Biogeographic Atlas of the Deep NW Pacific Fauna

edited by

Hanieh Saeedi and Angelika Brandt

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FOREWORD

Maria Baker – University of Southampton, UK &
Tammy Horton – National Oceanography Centre, Southampton, UK

Only 150 years ago, life in the deep oceans was virtually unknown. Reaching these depths was a goal of early explorers and naturalists, such as those of the Challenger Expedition (1872–76). They were rewarded with astonishing discoveries of a wealth of diverse life in the deep sea. Since these early ventures, expeditions to study this realm have increased in regularity and scope, continuing to reveal extraordinary life-forms across the globe.

Experts in deep-sea taxonomy and ecology have worked together for four Russian-German and German-Russian expeditions in the NW Pacific deep sea (Sea of Japan, Sea of Okhotsk, Kuril-Kamchatka abyssal plain and the Kuril-Kamchatka Trench). This book provides a summary of the findings of these experts following the many hours of subsequent sample-processing and analyses, revealing a treasure trove of critical fundamental knowledge of life in our deep oceans.

Human influence in remote deep-sea ecosystems is rapidly increasing. Exploitation of abiotic and biotic resources and the varied use of the vast space on the seafloor and deep water-column is realised through advancing technologies and the growing need by a growing population for materials, food and new genetic resources. Today, the entire deep ocean is affected by human pressures including fishing, pollution, climate change, with new emerging industries such as deep seabed mining on the horizon. A quarter of all species described on our planet are threatened with extinction due to human activities, yet most deep-sea animals are not yet even known to science. Their discovery and description of unknown species is at the heart of biology. Taxonomists provide this critical baseline knowledge. The Deep-Ocean Stewardship Initiative (www.dosi-project.org) has a vision of a healthy deep ocean able to contribute to the wider Earth system, through its sustainable management informed by independent science. The information gleaned by this project and published in the "Biogeographic Atlas of the Deep NW Pacific Fauna" will be used to further deep-ocean stewardship via the dedicated science-policy interface facilitated by DOSI.

In order to effectively manage activities in the deep sea, fundamental baseline biodiversity data are needed upon which to base predictive models and appropriate and operational legislation. Such datasets are rare, with basic information on the taxonomy, biodiversity, and biogeography of many faunal groups lacking, or found across numerous disparate sources. This new volume brings together for the first time this much-needed knowledge on the NW Pacific fauna > 2,000 m.

We wish to applaud the devoted and timely work of the chief editors of this book, Hanieh Saeedi and Angelika Brandt, for bringing together this rich, revealing and important work of global significance. The importance of taxonomic expertise in the provision of baseline biogeographic data is clearly evident in this book. A comparatively small group of dedicated experts worldwide work hard to identify, describe and study our deep-sea fauna gaining indispensable knowledge for humankind. We thank them all.

CHAPTER 1

INTRODUCTION

BIOGEOGRAPHIC ATLAS OF THE DEEP NW PACIFIC FAUNA

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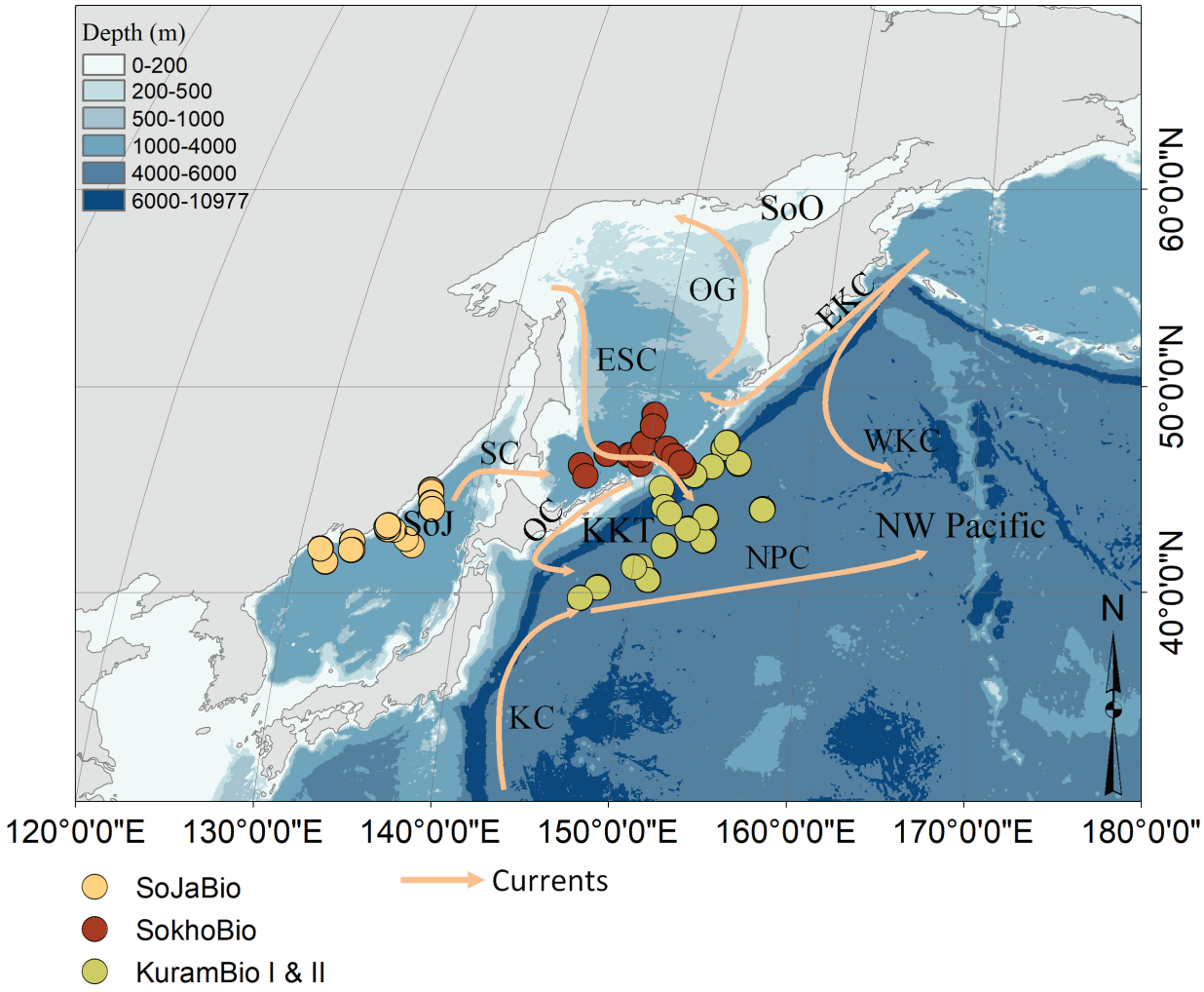
1. The deep NW Pacific

The deep sea is the largest, but the least explored environment on Earth. However, less than 0.0001% of the deep sea (deeper than 200 m) has been explored so far, making it the least explored environment on Earth (Brandt and Malyutina 2015; Danovaro et al. 2017). Deep-sea macrobenthos are speculated to comprise about 25 million species; meiofauna seems to be composed of 20 to 30 million species (Adrianov 2004), in contradiction with what was estimated previously for deep-sea macrofauna (between 0.5 and 10 million species) (Brandt et al. 2007a; Brandt et al. 2007b; Grassle and Maciolek 1992). Appeltans et al. (2012) predicted that 100,000 species will be described in the next 50 years if the rate of 2,000 new species description per year maintains in the future (Appeltans et al. 2012). Recent expeditions in the framework of the Census of Marine Life have documented that deep-sea biodiversity is very unevenly distributed in different oceans and ocean basins (Ramirez-Llodra et al. 2010). However, some mechanisms have been identified that can cause high local species concentrations (e.g., productivity and isolation) (Brandt et al. 2007a; Gibson et al. 2002; Levin et al. 2001; Saeedi et al. 2019a; Smith and Stockley 2005).

