Introduction

Seeps and vents of the Bering Sea

This special issue focuses on hydrothermal vent and methane seep fauna and communities in the Bering Sea. Although fragmentary information has been previously published on the hydrothermal vents, data on methane seep communities from the Bering Sea are presented here for the first time.

Hydrocarbon seeps and hydrothermal vents provide specific habitats that are influenced by seabed emissions of fluids rich in reduced compounds. Communities inhabiting hydrothermal vents and seeps below the photic zone, mostly depend on autochthonous primary organic matter synthesized by symbiotic and free-living microbes through chemoautolithotrophy or methanotrophy. Chemosynthetic communities are highly productive, compared to the surrounding benthic areas.

Discovered nearly 40 years ago (Corliss et al., 1979; Paull et al., 1984), and intensively studied since then (Van Dover, 2000; German et al., 2011; Levin et al., 2016 and others), vent and seep communities are still of great research interest. This includes: faunistic and ecological distinctiveness of chemosynthetic communities, adaptations to extreme conditions and understanding the evolution of marine ecosystems. Recent proposals for seabed mineral exploitation also require knowledge on chemosynthetic ecosystems for rational management decisions (Jones et al., 2020; Van Dover et al., 2018).

1. Previous biological research in the Bering Sea

The Bering Sea links the Pacific and Arctic Oceans (Fig. 1). The north-eastern part of the Sea is located on a vast shelf (depth <200 m) and is connected to the Chukchi Sea by the shallow (36 m) Bering Strait. The southwestern Bering Sea is deep-water, divided by underwater ridges into three basins (Aleutskaya, Bowers and Komandorskaya) with depths of more than 3000 m. It is connected to the Pacific Ocean through numerous straits (Dobrovolsky and Zalogin, 1982; Mazarovich, 2006).

Bering Sea continental slopes are among the most productive areas in the World Ocean, supporting the marine fisheries of the United States and Russia (Springer and McRoy, 1993; Springer et al., 1996; Sorokin, 1999; Shuntov, 2001; National Marine Fisheries Service, 2022). The high productivity and economic significance of the Bering Sea contribute to a considerable interest in its study (Zabanbark, 2009; Wiese et al., 2012; Crane and Ostrovskiy, 2015; Moore and Stabeno, 2015; Bergman et al., 2016; Portnyagin et al., 2016; Lavrenova et al., 2020). This interest has increased in recent decades, when significant changes in ecosystems have been registered (Huntington et al., 2020; Waga and Hirawake, 2020; Cai et al., 2021; Chylek et al., 2022; Logerwell et al., 2022).

The first regular studies of the deep-sea ecosystems of the Bering Sea began in the second half of the last century in the multidisciplinary expeditions of the R/V *Vityaz* (Kusakin and Chavtur, 2000). During the 5th, 8th, 10th, 13th and 16th cruises of the R/V *Vityaz*, extensive material was obtained on the deep-sea bottom communities of the Bering Sea (Research Vessel Vityaz, 1983; Vinogradova and Filatova, 1983). Together with faunistic studies of the shelf and the upper part of the continental slope (e.g., Deryugin, Ivanova, 1937; Filatova, 1938; Vinogradov, 1954; Lus and Kuznetsov, 1961; Neiman, 1961; Koblikov and Nadtochy, 2002; Nadtochy et al., 2008, 2017a, b; Shuntov et al., 2014 etc.), studies on biogeography and ecology including investigation of the composition, structure and functioning of deep-sea communities were conducted (e.g., Belyaev, 1960; Filatova, 1960; Filatova and Neiman, 1963; Filatova and Barsanova, 1964; Kuzneztsov, 1964; Galkin, Turpaeva, 1994; Shuntov, 2001; etc.).

2. Early discoveries of hydrothermal vents and methane seeps in the Bering Sea

However, despite intensive research, chemosynthetic communities were not known in the Bering Sea until 1990. In 1981, in the southern part of the Commander Basin, during the 12th cruise of the R/V *Vulkanologist*, positive forms of seabed relief were identified (Seliverstov, 1983), later described as the Volcanologists Massif and Piip Volcano (Seliverstov et al., 1986). Subsequently, scientific expeditions on the R/V *Vulkanologist* (1986-1989, 1991), R/V *Akademik Mstislav Keldysh* (1990), R/V *Professor Khromov* (2004), R/V Sonne (2009, 2016) intensively studied the massif (Sagalevich et al., 1992; Glasby et al., 2006; Seliverstov, 2009; Dullo et al., 2009; Werner et al., 2016). Data on the geological structure of the massif, its origin and hydrothermal activity were obtained (Bogdanova et al., 1990; Sagalevich et al., 1992; Taran et al., 1992; Torokhov and Taran, 1994; Yogodzinski et al., 1994; Bogdanov et al., 2006; Seliverstov, 2009; Melekestsev, 2014), and detailed bathymetric maps were produced (Baranov et al., 2021).

