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SOME FEATURES OF DISTRIBUTION AND POPULATION STRUCTURE OF *PSEUDOCALANUS ACUSPES* (GIESBRECHT, 1881) (COPEPODA, CRUSTACEA) IN THE SOUTHEASTERN BALTIC SEA

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Based on plankton samples collected in the southeastern Baltic Sea (SEB) during research cruises of the Shirshov Institute of Oceanology of RAS, the occurrence, spatial distribution, and size and age structure of the key copepod species, *Pseudocalanus acuspes*, were studied. The current state of the *P. acuspes* population in the SEB remains insufficiently described. Sampling was carried out with a WP2 plankton net (Ø = 56 cm, mesh size of 100 μm) in different seasons by vertical stratified haul method. The size and age structure of the *P. acuspes* population was evaluated under microscopes, and specimens were measured from the anterior margin of the cephalothorax to the tip of the caudal rami. Quantitative indicators, especially abundance, were 10-fold higher in the early spring than in summer and autumn. There was a direct positive correlation between the species abundance and salinity of the bottom water layer in the SEB. On the slope of Gdansk Deep, the highest abundance and biomass of this crustacean were noted, while in the coastal zone (down to a depth of 30 m), the species was practically not found, with the exception of single nauplii. Features of the vertical distribution were revealed: in spring and autumn, abundance and biomass of *P. acuspes* were the highest in a water layer below the halocline upper boundary, whereas in summer, in a cold intermediate layer. In different years and seasons, its population was represented by all developmental stages: juveniles (nauplii and copepodites) and adult individuals, mainly females. The proportion of nauplii was the highest in early spring (70% on average). It indicates active reproduction during this season, at water temperature of +4…+7 °C preferred by this arctic species. The size of adult individuals ranged 1.03 to 1.63 mm, and *P. acuspes* were smaller than copepods of other reported populations inhabiting various areas of the World Ocean.

Keywords: *Pseudocalanus*, abundance, biomass, population structure, zooplankton, southeastern Baltic Sea

Planktonic copepods *Pseudocalanus* Boeck, 1873 are widely distributed in the neritic zone of Arctic and boreal waters throughout the Northern Hemisphere. Calanoids of this genus often dominate zooplankton communities and are important in pelagic ecosystems as a key food source for many commercially valuable fish. Noteworthy, there are *Pseudocalanus* species exhibiting similar morphology, and this complicates species-level identification. This difficulty is compounded by the fact that several species frequently co-occur within one water area. In many studies, researchers do not differentiate between individual species and limit identification down to the genus level to avoid confusion.

The genus *Pseudocalanus* was previously considered to comprise six species [Corkett, McLaren, 1979]. Three were reported from Eurasian waters: *Pseudocalanus elongatus* (Brady, 1865), *P. gracilis* Sars G. O., 1903, and *P. major* Sars G. O., 1900 [Brodsky et al., 1983]. Following a revision by B. W. Frost [1989], the genus is considered to cover seven species. In the Atlantic Ocean basin, five *Pseudocalanus* species have been identified; in the North Sea, two, *P. elongatus* and *P. acuspes* Giesbrecht, 1881; and in the southern Baltic Sea, *P. acuspes* alone [Frost, 1989]. The species inhabiting the Baltic Sea was classified as *P. elongatus* [Aleksandrov et al., 2009; Flinkman et al., 1998; Möllmann et al., 2000; Polunina et al., 2021; Shchuka, 2002]. Morphological studies of the Baltic Sea specimens failed to provide a definitive assessment of crustacean composition in its different areas. The genetic analysis of *Pseudocalanus* copepods in the Arkona basin of the Baltic Sea confirmed the occurrence of *P. acuspes* [Bucklin et al., 2003]. For the Bornholm basin, two species were reported: *P. elongatus* and *P. acuspes*, with the latter prevailing in abundance [Grabbert et al., 2010; Renz, 2006]. In the Gulf of Finland and the central Baltic, only the occurrence of *P. acuspes* was confirmed [Holmborn et al., 2011].

The occurrence of *P. elongatus* in the southern Baltic Sea cannot be ruled out: this species may enter the Baltic Sea from the North Sea *via* bottom water advection or surface currents driven by strong westerly and northwesterly winds, primarily autumn and winter ones. Considering the ratio of these two species in the Bornholm basin, where only 2 *P. elongatus* specimens were identified among 262 copepods examined [Grabbert et al., 2010], its proportion in the southeastern Baltic Sea (hereinafter SEB) is expected to be negligible. *P. acuspes* and *P. elongatus* are morphologically and morphometrically similar. In the North Sea and the Arkona and Bornholm basins of the Baltic Sea, differentiating characteristics cover their reproductive timing, number of generations, egg production rates, *etc.* [Renz, 2006; Renz et al., 2007, 2008].

Contemporary data on *P. acuspes* population structure, sizes, and spatial distribution in SEB are still scarce. The aim of this work is to reveal features of *Pseudocalanus acuspes* horizontal and vertical distribution and describe its population structure in SEB.