The NW Pacific is one of the most productive, nutrient rich, and diverse regions of the World Ocean, and includes several deep-sea basins diverging in depths, hydrology, and isolation (Grebmeier et al. 2006; Leprieur et al. 2016; Renema et al. 2008; Saeedi et al. 2019b). The Sea of Japan, the warm temperate zone of the NW Pacific, and the Kuril-Kamchatka Trench (KKT) receive two major currents: the warm Tsushima and cold Oyashio currents (Fujikura et al. 2010; Su et al. 1990) (Map 1). The Tsushima Current splits from the Kuroshio Current and flows from off Kyushu into the Sea of Japan. The Oyashio Current flows southward through Japanese waters from off Hokkaido along the Pacific coast (Fujikura et al. 2010; Su et al. 1990). The tropical and subtropical parts of the western Pacific host the highest number of marine species around the world (Asaad et al. 2018; Crame 2000; Jablonski et al. 2006; Krug et al. 2008; Sanciangco et al. 2013). Some areas of the Sea of Japan, Sea of Okhotsk, and Kuril-Kamchatka Trench (KKT) have been specifically sampled and studied by deep-sea scientists (Brandt et al. 2020; Brandt and Malyutina 2015; Malyutina and Brandt 2013; Malyutina et al. 2018). In the next few paragraphs we review the geography and hydrology of these three ecosystems.

1.1. Sea of Japan

The Sea of Japan is a young and broadly enclosed marginal sea of the NW Pacific (Fujikura et al. 2010; Malyutina and Brandt 2013; Su et al. 1990). The Sea of Japan is geographically isolated and has an abnormally high level of dissolved oxygen in its deeper parts; however, its bottom-water oxygen level has declined up to 8–10% in the past three decades (Elsner et al. 2013; Huang et al. 2019; Huang et al. 2018). The abyssal depths of the Sea of Japan were formed in the Cenozoic as a caldera of the mainland (Malyutina and Brandt 2013). The largest and deepest part of the Sea of Japan is the Japan Basin, reaching a depth of ca. 3,800 m. The two other deep basins are the Yamato and the Tsushima (Ulleung), which are separated from the Japan Basin by the Yamato Rise (Fig. 1 in Malyutina & Brandt 2013). The Sea of Japan has been and still is connected



Map 1. Study area, sampling locations, and currents in three areas from four expeditions. Colored circles show 418 sampling effort coordinate points (per sampling gear per station per cruise) during four deep-sea cruises including Sea of Japan Biodiversity Study (SoJaBio, 2010), Kuril-Kamchatka Biodiversity Study (KuramBio I and II, 2012–2016), and Sea of Okhotsk Biodiversity Study (SokhoBio, 2015). The area KuramBio is represented by the two expeditions KuramBio I in 2012 (open abyssal of NW Pacific) and Sea of Okhotsk; SoJ: Sea of Japan; KKT: Kuril-Kamchatka Trench; EKC: East Kuril Current; ESC: East Sakhalin Current; KC: Kuroshio Current; NPC: North Pacific Current; OC: Oyashio Current; OG: Okhotsk Gyre; SC: Soya Warm Current; WKC: West Kuril Current. ArcMap 10.5.1 was used to create this figure.

to the Pacific Ocean through two shallow straits, the Tsushima Strait in the south (about 140 m depth), and the Tsugaru Strait between Honshu and Hokkaido in the north (about 130 m depth) (Malyutina and Brandt 2013). Two even shallower straits, the Soya Strait (La Perouse) between Hokkaido and Sakhalin (50–53 m depth), and the Tatar Strait between Sakhalin and the Asian continent (around 10 m depth) connect the Sea of Japan to the Sea of Okhotsk (Malyutina & Brandt 2013). However, the Sea of Japan is isolated by shallower straits compared to the Sea of Okhotsk and this isolation may affect species and community composition, endemicity, and biodiversity in this area (Brandt et al. 2019; Brandt et al. 2013; Golovan et al. 2013; Kamenev 2013; Malyutina and Brandt 2013; Saeedi et al. 2019b; Saeedi et al. 2019d; 2020).

1.2. Sea of Okhotsk

The Sea of Okhotsk is a marginal sea which is separated by the Kuril Islands (on the southeast) and the Kamchatka Peninsula (on the east) from the Pacific Ocean. The Sakhalin Islands are located in the western part of the Sea of Okhotsk where it is connected to the Sea of Japan on either side of Sakhalin. The total area of the Sea of Okhotsk is 1,616,700 km^2 and the abyssal zone occupies ca. 8% of this total area (Glukhovsky 1998; Malyutina et al. 2018). The Kuril Basin with a maximum depth of 3,372 m is the deepest and oldest part of the Sea of Okhotsk. There is water exchange between the abyssal Kuril Basin and the Pacific Ocean via the bathyal depths of the Krusenstern and Bussol straits allowing the exchange of reproductive propagules of the pelagic and benthic fauna between these two body waters (Malyutina et al. 2018; Tyler 2002).

1.3. Kuril-Kamchatka Trench (KKT)

The KKT is an oceanic trench in the NW Pacific. The Kamchatka Strait (KS) with a width of 190 km is located between the Kamchatka Peninsula and the Bering Island, and occupies 46% of the total area of the straits connecting the Bering Sea and the Pacific Ocean (Prants et al. 2013; Stabeno 1999). The maximum depth of the Kamchatka Strait, connecting the Kuril-Kamchatka Trench to the Aleutian Trench, is 4,420 m, and because it is deeper than the maximum depth of the Bering Sea, Kamchatka Strait water content can penetrate all the depths of the basin (Prants et al. 2013; Stabeno 1999). The KKT area is strongly influenced by the Kamchatka Current, which transports water from the Bering Sea (Prants et al. 2013; Sattarova and Artemova 2015). The water temperature of the Kamchatka Current ranges between 0 to 5°C in winter and 8 to 16°C in summer depending on winter conditions in the Okhotsk and Bering seas (Sattarova and Artemova 2015). The water transport through the KS and straits of the Aleutian Island chain plays an important role in the volume, heat, and nutrient fluxes between the Bering Sea and the North Pacific (Prants et al. 2013; Sattarova and Artemova 2015; Stabeno 1999). The climate of this area is controlled by monsoon circulation, which defines the climatological features and weather conditions, particularly large seasonal variations in temperature as well as air and water in the surface layers (Sattarova and Artemova 2015).

2. Expedition history and motivation

Several biological expeditions to the deep NW Pacific onboard the Russian RV *Vityaz* were performed between 1949 to 1966. The data found on faunal taxonomic description, hydrology, topography, chemical characteristics, and organic matter of the Kuril-Kamchatka Trench (KKT) and the adjacent abyssal plain area were reported in many publications (Belyaev 1989; Belyaev 1983; Ushakov 1953; Vinogradova 1977; Zenkevitch et al. 1955). Moreover, Sirenko et al. (2013) published a check list of species of free-living invertebrates of the Russian Far Eastern Seas. Isopoda (Crustacea) was one of the dominant taxa in species richness of the abyssal KKT area and one of the most well studied (Birstein 1970; 1971; Birstein 1963; Kussakin 1971; 1988; 1999; Kussakin and Vasina 1990; Kussakin 2004).

In the past decade, the biology of the bathyal, abyssal, and hadal faunas of all size classes (meio- macro-, and megabenthos) of the NW Pacific have been intensively investigated based on a Memorandum of Understanding (2007) between Russian and German partners. A total of four Russian-German and German-Russian expeditions (with the RV *Akademik M.A. Lavrentyev* and RV *Sonne*) have provided a wealth of data on the systematics, evolution, and biogeography of the deep-sea faunas of the Sea of Japan (SoJaBio 2010) (Malyutina and Brandt 2013), Sea of Okhotsk (SokhoBio 2015) (Malyutina et al. 2018), the Kuril-Kamchatka Trench (KKT), and the NW Pacific open abyssal plain adjacent to the KKT (KuramBio I and II, 2012–2016) (Brandt et al. 2019; Brandt et al. 2018; Brandt et al. 2020; Brandt and Malyutina 2015) (Map 1). All specimens were collected using standard gear (CTD, MUC (multicorer), GKG (giant box corer), EBS (epibenthic sledge), AGT (Agassiz Trawl), WT (bottom trawl) (Brandt and Malyutina 2014), BC (box corer) (Brandt et al. 2010), and PN (plankton net) (Chernyshev and Polyakova 2018) being deployed following a standardized method (Brandt and Malyutina 2014).

