



Research papers

The benthoneuston of the Black Sea: Composition and environmental factors influencing its nocturnal dynamic



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ABSTRACT

Plankton fauna nocturnally migrating from the sea-floor or near-bottom layer to the uppermost surface layer (benthoneuston) links benthic, benthopelagic, pelagic, and neustonic realms. We conducted five intervals of sampling (every 1–2 h during five nights) synchronously in the neustal (surface to 10-cm depth layer) and in the water column below to examine which taxa concentrate in the neustal, and under which circumstances they do so. We tested the following environmental factors: sea-floor biotope type, temperature, time after sunset, time to midnight, moon phase, and moon altitude. Of the 77 taxa recorded, about half (41) were found in the neustal. Among these, less than half (16) of the taxa showed a quantified attraction (by L-index) to the neustal and may be called the true benthoneuston. In contrast to the benthopelagic zone, where the contribution of the characteristic benthopelagic fauna exceeded 50%, the neustal was not dominated by a specific benthoneuston fauna. Nocturnal dynamics of the benthoneuston was mainly controlled by the proximity of the twilight time, then by the sea-floor biotope type and time to midnight. Neustonic taxa were more affected by moon illumination (moon phase and moon altitude) than those in the water column below. The benthoneuston in the studied area was represented by either juveniles or reproducing adults. This component of plankton communities is thus temporary and seasonal, at least in the temperate Black Sea. In the "high" summer-autumn season, contribution of benthoneuston to the coastal plankton communities is significant, whilst in winter this contribution may be negligible. The next step in the understanding of the role of benthoneuston should be associated with tropical areas where seasonal changes in reproduction are less distinctive and this group may represent an important permanent component of coastal communities.

1. Introduction

The water column encompasses three principal vertical ecological zones: (1) the uppermost neustal (a surface layer 10-cm thick (e.g. Zaitsev, 1961; Macquart-Moulin, 1968), (2) the lowermost near-bottom layer several tens of meters thick (e.g. Marshall and Merrett, 1977; Vereshchaka, 1995), and (3) the proper pelagic in between. Each of these zones is inhabited by a distinct fauna adapted to specific conditions, which include intensity of solar radiation, turbidity, physical (temperature, salinity, currents, absolute values and gradients) and chemical parameters. In addition to the pelagic fauna living in, and adapted to, the pelagic, there is a fauna migrating between adjacent biotopes: (1) benthopelagic taxa migrating between the benthic/near-bottom layer and the pelagic (Macquart-Moulin, 1965, 1968, 1973, 1984; Macquart-Moulin and Maycas, 1995) and (2) hyponeustonic taxa migrating between the neustal and water column (Champalbert and Macquart-Moulin 1970; Macquart-Moulin, 1972, 1984; Tully and

Ceidigh 1986, 1987; Macquart-Moulin and Maycas, 1995). Migrating animals can take advantage of both adjacent biotopes using one of them as a food reservoir and the second as a shelter (Vereshchaka, 1995; Vereshchaka and Anokhina, 2014, 2015).

There is, however, one more ecological possibility: a migration between all three biotopes, from the benthic/near-bottom realm through water column to the neustal. Since the amplitude of vertical migrations of the plankton is limited to the first hundreds of meters (Vinogradov, 1970), migrations from the benthos to the surface may occur only above the shelf and upper-slope regions. Such fauna migrating between benthic and neustonic realms has been studied over coral reefs (Alldredge and King, 1977; Porter and Porter, 1977; Hobson and Chess, 1979; Ohlhorst, 1982; Madhupratap et al., 1991) in tropical areas, continental slopes in the Mediterranean (e.g., Macquart-Moulin, 1968), and the shelves of the Azov and Black Seas (Zaitsev, 1961, 1971; Zakutsky, 1965a, 1965b). Over greater depths, regular connection between surface and bottom is lacking due

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to the restricted range of vertical migrations. This fauna has been known under different names (see review in the Introduction to Vereshchaka and Anokhina (2015)); hereby, we will use the term "benthoneuston" to emphasize the linkage between benthic and neustonic habitats, which this fauna provides. Benthoneuston is more abundant over flat sandy substrates than over rocky sea-floors, biodiversity is maximal over coral reefs (Alldredge and King, 1977; Porter, Porter, 1977).

In spite of the results above, the benthoneuston remains one of the poorly understood ecological groups in three basic aspects. First, methods should be developed and unified to recognize and separate this fauna from the rest of the migrating benthopelagic species, which are strays in the neustal. Second, the diversity and the role of the benthoneuston in the coastal communities remains nearly unknown. Third, a comprehensive assessment of environmental factors, which explain the distribution of the benthoneuston, has not yet been conducted. Recent studies devoted to the separation of the benthoneustonic species from the rest of the nocturnally migrating fauna, their distribution and temporal (diel, seasonal, and interannual) dynamics have been based on samples taken at a single site at a depth of 7 m (Vereshchaka and Anokhina, 2015). These authors offered and tested the L-index, which separates the neustonic animals and shows either their robust attraction to the neustal ($L > 0$), or avoidance / indifference ($L < 0 / \sim 0$) to this biotope. This index has not been tested since then.

