ISSN 1063-0740, Russian Journal of Marine Biology, 2024, Vol. 50, Suppl. 1, pp. S17–S34. © Pleiades Publishing, Ltd., 2024.

ORIGINAL PAPERS

Seasonal Variations in Structure and Distribution of Zooplankton Community in Vostok Bay (Peter the Great Bay, Northwestern Sea of Japan)

V. V. Kasyan[a, *] **(ORCID: 0000-0002-2745-3961) and A. Yu. Lazaryuk**[a, b] **(ORCID: 0000-0003-4231-9653)**

[a] *Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, 690041 Russia*

[b] *Il'ichev Pacific Oceanological Institute, Far Eastern Branch, Russian Academy of Sciences, Vladivostok, 690041 Russia*

**e-mail: valentina-k@yandex.ru*

Received July 20, 2024; revised October 3, 2024; accepted October 18, 2024

Abstract—The composition and spatial distribution of the zooplankton abundance and biomass in Vostok Bay during the period from July to November 2023 were analyzed. A total of 37 zooplankton taxa including neritic (71%) and oceanic (29%) species were identified. Copepods (*Acartia hudsonica*, *Oithona brevicornis*, *O. similis*, *Paracalanus parvus*, and *Pseudocalanus newmani*) and cladocerans (*Penilia avirostris* and *Podon leuckartii*) contributed more than 70% to the total zooplankton abundance and biomass. In the early summer, with southeasterly winds and freshening of surface water, the cold-water copepods *A. hudsonica*, *P. newmani*, and *O. similis* and the cladoceran *Podon leuckartii* dominated the total abundance and biomass; brackish-water copepods of the genera *Centropages*, *Tortanus*, and *Sinocalanus* were more abundant in the early summer than in the other seasons. In the late summer, with maximum warming of water in the bay, the warm-water copepods *P. parvus*, *O. brevicornis* and the cladoceran *P. avirostris* dominated the total abundance, while the copepod *P. parvus*, the cladoceran *P. avirostris*, and chaetognaths dominated the total biomass. In the fall, as the water cooled down to 8–11°C, with northerly winds and the change of the summer monsoon to the winter one, the copepods *P. newmani*, *O. brevicornis*, *O. similis* and copepod nauplii dominated the total abundance, while the copepods *P. newmani*, *O. brevicornis*,and chaetognaths dominated the total biomass. Three types of zooplankton assemblages (estuarine, mixed, and marine) spatially coincided with the shallow, transitional, and deep parts of the bay. In the early summer, the total abundance and biomass increased in the direction from the deep to the transitional parts; in the late summer and fall, the values of these parameters increased, vice versa, from the shallow toward the deep parts. The 25-year dynamics of the total zooplankton abundance and biomass during the summer and fall seasons showed a negative trend with a pronounced shift to lower values. A decrease was recorded in the contribution of large-sized and tropical/subtropical species such as copepods of the genera *Calanus*, *Eucalanus*, *Metridia*, *Labidocera*, *Sapphirina*, *Scolecithricella*, chaetognaths, gammarids, hyperiids, isopods, and salpids to the total zooplankton abundance.

Keywords: zooplankton composition, abundance, biomass, spatial distribution, Vostok Bay, northwestern Sea of Japan

DOI: 10.1134/S1063074024700500

INTRODUCTION

Knowledge of the structural and functional organization of aquatic ecosystems is impossible without studying plankton communities. Zooplankton (or mesozooplankton) is a crucially important secondary producer of pelagic communities that links primary producers with species of higher trophic levels [1, 2]. Changes in the structure and distribution of zooplankton community can affect biogeochemical cycles and energy fluxes in aquatic ecosystems [3, 4]. Zooplankton is also a useful indicator of environmental variations induced by climate change or pollution [5, 6]. Moreover, zooplankton makes a substantial contribution to the vertical transport of carbon [7].

The hydrology of the Vostok Bay depends on its topography, the rivers emptying in it, and on the composition of waters and dynamic processes in the adjacent part of the Peter the Great Bay (PGB), which are influenced by various environmental factors. In January, daily amounts of solar radiation are 3–4-fold lower than in June despite frequent fogs and dense stratus clouds in summer. In fall and winter, the PGB climate is formed by the Siberian High and is characterized by an increased background atmospheric pressure, up to 1030 hPa, and a prevailing northerly dry wind (with a wind frequency of 70–80%). In summer, the pressure is by 20 hPa lower due to the influence of the Far East depression (in northeastern China), and the southerly humid wind prevails with a lower frequency (about 60%) [8, 9]. Thus, the monsoon climate of the region is characterized by humid sea air with southerly winds in spring and summer and by dry continental air with northerly winds in fall and winter [10–12]. The wind has an average speed of about 5–6 m/s during the winter monsoon (October–March) and 4–5 m/s during the summer monsoon (April–September) [9]. The highest wind speeds (20 m/s or more) is recorded in summer during tropical cyclones (typhoons) and in winter during cold-air outbreaks caused by the movement of the Siberian High southeast [11]. In December–February, the cold-air outbreaks decrease air temperatures to –20°C or lower. In July–August, positive anomalies (27°C or more) were recorded at the coastal World Meteorological Organization (WMO) weather stations during tropical cyclones (from one to four annually). The values of summer/winter monsoon precipitation at the Nakhodka weather station, averaged from 1931 to 2015, differed 3.3-fold (520/160 mm), and the annual precipitation values ranged from 390 to 1150 mm [9, 13].

In winter, low air temperatures and the northwesterly winds over PGB maintain coastal polynyas with continuous ice formation and brine rejection. As a result, the shelf water is cold (from –1.7°C) and highly saline (up to 34.3 psu) [8]. In spring and summer, the temperature of the water column slowly increases, and the salinity decreases, forming a stable density stratification. During the southern monsoon, the water dynamics in shallow areas of PGB corresponds to the wind-driven water rise. During the southern monsoon, the wind blows into the apex of PGB and a two-layered current system arises in the shallow areas: the water moves in the direction of the wind in the upper layer and in the opposite direction in the lower, compensatory current. The water circulation in the deep-water (more than 50 m) part of the shelf is influenced by the cold Liman (Primorye) Current. In fall, the water layers of PGB rapidly cool mainly due to density convection (heat loss from the surface up to 750 W/m^2) and upwellingat the edge of the shelf and near the coast, formed by the northerly wind [14]. In winter monsoon, the Liman Current deviates south from the shelf edge due to the Siberian northwesterly jet and upwelling events [8].

Vostok Bay is an important area for world's and Russian marine biology research and a testing ground for scientific assessment of one of rational nature management approaches: a conflict-free combination of scientific, recreational, environmental, and nature-conservation education purposes with small-scale local businesses such as recreation/service, building, aquaculture, and trading [15]. Most plankton studies in the shelf zone of the northwestern Sea of Japan were conducted in economically significant waters (Peter the Great, Amur, Ussuri, and Posyet Bays) [16–18, 20–22]. However, the zooplankton community in small bodies of water such as Vostok Bay remains poorly studied. The first studies of the zooplankton community in Vostok Bay were launched in 1998 and lasted for several years. Since 2001 and up to the present time, such studies have been carried out episodically. Only few recent publications consider seasonal changes in the structure of zooplankton community [23]. In our study, we aimed to elucidate the composition and spatial distribution patterns of zooplankton, with focus on copepods, in Vostok Bay, contribute to the zooplankton research in Peter the Great Bay, and compare our data with those previously obtained. This study is expected to extend the knowledge of the biodiversity in Vostok Bay. However, further research is needed to identify the current trends in the marine coastal ecosystem.

MATERIALS AND METHODS

Vostok Bay is a secondary embayment of the larger Peter the Great Bay (PGB) located in the northwestern Sea of Japan (Fig. 1). Field studies in Vostok Bay included conductivity, temperature, and density (CTD) profiling at 29 stations and sampling at five planktonic stations (Fig. 1b). The water column monitoring using a CTD profiler started earlier (in June) and were carried out more frequently (twice a month). The dates of eleven CTD surveys in bay were June 6/13, July 7pn/10, August 8pn/15, September 7pn/13, October 11pn/13, and November 2pn of 2023 (where pn index is the survey day when a plankton net was used). Hydrological parameters such as water temperature (*T*, °C), salinity (S, psu), and concentrations of dissolved oxygen (O_2, mg/L and %) and chlorophyll *a* (Chl-*a*, μg/L) at the stations were measured with a SBE 19plus CTD profiler (Sea-Bird Electronics, United States). Data processing was performed using the SBE Data Processing Win32 software [24]. The CTD data archive has a depth resolution of 0.5 m. The coordinates of the observation points were recorded with a Garmin eTrex GPS receiver. To analyze the weather conditions, the archive of the Nakhodka weather station (WMO_ID = 31970) was used, which contains continuous series of regular (eight times a day) observations [13]. The distance between the weather station and Vostok Bay is about 14 km.

Zooplankton was sampled with a Juday net (with an opening area of 0.1 m^2, a filtering cone with a mesh size of 180 μm, and a hauling speedof 0.6–1.0 m/s) once a month. The entire column of water from the bottom to the surface was sampled withnet hauls (total sampling). The samples were fixed with a 4% formaldehyde solution. In the laboratory, all individuals were identified to the lowest taxonomic level possible and counted under a SZX7 stereomicroscope (Olympus, Japan) (10× eyepiece, 1× objective, magnification range of 8× to 56×). Synonymy of species was corrected according to [25, 26]. Zooplankton abundance was calculated by dividing the number of individuals by the filtered water volume and expressed in terms of