The goals of these expeditions were to study the biodiversity, biogeography, and evolution of the benthic organisms in different NW Pacific deep-sea environments. We aimed to compare more isolated deep-sea basins with more easily accessible ones (Sea of Japan vs. Sea of Okhotsk) and to test whether the hadal bottom of the trench of the KKT isolates the fauna from the Sea of Okhotsk to the fauna of the open NW Pacific area. The faunal composition of these areas comprising systematic, ecological, and biogeographical data, as well as evolution of protists, selected invertebrate taxa and fish, has been published in four scientific volumes, and includes the formal descriptions of many species, some genera, and one family (Brandt et al. 2020; Brandt and Malyutina 2015; Malyutina and Brandt 2013; Malyutina et al. 2018; Saeedi et al. 2020).

Based on these expeditions, the **Beneficial** project (**B**iog**e**ography of the **n**orthwest Pacific fauna. A benchmark study for **e**stimations o**f** alien **i**nvasions into the Ar**c**tic Ocean **i**n times of r**a**pid c**l**imate chance) was designed. The main aims of the Beneficial project were 1- digitizing the biodiversity and environmental data collected during our expeditions, 2- discovering the deep-sea biogeography and biodiversity patterns in the NW Pacific, 3- predicting the potential future distribution range shifts of key species from the NW Pacific to the Arctic Ocean under rapid climate change, and 4- compiling a novel book on the taxonomy and biogeography of the highly abundant key species. All the data, publications, and the book arising from this project provide crucial benchmarks and datasets for any deep-sea biodiversity assessment, and help predict the future status of the Arctic marine ecosystem in a changing environment (Brandt et al. 2020; Canonico et al. 2019; Saeedi et al. 2019b; Saeedi et al. 2019c; Saeedi et al. 2019d; 2020; Saeedi et al. 2019e).

3. The Beneficial project highlights

We mined and mobilized 7,042 unique deep-sea benthos taxa records, with 1,723 records at the species level (more than 50% at the species

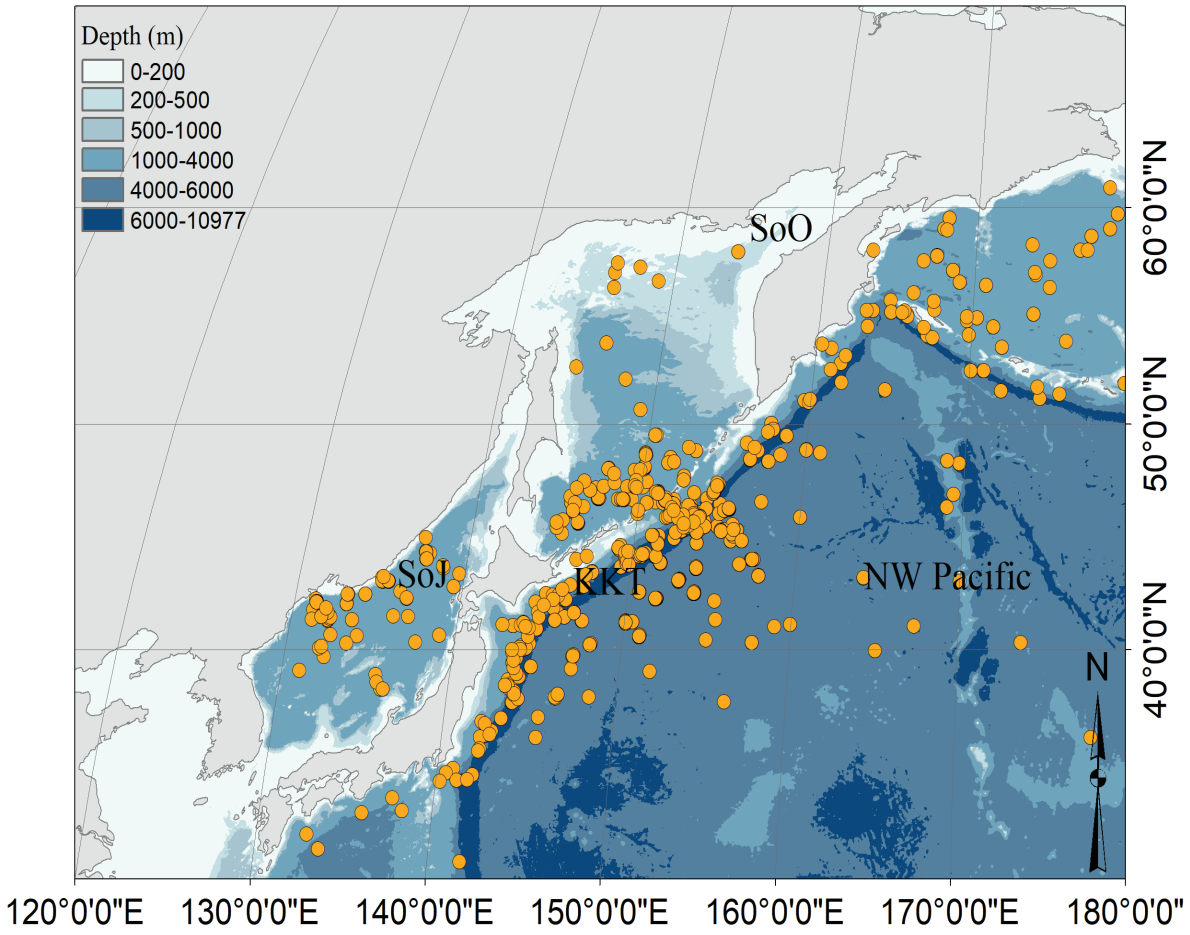
and genus level, the rest were at the higher taxa level, mostly family, order, and class) from our four deep-sea cruises including SoJaBio, SokhoBio, and KuramBio I and II (Saeedi et al. 2019e). Using this dataset and data collected from the open-access databases, we analysed species richness, endemicity, and community composition in the shallow and deep NW Pacific and its adjacent Arctic Ocean (Saeedi et al. 2020, Brandt et al. 2020; Canonico et al. 2019; Saeedi et al. 2019b; Saeedi et al. 2019c; Saeedi et al. 2019d; Saeedi et al. 2019e). Our findings supported the hypothesis that biodiversity, while highest in the tropics and coastal depths (mostly in the Philippines), decreases at the equator and decreases at depths below ca. 2,000 m (Saeedi et al. 2019b; Saeedi et al. 2019d). Despite high species richness in the eastern Philippines, the Yellow Sea and Gulf of Tonkin had the highest benthic species endemicity rates (ca. 70%), while the Aleutian Islands had the highest pelagic endemicity rate (ca. 45%) among all different ecoregions (Saeedi et al. 2019b; Saeedi et al. 2019d). Our generalized linear models (GAMs) showed that the combined effects of all environmental predictors produced the best model driving species richness in both shallow and deep sea in the NW Pacific (Saeedi et al. 2019b; Saeedi et al. 2019d; 2020). However, among all predictors, dissolved oxygen, bottom temperature, and salinity were the most important environmental drivers of the deep-sea species richness in the NW Pacific and the adjacent Arctic Ocean (Saeedi et al. 2019b; Saeedi et al. 2019d; 2020). These investigations should strengthen and inform marine protection plans as species richness and endemicity hotspots could be profoundly compelling in helping to pinpoint and prevent biodiversity loss.