MATERIAL AND METHODS

Material was sampled during research cruises conducted by the Shirshov Institute of Oceanology of RAS: the 135th cruise of the RV "Professor Shtokman," 03.04.2017–07.04.2017; the 48th cruise of the RV "Akademik Boris Petrov," 01.11.2021–11.11.2021; and the 61st cruise of the RV "Akademik Ioffe," 28.06.2022–12.07.2022. The study area encompassed both open-sea area (depths down to 110 m) and the coastal zone (depths < 30 m) within the exclusive economic zone of Russia, in SEB (Fig. 1).

Water temperature and salinity were measured by multiparameter probes Idronaut Ocean Seven 316S Plus and Sea & Sun CTD 90Mc having similar characteristics. At each station, while selecting zooplankton sampling layers, vertical profiles of several hydrological parameters were obtained with the CTD to determine positions of the thermocline and halocline.

Zooplankton was sampled during daylight hours with a WP2 plankton net (Ø = 56 cm, mesh size of 100 μm). The sampling strategies differed between the years. In 2017, sampling covered the following layers: 1) the upper mixed layer (hereinafter UML) (from the upper boundary of the thermocline to the surface); 2) the layer from the upper boundary of the halocline to the surface; 3) the layer from the bottom to the surface (full-depth haul). In 2021 and 2022, samples were taken

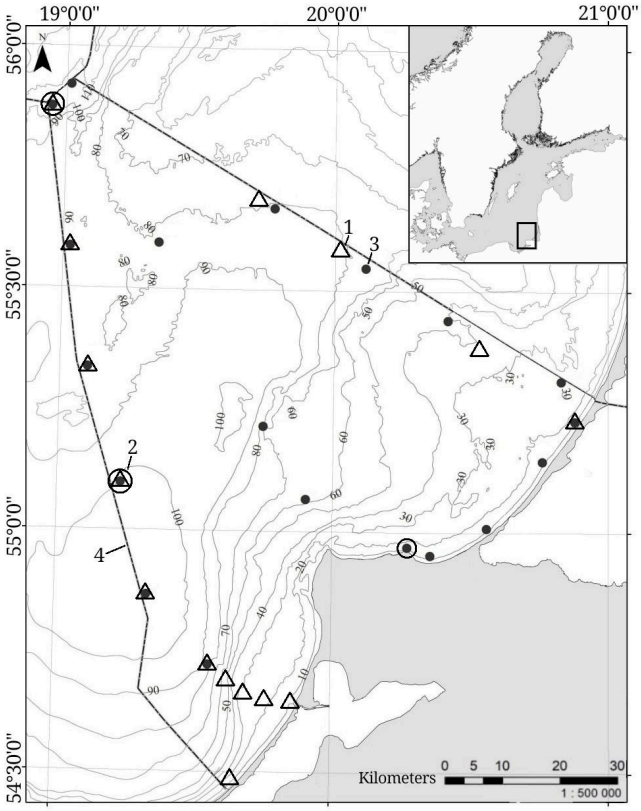

Fig. 1. Zooplankton sampling stations in the southeastern Baltic Sea. The research area is highlighted on the Baltic Sea map in the upper right corner. 1, stations in April 2017; 2, stations in July 2022; 3, stations in November 2021; 4, the borders of the exclusive economic zone of Russia

with a plankton catcher from the following layers: 1) UML; 2) the intermediate layer (from the upper boundary of the thermocline to the upper boundary of the halocline); 3) the layer below the halocline (from the bottom to the upper boundary of the halocline). Samples were preserved in a 4% formaldehyde solution. Their subsequent laboratory processing and statistical analysis followed standard procedures [Metodicheskie rekomendatsii, 1984]; biomass of copepods was calculated using length–weight regressions [Recommendations on Methods, 1985; Vinogradov, Shushkina, 1987]. In total, 77 samples were processed: 37 in 2017, 33 in 2021, and 7 in 2022.

To analyze *P. acuspes* size and age structure, 360 ind. were examined and classified into nauplii, copepodites (early ones, stages I–III; late ones, stages IV–V), and mature females and males. All specimens were measured under microscopes MBS-10 (Russia) at ×32 magnification and Olympus CX41 (Japan) at ×100 magnification. Total length of copepodites and adults was measured from the anterior end of the cephalosome to the posterior end of the urosome, excluding the caudal setae.

Data analysis involved MS Office Excel 2010 and SPSS Statistics 23.0. Spearman's rank correlation coefficient (R) was calculated, and one-way analysis of variance (ANOVA) was performed to compare size and age groups across all seasons and years. Chaddock scale was applied to evaluate the strength (the tightness) of correlations. Distribution maps were built in CorelDRAW Standard 2020 based on a map constructed in ArcGIS.