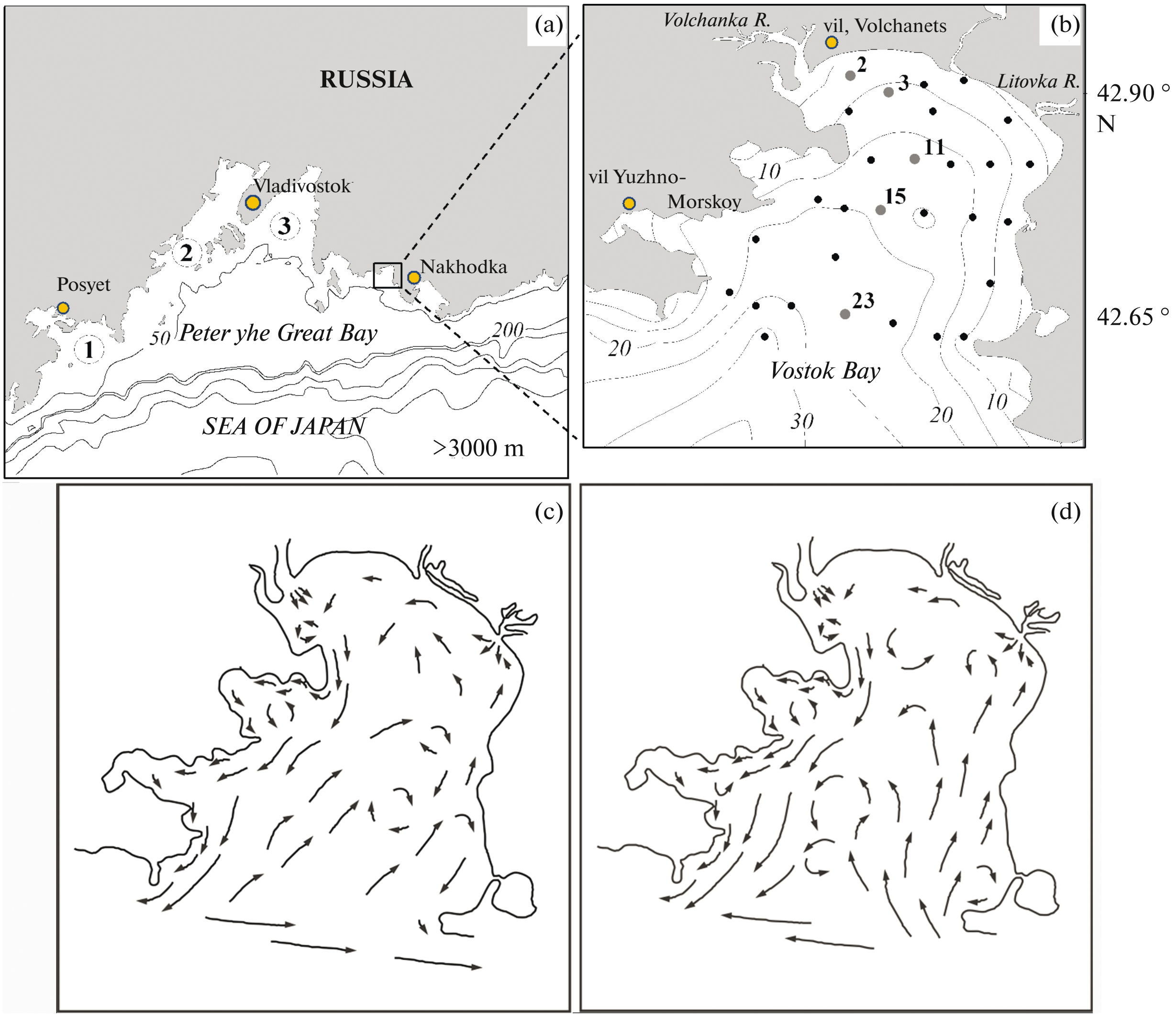

Fig. 1. Study area (a); bathymetric map with isobaths 10, 20, and 30 m (b); and the main surface (c) and near-bottom (d) currents according to Gayko [9, 10]. Black dots indicate hydrological stations; grey dots with numerals, plankton stations; black arrows, currents. (**1**) Posyet Bay; (**2**) Amur Bay; (**3**) Ussuri Bay.

individuals per cubic meter (ind./m^3). Biomass was calculated by multiplying the number of individuals per cubic meter by the wet weight of each individual according to Borisov et al. [27] and expressed in terms of milligrams of wet weight per cubic meter (mg WW/m^3).

For convenience of comparative analysis, in accordance with the bathymetry of the bay, we identified three parts and referred to them as shallow (stns. 2, 3), transitional (stns. 11, 15), and deep (stn. 23), which were bounded by the 10- and 20-m isobaths, respectively (Fig. 1b).

To assess similarity between the zooplankton assemblages in the study area, the cluster analysis and the non-metric multidimensional scaling (nMDS) algorithm were used [28]. The Bray–Curtis similarity was calculated as log(X+1) transformation of the species/taxa abundance [29]. The cluster analysis was applied for average group sorting. The SIMPER (Similarity Percentage) procedure was used to assess the average percentage contribution of each zooplankton species/taxa to the overall dissimilarity, the contribution of each species to the average intra-group similarity with the standard deviation, and the contribution of each species to the average between-group dissimilarity [30]. The diversity was calculated using the Shannon–Wiener index (H') as follows:

$$H' = -\Sigma\left(p_i \ln p_i\right),$$

where H' is the diversity index, p_i is the proportion of each group in the sample, and $\ln p_i$ is the natural logarithm of this proportion [31]. The species richness was calculated using the Margalef's index (D') as a simple measure of species richness, $D' = (S - 1)/\ln N$ [32]. For estimating evenness of species, the Pielou's evenness index (J') was used [33]. The evenness index was calculated by the following formula:

$$J' = H'/\ln S,$$

where H' is the Shannon–Wiener index, and S is the total number of species in the sample.

The relationships between the quantitative values of zooplankton and the environmental variables were assessed using the Spearman's rank order correlation. The BEST analysis (BIO-ENV algorithm), which best explains observed patterns of zooplankton distribution, was carried out to test the relationships between the environmental variables and the abundance. The environmental variables were log-transformed, normalized, and computed for Euclidean distances. To determine significance of the relationships between the similarity matrices (biological data and environmental variables), the RELATE test was used. Multivariate analyses were performed using PRIMER ver. 6 [28]. The map of the sampling stations was composed using Ocean Data View ver. 4 [34].

RESULTS

Environmental Conditions

The weather in the eastern part of PGB during the summer field studies (between the CTD surveys in Vostok Bay from June 6 to September 7) showed typical climatic features of the summer monsoon. During this monsoon period, the winds of southerly direction prevailed (the frequency of SE–SW winds was 44%; NE–NW, 18%); tropical cyclones brought heavy rains (115, 95, and 350 mm in June, July, and August, respectively) and significantly increased the average daily air temperature (higher than 27°C) and air humidity (up to 100%). In the fall season (from September 13 to November 2),with northerly winds and the change of the summer monsoon to the winter one (NE–NW, 41%; SE–SW, 18%), dry continental air coming from Siberia contributed to lower air temperatures (with a trend of 7.5°C per month) and minimal precipitation (17 and 14 mm in September and October, respectively) [13].

The results of monthly CTD surveys in Vostok Bay in 2023 showed the influence of weather conditions on the bay's hydrology. The water temperature, salinity, oxygen concentration, and chlorophyll *a* measured in the surface and near-bottom layers of water at 29 stations from June to November are presented in Fig. 2. Figure 3 shows the CTD profiles measured at stn. 15 located in the middle of the bay where the depth is about 20 m. These profiles characterize the water stratification on the days of plankton sampling. The CTD data on June 6 were $2.6 \le T \le 15.3$°C, $32 \le S \le 33.7$ psu, Chl-$a \le 9.5$ μg/L, and $8.2 \le O_2 \le 11.2$ mg/L or $80 \le O_2 \le 110$%. Over the following 4–5 weeks, the air temperature increased from 15 to 20°C and the atmospheric cyclones brought heavy rains (about 160 mm) and strong winds up to 6 m/s (mainly southerly, with gusts to 17 m/s). The CTD data on July showed significant changes in the ranges of measured parameters. Thus, the temperature in the water column increased by 5–10°C, the salinity (average in the column) decreased by 1 psu, and its value in the surface layer (0–2 m) decreased to 15–25 psu (Figs. 2, 3). In addition, the chlorophyll *a* concentration in the surface and the column increased 4–6-fold, to 5–8 μg/L or more, and in the near-bottom layer did not change, 1–3 μg/L. The spatial distribution of values of the water parameters was highly uneven (Fig. 4). Thus, the surface layer in the northern and western parts of the bay was freshened ($15 < S < 28$ psu) by the river runoff, and in the southeastern part, there was a high salinity (≥30 psu) due to the inflow of water from PGB. The highest chlorophyll *a* concentration (25 μg/L) was found in the northern and western part of the bay where the river empties. This distribution of salinity and chlorophyll *a* concentration values indicates the cyclonic water dynamics in Vostok Bay (i.e., the water moving counterclockwise).

The August surveys were also preceded by warm weather (up to 27°C) with heavy precipitation (about 180 mm). The sea surface temperature (SST) on August 8 reached a maximum of 21–24°C; near the bottom, it increased slightly. The ranges of salinity, chlorophyll *a* and dissolved oxygen concentration values remained almost unchanged (Figs. 2, 3).

The weather in the next half of August remained warm and rainy (about 200 mm). On September 1, the precipitation stopped and the wind had low speeds. The water temperature stratification of Vostok Bay in the early fall was almost uniform. Thus, on September 7, the temperature at stn. 15 ranged within 19.5–21.7°C, while the salinity had a linear increase from 29.7 psu (on the surface) to 31.3 (horizon 5 m) and up to 32.5 (near the bottom) (Fig. 3). The river runoff and PGB waters flowing along the eastern coast of the bay supported the heterogeneity of the spatial distribution of salinity and temperature values in the surface layer: with minima of 28 psu/20.5°C in the northwestern and maxima of 31.47 psu/21.5°C in the southeastern parts of the bay (Fig. 4). The chlorophyll *a* concentration in the surface layer was not higher than 1 μg/L (decreased 4–6-fold within the month). Chl-*a* near the bottom increased 1.5-fold (3 μg/L). The oxygen concentration in the water column on September 7 ranged within 50–110% or 4–8 mg/L.

In the fall season, the river runoff reduced, the cold continental air decreased the temperature of the water surface layer and, as a result, its density increased and vertical convection occurred. Under northerly winds, a combined dynamic process was observed in Vostok Bay: a wind-driven surface current flowing south from the apex of the bay with a simultaneous compensating inflow along its eastern coast and into the near-bottom