4. Book outline

This book is designed as a guide, synthesis, and review of the current knowledge of the benthic fauna in the NW Pacific. This book includes benthic species that are distributed in the bathyal and abyssal zones (below 2,000 m) of the NW Pacific (latitude ca. 30 to 60°N, longitude ca. 120 to 180°E) (Map 2). This book consists of 21 chapters, with an introduction followed by 20 chapters on taxonomy and biogeography of different deep-sea taxa including Porifera, Cnidaria, Brachiopoda, Entoprocta, Nemertea, Solenogastres, Bivalvia, Sipuncula, Polychaeta, Echiura, Nematoda, Kinorhyncha, Pygnogonida, Ascothoracida, Ostracoda, Decapoda, Amphipoda, Isopoda, Ascothoracida, Tanaidacea, Echinoidea and Asteroidea. The editors worked closely with the authors and ensured that the work being produced has suitable literary merit and is free from inconsistencies, including grammatical and spelling errors. However, all the chapters proofread by the authors and all authors must take public responsibility for the content of their chapter. A total number of 2,503 distribution records belonged to 503 deep-sea taxa were used in the 20 chapters of this book (Map 2). A list of species represented in this book is given in supplementary table 1 (https://doi.org/10.3897/ab.e51315.suppl-1). The highest numbers of distribution records used in this book were from latitudes 40–48°N belonging to the materials were collected during the four joint Russia-Germany expeditions (Map 3).

5. Taxonomic impediment

In this book, we aimed to include chapters on the major groups of benthic fauna that are especial-



Map 2. Distribution records of all 503 deep-sea taxa used in 20 chapters of this book (see supplementary table 1).

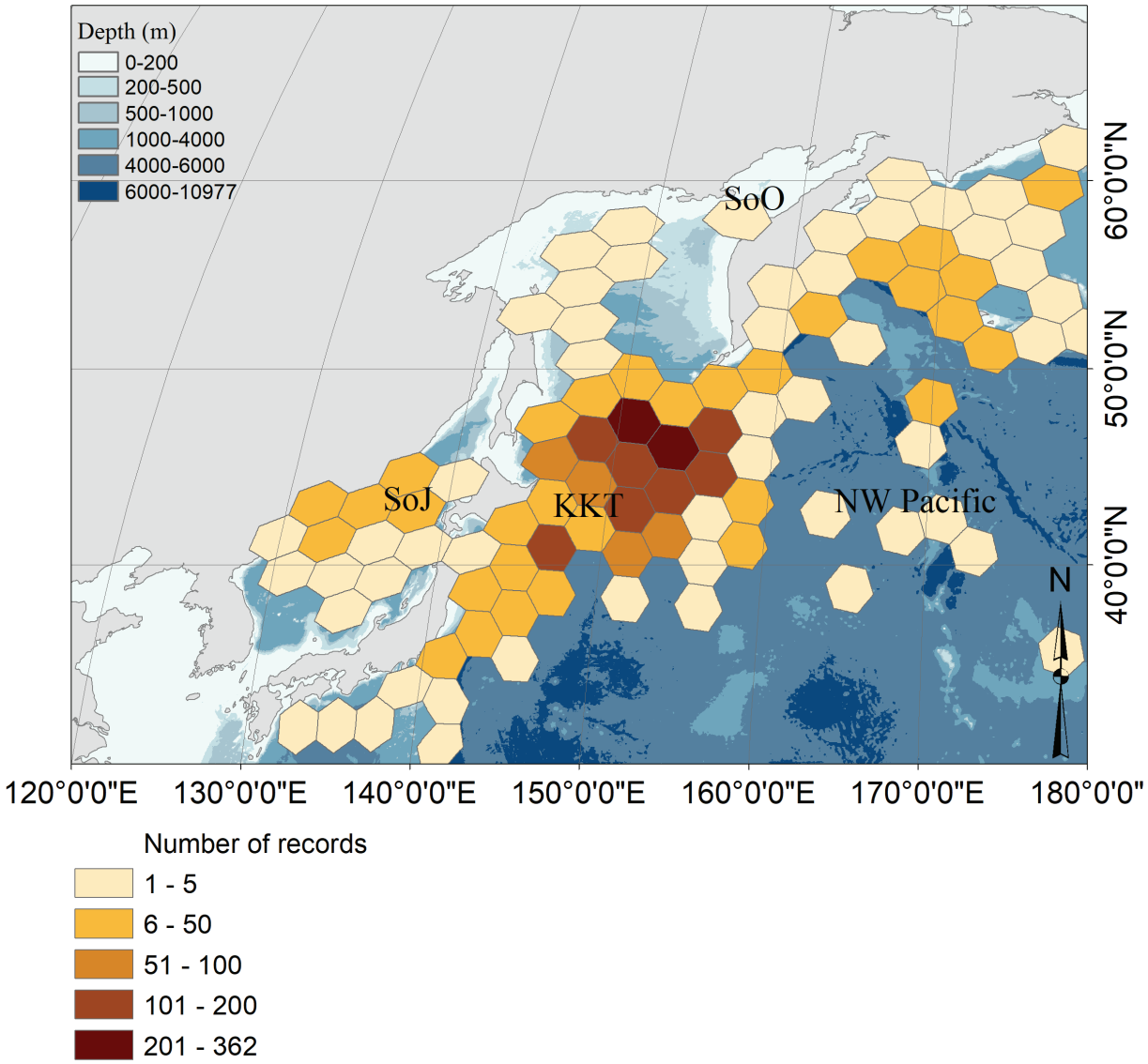
ly species rich (or being very diverse). However, for some taxa including Bryozoa, Harpacticoida, Crinoidea, Ophiuroidea, Holothuroidea, and Tunicata we were not able to find expert taxonomists with the time and/or the necessary skills to complete chapters.

6. Impacts of this book

In times of rapid climate change and increasing anthropogenic impact, a compilation of life at the seafloor in the deep sea, where environmental parameters resemble those of the Arctic Ocean, is urgently needed. To date; however, there has been no compilation and synthesis of deep-sea biodiversity in the deep NW Pacific excluding Sirenko's (2013) species list of free-living invertebrates of the Russian Far Eastern seas (Sirenko 2013). It is thus necessary to accurately assess deep-sea areas to establish biodiversity conservation plans and Marine Protected Areas (MPAs).

6.1. Biodiversity and ecosystem services

Based on such urgent needs, this book is very timely and provides not only insights into NW Pacific deep-sea benthic biodiversity and species compositions; but also forms a fundamental regional study of the NW Pacific required for understanding the ecosystem services (e.g., culture and human well-being, fisheries, water



Map 3. Total number of distribution records used in 20 chapters of this book calculated per ca. 50,000 km^2 hexagonal cells. The highest numbers of distribution records (100 to 362 records) used in this book were from latitudes 40–48°N belonging to the materials were collected during our four expeditions.

circulation and CO_2 exchange, and nutrient cycling) and decision-making assessments in order to prioritize conservation criteria across multiple biodiversity conservation initiatives and groups such as the Deep Ocean Stewardship Initiative (DOSI), International Seabed Authority (ISA), the Polar Prediction Project (PPP), the Intergovernmental Panel on Climate Change (IPCC), and Conservation of Arctic Flora and Fauna (CAFF). This book also represents an important backbone study for the United Nations Decade of Ocean Science for Sustainable Development assessment (2021–2030) to ensure that ocean science can support nations' activities to sustainably manage the oceans and to in particular to reach the goals of the 2030 Agenda for Sustainable Development such as sustainable consumption and production, natural resources management, effective institutions, good governance, and the rule of law and peaceful societies.

6.2. Climate change implications

Understanding and preserving the biodiversity of the NW Pacific is an important challenge in this area of rapid climate change, particularly given the potential of alien species invasions into the Arctic Ocean. There are already many benthic species shared between the NW Pacific and the adjacent Arctic Ocean (Saeedi et al. 2019d). Initially, an embayment of the North Pacific, the deep Arctic Ocean was impacted by the northern Pacific fauna until ca. 80 million years prior to the deep-water connection closed (Bodil et al. 2011). As Arctic Sea ice loss continues with its implications for governance, economics, and society (Carmack et al. 2015), this book provides information on highly abundant key species which might potentially invade the Arctic Ocean in future (both from hadal and also shallower deep-sea depths of the NW Pacific) under climate change scenarios including decreasing sea-ice conditions. Our data and book will serve as a solid basis and benchmark for predicting potential species invasions or migrations supported by the retreat of the Arctic Ocean sea ice.