RESULTS

Hydrological conditions. In SEB waters, the upper layer began to warm in spring, and at depths of 10–20 m, a seasonal thermocline and UML were formed (Fig. 2). Water temperature in UML ranged within +4.2…+7.1 °C averaging +5.2 °C: this is indicative of the early spring biological season (winter-to-spring transition). The highest temperatures were recorded near the shore. The cold intermediate layer (hereinafter CIL) occurred at depths of 16–55 m, with the core at 45–46 m and water temperature of +3.4 °C. Above the halocline, water was weakly stratified. There, salinity ranged 7.2–8.7 psu (2a in Fig. 2). The upper boundary of the halocline was located at depths of 55–65 m. Within the halocline, water temperature varied +3.9 to +7.3 °C, and salinity increased with depth. On the slopes of the Gdansk Deep, near-bottom temperature and salinity were +7.5…+7.7 °C and 13.7 psu, respectively; on the slopes of the Gotland Deep, the values were of +6.8 °C and 12.4 psu.

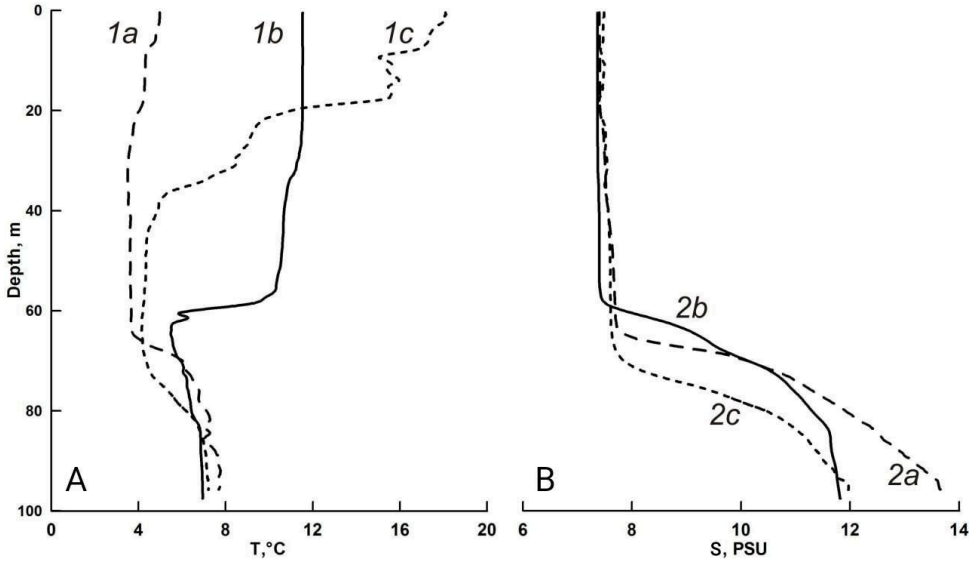

Fig. 2. Vertical distribution of thermohaline indicators on the northeastern slope of the Gdansk Deep in different seasons of the study. A, water temperature, °C; B, water salinity, psu. 1a, 2a, spring 2017; 1b, 2b, autumn 2021; 1c, 2c, summer 2022

In summer, stepped stratification was observed in the upper layer of water (Fig. 2A) suggesting the pulsed nature of the warming. The thickness of UML on the northern slope of the Gdansk Deep did not exceed 10 m; the temperature was of +18.1 °C, and salinity was of 7.5 psu. The most pronounced temperature gradients were associated with a well-defined CIL: a remnant of autumn and winter cooling. The core of CIL was located at 65 m; the water temperature was of 4.1 °C, and the salinity value was similar to that for UML, 7.6 psu. In the bottom layer, the temperature reached +6.0…+7.0 °C, and the salinity increased to 12.0 psu (2c in Fig. 2).

In autumn, cooling of UML and deepening of the seasonal thermocline down to the depth of the permanent halocline were recorded (Fig. 2). Although temperature variations within this layer were minor, a detailed analysis of the data allowed us to identify UML with a lower boundary of 35–47 m, temperature values of +9.8…+11.8 °C, and salinity of 7.1–7.4 psu. CIL was relatively thin (about 10 m); its core was located at 48–58 m, and thermohaline indicators were +4.4…+4.6 °C and 7.6–8.5 psu. The halocline depths ranged within 55–65 m, water temperature and salinity were of +5.8…+11 °C and 6.8–9.0 psu, respectively (Fig. 2). The bottom layer, from a depth of 65–75 m, had the temperature of +5.4…+6.8 °C and salinity of 9.0–11.7 psu.

On the slope of the Gdansk Deep, bottom water temperatures were consistent across all seasons and years: +7…+8 °C. Bottom salinity in April 2017 was approximately 2 psu higher than in subsequent years (Fig. 2).

Quantitative indicators and distribution patterns. Substantial seasonal variations were observed in quantitative indicators of *P. acuspes* in SEB. In spring, the abundance of this copepod ranged within 0.01–57.9 thousand ind.·m^{-3} averaging 17.1 thousand ind.·m^{-3}, *i. e.*, about 13% of the total zooplankton abundance. Its biomass ranged within 0.1–521.3 mg·m^{-3} averaging 152.4 mg·m^{-3}, *i. e.*, 21% of the total zooplankton biomass. In summer, the abundance of all *P. acuspes* stages in the open sea ranged 1.3–1.9 thousand ind.·m^{-3} (1.6 thousand ind.·m^{-3} on average), whereas the biomass ranged within 27–53 mg·m^{-3} (40 mg·m^{-3} on average). In autumn, the abundance reached a peak of 7.2 thousand ind.·m^{-3} averaging 1.4 thousand ind.·m^{-3}, *i. e.*, 13.3% of the total zooplankton abundance.