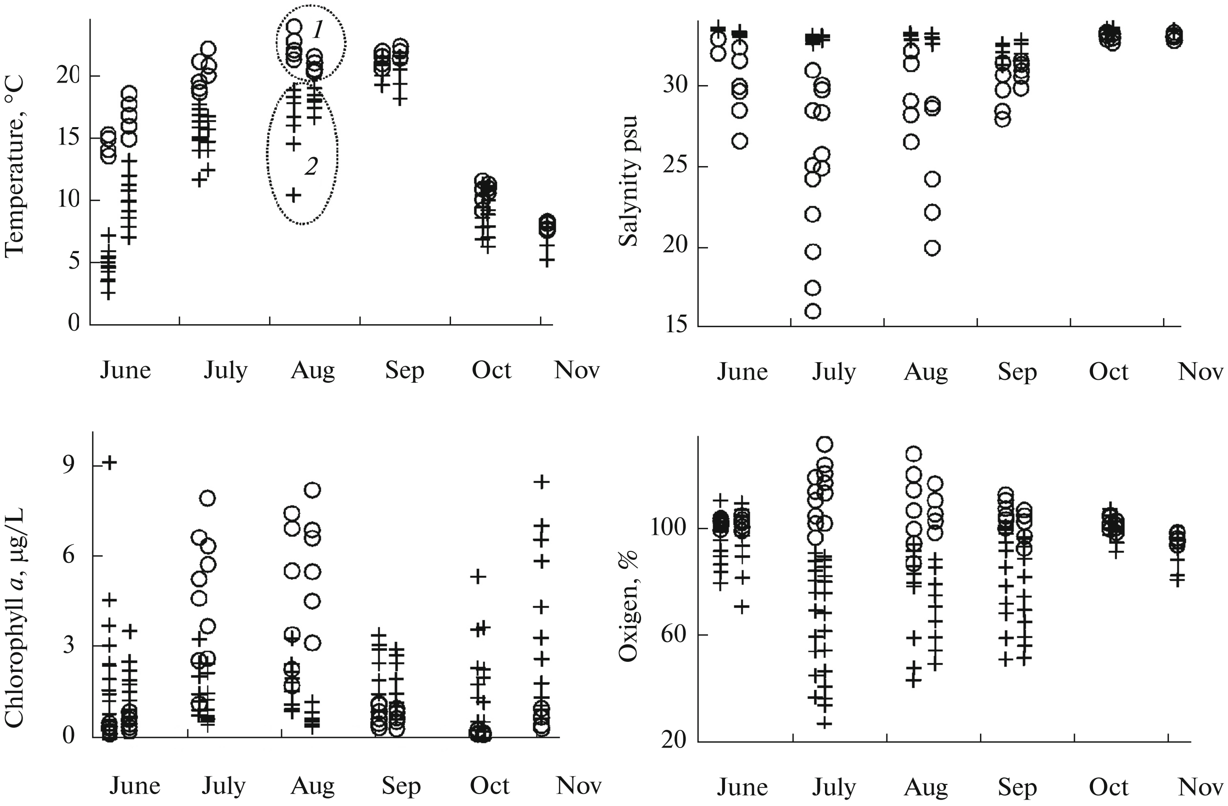

Fig. 2. Temperature (°C), salinity (psu), chlorophyll *a*(µg/L), and dissolved oxygen (%) concentrations in the surface (*1,* circle) and near-bottom layers (*2*, cross symbol) in Vostok Bay from June to November 2023.

layer. The T, S, and O_2 stratifications of the bay water gradually became more homogeneous due to these processes. The CTD data on October 11 and 13 were $6 \leq T \leq 11.4$°C, $32.8 \leq S \leq 33.65$ psu, Chl-*a* ≤ 5.4 µg/L, and $8.5 \leq O_2 \leq 9.8$ mg/L or $92 \leq O_2 \leq 107\%$. After 3 weeks (November), the water column of the bay had the same salinity, but cooled by 1–3°C ($5.2 \leq T \leq 8$°C). However, the chlorophyll *a* near the bottom increased (Chl-*a* ≤ 8 µg/L), and the dissolved oxygen slightly decreased ($8 \leq O_2 \leq 9.5$ mg/L or $80 \leq O_2 \leq 98\%$).

Zooplankton Community Structure

A total of 37 zooplankton taxa were identified, including neritic (71%) and oceanic (29%) species (Table 1). Copepods (79.4%), e.g., *Oithona similis* (18.9%), *Oithona brevicornis* (17.6%), *Pseudocalanus newmani* (13.4%), *Paracalanus parvus* (12.2%), and *Acartia hudsonica* (8.0%), and cladocerans (12.7%), e.g., *Podon leuckartii* (6.1%) and *Penilia avirostris* (5.9%), clearly dominated the zooplankton total abundance and biomass. Based on the cluster analysis of zooplankton abundance, the stations were divided into three types corresponding to the early summer, late summer, and fall seasons, which were represented by estuarine, mixed, and marine zooplankton assemblages (Fig. 5). The assemblages spatially coincided with the shallow, transitional, and deep parts of the bay, respectively. In the early summer (July), the zooplankton community did not divide into distinct assemblages. In the late summer (August and September), the zooplankton community divided into the estuarine assemblage located in the northern, shallow part, the mixed assemblage located in the transitional part, and the marine assemblage located in the deep part of the bay. In the fall (October and November), the difference in the zooplankton composition between the deep and transitional parts was high, while the difference in the zooplankton composition between the transitional and shallow parts was low.

The results of ANOSIM showed that the zooplankton assemblages differed significantly ($P < 0.001$; Global $R = 0.884$) between the shallow, transitional, and deep partsin all three seasons (Table 2). According to the results of SIMPER, the dissimilarity of zooplankton assemblages between the early summer and late summer seasons was the highest. The zooplankton assemblages had higher dissimilarities in the deep part than in the shallow part, and the dissimilarities were the highest in the late summer and the lowest in the early summer (Table 2).

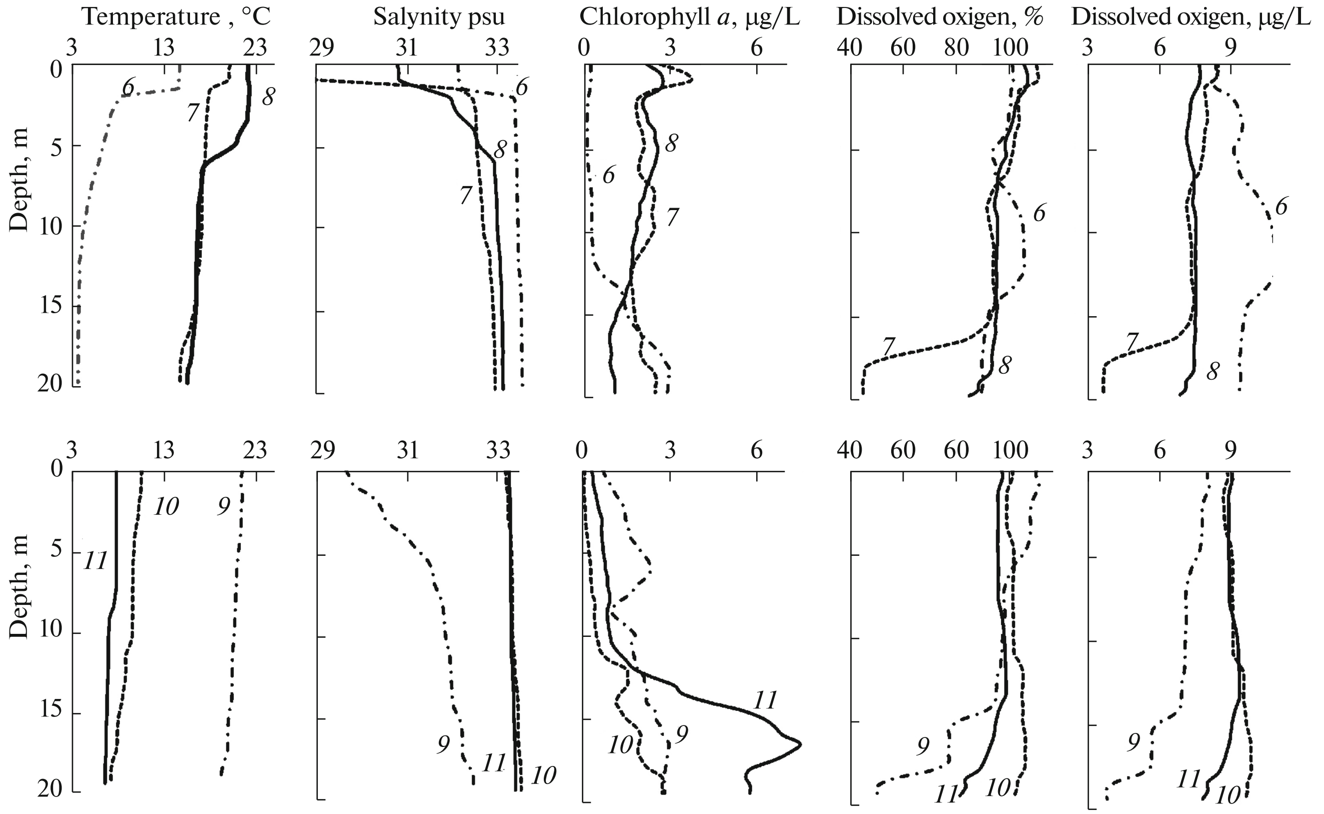

Fig. 3. Water temperature (°C), salinity (psu), chlorophyll *a* (μg/L), and dissolved oxygen (% and mg/L) concentrations at stn. 15 in June (*6*), July (*7*), August (*8*), September (*9*), October (*10*), and November (*11*).

Seasonal Variations in Zooplankton Community

In the early summer, the species richness in the three parts was 18–19 species per each. The peak of species richness (21–22 species) was recorded in the late summer from the transitional and deep parts. In the fall, the species richness in the shallow and transitional parts reduced sharply to 13; in the deep part, the species richness was higher than 15. The diversity (Shannon's, Margalef's,and Pielou'sevenness) of the zooplankton community in Vostok Bay is shown in Table 3. The lowest values of biodiversityindexes were found in the shallow part.

The average values of total zooplankton abundance were maximum in the early summer and showed a tendency to decrease twofold by the fall (Table 1). The significant differences in zooplankton abundance between the shallow, transitional, and deep parts were found only in the late summer (Table 2). In this season, the copepods *O. brevicornis*, *P. parvus*, and cladocerans made the greatest contribution to the estuarine zooplankton assemblage located in the shallowpart; the copepods *O. similis*, *O. brevicornis*, and *P. parvus*, to the mixed zooplankton assemblage locatedin the transitional part; the copepods *O. brevicornis,P. parvus*, cladocerans, and chaetognaths, to the marine zooplankton assemblage located in the deep part (Fig. 6a). In the early summer, no significant differences in zooplankton abundance were found between all parts.The copepods *A. hudsonica*, *O. similis, P. newmani*, and cladocerans dominated in abundance. In the fall, no significant differences in zooplankton abundance were found between the shallow and transitional parts; nevertheless, significant differences in abundance were found between the transitional and deep parts. The greatest contribution (over 50%) to the zooplankton community similarity between the shallow and transitional parts was made by the copepod *P. newmani* and copepod nauplii; in the deep part, by the copepods *O. similis* and *P. newmani* (Table 1). The mean total abundance was the highest in the transitional and deep partsduringthe early summer and late summer, respectively (Fig. 6a).