In 1990, on the 22nd cruise of the R/V *Akademik Mstislav Keldysh*, four dives of the HOVs Mir-1 and Mir-2 were conducted in the vicinity of the Piip Volcano. These studies provided data on the composition, structure, and distribution of the communities for the first time (Sagalevich et al., 1992). Numerous hydrothermal vents, active edifices, and extensive bacterial mats were identified on the Northern (min depth 368 m) and Southern (min depth 464 m) summits of the volcano, and chemosymbiotrophic bivalves, *Calyptogena pacifica,* were found on the Southern Summit. The Piip Volcano thus became the northernmost active hydrothermal vent area in the Pacific Ocean.

In addition to hydrothermal vent activity, in the western Bering Sea on the Koryak slope, possible gas hydrate-bearing structures were identified in the Khatyr sedimentary basin (Gretskaya and Petrovskaya, 2010), in close proximity to which high-intensity methane anomalies (up to 1600 nl/l) in the bottom layer were recorded in 1992 (Shakirov, 2018), suggesting the presence of seeps. Chemosymbiotrophic bivalve molluscs of the families Vesicomyidae (Pliocardiinae) and Solemyidae were found in the by-catch of bottom trawls at depths of 160-740 m (Danilin, 2013; Kolpakov et al., 2019). This area is proposed to name after Chingiz M. Nigmatullin (AtlantNIRO, Kaliningrad, Russia), who collected vesicomyids on the Koryak slope for the first time (Danilin, 2013).

3. Results of the cruises of R/V *Akademik M.A. Lavrentyev* (2016-2021)

From 2016 to 2021, three expeditions on the R/V *Akademik M.A. Lavrentyev* studied deep-sea hydrothermal vent and methane seep ecosystems in the western part of the Bering Sea using the ROV *Comanche 18*. A total of 32 dives were performed on the Volcanologists Massif and adjacent areas (368-4278 m) and 16 dives on the Koryak slope (356-906 m). The observations were accompanied by CTD measurements, photography and video recording, sampling of fauna, water, and bottom sediments. During the expeditions, new data on the ecosystems of the Piip Volcano were obtained (Galkin and Ivin, 2019; Marin, 2020; Demina et al., 2021 and others); on the Koryak slope, the presence of chemosynthesis-based communities in the upper bathyal zone, at the depths 400-695 m, were confirmed and studied using the ROV.

Early studies of video and still images and collected specimens showed that the benthic communities were characterized by a high abundance and diversity of meio-, macro- and megafauna, with a pronounced vertical and horizontal zonation in faunal distribution (Sanamyan et al., 2018, 2021; Sanamyan & Sanamyan, 2018; Galkin, Ivin, 2019; Galkin et al., 2019; Vinogradov and Galkin, 2019; Adrianov and Maiorova, 2020; Mordukhovich et al., 2020; Rybakova et al., 2020; Garlitska et al., 2022; Menshenina and Tabachnik, 2022; Mordukhovich et al., 2022; Tabachnik et al., 2022; Zograf and Mordukhovich, 2022; Kantor et al., 2023; Nekhaev, 2023).

A more detailed description of the results of cruises of the R/V *Akademik M.A. Lavrentyev* (2016-2021) forms the basis of this special issue of 22 articles on the chemosynthetic communities. The paper by Demina et al. (2022, this issue) examines the composition of the issuing fluids and the distribution of essential and potentially toxic chemical elements in the benthic organisms, biotope water, and surface sediments in the methane seep areas of the Bering Sea.

Fungal diversity in vicinity of the Piip Volcano and the composition of the major fatty acids in fungi strains are studied in the paper by Borzykh et al. (2022, this issue). A total of 11 species from three Ascomycota genera (*Aspergillus*, *Penicillium*, and *Cladosporium*) were recorded.