The biomass of this copepod ranged within 0.1–143.1 mg·m^{-3} averaging 32.1 mg·m^{-3}, *i. e.*, 16.6% of the total zooplankton biomass. Overall, the highest quantitative indicators for *P. acuspes* were recorded in spring. Across all seasons, this copepod comprised 13–24% of the total zooplankton abundance and 17–29% of the total zooplankton biomass in SEB; this allowed classifying the species as a subdominant one.

The analysis of *P. acuspes* spatial distribution revealed noticeable differences between the coastal zone and the open-sea area. In spring, high abundance, 13–58 thousand ind.·m^{-3}, was recorded at deep-water stations on the slopes of the Gdansk and Gotland deeps (Fig. 3A). This copepod accounted for approximately 15% of the total zooplankton abundance. In the coastal zone (at depth < 30 m), the abundance was significantly lower, 0.04–4 thousand ind.·m^{-3}, with a reduced contribution to the total zooplankton community, 2%. The coastal population of *P. acuspes* was dominated by juveniles: nauplii and early copepodites.

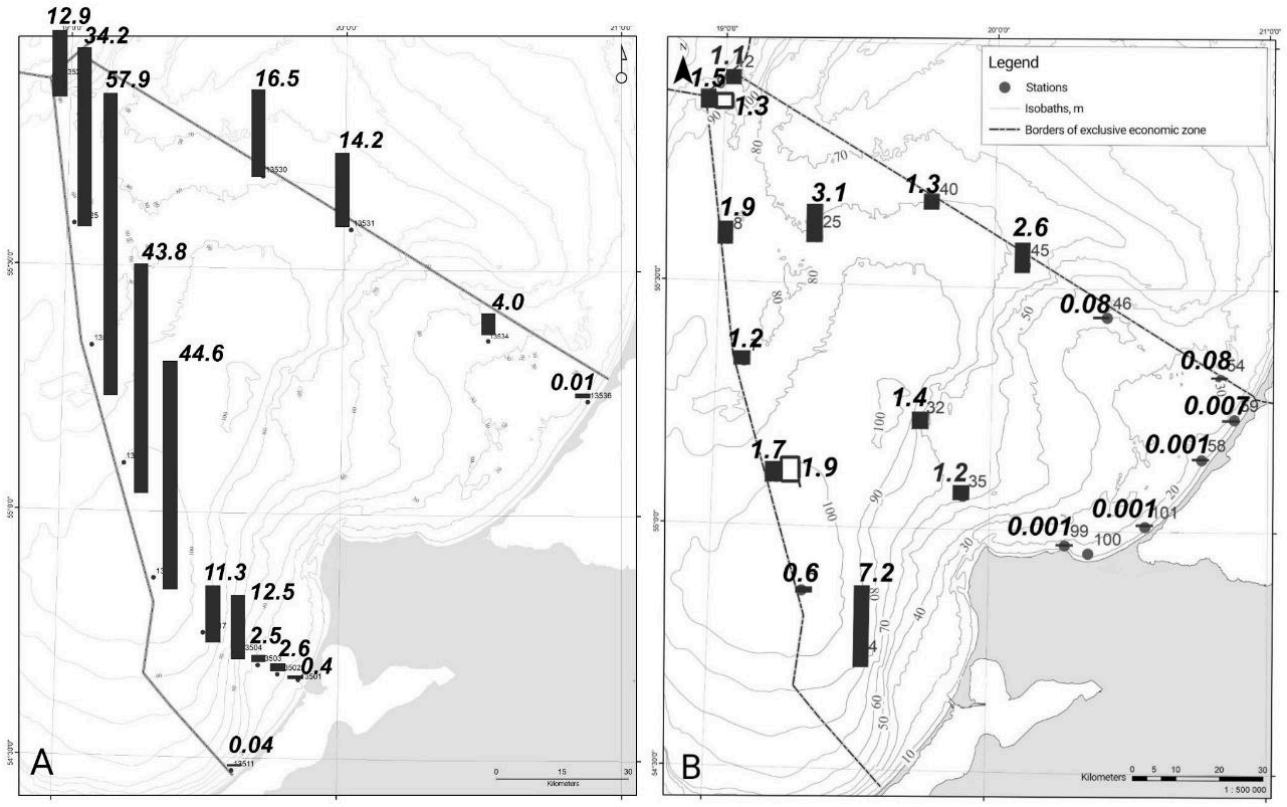

Fig. 3. Spatial distribution of *Pseudocalanus acuspes* (by abundance, thousand ind.·m^{-3}) in the southeastern Baltic Sea: A, April 2017; B, July 2022 (white columns) and November 2021 (black columns)

In summer, there were no *P. acuspes* at coastal stations. At deep-water stations in the Gdansk and Gotland deeps, the species accounted for 24% of the total zooplankton abundance and 21% of the total zooplankton biomass (Fig. 3B).