The average values of total zooplankton biomass were maximum in the early summer and showed tendency to decrease by the fall (Table 1). In the early summer, the highest biomasses were recorded from all stations (Fig. 6b). In the shallow and transitional parts, the copepods *A. hudsonica*, *O. similis* and cladocerans accounted for >80% in total biomass; the stations of the deep part were characterized by generally high concentrations of *P. newmani*. In the late summer, the highest biomasses were recorded from the deep part where the copepods *O. similis*, *P. parvus*,

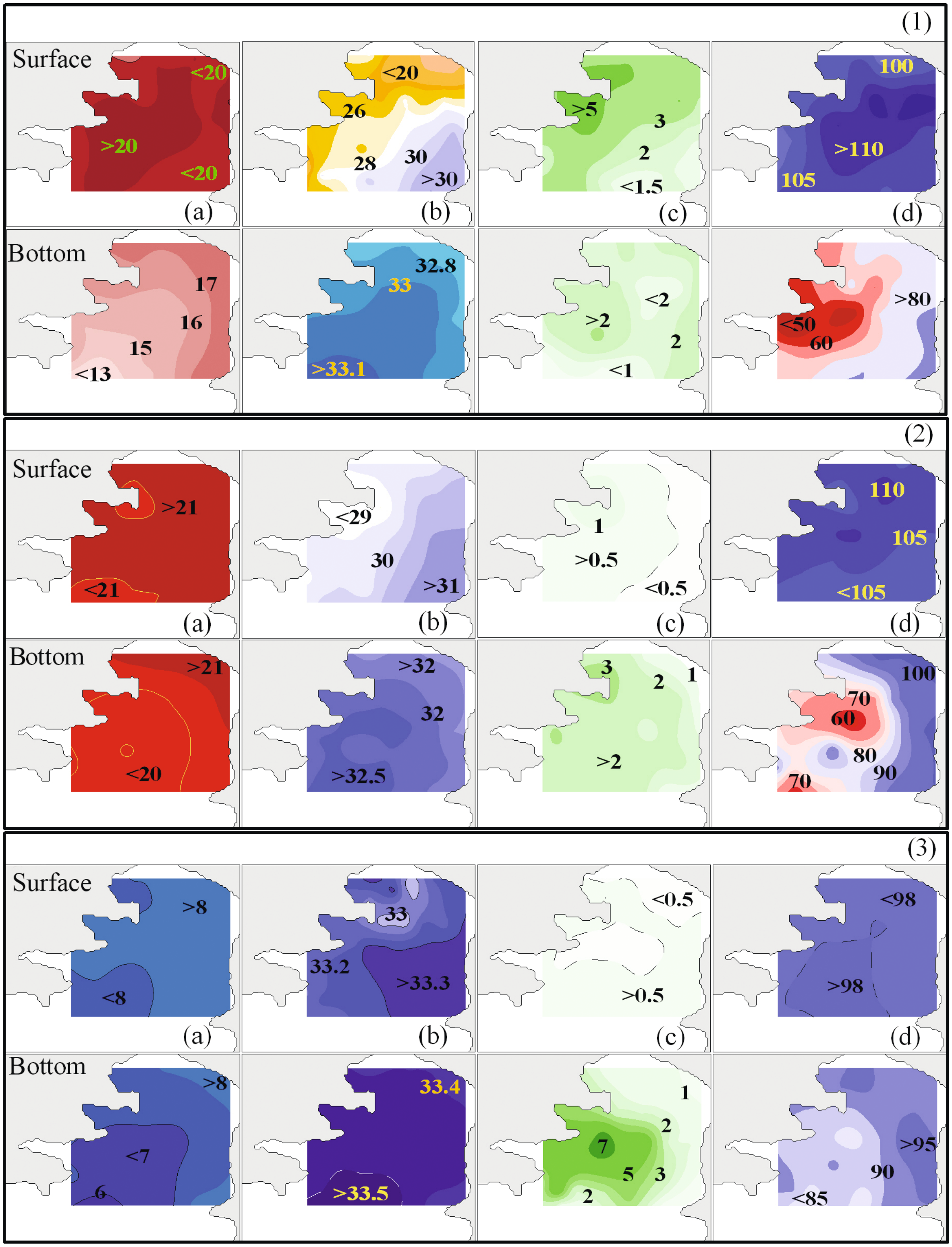

Fig. 4. (a) Water temperature (°C), (b) salinity (psu), (c) chlorophyll *a* (μg/L), and (d) dissolved oxygen (%) concentrations in the surface and near-bottom layersat the CTD stations in July (1), September (2), and November (3).

Table 1. Abundance (ind./m^3, numerator) and biomass (mg WW /m^3, denominator) of zooplankton in the shallow, transitional, and deep partsof Vostok Bay from July to November

Taxon	Early summer			Late summer			Fall		
	shallow	transitional	deep	shallow	transitional	deep	shallow	transitional	deep
Appendicularia	5.3/0.2	2.4/0.1	2.2/0.1	33.3/1.0	77.5/2.3	133.3/4.0	13.3/0.4	9.8/0.3	25.5/0.8
Chaetognatha	5.3/0.5	7.8/0.8	6.6/0.7	*33.5/3.3*	163.9/16.4	*716.6/71.7*	322.6/32.3	205.4/20.5	100.1/10.1
Cladocera									
Podon leuckartii	*1573.3/47.2*	*1580.8/47.4*	*1222.2/36.7*	0.0/0.0	0.0/0.0	0.0/0.0	82.6/2.5	35.2/1.1	5.7/0.2
Pleopis polyphemoides	0.0/0.0	0.0/0.0	0.0/0.0	2.4/0.1	68.5/2.1	116.6/3.5	0.0/0.0	0.0/0.0	0.0/0.0
Evadne nordmanni	0.5/0.1	6.1/0.2	11.1/0.3	0.0/0.0	0.0/0.0	0.0/0.0	42.6/1.3	23.5/0.7	5.5/0.2
Pseudevadne tergestina	0.0/0.0	0.0/0.0	0.0/0.0	4.0/0.1	15.7/0.5	103.3/3.1	0.0/0.0	0.0/0.0	0.0/0.0
Penilia avirostris	0.0/0.0	0.0/0.0	0.0/0.0	168.0/5.0	621.1/18.6	*3211.1/96.3*	0.0/0.0	0.0/0.0	0.0/0.0
Scyphozoa	0.5/0.1	1.2/0.2	0.6/0.1	6.6/0.3	18.1/0.7	22.2/0.9	13.6/0.5	5.8/0.2	1.1/0.05
Copepoda									
Acartia hudsonica	*2240.1/67.2*	*3161.7/94.9*	*666.6/20.0*	0.0/0.0	0.0/0.0	0.0/0.0	20.5/0.6	7.4/0.2	1.1/0.04
Acartia omorii	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	42.6/1.3	250.1/7.5	0.0/0.0	0.0/0.0	0.0/0.0
Acartia pacifica	0.0/0.0	0.0/0.0	0.0/0.0	1.7/0.05	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Calanus pacificus	0.5/0.4	0.9/0.8	2.2/1.8	0.0/0.0	0.1/0.1	0.5/0.4	0.0/0.0	0.0/0.0	0.0/0.0
Centropages abdominalis	1.3/0.2	0.8/0.1	0.4/0.1	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Centropages tenuiremis	0.0/0.0	0.0/0.0	0.0/0.0	20.2/1.1	5.3/0.3	5.1/0.3	0.0/0.0	0.0/0.0	0.0/0.0
Labidocera japonica	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.3/0.1	4.3/1.1	0.0/0.0	0.0/0.0	0.0/0.0
Neocalanus plumchrus	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.4/0.3	0.6/0.5	1.7/1.4
Oithona brevicornis	0.0/0.0	0.5/0.1	0.0/0.0	*333.3/3.3*	*2119.2/21.2*	*1355.5/13.6*	1760.3/17.6	*1306.6/13.1*	*811.1/8.1*
Oithona nana	0.0/0.0	0.5/0.1	0.0/0.0	0.0/0.0	0.0/0.0	35.1/0.4	0.0/0.0	0.0/0.0	0.0/0.0
Oithona similis	*4213.3/42.1*	*4617.6/46.2*	*3555.5/35.6*	46.6/0.5	297.4/3.0	*2188.8/21.9*	293.3/2.9	*272.7/2.7*	*1533.3/15.3*
Paracalanus parvus	0.0/0.0	0.0/0.0	0.0/0.0	*320.1/9.6*	*1633.8/49.0*	*5688.8/170*	13.3/0.4	9.2/0.3	8.9/0.3
Pseudocalanus minutus	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	22.2/0.7

Table 1. (Contd.)

Taxon	Early summer			Late summer			Fall		
	shallow	transitional	deep	shallow	transitional	deep	shallow	transitional	deep
Pseudocalanus newmani	*1013.3/30.4*	*1580.8/47.4*	*2222.2/66.7*	0.0/0.0	0.0/0.0	0.0/0.0	*1146.6/34.4*	*1431.9/43.1*	*2855.5/85.7*
Pseudodiaptomus marinus	0.0/0.0	0.0/0.0	0.0/0.0	0.1/0.003	0.0/0.0	0.0/0.0	0.0/0.0	0.2/0.01	0.6/0.02
Sinocalanus tenellus	0.1/0.01	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Tortanus derjugini	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.2/0.01	5.0/0.3	0.0/0.0	0.0/0.0	0.0/0.0
Tortanus discaudatus	0.0/0.0	0.5/0.03	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	4.0/0.2	0.0/0.0	0.2/0.01
Harpacticoida	0.01/0.001	0.01/0.001	0.0/0.0	0.6/0.01	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0
Copepod nauplii	373.3/0.4	85.3/0.1	44.4/0.05	13.3/0.01	30.1/0.03	26.1/0.03	*1440.1/1.4*	*1184.9/1.2*	*1177.7/1.2*
Fish ova and larvae	0.8/0.05	2.3/0.1	6.6/0.3	0.1/0.003	0.4/0.01	1.1/0.02	0.0/0.0	0.0/0.0	0.0/0.0
Mysida, larvae	0.2/0.3	0.6/0.5	0.4/0.3	0.0/0.0	0.5/0.04	6.5/6.4	0.0/0.0	0.0/0.0	0.0/0.0
Decapoda, larvae	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	1.7/1.6	10.3/10.1	0.0/0.0	0.0/0.0	0.0/0.0
Polychaeta, larvae	4.0/0.2	4.8/0.2	6.6/0.3	6.6/0.3	38.9/1.6	133.3/5.3	18.6/0.7	10.2/0.4	44.4/1.8
Cirripedia, nauplii, cypris	8.1/0.3	10.9/0.4	4.4/0.2	6.6/0.3	26.1/1.0	36.1/1.4	6.7/0.3	25.4/1.0	12.2/0.5
Gastropoda, larvae	2.6/0.1	4.8/0.2	2.2/0.1	4.6/0.1	7.9/0.2	25.1/0.5	0.0/0.0	2.9/0.1	3.3/0.1
Echinodermata, larvae	80.1/4.0	147.8/7.4	44.4/2.2	14.6/0.7	110.2/5.5	161.1/8.1	53.3/2.7	42.6/2.1	27.7/1.4
Bivalvia, larvae	160.0/1.6	72.7/0.7	22.2/0.2	*33.3/0.3*	112.5/1.1	705.5/7.1	126.6/1.6	67.2/0.7	138.8/1.4
Phoronida, larvae	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	0.0/0.0	100.1/2.8	26.1/0.7	233.3/5.7
Total abundance	9682.6	11290.5	7821.5	1048.2	5392.6	14941	5458.1	4668.3	7010.6
Average of total abundance	9598.2 ±5 69.1			7427.3 ± 459.7			5612.3 ± 395.6		
Total biomass	194.9	247.1	165.3	25.9	127.3	437.5	102.1	88.5	128.9
Average of total biomass	202.4 ± 54.6			196.9 ± 52.8			106.5 ± 36.9		

The underlined values are for the species that contributed >10% to community dissimilarities between the bay'sparts; the values highlighted in italics are for the species that contributed >10% to community similarities between the bay'sparts.