6.3. Community and citizen science

This book is published as open-access and is this publically available to a broad range of communities including the deep-sea researchers and citizen scientists. The book contains taxonomic information and images that can be used by scientists as identification keys or for citizen science projects such as iNaturalist. The geographic distribution data provided in this book are a significant contribution to the open-access database communities, including the Global Biodiversity Information Facility (GBIF) and Ocean Biogeographic Information System (OBIS).

6.4. Science-policy interface

This book integrates information on distribution and biodiversity of many unique deep-sea species in the NW Pacific for the first time, providing fundamental information required by intergovernmental bodies such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES). This information can be used to assess the present and future status of deep-sea biodiversity as requested by governors and decision makers to improve the strategic plans for the conservation and sustainable use of biodiversity, long-term human well-being, and sustainable development.

Acknowledgements

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CHAPTER 2
PORIFERA

TAXONOMY AND BIOGEOGRAPHY OF PORIFERA ALONG THE NW PACIFIC

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1. Introduction

1.1. Biology and Ecology

Despite being the largest biome on Earth, deep-sea environments remain poorly mapped and understood, with our current knowledge of sponge distribution biased to regions with a history of deep-sea research (Hogg et al. 2010; Ramirez-Llodra et al. 2010). In the deep sea, below 2,000 m, 60 sponge families, 158 genera and 387 species are known to science (OBIS 2019). Globally, 4% of sponge species are known to occur at depths greater than 2,000 m and these are dominated by firstly demosponges (66% families, and 55% of both genera and species) and secondly hexactinellids (glass sponges) (23% families, 41% genera, and 44% species). Calcareous (five families, five genera, five spp.) and homoscleromorph sponges (1 family, genus and species) are not known to be rich in species, genera or families in the deep sea (van Soest et al. 2012).

In general, demosponges are far more dominant in the deep NW Pacific Ocean, in terms of species, compared to hexactinellids; however, there is variability noted in abundance, with the Sea of Okhotsk greatly dominated by hexactinellid individuals, whereas demosponge individuals dominate the Kuril-Kamchatka abyssal plain (Downey and Janussen 2015; Downey et al., 2018). Only one calcareous sponge specimen is known from the NW Pacific (Koltun 1970). All demosponges are composed of siliceous spicules and/or skeleton of spongin fibres, hexactinellids (glass sponges), are composed entirely of siliceous spicules, and calcareous sponges have calcified spicules (Van Soest et al. 2012). Many irregular growth forms are found within the demosponge class (Bergquist 1978); however, in the deep NW Pacific Ocean, stalked sponges were dominant (Figure 1). Hexactinellids are generally symmetrical, and can be composed of a stalk with a cup, or vase-like in shape, and these growth forms were both encountered in the NW Pacific Ocean. The small calcareous specimen

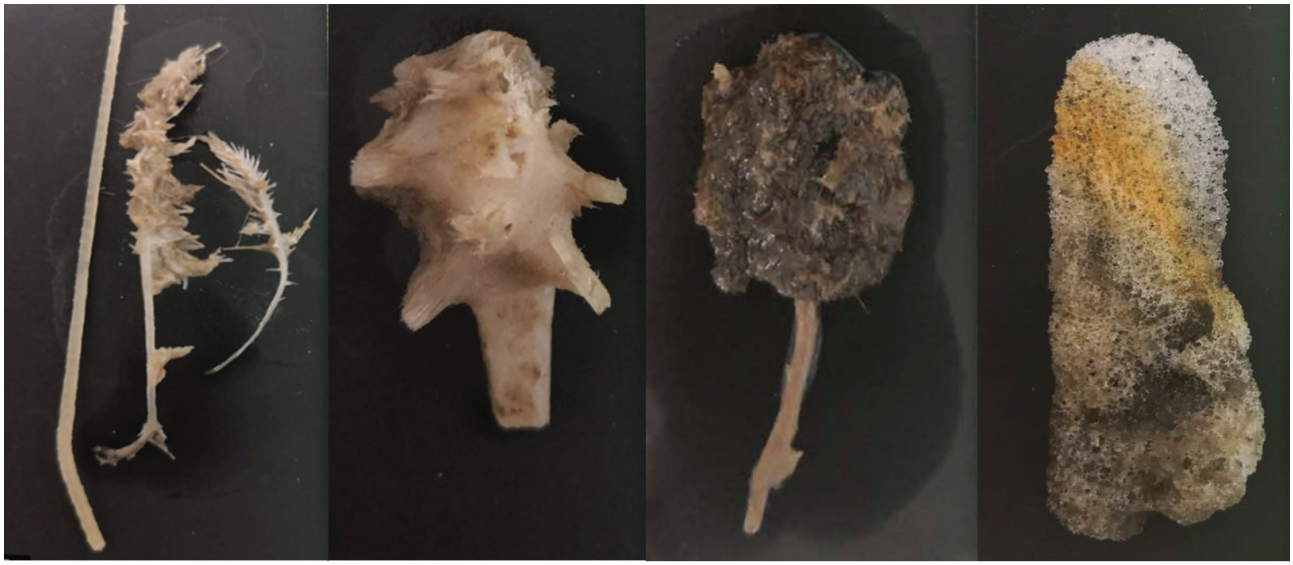


Figure 1. From left to right, several examples of branched carnivorous sponges and stalk and cup, and vase morphologies of hexactinellid sponges from the NW Pacific.

has not been observed by our team; however, it was likely to be either encrusting or tubular in morphology. Many hexactinellids and several deep-sea demosponge genera possess basal root tufts, stalks, and a fringe at the base of their bodies, which enable them to successfully anchor their bodies in deep-sea environments, where soft sediments are common (van Soest et al. 2012).

Sponges are generally filter feeders; however, in the deep sea, food supply can be scarce, and limited to particular seasons or oceanic current systems, and so sponge genera and species that live in this part of the ocean are highly adapted to sporadic food supplies (Gage and Tyler 1991; Smith et al. 2008). It has been found that filter-feeding sponges in the same habitat consume picoplankton to different efficiencies (Perea-Blázquez et al. 2013), and so despite food limitation, potentially many species can thrive in deep-sea regions. Hexactinellid sponges are often dominant components in the deep sea, including sectors of the NW Pacific (Koltun 1966, 1967, 1970; Downey et al. 2018), and contribute significantly to the biomass, species diversity and abundance in all deep-sea oceans (Tabachnick 1994; Reiswig 2002; Leys 2003). However, one diverse and abundant deep-sea sponge family has evolved carnivory, the Cladorhizidae Dendy, 1922, within the Demospongiae Sollas, 1885 class (Hestetun et al. 2016), likely as a novel adaptive response to reduced nutrient supply in the deep sea (Vacelet and Boury-Esnault 1995, 1996). These sponges have modified micro-skeletal features that are hook-like, enabling them to catch small invertebrates, such as crustaceans (Vacelet and Duport 2004). The Cladorhizidae family dominate in terms of species richness in the NW Pacific Ocean (Koltun 1970), particularly in the Sea of Okhotsk, in which they comprise two-thirds of all demosponges, and the Kuril-Kamchatka abyssal plain, in which nearly 90% of demosponge species are from this carnivorous family (Downey and Janussen 2015; Downey et al. 2018). Global analyses have indicated that the NW Pacific Ocean may be a global hotspot of this carnivorous family, with one known endemic genus (*Koltunicladia* Hestetun, Vacelet, Boury-Esnault, Borchiellini, Kelly, Rios, Cristobo & Rapp, 2016) and at this point 20% (35 spp.) of all known Cladorhizid species (173 spp., WORMS 2019), which includes identified species morphotypes from recent studies that have not been formerly described.