In autumn, the highest values (3.1–7.2 thousand ind.·m^{-3}) were noted at stations on the slopes of the Gdansk and Gotland deeps; *P. acuspes* constituted an average of 12% of the total zooplankton abundance. In the coastal zone, its abundance did not exceed 100 ind.·m^{-3}, and the proportion in zooplankton was only 0.2% (Fig. 3B).

The mean abundance of *P. acuspes* was more than 10 times lower in summer and autumn than in early spring.

The following features of seasonal vertical distribution were revealed: in spring and autumn, the maximum *P. acuspes* abundance and biomass were recorded in the layer below the halocline, whereas in summer, peaks were registered in CIL (Fig. 4).

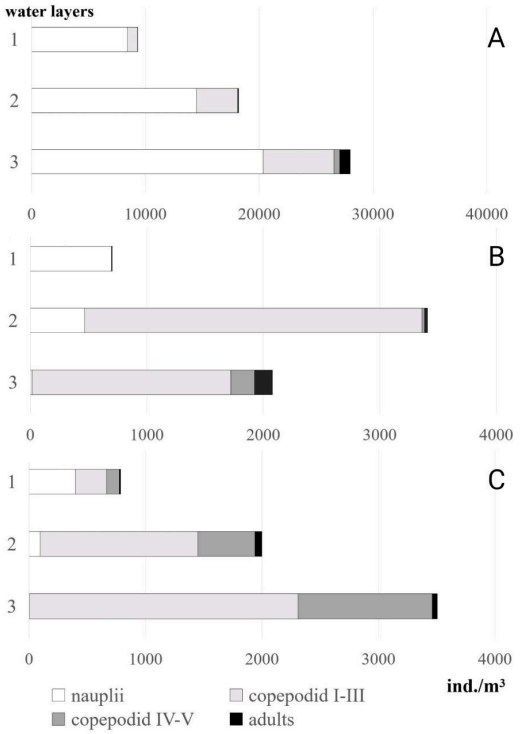

Fig. 4. The structure of *Pseudocalanus acuspes* population (by abundance, ind.·m^{-3}) in different water layers in the southeastern Baltic Sea in April 2017 (A), July 2022 (B), and November 2021 (C). A, B: 1, from the surface to the thermocline upper boundary; 2, from the surface to the halocline upper boundary; 3, from the surface to the bottom. C: 1, from the surface the thermocline upper boundary; 2, from the thermocline upper boundary to the halocline upper boundary; 3, from the halocline upper boundary to the bottom

Population structure. During the study period, the *P. acuspes* population comprised all developmental stages: nauplii, copepodites, and adult females and males. In spring, nauplii were predominant in UML (83–100%); the proportion of early copepodites did not exceed 17%, and proportions of late copepodites and adults constituted less than 1% (Fig. 4A). Throughout the water column, nauplii also prevailed accounting for 10–100% of the total population (67% on average). Proportions of early copepodites ranged within 5–41% (24% on average); late copepodites, within 0.2–11% (2% on average); and adults, within 0.6–37% (6% on average). Adult specimens consisted almost exclusively of females: the ratio was about 100% (males were exceptionally rare). In the coastal zone, the *P. acuspes* population was represented by nauplii alone (100%).

In summer, nauplii remained dominant in UML: 85 to 100% of the population (Fig. 4B). Within the thermocline, with a decrease in water temperature, the proportion of nauplii declined to 16%, while copepodites I–III reached 83% of the total population. The proportion of late copepodites and adults did not exceed 1% in these two layers. Below the upper boundary of the halocline, copepodites IV–V and adults appeared (10.5 and 8.5% on average, respectively). In this layer, the proportion of early copepodites was approximately 80%, while that of nauplii did not exceed 1% of the total abundance.

In autumn, *P. acuspes* nauplii were predominant in UML: 28 to 92% of the total population (52% on average) (Fig. 4C). The proportion of early copepodites averaged 33%, while that of the late ones was 13%. The presence of adults was recorded in this layer (approximately 3%): a phenomenon not observed

in previous seasons and likely resulting from the deepening of the thermocline and water mixing during autumn. Copepodites dominated the intermediate layer (early copepodites accounted for 47–86%, and late ones, for 12–43%); average proportions of nauplii and adults did not exceed 4%. Below the halocline peak, early copepodites prevailed: 62 to 74%. The proportion of late copepodites varied 24 to 38%, and that of nauplii did not exceed 0.3%. Adults constituted up to 3%, and females predominated (over 90%). In the coastal zone, nauplii prevailed: their proportion varied 60 to 100% (75% on average). The rest of the population consisted of early copepodites (late copepodites and adults were absent).