Papers by Adrianov and Maiorova (2022a, 2022b, this issue) focus on taxonomy, ecology and distribution of kinorhynchs. Three species of kinorhynchs, including one new to science were found for the first time in cold methane seeps in the Bering Sea and in the Pacific as a whole. The paper by Mordukhovich et al. (2023, this issue) contains an analysis of morphological and molecular data and distribution of the genus *Desmodora* (Nematoda), which is the dominant genus in the hydrothermal vent communities of the Piip Volcano. Three new species were described, two of which appeared to specialize for hydrothermal vents. Stabile isotope and fatty lipid analyses of *Desmodora* from vent habitats confirmed the consumption of chemosynthetically derived organic matter.

Demospongiae were abundant at hydrothermal vent habitats and at their periphery (Shilov et al. 2022, this issue), with a pronounced dominance of a single newly described species. Isotopic analysis of this species suggests possible symbiosis with chemosynthetic bacteria. The vertical distributions of demosponges were characterized by a distinct zonation pattern. Altogether four new species of vulcanellid sponges were described.

Cnidarians were very numerous and diverse in both chemosynthetic and regular habitats. The paper by Prudkovsky et al. (2022, this issue) addresses the taxonomic diversity and distribution of hydrozoans from the Volcanologists Massif and the adjacent area (~3360–3930 m depth) and at methane seep communities on the Koryak slope (~660 m depth). Two new species of large hydrozoans were described. In methane seep habitats, hydroids were particularly varied and abundant, forming numerous so-called "hydroid bushes" attached to carbonate crusts and pebbles. Two mass species of sea anemones of the genus *Sagartiogeton* were reported from reducing environments of the Bering Sea (Sanamyan et al., 2023, this issue). One species was found at both seep and background sites on the Koryak slope and at hydrothermal vents on the Piip Volcano. Another new species formed crowded settlements in hydrothermal vent areas on the Northern summit of the Piip Volcano. Isotope analysis showed a non-chemosynthetic origin of food for both species and no site-specific differences between anemones from background and methane seep communities.

The composition and structure of the polychaete fauna from the Piip Volcano and the Koryak slope were examined in papers by Alalykina (2022, this issue) and Alalykina and Polyakova (2022, this issue). Two new species of the genus *Ophryotrocha* from methane seep habitats were described using morphology and molecular data. Considerable differences were revealed between polychaete assemblages of the vent, seep, and background habitats.

The paper by Chernyshev and Polyakova (2022, this issue) contains a phylogenetic analysis of nemerteans from different regions of the World Ocean, including four species collected from the Bering Sea, based on five gene markers. One new species of genus *Cerebratulus* was described.

Crustaceans were found to be very abundant in the vent and seep habitats including bacterial mats and *Calyptogena*-beds. The distribution of Leptostracans (Phyllocarida), known from reducing habitats, was discussed and a new species, from the hydrothermal vent fields of the Piip Volcano, was identified through molecular and morphological analysis (Hirata et al. 2023, this issue). The body surface of the new species was covered with a variety of epibiotic bacteria. The paper by Malyutina & Golovan (2022, this issue) focuses on fauna of asellote isopods. Three species were found at hydrothermal vents of the Piip Volcano, including two new species of the family Munnopsidae. Munnopsids were one of the most abundant macrofaunal species on bacterial mats on the Southern summit of the volcano with a density of up to 40 individuals per square decimetre. Morphological adaptations of these species for reducing habitats are discussed. Paramunnid isopods from the vicinity of methane seep area on the Koryak slope were studied in the paper by Golovan and Malyutina (2022, this issue). Four species were found, two of which are new to science and the first paramunnids known from the bathyal of the Bering Sea. Deep-sea colonization is also discussed in the paper by Kireev et al. (2023, this issue) for the amphipod family Caprellidae. Among the three caprellid species collected from the Volcanologists Massif, there was a new species of the subfamily Paracercopinae and a first recorded abyssal species for the subfamily.

The paper by Nekhaev et al. (2022, this issue) examines the composition, distribution and ecology of shell-bearing gastropods from seep and vent habitats of the Bering Sea. Of 27 recognizable taxonomic units (RTUs), at least six presumably belong to new species. Only nine RTUs were found on the Piip Volcano, among which there was one new species of the family Provannidae, described in the paper by Chaban et al. (2022, this issue) as potentially obligate for chemosynthesis-based communities. Nineteen RTUs were identified in the methane seeps of the Koryak slope, however no taxa specific for chemosynthesis-based communities were recorded. On the Koryak slope, a low density of gastropods, with relatively high species diversity, was observed, while in the hydrothermal zone of the Piip Volcano low species diversity in aggregated settlements was recorded.