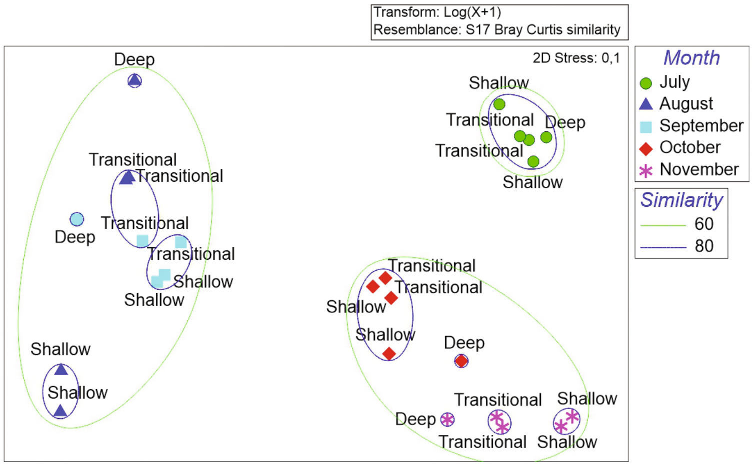

Fig 5. nMDS ordination plot based on zooplankton abundance in the shallow, transitional, and deep parts of Vostok Bay.

and chaetognaths accounted for >60% in total biomass; in the shallow part, *P. parvus* and cladocerans accounted for >50% in total biomass; the stations of the transitional part were characterized by generally high concentrations of the copepods *O. brevicornis* and *P. parvus*. In the fall, the copepods *O. brevicornis* and chaetognaths showed record-breaking biomasses in the shallow and transitional parts, while the copepods *O. similis* and *P. newmani* accounted for more than 70% in total biomass of the deep part (Fig. 6b).

Each abundant zooplankton taxon showed its characteristic preference for spatial distribution: cladocerans had high average values of total abundance in all the parts during the early summer and in the deep part during the late summer (Fig. 6a). Chaetognaths were concentrated in the deep part, with some exceptions during the fall when they occurred in the shallow part. The cold-water copepods *O. similis* and *P. newmani* were abundant in all the parts, while the brackish-water copepod *A.hudsonica* dominated the shallow and transitional parts during the early summer. The warm-water copepods *O. brevicornis* and *P. parvus* were abundant in the transitional and deep parts during the late summer; and in the shallow and transitional parts during the fall. The copepod nauplii were concentrated in the shallow part, but in the fall, higher abundances of copepod nauplii were in the deep part with high microalgae concentrations (cells were not counted).

In the early summer, based on the SIMPER analysis, the small-sized copepods *A.hudsonica*, *O. similis*, *P. newmani*, copepod nauplii, Bivalvia larvae, and Echinodermata larvae together contributed <10% to the zooplankton community dissimilarity between the shallow and transitional parts. The maximum degree of dissimilarity was between the shallow and deep parts where the copepods *A. hudsonica*, *O. similis*, *P. newmani*, copepod nauplii, and Bivalvia larvae were the major contributors to the community dissimilarities. The dissimilarity between the transitional and deep parts was determined by the copepods *A. hudsonica*, *O. similis*, *P. newmani*, Echinodermata larvae, and Cladocera (Table 1).

The results of SIMPER showed that in the late summer, the small-sized copepods *O. brevicornis*, *O. similis*, *P. parvus*, appendicularians, chaetognaths, cladocerans, and bivalve larvae made the greatest contribution to the dissimilarity (>50%) between the shal-

Table 2. Comparison of zooplankton assemblages between the shallow, transitional, and deep parts in Vostok Bay as inferred from ANOSIM (*R* value and *P* significance level) and SIMPER

Season	ANOSIM		SIMPER average dissimilarity, %	Season	SIMPER average dissimilarity, %		
	R	*P*, %			shallow and transitional	shallow and deep	transitional and deep
Early summer and Late summer	0.98	0.1	76.47	Early summer	9.33	17.49	14.92
Early summer and Fall	0.95	0.1	56.07	Late summer	44.68	57.76	36.24
Late summer and Fall	0.83	0.1	63.33	Fall	31.72	36.23	34.85

Table 3. Diversity of zooplankton community in Vostok Bay from July to November

Station	Total of species, *S*	Total of individuals, *N*	Margalef's index, *D'*	Pielou's evenness, *J'*	Shannon–Wiener index, *H'*
J2	16	62	3.63	0.94	2.61
J3	17	57	3.95	0.86	2.46
J11	19	61	4.38	0.87	2.58
J15	19	59	4.41	0.88	2.59
J23	18	55	4.23	0.88	2.57
A2	10	42	2.40	0.85	2.19
A3	11	34	2.82	0.81	2.17
A11	21	79	4.58	0.92	2.81
A15	22	75	4.86	0.91	2.82
A23	21	98	4.36	0.94	2.88
S2	15	55	3.49	0.96	2.61
S3	18	55	3.25	0.96	2.79
S11	17	58	3.94	0.95	2.69
S15	17	60	3.91	0.94	2.68
S23	16	71	3.52	0.96	2.67
O2	14	71	3.05	0.98	2.59
O3	17	76	3.69	0.96	2.73
O11	17	74	3.72	0.95	2.71
O15	18	61	4.13	0.92	2.68
O23	16	59	3.68	0.94	2.62
N2	13	39	3.28	0.93	2.38
N3	13	46	3.12	0.94	2.40
N11	13	42	3.20	0.92	2.36
N15	13	43	3.18	0.92	2.38
N23	15	58	3.44	0.88	2.41

Sampling months are July (J), August (A), September (S), October (O), and November (N). The plankton stations nos.: 2, 3, 11, 15, and 23.

low and deepparts. The above-listed taxa and echinoderm larvae contributed more than 40% to the dissimilarity between the shallowand transitional parts. The minimum contribution to the dissimilarity between the transitional and deep parts was made by the copepods *A. hudsonica*, *O. brevicornis*, *O. similis*, *P. parvus*, appendicularians, chaetognaths, cladocerans, bivalve larvae, and echinoderm larvae (Table 1).

In the fall, the major contributors to the zooplankton dissimilarity between the shallow and deep partswere the copepods *O. brevicornis*, *O. similis, P. newmani*, copepod nauplii, chaetognaths, cladocerans, Phoronida larvae, bivalve larvae, and echinoderm larvae. The contributors to the dissimilarity between the shallow and transitional parts, as well as between the transitional and deep parts, were the above-listed species with equal proportions, except cladocerans and chaetognaths. In addition, as the SIMPER showed, the copepods *A. hudsonica*, *O. similis, O. brevicornis*, *P. parvus*, *P. newmani*, copepod nauplii, cladocerans, and chaetognaths together contributed >10% to the zooplankton community similarities within each of the parts in each season (Table 1).

Factors Influencing the Community Structure

Average values of the following parameters for the shallow, transitional, and deep parts of Vostok Bay are provided in Table 4: sea surface temperature (SST, °C) and sea bottom temperature (SBT, °C); sea surface salinity (SSS, psu) and sea bottom salinity (SBS, psu); sea surface chlorophyll *a* (SChl a, μg/L) and bottom chlorophyll *a* (BChl a, μg/L) concentrations; sea surface dissolved oxygen (O_2, mg/L) and bottom dissolved oxygen (BO_2, mg/L) concentrations.

According to the BIO-ENV analysis (Table 5), SST, SBT, and SBS were the best combination of environment variables to explain the variance in the community structure based on abundance in the early summer ($\rho = 0.842$). A combination of SBT, SChl *a*, O_2 concentrations, and depth best explained it in the

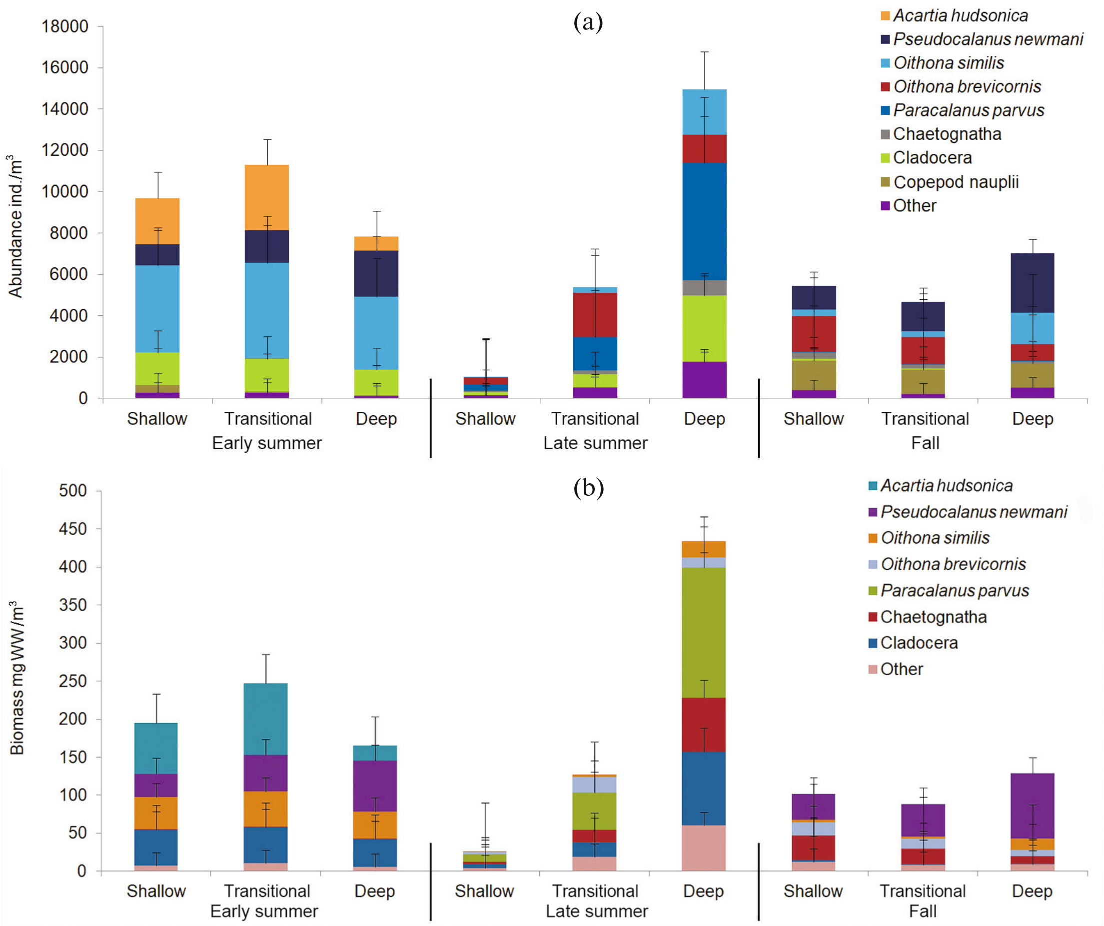

Fig. 6. Seasonal variations in the (a) abundance (ind./m^3) and (b) biomass (mg WW/m^3) of dominant species/taxa in theshallow, transitional, and deep parts during early summer, late summer, and fall.

late summer (ρ = 0.773), while SST, SBT and BO$_2$ concentration were the best combination to explain the differences in the quantitative distribution of zooplankton community in the fall (ρ = 0.672).