A significant positive correlation was found between the total species abundance and bottom water salinity in SEB across all three seasons ($R = 0.51$; $p = 0.002$; $n = 31$). In spring, when the surface water layer had not yet warmed and was cooler than the bottom layer (mean surface water temperature was +5.2 °C, and bottom water temperature was +6.0 °C), a strong positive correlation was established between the total species abundance and bottom salinity ($R = 0.70$; $p = 0.002$; $n = 15$), as well as between the total species abundance and bottom water temperature ($R = 0.60$; $p = 0.009$; $n = 15$). A feature of the *P. acuspes* vertical distribution was the fact that nauplii were highly abundant in the surface layer. Furthermore, a negative correlation was recorded between nauplii abundance and surface water temperature ($R = -0.64$; $p = 0.005$; $n = 15$). In summer, a strong positive correlation was registered between the abundance of late copepodites and adults and water salinity ($R = 0.83$; $p = 0.021$; $n = 7$). A strong negative correlation was revealed between the abundance of early copepodites and water temperature ($R = -0.87$; $p = 0.011$; $n = 7$). In autumn, there were no significant correlations between copepod abundance and thermohaline parameters in UML. Below the halocline, a negative correlation was observed between the total abundance of *P. acuspes* and bottom water temperature ($R = -0.54$; $p = 0.019$; $n = 15$), and a positive correlation was found between the total abundance and bottom salinity ($R = 0.48$; $p = 0.035$; $n = 15$).

Size structure. The population consisted of different developmental stages, with each characterized by its own size ranges. Body length of nauplii was of 0.18–0.43 mm, with the largest specimens recorded in spring (Table 1). Early copepodites (I–III) were of 0.45–0.70 mm, while late copepodites (IV–V) had the length of 0.88–1.38 mm (Table 1). Adults measured 1.01–1.63 mm. Importantly, females were significantly larger than males (Table 1), that is common for calanoids. All groups, except for early copepodites, were larger in spring than in summer and autumn.

Table 1. Mean body length and its range (in parentheses) in *Pseudocalanus acuspes* individuals of different age (mm) in April 2017, July 2022, and November 2021

Stage	April 2017	July 2022	November 2021
Nauplii	0.31 (0.20–0.43)	0.19 (0.15–0.25)	0.28 (0.18–0.38)
Copepodites I–III	0.61 (0.45–0.78)	0.81 (0.70–0.93)	0.69 (0.50–0.80)
Copepodites IV–V	1.19 (0.88–1.38)	1.10 (0.95–1.23)	0.95 (0.88–1.05)
Females	1.36 (1.20–1.63)	1.34 (1.18–1.55)	1.25 (1.03–1.49)
Males	1.25 (1.05–1.33)	1.19 (1.01–1.30)	1.24 (1.18–1.46)

Nauplii were noticeably smaller in summer than in spring and autumn ($F = 32.7$; $P < 0.001$), while sizes of spring and autumn nauplii did not differ much ($F = 32.7$; $P = 0.013$). Early copepodites were significantly smaller in spring than in summer and autumn ($F = 34.2$; $P < 0.001$). Sizes of late copepodites differed noticeably across all seasons; those were the largest in spring and the smallest

in autumn ($F = 13.0$; $P < 0.001$). In spring and summer, body lengths of females did not differ ($F = 6.2$; $P = 0.35$); in autumn, those were shorter than in spring ($F = 6.2$; $P = 0.002$), but these differences were not statistically significant ($F = 6.2$; $P = 0.098$). No noticeable differences in body length of males were established across all seasons ($F = 2.5$; $P = 0.092$).

DISCUSSION

Analysis of thermohaline conditions in SEB during our study revealed key patterns: below the halocline, the temperature in more saline layer remained stable across all seasons varying by less than 1 °C, and values of the surface salinity showed minimal fluctuations. The position and structure of the halocline varied only slightly. Strong density stratification in SEB restricts vertical water exchange and limits deep-water aeration. During the period analyzed, temperatures from the surface water layer down to the density gap (the upper boundary of the halocline) were primarily governed by convection and varied widely; temperatures below the halocline remained constant across all seasons. Vertical salinity distribution was similar in summer 2022 and autumn 2021, but different in spring 2017: bottom salinity reached 14 psu *vs.* ≤ 12 psu in other seasons. These features seem to be mediated by major inflows of North Sea water into the Baltic Sea in 2014–2016 [Naumann et al., 2016]. Such inflows are rare, but dense, oxygen-rich, and saline waters spread through Baltic Sea depressions [Matthäus et al., 2006]; apparently, this was observed in spring 2017.

P. acuspes abundance in SEB ranged 0.01 to 57.9 thousand ind.·m^{-3} during the study period. The fact that it was 13–29% of the total zooplankton abundance and biomass allowed referring the species to subdominant ones in the zooplankton community in SEB. Most specimens, particularly late copepodites and adults, occurred at depths exceeding 55 m, in the high-salinity layer, below the halocline. In contrast, the occurrence of this copepod in the coastal zone was limited to sporadic records of nauplii. So, in SEB, the highest *P. acuspes* abundance was registered deeper than 55 m.