Five species of deep-sea acorn worms (Enteropneusta) were found in the Bering Sea on the Volcanologists Massif and adjacent area at depths between 1830 and 4278 m and on the Koryak slope between 419 and 662 m (Ezhova et al., 2022, this issue). Four of the species were only observed: two on the Koryak slope in the vicinity of methane seeps and two on the Volcanologists Massif. The fifth species was collected and examined using morphological and molecular methods. The abundance of this species in the soft-sediment community at the depth 1830–2290 m was up to 12 specimens per m^2, the highest ever recorded for any deep-sea enteropneusts. Holothurians, in particular, the genus *Pannychia,* were another dominant group of megafauna on the slopes of the Volcanologists Massif. On the basis of molecular analysis and morphological comparison, two species of *Pannychia* with different distribution patterns were distinguished (Ogawa et al., 2022, this issue).

The preliminary studies have suggested that the high abundance of acorn worms on the slopes of the Volcanologists Massif was supported by high phytoplankton productivity in the photic layer (Ezhova et al., 2021). This assumption was confirmed by the results of studying the food preferences of four common deep-sea species of holothurians on the slopes of the Volcanologists Massif based on stable isotope and fatty acid analyses (Rodkina et al., 2023, this issue). A large amount of primary production in the upper layers of the Bering Sea provides high quality sedimentary organic matter for deposit feeders, even at the greatest depths. Moreover, some dominant species in areas of hydrothermal vents and cold seeps preferentially consume organic matter of photosynthetic origin (Sanamyan et al., 2023, this issue). At the same time, organic matter of chemosynthetic origin forms a great contribution to the diet of some species of meio- and macrofauna (Mordukhovich et al., 2023, this issue; Shilov et al., 2023, this issue).

In general, 335 macrofaunal species were identified from benthic communities on the Koryak slope at the depths from 400 m to 695 m. The shallower methane seeps (400-429 m) were dominated by background species, despite numerous extensive bacterial mats and the high potential toxicity of the environment. E.g., seeps at 417–429 m were dominated by the echinoid *Brisaster latifrons* with a population density on bacterial mats four times higher than in background areas. The deepest seep communities at 647–695 m were dominated by the chemosymbiotrophic pliocardiine *Calyptogena pacifica* and were characterized by the highest species richness, relatively high evenness and strong variations in the composition and structure. The pattern of variation in diversity with depth could be related, in part, to increased habitat heterogeneity associated with carbonate crusts and clam beds occurring only at deeper methane seeps. Four chemosymbiotrophic species were recorded at 647–695 m and only one was found at shallower depths. Polychaetes of the genus *Neosabellides* and *Ophryotrocha*, potentially obligate to reducing habitats, occurred in methane seep communities at all depths (Rybakova et al., 2022, this issue).

The distinctive features of macro- and megafaunal vent communities of the Piip Volcano were the significant number of taxa, obligate for reducing habitats, at different taxonomic levels, including family- and subfamily-levels, and abundances of sedentary organisms, including sea anemones, demosponges, calcareous sponges and benthopelagic Trachimedusa. In total, 130 species of macro- and megafauna were found, of which ~25% were new to science. Of the fauna, 9 species (7%) were obligate, or potentially obligate, to environments with access to reduced chemicals (Rybakova et al., 2023, in this issue).

The articles in this special issue are part of an ongoing study of chemosynthesis-based communities of the Bering Sea. Investigations of collected materials are still underway to will clarify taxonomy of different species, their ecology, distribution patterns, and relationships of chemosynthesis-based ecosystems from different regions.