Deep-sea sponges are characteristically slow growing, can reach vast sizes, and are often long-lived (Hogg et al. 2010). Growth measurements of NW Pacific sponges have not been undertaken; however, deep-sea sponges in other sectors of the North Pacific have indicated that hexactinellid species grew very slowly, at 1.98 cm per year and individuals were likely to be 220 years old (Leys and Lauzon 1998). Another study dated deep-sea hexactinellid siliceous spicules from another species, and estimated an age of 11,000 years (Jochum et al. 2012). Due to their long lives, some deep-sea sponges can exhibit gigantism, growing to immense sizes, with the largest known individual, a hexactinellid from 2,117 m depth from the NW Hawaiian Islands, which was greater than 3.5 m in length (Wagner and Kelley 2016). However, in the NW Pacific Ocean, referring to the Sea of Okhotsk and the Kuril-Kamchatka abyssal plain, most sponges were less than 2 cm in height, with only small numbers of demosponges (typically from the Cladorhizidae family), and stalked hexactinellids, achieving

sizes greater than 5 cm (Downey and Janussen 2015). This dominance of smaller specimens could partly be due to the use of the epi-benthic sledge, which collects smaller macrofauna, picking up greater numbers of younger sponges and/or species exhibiting dwarfism. The use of trawl gear damages sponges, and so fragile glass sponges could have been significantly larger in the NW Pacific, and more characteristically typical of gigantism as seen in other sectors of the North Pacific Ocean.

Despite the likely slow-life of deep-sea sponges, recent research has found that these sponges are far more dynamic. There are few long-term studies of sponge demography and metabolism; however, one long-term study of hexactinellids in the adjacent NE Pacific found that these sponges responded positively to increases in food particulates, increasing their density and body size, and these fluctuated with changes in the ocean currents and gyres in this region (Kahn et al. 2012). This indicates that NW Pacific sponges could respond in a similar fashion, likely being dynamic in their response to seasonal changes in food supply. Sponge metabolisms are known to vary considerably (Witte and Graf 1996), between species, genera, and families; however, there are no known studies in the NW Pacific Ocean. One study in the Southern Ocean, which has highly seasonal productive waters, found that some sponges had a 25% metabolic decrease in the food-poor winter, compared to up to a 6-fold increase in the food-rich summer months (Morley et al. 2016). This could indicate that deep-sea sponges are likely to be able to adjust their metabolic physiology, at species level, to feed, grow, and reproduce when conditions alter in the deep sea. Our knowledge of growth, metabolism, and demography of many sponge species, particularly smaller and encrusting deep-sea sponges, is limited, due to the difficulty in sampling and monitoring species that grow very slowly and variably (McMurray et al. 2008).

Deep-sea sponges are likely to be 'K-strategists', with low reproduction rates and reproductive efforts due to limited energy availability (Ramirez-Llodra et al. 2010). No reproductive research has been undertaken on NW Pacific deep-sea sponges; however, reproduction is expected to be seasonal, with key triggers for reproduction likely to be a rise in water temperature and/or primary production (Lanna et al. 2007; Hogg et al. 2010). Most sponge species are hermaphrodites; however, in some species, separate individuals produce sperm and egg cells. Patterns of sexual and asexual reproduction vary from one family to another; however, they are still poorly known, especially for deep-sea species (Hogg et al. 2010). Sponges currently known from the NW Pacific, according to general literature on sponge reproduction (Ereskovsky 2018), are likely to be hermaphrodites which exhibit viviparity (eggs are retained in the body until they develop), which includes hexactinellids and most of the demosponges found in this region. A small selection of demosponges in the deep NW Pacific, in the families and order of Polymastiidae, Suberitidae, and Tetractinellida, are typically not hermaphrodites, and practice oviparity (eggs develop outside of the sponge). Many of the NW Pacific sponges are likely to produce lecithotrophic (non-feeding) larvae, which enable sponges to disperse and thereby have broader ranges (Maldonado 2006). Most sponges are also likely to reproduce asexually, by either budding, fragmentation or gemmulogensis.

Despite little being known about the specific reproductive strategies of deep-sea sponges, it appears that there are likely multiple reproductive options. In the NW Pacific Ocean, sponges are more likely to be hermaphrodites, they also, more often than not, protect their eggs, they generally release larvae that could disperse across the vast deep-sea regions, and they can reproduce both sexually and asexually, which could increase their opportunities to increase their abundance and distribution when the environment changes rapidly.

1.2. Habitat

Most deep-sea habitats are heterotrophic, dependent upon the flux of organic matter (marine snow) photosynthetically produced in the surface ocean (Ramirez-Llodra et al. 2010). Food limitation has and continues to shape many deep-sea habitats, yielding some of the lowest biomass and productivity of faunal communities (Rex et al. 2006; Rowe et al., 2008). However, this is not the case with seamounts, seabed beneath upwelling regions, and canyons, which have higher levels of productivity, and therefore, biomass and diversity, due to topographic modification of currents and enhanced food particle transport (Ramirez-Llodra et al. 2010). Large sectors of the NW Pacific Ocean are known to be areas of upwelling, such as the Sea of Okhotsk, the Kuril-Kamchatka Trench, Kamchatka Peninsula, Sea of Japan, and the Bering Sea (Zhabin et al. 2017). Results from the Sea of Okhotsk indicate that sponges in this region are richer and more abundant than areas sampled on the Kuril-Kamchatka abyssal plain, which is not in an area of upwelling (Downey et al. 2018). However, we do not know enough about other regions in this sector to understand the potential role of upwelling in structuring sponge habitats; however, there is the possibility that sponge fauna could be richer in these regions.

So far, 28 deep-sea habitats have been described globally, and geological, physical and geochemical processes (GOODS 2009; Ramirez-Llodra et al. 2010) likely drive their differences. For many of these habitats, their coverage is still unknown and very few of them have been sampled adequately. Much of the Sea of Okhotsk and Kuril-Kamchatka abyssal plain were found to be composed of fine muds, with occasional stones, which appeared to be more common in the Sea of Okhotsk. Some deep-sea sponges anchor themselves on hard substrata, such as rock, cobbles and gravel found on ridges and trenches, which have been found in this region (Downey and Janussen 2015; Downey et al. 2018). Sponges are typically more diverse on harder substrates (Ramirez-Llodra et al. 2010; van Soest et al. 2012), and this could partly explain the differences in richness and composition of sponge habitats found closer to the Kuril islands (Downey et al. 2018). However, hard substrate habitats are not present throughout most of the deep sea, and that includes the NW Pacific Ocean too. Several demosponge and hexactinellid families and genera, are adapted to live in these soft-bottom, bathyal and abyssal environments (75% of the deep-sea floor) (Hogg et al. 2010), and many of these were encountered in the Kuril-Kamchatka abyssal plain, although they tended to be less diverse sponge habitats (Downey and Janussen 2015).

Deep-sea sponges are known to provide living, complex-structured habitat on the seabed, and sponge habitats are found to be potentially

significant centres of invertebrate and vertebrate (fish) diversity (Klitgaard 1995; McCormick 1994; Cleary and de Voogd 2007; Hogg et al. 2010). Tubes and stalks of dead and living sponges provide elevated structures in the vast areas of soft, muddy floor in bathyal and abyssal regions. They act as habitat structures for many encrusting and motile suspension feeders, producing 'habitat islands' in the deep sea which can be used as nurseries, feeding platforms, and areas of refuge for predators and prey (Beaulieu 2001). Complex, hard substrate is scarce in the deep sea, and so episodic recruitment of living (and the death of sponges) creates habitats, that are likely to play a critical role in deep-sea biodiversity, as they increase the area and type of micro-habitats at differing stages of succession (Hogg et al. 2010). In the NW Pacific Ocean, several dead sponge stalks were found that were encrusted with corals (refer to Chapter 15), which highlights that some sponges do provide deep-sea habitat in this sector of the ocean. However, our current understanding of the roles sponges play in sustaining deep-sea biodiversity, and the connectivity of these habitats of the NW Pacific Ocean, remains limited due to the difficulty in sampling and monitoring these patchy habitats.