A high proportion of juveniles, especially nauplii, was observed in spring, and this indicated active population reproduction during the season under low water temperatures (+4…+7 °C) preferred by this arctic-boreal species. The analysis of quantitative data from other Baltic Sea areas showed that the maximum values of the *P. acuspes* abundance in the Bornholm basin were reported for spring: 869 thousand ind.·m^{-3} in April 2003 and 618 thousand ind.·m^{-3} in May 2002 [Renz, 2006]. Similarly, a peak, 11 thousand ind.·m^{-3}, was recorded in the Gdansk Bay in March 2007 [Dzierzbicka-Glowacka et al., 2013]. In SEB during early spring, with water temperatures of +4…+7 °C, the abundance of this species was orders of magnitude higher than that during summer and autumn. It can be assumed that the high abundance of *P. acuspes* in spring 2017 is mediated by the inflow of North Sea water into SEB reported for 2014–2016 [Naumann et al., 2016]. A rise in bottom salinity in April 2017 seems to form specific conditions that could favorably affect the local development of the copepod. However, it cannot be excluded that individuals from the western sites of the sea were brought there with the inflow.

Analysis of data on the quantitative development of *P. acuspes* under thermohaline conditions of other water areas showed as follows. In the northern Pacific Ocean, in the Avacha Bay, this species was the dominant one across all seasons in 1988–1989 constituting 20–55% of the total copepod abundance. It was abundant in summer and autumn [Samatov, 2001], though the surface temperature fluctuated +11 to +21 °C in July–August [Potapov, 2014], and salinity varied 1 to 25 psu. The abundance of the species peaked at 32 psu in the bottom water layer [Lepskaya et al., 2014]. The Chukchi Sea is inhabited by four *Pseudocalanus* species, with *P. acuspes* comprising 50 to 90% of their total biomass.

Meanwhile, its abundance decreases in areas with water temperature higher than +10 °C [Ershova et al., 2017]. In the White Sea, two species were identified: *P. minutus* and *P. acuspes* [Markhaseva et al., 2012]. In the open White Sea, summer water temperature does not exceed +15 °C; in coastal areas, it reaches +20 °C; in winter, it drops to negative values. In the open sea, salinity is 28–30 psu, while in coastal areas, it decreases to 0–5 psu [Maksimova, Chugainova, 2014]. In the White Sea, the reproductive intensity of *P. acuspes* is the highest at +9 °C; both the reproductive rate and population production declined with the water temperature rise to +12 °C [Ershova et al., 2016]. Accordingly, the species inhabits waters with salinity from 1 to 30 psu and temperature from negative values to +20 °C.

SEB exhibits strong water stratification. Long-term data indicate that surface salinity typically ranges within 6–8 psu across all seasons, while water temperature varies within +3…+18 °C. A permanent halocline is formed at depths of 55–70 m; in the bottom water layer, salinity reaches 9–14 psu, and temperature is +3.2…+7.0 °C [Dubravin, 2017]. Thus, the salinity and temperature ranges in SEB correspond to the ranges of *P. acuspes* occurrence and reproduction.

During this study, the population comprised all age groups, including adults: both females and males. Previous research showed that in the southern Baltic Sea, only one generation of *P. acuspes* was formed within a year. The abundance of nauplii peaked in March; that of copepodites I, in May; the abundance of copepodites II, in July; and that of copepodites III–IV, in September and October. The overwintering group typically consisted of late copepodites and adults [Renz, Hirche, 2004]. In SEB, according to our data, the proportion of males was extremely low: it did not exceed 5% of the mature population in spring and summer and rose to 10% in autumn. Such a low proportion of males may be governed by their shorter lifespan: unlike females, males cease feeding upon reaching maturity [Corkett, McLaren, 1979; Renz, Hirche, 2004]. In the western Baltic Sea (the Arkona and Bornholm basins), the male-to-female ratio was 1 : 5 within April–July 2004 [Renz, Hirche, 2004]. The presence of all age stages, *inter alia* adults, allows this population in SEB to be classified as self-sustaining. More frequent sampling throughout a year is required to fully characterize the seasonal development and reproduction of the species in SEB. In spring, almost all age groups were larger than in summer and autumn. Copepods are known to exhibit pronounced seasonal and interannual variability in body size driven chiefly by key environmental factors, water temperature and food availability, both affecting the developmental duration and the growth of different age stages [Brodsky et al., 1983]. Water temperature alone can account for more than 90% of the variability in copepod growth rates [Huntley, Lopez, 1992]. Individuals are likely to grow large in spring, at low temperatures.

In SEB, body length of *P. acuspes* females ranged within 1.03–1.63 mm, while that of males, within 1.01–1.46 mm. The maximum sizes of specimens, 1.05–1.63 mm, were recorded in spring, when the temperature was low throughout the water column. In summer, in the Avacha Bay (the Pacific Ocean), *P. acuspes* adults reached 1.45–2.20 mm [Samatov, 2001], and in the White Sea, 0.95–1.81 mm [Markhaseva et al., 2012]. Thus, this copepod was the smallest in the Baltic Sea as compared to specimens of this species recorded in the other regions of the Northern Hemisphere.