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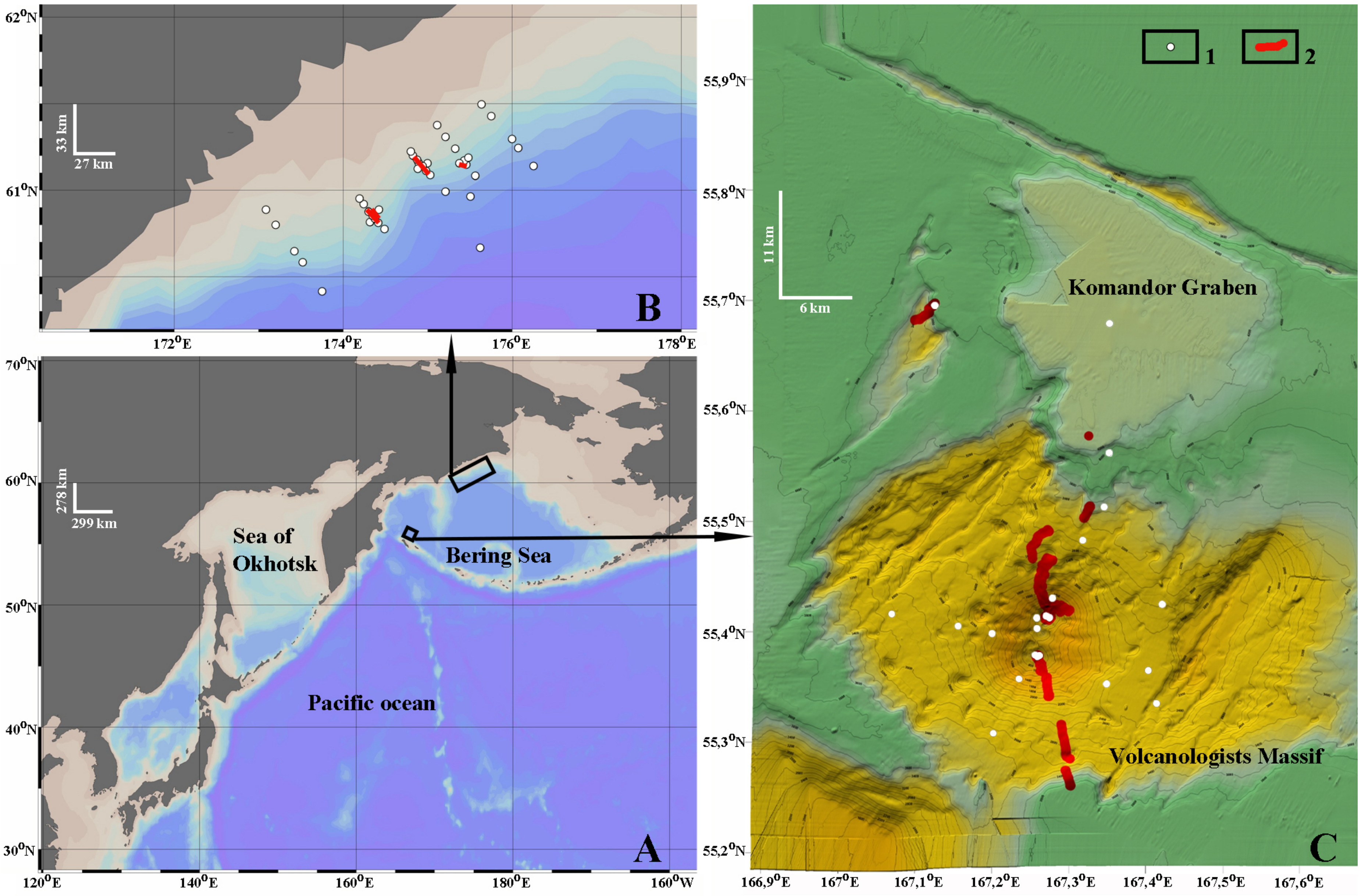
Figure captions

Figure 1. Map of the study areas. A – general map; B – area of the Koryak slope; C – area of the Volcanologists Massif (Baranov et al., 2021). 1 – CTD and gas-geochemical stations; 2 – ROV tracks.



62⁰N
61⁰N
33 km
27 km
172⁰E
174⁰E
176⁰E
178⁰E
B
70⁰N
60⁰N
50⁰N
40⁰N
30⁰N
278 km
299 km
Sea of Okhotsk
Bering Sea
Pacific ocean
120⁰E
140⁰E
160⁰E
180⁰E
160⁰W
A
1
2
55,9⁰N
55,8⁰N
55,7⁰N
55,6⁰N
55,5⁰N
55,4⁰N
55,3⁰N
55,2⁰N
11 km
6 km
Komandor Graben
Volcanologists Massif
166,9⁰E
167⁰E
167,1⁰E
167,2⁰E
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