The correlations between the abundance of oceanic copepods and the depth were positive ($p < 0.05$) (Table 6). The abundance of cold-water copepods was negatively correlated with the temperature at the surface and near

Table 4. Environmental variables (mean ± SD) at the plankton stations in Vostok Bay from July to November 2023

Variables	Early summer			Late summer			Fall		
	shallow	transitional	deep	shallow	transitional	deep	shallow	transitional	deep
SST	20.5 ± 1.0	20.4 ± 1.1	20.9 ± 1.3	22.2 ± 1.2	21.4 ± 0.6	21.5 ± 1.1	9.2 ± 1.4	12.1 ± 1.4	12.1 ± 2.3
SBT	16.0 ± 2.6	15.1 ± 2.9	14.3 ± 3.6	19.4 ± 2.9	17.0 ± 2.3	16.4 ± 2.7	8.8 ± 0.5	10.5 ± 0.7	9.8 ± 0.2
SSS	22.5 ± 0.2	27.6 ± 0.5	29.2 ± 0.4	29.2 ± 0.5	28.9 ± 0.7	29.6 ± 1.4	33.1 ± 0.1	32.5 ± 0.2	32.7 ± 0.2
SBS	33.0 ± 0.3	33.1 ± 0.9	33.1 ±0.5	32.3 ± 0.9	33.0 ± 0.6	33.1 ± 0.4	33.4 ± 0.1	33.2 ± 0.1	33.3 ± 0.1
SChl *a*	4.6 ± 0.3	3.5 ± 0.5	2.3 ±0.2	2.9 ± 0.5	3.0 ± 0.7	2.5 ± 1.0	0.5 ± 0.3	0.5 ± 0.2	0.5 ± 0.3
BChl *a*	1.6 ± 0.8	1.3 ± 0.2	0.8 ±0.3	2.0 ± 0.2	1.3 ± 0.1	1.3 ± 0.1	1.0 ± 0.2	3.0 ± 0.7	3.2 ± 1.2
O$_2$	9.4 ± 0.5	8.9 ± 0.4	8.3 ± 0.3	8.2 ± 0.4	8.4 ± 0.2	7.9 ± 0.1	9.3 ± 0.1	8.9 ± 0.1	8.9 ± 0.2
BO$_2$	6.3 ± 0.2	5.4 ± 0.1	7.3 ± 0.4	6.0 ± 0.1	5.6 ± 0.8	6.8 ± 0.4	9.4 ± 0.3	8.4 ± 0.5	7.8 ± 0.3

Abbreviations of environmental variables are as follows: sea surface (SST) and bottom (SBT) temperature (°C); sea surface (SSS) and bottom (SBS) salinity (psu); surface (SChl *a*) and bottom (BChl *a*) chlorophyll *a* concentration (μg/L); surface (O$_2$) and bottom (BO$_2$) oxygen concentration (mg/L).

Table 5. Results of BIO-ENV analysis showing the best environmental variables predicting variations in zooplankton abundances during three seasons

Early summer		Late summer		Fall	
significant environmental variables	spearman ρ	significant environmental variables	spearman ρ	significant environmental variables	spearman ρ
SST, SBT and SBS	0.842	SBT, SChl *a*, O_2andD	0.773	SST, SBT and BO_2	0.672
SST, SBT, SBS,SChl *a* and O_2	0.833	SBT, SChl *a* and O_2	0.762	SST, SBT, SSS, SChl *a* and BO_2	0.668
SST, SBT, SBS,BChl *a* and O_2	0.828	SBT, SSS, SChl *a*, O_2andD	0.756	SST and SBT	0.657
SST, SSS,SChl *a*, O_2 and D	0.821	SBT, SChl *a*, BChl *a*, O_2andD	0.742	SBT, SChl *a* and BO_2	0.653

For explanation of the abbreviations of the environmental variables, see Table 4.

Table 6. Spearman's rank order correlations showing the environmental variables predicting abundances of zooplankton taxa

Taxon	SST	SBT	SSS	SBS	SChl *a*	BChl *a*	O_2	BO_2	Depth
CopCold	**–0.522**	**–0.488**	0.002	0.249	0.049	–0.112	**0.445**	–0.025	0.303
CopWarm	0.424	0.156	0.253	0.119	–0.174	–0.105	–0.428	0.095	0.178
CopNerit	0.089	0.028	–0.301	–0.047	0.391	–0.229	–0.110	–0.322	0.372
CopOcean	–0.013	–0.131	–0.065	0.193	–0.144	0.017	–0.181	–0.109	**0.752**
Chaet	0.352	0.086	0.188	0.243	–0.184	–0.140	–0.338	0.154	0.233
Clad	**0.622**	**0.504**	**–0.633**	–0.413	**0.702**	–0.331	**–0.574**	**–0.565**	0.043
Append	0.104	0.368	–0.145	–0.212	–0.390	**0.480**	–0.238	–0.002	0.070

CopCold means abundance (ind./m^3) ofcold-water copepods; CopWarm, abundance of warm-water copepods; CopNerit, abundance of neritic copepods; CopOcean, abundance of oceanic copepods; Chaet, abundance of chaetognaths; Clad, abundance of cladocerans; and Append, abundance of appendicularians. For explanation of the abbreviations of the environmental variables, see Table 1. Significant correlations (p< 0.05) are highlighted in bold.

the bottom, while itshowed a positive correlation with the oxygen concentration at the surface. In contrast, the abundance of cladocerans showed a negative correlation with the salinity at the surface and the oxygen concentration andwas positively correlated with the temperature at the surface and at the bottom. The correlations between the environmental variables and quantitative values of other zooplankton taxa considered in the analysis were non-significant.

DISCUSSION

Species in zooplankton assemblages are always associated with distribution of water masses [12, 21, 35, 36]. In our study, three types of zooplankton assemblages (estuarine, mixed, and marine) spatially coincided with the shallow, transitional, and deep parts, and their distribution was consistent with the general pattern of the water masses in the bay [9, 10]. In all three seasons, small-sized copepods and cladocerans dominated the zooplankton community, and each species showed seasonal dominance in the total abundance. The copepods *A. hudsonica*, *O. similis*, *P. newmani* and the cladoceran *P. leuckartii* were abundant in the early summer; the copepods *O. brevicornis*, *P. parvus*, and the cladoceran *P. avirostris*, in the late summer; the copepods *O. similis*, *P. newmani*, and copepod nauplii, in the fall. Brackish-watercopepods of the genera *Acartia*, *Centropages*, *Tortanus*, and *Sinocalanus* and cladocerans usually show negative relationships with water salinity [12] and occur in the shallow zone, but can also spread to the inner shelf zone (to a depth of 50 m) [17]. The marine zooplankton assemblage was characterized by oceanic species, e.g., large-sized copepods of the genera *Calanus*, *Eucalanus*, *Labidocera*, *Metridia*, and *Neocalanus* and chaetognaths [17, 37]. During the summer and fall seasons from 2002 to 2013, the higher zooplankton abundance was recorded from the shallow zone (up to 10 m) [17], while in the present study, a higher zooplankton abundance was recorded from the deep zone (deeper than 20 m).

Some specific features of the species composition and abundance of zooplankton can persist for some time and then change dramatically, which givesthe community a different state. These processes correspond to the well-known concept of seasonal plankton succession in hydrobiology, where temporarily stable states are defined as seasons in plankton [38]. These seasons are not related to some calendar periods, but change when water temperature reaches certain values [35]. In PGB, from seven to nine such seasons can be observed during the year, and, from year to year, the pattern of seasonal sequence and features repeats itself but not necessarily at the same time [12]. In May, the Liman Current, after deviating north under the effect of the southern monsoon, transports cold-water oceanic copepods to the coastal zone. In August and September, as the monsoon weakens and off-shore currents develop, the allochthonous copepods *Oithona brevicornis*, *Paracalanus parvus*, and *Calanus pacificus* enter coastal waters. The proportion of oceanic species in the coastal zooplankton community depends on the monsoon speed [21, 22]. During the summer monsoon of 2023, the average wind speed was below 5 m/s, and the contribution of the oceanic species to the zooplankton community was not greater than 29%.

In our study, the boundaries between the shallow, transitional, and deep parts of the bay, characterized by estuarine, mixed, and marine assemblages, respectively, were not stable throughout all three seasons. In the early summer, with a prevalence of southeasterly winds and a decrease in salinity in the surface layer (see Fig. 4), there were nosignificant differences in zooplankton community between all parts of the bay. Due to the cyclonic circulation, the surface water in the northern part of Vostok Bay (freshened by river runoff) was carried to the southwestern part, while the water column located east was influenced by the PGB water. In addition, the high abundance of brackish-water cladocerans found in the deep part is probably a result of cyclonic water circulation in Vostok Bay. In the late summer, significant differences in zooplankton community were found between the shallow, transitional, and deep parts of the bay, apparently, due to the uniform warming of the water column, low hydrodynamics of waters, and low effect of river discharge in all the parts, which was also consistent with previous environmental observations [9, 10, 39, 40]. In the fall, differences in zooplankton community were observed only between the transitional and deep parts, with a boundary between them running in the inner shelf (above 20 m depth). In this season, the northerly wind drives the surface water from the bay and induces compensatory currents (directed north) in the near-bottom layer and along the eastern coast. Thus, the formation of the boundary between the shallow, transitional, and deep parts of the bay is due to the predominance of cyclonic water circulation with coastal currents in the surface layer and compensatory currents near the bottom. However, this circulation in the summer season, under a southeasterly wind, is accompanied by the effect of wind-driven water level setup to the northern part of the bay; in the fall, the opposite effect is observed with a northerly wind.