P. acuspes distribution in SEB is patchy, with aggregations in terms of abundance and biomass deeper than 55–65 m in the open-sea area, where the halocline is well-developed. The smaller size of adults in the Baltic Sea than in other areas of the range of this species and low proportion of males in the population seem to result from the isolation of the Baltic population from the other ones. As hypothesized, this arctic-boreal species survived in the Baltic Sea as a component of a cold-water relict fauna, as a remnant of geological glacial processes that occurred approximately 10,000 years ago [Renz, 2006].

The hydrological conditions of the Baltic Sea and the specific ecology of *P. acuspes* have facilitated its survival at more southern latitudes, at the edge of its range. However, the revealed population structure and small size of individuals allow suggesting that the Baltic Sea population of this copepod exists under suboptimal conditions.

Conclusions:

1. Substantial interannual and seasonal variations in *Pseudocalanus acuspes* abundance and biomass were revealed in zooplankton of the southeastern Baltic Sea (SEB). On average, this species accounted for 17–29% of the total zooplankton biomass being a subdominant one in the planktonic community. In spring 2017, the quantitative indicators of *P. acuspes* were 4–10 times higher than in summer and autumn in subsequent years. This peak seemed to result from elevated near-bottom salinity which creates favorable conditions for the development of this species in the Baltic Sea.
2. In SEB, the highest abundance of *P. acuspes* was recorded on the northeastern slope of the Gdansk Deep. This species was rare in the coastal zone and primarily represented by early juvenile stages. The analysis of vertical distribution showed as follows: in spring and autumn, the maximum abundance and biomass of this copepod were registered below the upper boundary of the halocline (deeper than 55 m), while in summer, the highest value was recorded within the cold intermediate layer. A significant positive correlation was found between the total abundance of the species and the near-bottom salinity in SEB.
3. The *P. acuspes* population in SEB covered all developmental stages: nauplii, copepodites, and adults. In spring, the proportion of nauplii was the highest (70% on average) indicating active reproduction at low water temperature (it is preferable for arctic-boreal copepods). In other seasons, the population was dominated by copepodites, chiefly early one. In autumn, the proportion of older age groups increased. Adults were predominantly comprised of females (the proportion of males was low).
4. The size of adult specimens ranged within 1.01–1.63 mm, and *P. acuspes* were smaller than those reported from other water areas of the Northern Hemisphere.

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ОСОБЕННОСТИ РАСПРЕДЕЛЕНИЯ И СТРУКТУРА ПОПУЛЯЦИИ *PSEUDOCALANUS ACUSPES* (GIESBRECHT, 1881) (COPEPODA, CRUSTACEA) В ЮГО-ВОСТОЧНОЙ ЧАСТИ БАЛТИЙСКОГО МОРЯ

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По материалам планктонных сборов, проведённых в юго-восточной части Балтийского моря (ЮВБ) на НИС Института океанологии имени П. П. Ширшова РАН, исследовали встречаемость, пространственное распределение и размерно-возрастную структуру популяции ключевого для экосистемы вида веслоногих ракообразных — *Pseudocalanus acuspes*. Современное состояние популяции *P. acuspes* в ЮВБ описано недостаточно полно. Пробы отбирали планктонной сетью WP2 (Ø = 56 см, размер ячеи 100 мкм) в разные сезоны методом вертикальных

послойных ловов. Размерно-возрастную структуру популяции *P. acuspes* оценивали с использованием микроскопов, измеряли длину особей от начала цефалоторакса до конца фуркальных ветвей. Установлено, что в ранневесенний период количественные показатели, особенно численность *P. acuspes*, были в десятки раз выше, чем летом и осенью. Выявлено наличие прямой положительной средней связи между общей численностью вида и придонной солёностью вод в ЮВБ. На склоне Гданьской впадины отмечена максимальная численность и биомасса особей, в то время как в прибрежной зоне (до глубины 30 м) этот вид практически не встречался, за исключением единичных науплиусов. Выявлены особенности вертикального распределения: в весенний и осенний периоды численность и биомасса *P. acuspes* были максимальными ниже верхней границы галоклина, тогда как летом — в холодном промежуточном слое. Популяция этого вида в разные годы и сезоны была представлена всеми возрастными стадиями — ювенильными (науплиусами и копеподитами) и взрослыми особями, преимущественно самками. Максимальная доля науплиусов отмечена ранней весной (в среднем 70 %), что указывает на активное размножение рачков при температуре воды +4…+7 °C, предпочтительной для этого аркто-бореального вида. Размеры половозрелых особей варьировали от 1,03 до 1,63 мм; рачки были мельче, чем в других районах Мирового океана.

Ключевые слова: *Pseudocalanus*, численность, биомасса, структура популяции, зоопланктон, юго-восточная часть Балтийского моря