1.3. Geographical Distribution

There are currently 3907 online records of deep-sea (>2,000 m) sponges globally, with over half of these records from the North Pacific Ocean (OBIS 2019). Previously, our knowledge of North Pacific Ocean sponge fauna had been partial (e.g. reviewed in Downey and Janussen, 2015; Downey et al. 2018), with less than 6% of databased global sponge distribution records found in this deep-sea region in 2017. However, our knowledge of deep-sea sponge fauna in the NW Pacific Ocean has increased with the systematic sampling during the Russian-German collaboration in the NW Pacific Ocean (refer to Chapter 1). Over 700 sponge specimens were retrieved from these four expeditions in this region, and results from the identified fauna from the Sea of Okhotsk and the Kuril-Kamchatka abyssal plain indicate that many of the sponges are likely to be endemic to the NW Pacific Ocean (Downey and Janussen 2015; Downey et al. 2018). Over two-thirds of sponges found in the Sea of Okhotsk and Bussol Strait are likely endemic, and a third of sponges found in the Kuril-Kamchatka abyssal plain, are likely to be endemic to the NW Pacific Ocean (Downey et al. 2018; Downey and Janussen 2015). Despite high levels of endemism in the semi-enclosed Sea of Okhotsk, likely due to the limited number of deep-sea straits, some species were found to have much broader distributions throughout the North and NW Pacific Ocean. These broader longitudinal, latitudinal and depth distributions were more common in the Kuril-Kamchatka abyssal plain, which found that these species were generally found throughout the North Pacific Ocean (Downey and Janussen 2015). It was also found that hexactinellids had much greater depth distributions (eurybathy), than demosponges, with only 15% of demosponges were found to have broad depth distributions (Downey and Janussen 2015; Downey et al. 2018).

In the deep sea, rarity is considered a characteristic of taxa, with ca. 74% of macrofaunal species were found in less than 10% of samples in the West Atlantic, and 25% of species were singletons (Carney 1997). Within the NW Pacific Ocean, more than half of sponge species found on the

Kuril-Kamchatka abyssal plain, and nearly two-thirds of species from the Sea of Okhotsk, are rare through geographical limitation, only being found at one station (Downey and Janussen 2015; Downey et al. 2018). Several stations, particularly in the Sea of Okhotsk, were found to have high levels of localised diversity, despite most stations having found very few or no sponges in the adjacent abyssal plain.

The majority of deep-sea sponge records are from the lower bathyal and abyssal depths, with less than 1% (19 records) of deep-sea records from the hadal (>6,000 m) (OBIS 2019). Hadal regions are common throughout the North Pacific Ocean, as well as around Indonesia, Puerto Rico in the Atlantic Ocean, and the South Sandwich Islands in the Southern Ocean (GOODS 2009). The most recent expedition to the Kuril-Kamchatka Trench hadal region has yielded 87 sponge specimens, with several demosponges and hexactinellids achieving depth records greater than all previously collected deep-sea sponges (Koltun 1959; Vacelet and Boury-Esnault 1995; van Soest et al. 2012).

2. Objectives

The main objectives of this study were to analyse our current knowledge of deep-sea sponge species, genera, and family diversity, endemism and richness, sponge abundance, and latitudinal and depth gradients in the NW Pacific Ocean, as well as to investigate deep-sea faunal biogeographical patterns within this region and with adjacent deep-sea regions utilising new and previously identified sponge collections.

3. Material and Methods

3.1. Coverage Area and Occurrence Data

Sponge specimens were collected on four separate expeditions in the NW Pacific (Sea of Japan, Sea of Okhotsk, Kuril-Kamchatka abyssal plain and the Kuril-Kamchatka Trench), using Agassiz trawls, epi-benthic sledges and box corers, a joint collaboration between the Russians and Germans, between 2010 and 2016 (refer to Chapter 1 in this issue). All previous deep-sea data from this study region was collated from OBIS (2019) and additional publications (Hôzawa 1918; Okada 1932; Koltun 1955, 1958, 1959, 1962, 1966, 1967, 1970; Samaai and Krasokhin 2002; Ereskovsky and Willenz 2007). Maps have been produced, documenting most of the deep-sea sponge species found in the NW Pacific Ocean, including both widely distributed, and species that have only been found once. Data for these species distributions was compiled from these new expeditions, as well as previously published data. In this study, the NW Pacific Ocean was defined as 120–180°E and 40–60°N. All sponge taxonomy was checked using World Porifera Database (WPD: Van Soest et al. 2019); however, several hexactinellid species described by Koltun (1967), have not yet been accepted by WPD, but were considered as a distinct species morphotypes despite current uncertainty. This sector of the NW Pacific Ocean contains several distinct deep-sea areas: abyssal plains, abyssal basins of the semi-enclosed Sea of Okhotsk, Sea of Japan and the Bering Sea, the hadal Kuril-Kamchatka Trench, and the Emperor Seamounts.

3.2. Depth Gradient

All deep-sea sponge data was collated for the NW Pacific Ocean; however, only sponge records from depths greater than 2,000 m were used to analyse variations in species diversity at depth. Depths were categorised into both stenobathic (restricted) zones: lower bathyal (2,000–3,000 m), abyssal (3,000–6,000 m), and hadal (6,000 m +). Eurybathic (species occurring across multiple depths) zones were also included to determine which species had broad depth distributions in the deep sea. Shallower depth data from these deep-sea species was added into a table to fully understand biogeographic patterns, and potentially enable our understanding of submergence and emergence processes.

3.3. Latitudinal Gradient

In this study region, the temperate and sub-polar NW Pacific Ocean has a latitudinal gradient of 40–60°N. In some deep-sea species, there is a known reduction in diversity with increasing latitudinal gradient (Gray 2001), and therefore latitudinal data was utilised to determine if there was a reduction in species with an increased latitude at these depths. Five-degree latitude intervals were compiled, and longitudinal and depth ranges of stations were recorded for overview. Each unique latitude and longitude was taken to be a station, so that sampling intensity could also be explored in these latitudinal bands.

4. Results

4.1. Richness Patterns

The minimum number of known sponge specimens from this deep-sea region is 938, which is likely an underestimation of sponge records from below 2,000 m, as older records did not always provide exact numbers of specimens (Table 1). Overall, results indicate that hexactinellid sponges are far more abundant throughout the NW Pacific deep sea, with close to 60% of known specimens found in this class. Nearly 40% of specimens found are from the demosponge class, with the remaining few percent not yet identified from the phylum. These are similar to findings from the Sea of Okhotsk, which found 74% hexactinellid species and 26% demosponges (Downey et al. 2015). However, they are in opposition to sponges collected in the Kuril-Kamchatka abyssal plain, which found that 57% of specimens were demosponges, and 43% were hexactinellids (Downey et al. 2018). So far, only one calcareous sponge specimen has been found (Order: Calcarea Bowerbank, 1862) in the deep-sea sector of the NW Pacific, which is not unexpected, as only one calcareous species (*Sycon escanabense* Duplessis and Reiswig, 2000) has so far been found in the adjacent abyssal NE Pacific region (Duplessis and Reiswig 2000) and only 145 specimens of calcareous sponges are known from below 2,000 m (OBIS 2019).

This region has so far yielded at least 70 sponge species morphotypes, and 2 subspecies, with many new species not yet fully described from recent expeditions, including specimens from the Sea of Japan, and many from the most recent Kuril-Kamchatka Trench expedition (Table 2). These 70 species morphotypes are found within 28 genera, and 17 families. These are conservative lower estimates of the species, genera and family richness from the deep NW Pacific Ocean, with the numbers likely to increase substantially with each new expedition into this region.

Table 1. Numbers of families, genera, species and specimens of demosponges and hexactinellids found in the NW Pacific deep sea.