The present paper is aimed to fill a gap in our knowledge of the benthoneuston ecology and addresses to the following questions: How diverse is the proper benthoneustonic fauna at depths 10–40 m in the Black Sea? Is the L-index (Vereshchaka and Anokhina, 2015) appropriate for a wider depth range? Which of the environmental variables have the largest effect on species and biomass distribution of benthoneuston (temperature, local sea-floor biotope, time, solar illumination, lunar phase)? Do these differ among various taxonomic groups? In order to address these points, we extended the former observation range (Vereshchaka and Anokhina, 2015) to depths 10, 20 and 40 m, where three types of the sea-floor substrates were recorded (rocks, shelly sands, and oozes, respectively); we also tried to test the widest possible temperature range, different moon phases and moon altitudes within the same season (in order to minimize a seasonal factor).

2. Methods

Samples were taken off the Golubaja ("Blue") Bay near Novorossiysk (see map in Vereshchaka and Anokhina (2016), Fig. 2), where environmental parameters were characteristic for the Northeast coast of the Black Sea (Pasternak, 1983; Lebedeva et al., 2003). The sampling strategy was similar to that of Vereshchaka and Anokhina (2017; Fig. 1) and the same environmental factors were tested as possible proxy cues for the plankton communities: the type of the sea-floor biotopes (SFB,) temperature (T), moon phase and moon altitude (MP and MA), time after sunset (TAS), and time to midnight (TTM). We focused at a short period between mid-August and mid-September when the benthopelagic biodiversity at the site was the highest (Vereshchaka and Anokhina, 2014). Meteorological conditions during all observations were similar: mostly clear sky, no waves (and no tides in the Black Sea). No significant salinity gradients existed in this period above studied depths.

Each of five nocturnal observations included 6–7 hauls taken every 1–2 h over 10, 20, and 40 m (Table 1). We took two sets of samples: in the water column (from the surface to the near-bottom layer) and in the neustal zone (upper 10 cm), similar to previous methods (Vereshchaka and Anokhina, 2015). Water column stations were taken with a Judey net (mouth area 0.1 m^2 , mesh size $180 \mu\text{m}$), towed at 50 cm s^{-1} . Synchronously, just after retrieval of Judey net, we took hauls with a neustonic net (frame $10 \times 65 \text{ cm}$, mesh size same as in Judey net). The net was towed at a distance of 10 m (0.65 m^{-3} filtered

every time). All samples were accompanied by measurements of surface temperature with Spindler thermometer and meteorological data.

Preservation of samples, identification of taxa, estimation of abundance and biomass was identical to those by Vereshchaka and Anokhina (2015).

In order to establish possible relationships between plankton assemblages and environmental factors, Canonical Correspondence Analysis (CCA: Ter Braak, 1986) was performed. CCA is a multivariate constrained ordination technique that extracts major gradients among combinations of explanatory variables in a dataset. We used such plankton assemblage characteristics as abundances of each benthopelagic taxa recorded in the water column twice or more, total abundance (**NB**) and biomass (**BB**) of benthopelagic fauna, and the proportion of the benthopelagic animals in the total plankton biomass (**SB**). For each of plankton taxon we calculated the L-index: $L = \log(N_1/N_2)$, where N_1 and N_2 are simultaneous abundances of the identified unit (sex/age stage, species, major taxa) in the neustal zone and in the water column, respectively (Vereshchaka and Anokhina, 2015). If L significantly differs from 0 (we use t -test), the group either prefers the neustal zone (L positive) or avoids it (L negative). Otherwise, the group is evenly distributed in both zones.

As environmental variables, we tested the following factors (see Fig. 1 in Vereshchaka and Anokhina (2017)):

- Sea-floor biotope type (*SFB*): a qualitative variable, determined at each site with the use of scuba.
- Temperature (T): measured at the beginning and at the end of hauls at the surface and further averaged.
- Time after sunset (TAS): a variable indicating time-lag between "black-out" in the environment and uprise of migrants, estimated with a precision of 0.1 h after astronomical sunset.
- Time to midnight (TTM): a variable indicating residual solar illumination, calculated with a precision of 0.1 h as the time interval between the beginning of a sample and "midnight," the middle between sunset and sunrise.
- Moon phase (MP): a variable indicating parent luminous intensity of moon, grouped into three rough conditional states: 1 (new moon, 0% illumination), 2 (nearly crescent, 10–35% of potential disk illumination), and 3 (nearly full moon, 90–92% of potential disk illumination).
- Moon altitude (MA): a variable indicating share of lunar illumination penetrating to the environment, calculated as $\sin A$, where A is the angle of the moon ascent (expressed in radians); MA was grouped into three rough conditional states: 0 ($\sin A \leq 0$), 1 ($0 \leq \sin A \leq 0.1$), 2 ($0.1 \leq \sin A \leq 0.3$), and 3 ($0.3 \leq \sin A$).

Such pair of parameters as TAS - TTM and MP - MA , although looking similar, represent independent variables moderating impact of solar and lunar illumination, respectively.

Benthopelagic assemblages were discriminated via non-metric multidimensional scaling after computing Bray-Curtis similarity indices. Species were represented by their standardized abundances ($\text{ind.} \cdot \text{m}^{-3}$). The contributions that individual species made to assemblages dissimilarities were calculated with use of the SIMPER algorithm. Correlations between individual environmental factors and species abundance and total abundance/biomass were calculated via one-way ANOSIM.

Calculations and analyses were carried out with use of Excel, STATISTICA, and PAST 3.04 (Hammer et al., 2001). Correlations were considered significant if $p < 0.05$.

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