggregations shift to deeper and more oxygen-depleted layers of the sea at [O2] = 10-25 μM. In the first half of winter, the sound scattering by the daytime deep-sea mesoplankton aggregations weakens, indicating that the aggregations become less tight. The mesoplankton vertical diel migration depth is rather shallow in the Black Sea due to poor ventilation.

The persistent diapause SSL is observed from spring to autumn in the suboxic zone at very low [O2] < 10 μM. This layer does not exceed 5-10 m in thickness. However, the volume scattering strength in this layer may exceed that in the overlying daytime SSL, which may indicate tighter diapausing hypoxia-tolerant mesoplankton aggregations in the lower part of the suboxic zone. The diapause SSL may appear early in spring; at least, we observed it at the beginning of April. At the end of summer, the core of this layer is located particularly deep, between the oxy-isolines of 3-6 μM.

For measurements of mesoplankton SSLs, it is beneficial to employ an acoustic device with a side-looking transducer that transmits pulses at the ultrasound frequency at 3 different angles. This allows one to work with combinations of acoustic beam data, using data of an inclined beam as a reference for the background signal. This helps to reduce the noise associated with suspended particles, to equalize the background scattering level of the echogram and to determine the predominant orientation of mesoplankton species. If the specimens that scatter sound have an elongated shape, then using acoustic sounding at different angles can provide information on the orientation of the zooplankton, which may indicate its behavioral features. Hence, it is shown that the backscattering amplitude of sound is on average the same for all 3 acoustic beams in the upper layer of the Black Sea due to the random distribution of the orientation of specimens during feeding. Below the Black Sea euphotic zone, more precisely in the lower part of the oxycline, where the oxygen content in the water becomes less than 200 μM, the orientation of migrating specimens becomes ordered. The specimens are mainly oriented vertically in daytime aggregations in the hypoxic zone and in diapause clusters in the suboxic zone. Fluctuations of the SSLs are subject to interannual changes. It is necessary to maintain the moored profiling acoustic observatories in the Black Sea for a detailed analysis of year-to-year variability.

Data availability. Underlying research data can be accessed via DOI: 10.13140/RG.2.2.28470.73285, License CC BY-NC 4.0.

Author contributions. AO analyzed the moored profiler Aqualog data and wrote the paper. VS deployed the mooring and handled the profiler sensors. DS is a design engineer of the profiler who also maintained the profiler.

Competing interests. The authors declare that they have no conflict of interest

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