The most pronounced changes in the zooplankton structure and abundance in the coastal zone, which is subject to intensive exchange with adjacent deep-sea areas, occur rather between long-term periods, sometimes decades, than between years [21, 41]. Both neritic species, which spend all their lives in shallow waters, and oceanic species are present in the coastal zooplankton community. Most oceanic species make vertical migrations during their ontogeny because they cannot spawn in shallow waters, use coastal waters only for feeding, and their presence in coastal waters may vary between years [16, 42]. Thus, in the early 1930s, tropical and subtropical species (e.g.,the copepods *Labidocera pavo*, *Labidocera japonica*, *Labidocera bipinnata*, *Epilabidocera amphitrites*, and *Acartia plumosa*) dominated the zooplankton of Posyet Bay (southwestern PGB). In the late 1960s, cold-water small-sized species (e.g., copepods of the genera *Acartia*, *Oithona*, *Pseudocalanus*, and *Pseudodiaptomus*) began to dominate the zooplankton community in Posyet Bay; the dominance of these species lasted until the late 1980s [16, 18–20]. The change in the climate regime, recorded in the early 1990s, was accompanied by increases in the average annual air temperature by 1°C, in the level of the Sea of Japan by 5.9 cm, and in the thermohaline characteristics of the surface layer which showed opposite trends, +1.4°C and –1.3 psu [43–45]. This change led to significant rearrangements in the coastal zooplankton community, in particular, to the appearance of oceanic large-sized copepods and chaetognaths. As a result, the total biomass of zooplankton increased 2–3-fold and averaged at 2000 mg WW/m^3 [35]. The warming in the winter caused shallower convection in the Sea of Japan and, therefore, the seasonal renewal of nutrients in the near-surface layer became weaker, which caused the carrying capacity to decrease with a 1–2 year lag. The coastal community returned to its neritic state only in the early 2000s (with a dominance of small-sized copepods, the total biomass decreased to 1500 mg WW/m^3), and the subsequent changes were accompanied by a decrease in the level of total abundance and biomass [12].

A comparison of the current status of the zooplankton community in Vostok Bay with observations during the summer and fall seasons of 1998, 2000, 2006, and 2015 revealed a negative trend in the total abundance and biomass with a marked shift towards lower values [23, 40, 46, 47]. In the late 1990s, the community was dominated by taxa of large-sized allochthonous organisms (copepods and chaetognaths) which had been transported to Vostok Bay from the deep-sea areas of PGB [23, 46]. Since the mid-2000s, neritic species (small-sized copepods and cladocerans), with their relatively low total abundance and biomass, dominated the zooplankton community in Vostok Bay. Currently, the zooplankton is in a stable "neritic state", with small-sized copepods of the genera *Acartia*, *Pseudocalanus*, *Paracalanus*, *Oithona* and cladocerans dominating the community. It is important to note that the contribution of tropical, subtropical, and allochthonous species such as copepods of the genera *Calanus*, *Eucalanus*, *Metridia*, *Labidocera*, *Sapphirina*, *Scolecithricella*, chaetognaths, gammarids, hyperiids, isopods, and salpids to the total zooplankton abundance and biomass decreased. In addition, in recent years (2015–2023), the rate of decrease in the total zooplankton biomass in Vostok Bay increased twofold, whereas the biomass of allochthonous species began to increase in winter (http://marbank.dvo.ru/index.php/ru/), which may be a consequence of the early spawning of these species under conditions of the winter increase in water temperature and a sharp strengthening of the winter monsoon [9, 48, 49]. During the winter of 2022–2023, the average air temperature at the Nakhodka weather station was–3.65°C and the precipitation was 156 mm, i.e., the winter monsoon was warmer (for example, the temperature during the abnormally cold winter monsoon of 2011–2012 and the winter monsoon of 2017–2018 were lower than –6°C, while during the warm winter monsoon of 2018–2019, it was about –2.9°C).

Variations in proportions of oceanic species in the coastal zooplankton depend on fluctuations in the Okhotsk and North Pacific climate indices that characterize the intensity of the summer monsoon off the southern Primorsky krai coast [12]. Both indices indicated a sharp weakening of the summer monsoon between the 1980s and 2000s [50]. The summer monsoons in 2000–2023 off the PGB coast had the average wind speed of about 5 m/s, except the values during 2017–2020 when the speed was 20–30% lower [9, 13]. Consequently, since the early 2000s, the summer monsoon has gradually weakened with a minimum in 2017–2020. In 2021, the wind speed of the summer monsoon increased again to values greater than 5 m/s. Nevertheless, the summer monsoons of 2017 and 2021 were warm (with average air temperatures of 15 and 15.5°C, respectively), while the monsoons of 2018–2020 were relatively cool (about 14.5°C). The summer of 2021 was abnormally dry (83, 6, and 105 mm in June, July, and August, respectively). The strengthening of the winter monsoon and the weakening of the summer monsoon off southern Primorsky krai might be caused by the effect of the interannual GAO-ENSO (Global Atmosphere Oscillation and El Niño–Southern Oscillation) [49, 51–53]. The summer monsoon of 2023 had an average wind speed below 5 m/s, an air temperature of 16°C, and a precipitation of 706 mm [13]. This was an extremely warm summer monsoon since 1932.

The biomass of zooplankton in Vostok Bay depends mainly on the degree of expansion of allochthonous zooplankton species, e.g., large-sized copepods and chaetognaths from the deep-sea areas of PGB. Chaetognaths are known to be major allochthonous predators preying on small-sized copepods in shallow waters, with their abundance positively correlating with the intensity of the summer monsoon. The contribution of other allochthonous species to the zooplankton increases during periods of strengthening of the summer monsoon [12, 21]. In our study, we did not find the significant changes in the zooplankton community structure that had been observed during the periods of strengthening of the summer monsoon off the southern Primorsky krai coast in the 1990s [12, 35]. It is likely that the time lag of several years, with a delay in zooplankton changes, reflects the asynchronous response of marine ecosystems to environmental changes. The increase in the abundance of predators leads to a lower biomass of phytophages with a lag of 3–5 years (determined by their life span). As a result, the total biomass of zooplankton significantly decreases. It should be noted that the coastal waters of Vostok Bay are subject to anthropogenic pressure [39, 40]. Nevertheless, no evidence of its direct effect on the zooplankton community has been obtained to date.

The variations in the direction of currents of the cross-shelf circulation as a result of the summer monsoon weakening from the 2000s to 2020 [12, 21, 51] and the long-term positive anomaly of water temperature in the cold half of the year in Vostok Bay [9] may be the major explanation for the low values of abundance and diversity of zooplankton formed in the summer and fall seasons, in particular, a decrease in the proportion of oceanic copepods and chaetognaths, as well as some tropical and subtropical taxa. Nevertheless, the data that we obtained does not contradict the general patternsin the structure and distribution of zooplankton in PGB and is consistent with the previously formulated concept of modern climate changes in the ecosystem of the northwestern Sea of Japan towards reduction in the carrying capacity and increasein the efficiency of its functioning [21, 44]. Furthermore, the isolation of the zooplankton community of Vostok Bay from the deep-sea zooplankton community of PGB will contribute to a decrease in predation within the bay and, thus, an increase in the food supply for planktivorous fish [54].

CONCLUSIONS

We identified a total of 37 zooplankton taxa including neritic (71%) and oceanic (29%) species. Copepods (e.g., *Oithona similis*, *Oithona brevicornis*, *Pseudocalanus newmani*, *Paracalanus parvus*, and *Acartia hudsonica*) and cladocerans (*Podon leuckartii* and *Penilia avirostris*) dominated the zooplankton community. The average values of total zooplankton abundance and biomass were maximum in the early summer due to cold-water copepods and cladocerans and showed a tendency to decrease twofold by the fall.

The seasonal dynamics of the zooplankton abundance was determined by the pattern of wind-driven cross-shelf water circulation formed by prevailing monsoon winds. In the early summer, an increase in the total abundance and biomass of zooplankton was observed in the direction from the deep to the transitionalparts of the bay; in the late summer and fall, vice versa, from the shallow towards the deep parts. The 25-year dynamics of the total zooplankton abundance and biomass had a negative and noticeable trend to lower values. There was also a decrease in the contribution of large-sized taxa and tropical/subtropical copepods to the total zooplankton abundance. In recent decade, the rate of decline in the summer–fall total biomass of zooplankton has increased two fold, while the biomass of allochthonous species has begun to increase sharply in winter.The zooplankton community is strongly influenced by variations in the environmental conditions in Vostok Bay, which determines the functioning of the bay ecosystem in general.

ACKNOWLEDGMENTS

Weare grateful to the administration of the A.V. Zhirmunsky National Scientific Center of Marine Biology, Far Eastern Branch, Russian Academy of Sciences (NSCMB FEB RAS), to the oceanographic research team of the Deepwater Equipment Department, NSCMB FEB RAS, for collecting plankton samples and for measuring the environmental parameters, and also to the captain and crew of the R/V *Vityaz* for their comprehensive assistance. Special thanks are due to Evgeny Shvetsov for his proofreading the English. We also thank anonymous reviewers whose valuable comments and suggestions substantially improved the manuscript.

FUNDING

This study was supportedby the State Assignments no. 123080800009-5 and no. 24021900011-9.

ETHICS APPROVAL
AND CONSENT TO PARTICIPATE

This work does not contain any studies involving human and animal subjects.

CONFLICT OF INTEREST

The authors of this work declare that they have no conflicts of interest.

REFERENCES

1. Robert, D., Murphy, H.M., Jenkins, G.P., and Fortier, L., Poor taxonomical knowledge of larval fish prey preference is impeding our ability to assess the existence of a “critical period” driving year-class strength, *ICES J. Mar. Sci.*, 2014, vol. 71, pp. 2042–2052.
2. Turner, J.T., The importance of small planktonic copepods and their roles in pelagic marine food webs, *Zool. Stud.*, 2004, vol. 43, pp. 255–266.
3. Brun, P., Stamieszkin, K., Visser, A.W., et al., Climate change has altered zooplankton-fuelled carbon export in the North Atlantic, *Nat. Ecol. Evol.*, 2019, vol. 3, pp. 416–423.
4. Mitra, A., Castellani, C., Gentleman, W.C., et al., Bridging the gap between marine biogeochemical and fisheries sciences; configuring the zooplankton link, *Prog. Oceanogr.*, 2014, vol. 129, pp. 176–199.
5. Batchelder, H.P., Daly, K.L., Davis, C.S., et al., Climate impacts on zooplankton population dynamics in coastal marine ecosystems, *Oceanography*, 2013, vol. 26, pp. 34–51.
6. Hays, G.C., Richardson, A.J., and Robinson, C., Climate change and marine plankton, *Trends Ecol. Evol.*, 2005, vol. 20, pp. 337–344.
7. Steinberg, D.K. and Landry, M.R., Zooplankton and the ocean carbon cycle, *Annu. Rev. Mar. Sci.*, 2017, vol. 9, pp. 413–444.
8. Danchenkov, M.A., *Okeanografiya zaliva Petra Velikogo* (Oceanography of Peter the Great Bay), Vladivostok: Novy Format, 2022.
9. Gayko, L.A., *Gidrometeorologicheskii rezhim zaliva Vostok* (*Yaponskoe more*) (Hydrometeorological Regime of Vostok Bay, Sea of Japan), Vladivostok: Tikhookean. Okeanol. Inst., Dal’nevost. Otd. Ross. Akad. Nauk, 2017.
10. Gayko, L.A., *Osobennosti gidrometeorologicheskogo rezhima pribrezhnoi zony zaliva Petra Velikogo* (*Yaponskoe more*) (Specifics of Hydrometeorological Regime of the Coastal Zone in Peter the Great Bay, Sea of Japan), Vladivostok: Dal’nauka, 2005.
11. Grigorieva, N.I. and Kashenko, S.D., Study of interannual and seasonal variability of thermohaline conditions in Vostok Bay (Peter the Great Bay, Sea of Japan), *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2010, vol. 162, pp. 242–255.
12. Zuenko, Yu.I. and Nadtochy, V.V., General features of seasonal and interannual dynamics for the zooplankton community in the Amur Bay (Peter the Great Bay, Japan Sea), *Tr. VNIRO*, 2018, vol. 173, pp. 157–170.
13. Archive of the Nakhodka meteorological station, WMO_ID = 31970. https://rp5.ru. Accessed February 2024.
14. Goncharenko, I.A., Federyakov, V.G., Lazaryuk, A.Yu., and Ponomarev, V.I., Thematic processing of the AVHRR data illustrated by the example of studying the coastal upwelling, *Issled. Zemli Kosmosa*, 1993, vol. 2, pp. 97–107.
15. Dolganov, S.M. and Tyurin, A.N., Marine Reserve “Zaliv Vostok”, *Biota Sreda Zapoved. Dal’nego Vost.*, 2014, vol. 1, pp. 9–24.
16. Brodsky, K.A., Species composition of copepods and cladocerans in the Posyet and Amur Bays (Sea of Japan) in connection with the long-term temperature fluctuations, *Biol. Morya* (Vladivostok), 1981, vol. 5, pp. 21–27.
17. Dolganova, N.T. and Nadtochiy, V.V., Composition, seasonal and interannual dynamics of zooplankton in Peter the Great Bay (Sea of Japan), *Izv. Tikhookean.*

Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr., 2015, vol. 181, pp. 169–190.

18. Kos, M.S., Reducing the role of warm-water elements in the plankton of Posyet Bay (Sea of Japan), *Dokl. Akad. Nauk SSSR*, 1969, vol. 184, no. 4, pp. 951–954.
19. Kos, M.S., Zooplankton in Posyet Bay, in *Pribrezhnie soobshestva dal'nevostochnih morey* (Coastal Communities of Far Eastern Seas), Vladivostok: Dal'nevost. Nauchn. Tsentr, Akad. Nauk SSSR, 1976, pp. 64–93.
20. Kos, M.S., Seasonal dynamics of zooplankton composition, structure and distribution in Posyet Bay (Sea of Japan), *Morsk. Issled.*, 1977, vol. 19, no. 27, pp. 29–56.
21. Nadtochiy, V.V. and Zuenko, Yu.I., Mechanisms of subtropical plankton transport into the coastal waters of southern Primorye, a case of *Paracalanus parvus*, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2016, vol. 184, pp. 241–252.
22. Zuenko, Yu.I., Nadtochiy, V.V., and Selina, M.S., Oceanographic processes and plankton succession in the coastal zone of the Japan Sea in summer season, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2004, vol. 135, pp. 144–177.
23. Shkoldina, L.S., About the zooplankton of the Vostok Bay marine reserve, in *Materialy konferentsii po prirodnym zapovednikam* (Proc. Far East. Conf. Nature Reserves), Vladivostok: Dal'nauka, 2001, pp. 317–318.
24. Operator's manual, SBE Data Processing 7.23.2. http://www.seabird.com. Accessed February 2024.
25. WoRMS Editorial Board, World Register of Marine Species, 2015. http://www.marinespecies.org. Accessed August 2023.
26. Razouls, C., Desreumaux, N., Kouwenberg, J., and de Bovee, F., Biodiversity of Marine Planktonic Copepods (morphology, geographic distribution and biological data), Sorbonne University, CNRS, 2005–2023. http://copepodes.obs–banyuls.fr/en/. Accessed August 2023.
27. Borisov, B.M., Volkov, A.F., Gorbatenko, K.M., et al., Standard tables of the wet weight and some biochemical parameters (calorie content, fats, proteins, carbohydrates, and the mineral rest) of zooplankton in the Far East seas, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2004, vol. 138, pp. 355–367.
28. Clark, K.R. and Warwick, R.M., *Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*, Plymouth: PRIMER–E, 2001.
29. Bray, J.R. and Curtis, J.T., An ordination of the upland forest communities of Southern Wisconsin, *Ecol. Monogr.*, 1957, vol. 27, pp. 325–349.
30. Clarke, K.R. and Ainsworth, M., A method of linking multivariate community structure to environmental variables, *Mar. Ecol.: Prog. Ser.*, 1993, vol. 92, pp. 205–219.
31. Shannon, C.E. and Weaver, W., *The Mathematical Theory of Communications*, Chicago: Univ. Illinois Press, 1964.
32. Margalef, R., Temporal succession and spatial heterogeneity in phytoplankton, in *Perspectives in Marine Biology*, Buzzati-Traverso, Ed., Berkeley, CA: Univ. Calif. Press, 1958, pp. 323–347.
33. Pielou, E.C., The measurement of diversity in different types of biological collections, *J. Theor. Biol.*, 1966, vol. 13, pp. 131–144.
34. Schlitzer, R., *Ocean Data View*, Bremerhaven: Alfred Wegener Inst., 2012. http://odv.awi.de. Accessed February 2024.
35. Nadtochiy, V.V. and Zuenko, Yu.I., Year-to-year variability of spring-summer plankton in Peter the Great Bay, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2000, vol. 127, pp. 281–300.
36. Zuenko, Yu.I., Application of a lower trophic level model to a coastal sea ecosystem, *Ecol. Model.*, 2007, vol. 202, nos. 1–2, pp. 132–143.
37. Nadtochiy, V.V., Rachkov, V.I., and Bokhan, L.N., Interannual dynamics of zooplankton in the Amur Bay, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2012, vol. 171, pp. 186–198.
38. Kiselev, I.A., *Plankton morei i kontinental'nykh vodoemov* (Plankton of Seas and Continental Water Bodies), vol. 1: *Vvodnye i obshchie voprosy planktologii* (Introductory and Common Issues of Planktology), Leningrad: Nauka, 1969.
39. Khristoforova, N.K., Lazaryuk, A.Yu., Zhuravel, E.V., et al., Vostok Bay: Interseasonal changes in hydrological, hydrochemical and microbiological properties, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2023, vol. 203, no. 4, pp. 906–924.
40. Tishchenko, P.P., Tishchenko, P.Ya., Elovskaya, O.A., et al., Conditions for primary production of phytoplankton in the Vostok Bay (Japan Sea) in spring 2016, *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2019, vol. 198, pp. 164–185.
41. Kasyan, V.V., Spatial and temporal changes of species composition and population density of copepods (Crustacea: Copepoda) in the Far Eastern Marine Reserve, Sea of Japan, *Morsk. Biol. Zh.*, 2017, vol. 2, no. 1, pp. 43–55. https://doi.org/10.21072/mbj.2017.02.1.05
42. Brodsky, K.A., *Fauna veslonogikh rachkov* (*Calanoida*) *i zoogeograficheskoe raionirovanie severnoi chasti Tikhogo okeana i sopredel'nykh vod* (Fauna of Copepods (Calanoida) and Zoogeographic Zoning of the North Pacific Ocean and Adjacent Waters), Moscow: Akad. Nauk SSSR, 1957.
43. Kang, Y.S., Jung, S., Zuenko, Y., et al., Regional differences in response of mesozooplankton to long-term oceanographic changes (regime shifts) in the northeastern Asian marginal seas, *Prog. Oceanogr.*, 2012, vols. 97–100, pp. 120–134.
44. Zuenko, Yu.I., Dolganova, N.T., and Nadtochiy, V.V., Forecasting of climate change influence on zooplankton in the Japan Sea, *Pac. Oceanogr.*, 2010, vol. 5, no. 1, pp. 6–18.
45. Rostov, I.D., Rudykh, N.I., Rostov, V.I., and Vorontsov, A.A., Manifestations of global climate change in the northern Japan Sea coastal water, *Vestn. Dal'nevost. Otd. Ross. Akad. Nauk*, 2016, vol. 5, pp. 163–181.
46. Omelyanenko, V.A., Coastal meroplankton of Peter the Great Bay, Sea of Japan, *Extended Abstract of Cand. Sci. (Biol.) Dissertation*, Vladivostok, 2006.
47. *Otchet of nauchno-issledovatel'skoi rabote "Vzaimosvyaz' mezhdu gidrokhimicheskimi i biologicheskimi protsessami*

v morskikh ekosistemakh v usloviyakh sovremennoi khozyaistvennoi deyatel'nosti i izmeneniya klimata" (Report on the Research "The Relationship Between Hydrochemical and Biological Processes in Marine Ecosystems under the Conditions of Modern Economic Activity and Climate Change"), Vladivostok: Tikhookean. Okeanol. Inst., Dal'nevost. Otd. Ross. Akad. Nauk, 2017, no. 01201363041, pp. 107–134.

48. Luchin, V.A., Tikhomirova, E.A., and Kruts, A.A., Oceanographic regime of the waters of Peter the Great Bay (Sea of Japan), *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2005, vol. 140, pp. 130–169.
49. Ponomarev, V.I., Dmitrieva, E.V., Shkorba, S.P., and Karnaukhov, A.A., Change of the global climate regime at the turn of the XX–XXI centuries, *Vestn. Mosk. Gos. Tekh. Univ. im. N.E. Baumana*, 2018, vol. 21, no. 1, pp. 160–169.
50. Zuenko, Yu.I., Aseeva, N.L., Glebova, S.Yu., et al., Modern changes in the ecosystem of the Sea of Okhotsk (2008–2018), *Izv. Tikhookean. Nauchno-Issled. Inst. Rybn. Khoz. Okeanogr.*, 2019, vol. 197, pp. 35–61.
51. Byshev, V.I., Neiman, V.G., Ponomarev, V.I., et al., The influence of global atmospheric oscillation on formation of climate anomalies in the Russian Far East, *Dokl. Earth Sci.*, 2014, vol. 458, no. 1, pp. 1116–1120.
52. Kawamura, H. and Wu,P., Formation mechanism of Japan Sea Proper Water in the flux center off Vladivostok, *J. Geophys. Res.*, 1998, vol.103, pp. 21611–21622.
53. Fayman, P., Prants, S., Budyansky, M., and Uleysky, M.Y., Coastal summer eddies in the Peter the Great Bay of the Japan Sea: In situ data, numerical modeling and Lagrangian analysis, *Cont. Shelf Res.*, 2019, vol. 181, pp. 143–155.
54. Primamedia, *Rybaki Primor'ya massovo vykhodyat v zaliv Vostok za mintaem* (Many Fishermen of Primorsky Krai Set out to Vostok Bay to Catch Walleye Pollock). https://primamedia.ru/news/1708811/. Accessed May 3, 2024.