	Deep-sea families	Deep-sea genera	Deep-sea species*	No. of specimens
Porifera	-	-	-	48
Demospongiae	10	17	46**	347
Hexactinellida	6	10	23***	542
Calcarea	1	1	1	1
Total	17	28	70	938

*including those that are not fully described species
**15 not fully described species (30 accepted species). Some aff. (species affinis) species.
***5 are not fully described species. (1 species includes a subspecies). Several aff. (species affinis) species.

Two-thirds of these species morphotypes are demosponges, with the remaining third found to be hexactinellids, and 1% calcareous sponges. In general, demosponges are twice as diverse in genera and families represented in the deep NW Pacific Ocean compared with hexactinellids, with demosponge species found within 17 genera, and 10 families, whereas, and hexactinellids are found within 10 genera and 6 families.

Over a third (26 spp.) of deep-sea species morphotypes found in the NW Pacific Ocean are either new to the region or new to science (Downey and Janussen 2015; Downey et al. 2018). Fifteen new species are currently being described, and eleven species are new to this region. Of the fifteen new species, thirteen are demosponges from the Cladorhizidae family. The eleven new species to this region include nine demosponges in nine genera, and two hexactinellids in two genera. Six of the demosponge genera and one of the hexactinellid genera, have never been recorded from this deep-sea sector of the ocean. Very little is known about the calcareous specimen; however, it is likely to be a new species, and potentially a new genus.

There is a high likelihood that more new cladorhizid species will be described from the Kuril-Kamchatka Trench, including an undescribed *Asbestopluma sp*. from 9,013 m, and 6 cladorhizid specimens from between 8,111–8,358 m. Until now, the deepest known living sponge, a cladorhizid (*Lycopodina occidentalis* (Lambe, 1893)), was collected from this region (8,840 m), (Koltun 1959; Vacelet and Boury-Esnault 1995; van Soest et al. 2012), and this new *Asbestopluma* (*Asbestopluma*) Topsent, 1901 record, is nearly 200 m deeper. However, one unidentified hexactinellid sponge from the same region and expedition was collected from a greater depth of 9,292–9,301 m, up to 461 m deeper than the previously deepest known record for all sponges in the global oceans. However, more importantly, it is more than 2,500 m deeper than the previously found glass sponges globally (Lévi 1964; OBIS 2019) and from this region (Koltun 1966, 1967).

Currently, more than half of species found in this region (35 spp.) are from the Cladorhizidae family (including species morphotyped but not yet to be fully described), which indicates the diversity and

dominance of this demosponge family within this region (Table 2). However, this does not include an additional 29 specimens from the recent Kuril-Kamchatka Trench expedition, which have not been identified to species level, and are likely to increase species numbers from this family further. Six genera are represented from this family, with *Asbestopluma* (A.) dominating in terms of species (13 spp.), followed by *Chondrocladia* Thomson, 1873 and *Cladorhiza* Sars, 1872 (both 8 spp.). All other demosponge families (9), are generally only represented by one or two genera in the NW Pacific Ocean (total of 11 species).

Previously, Koltun (1970) had documented 15 species of carnivorous sponges in the deep NW Pacific Ocean, which has now more than doubled in number after these recent NW Pacific Ocean campaigns (Table 2). No carnivorous sponges were found in the Sea of Japan; however, 11 spp. were found on the Kuril-Kamchatka abyssal plain, 15 spp. in the Sea of Okhotsk, two spp. at the northern end of the Emperor Seamounts, and seven spp. currently from the Kuril-Kamchatka Trench. Hexactinellids are far more abundant than demosponges in the deep NW Pacific Ocean, despite not being as species rich as demosponges. However, two hexactinellid families were found to be particularly diverse in either genera and/or species in the deep NW Pacific Ocean. Both the Hyalonematidae Gray, 1857 and Rossellidae Schulze, 1885 families are represented by eight spp., which accounts for close to a quarter of species found in this region. The Hyalonematidae family are only represented by the species-rich genus *Hyalonema* Gray, 1832, whereas the Rossellidae family are represented by five genera, with *Bathydorus* Schulze, 1886 and *Caulophacus* Schulze, 1886 dominating in numbers of species.

Recent studies, which explored the diversity of sponge species, using a Shannon-Wiener index, in the Sea of Okhotsk and the Kuril-Kamchatka abyssal plain, found that the Sea of Okhotsk was generally far more diverse, particularly the NE sector of the basin and the Bussol Strait, than the adjacent abyssal plain (Downey et al. 2018). Stations in the northern and central sector of the Kuril-Kamchatka abyssal plain tended to be slightly richer than those in the southern sector (Downey and Janussen 2015). However, sites sampled in the Sea of Okhotsk tended to be shallower than in the adjacent Kuril-Kamchatka abyssal plain. All sites sampled in these adjacent regions are found to be fairly even too, with evenness found to be slightly greater in the Kuril-Kamchatka abyssal plain (Downey and Janussen 2015). Diversity and evenness measures have not been analysed for the Sea of Japan and the Kuril-Kamchatka Trench; however, it is likely that the sparsity of samples for the Sea of Japan represents low sponge diversity and evenness; however, the hadal sector of the Kuril-Kamchatka Trench could yield similar levels of diversity and evenness to the adjacent abyssal plain.

Sampling across the deep NW Pacific Ocean has been sporadic, with depths and longitudinal ranges varying considerably in this region, and therefore analysis of latitudinal changes in diversity is complex. However, results indicate that 45-50°N latitude band appears to be the richest in species, with nearly twice as many found than the next richest latitudinal band (40–45°N) (Table 3). Depth ranges were similar for both of these species-rich latitudinal bands; however, there were at least 50% more unique sampling stations in the richest latitudinal band, and therefore, if the second-most rich band had had more

Table 2. List of all species morphotypes and subspecies of deep-sea sponges found in the NW Pacific. Depth, longitude and latitude include all information about a species distribution.

Class	Family	Species	Depth range	Latitudinal range	Longitudinal range	Distribution
Calcarea Bowerbank, 1862	-	-	5,005–5,045 m	44 N	156 E	Kuril-Kamchatka abyssal plain
Demospongiae Sollas, 1885	Acarnidae Dendy, 1922	*Cornulum clathriata* (Koltun, 1955)	89–2,440 m	51–53 N	170 E – 170 W	Aleutian Islands
Demospongiae Sollas, 1885	Acarnidae Dendy, 1922	*Megaciella ochotensis* (Koltun, 1959)	83–3,363 m	46–59 N	147–156 E	Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Abyssocladia claviformis* Koltun, 1970	5,005–6,069 m	33–44 N	149–156 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Abyssocladia koltuni* (Ereskovsky and Willenz, 2007)	500–2,358 m	46–50 N	145–151 E	Sea of Okhotsk and Bussol Strait
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 1*	3,307 m	46 N	146 E	Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 2*	3,307 m	46 N	146 E	Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 3*	3,299–3,366 m	46–48 N	147–151 E	Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 4*	3,347–3,350 m	48 N	150 E	Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 5*	3,361–4,469 m	46 N	152 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 6*	3,350 m	48 N	150 E	Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 7*	3,347–3,351 m	48 N	150 E	Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 8*	3,301–3,351 m	48 N	150–151 E	Sea of Okhotsk

Class	Family	Species	Depth range	Latitudinal range	Longitudinal range	Distribution
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 9*	3,248–3,377 m	46 N	152 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) sp. nov 10*	3,347–3,350m	48 N	150 E	Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) biserialis* (Ridley and Dendy, 1886)	941–6,282 m	42 S – 48 N	150 E – 118 W	Pacific Ocean and Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) ramosa* Koltun, 1958	188–3,347 m	45–51 N	147 E – 173 W	N/NW Pacific Ocean and Bussol Strait
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Asbestopluma (Asbestopluma) wolffi* Lévi, 1964	6,675–8,120 m	43–45 N	149–153 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Chondrocladia (Chondrocladia) sp. nov 1*	5,125–5,127 m	42 N	152 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Chondrocladia (Chondrocladia) clavata* Ridley and Dendy, 1886	25–5,711 m	78 S – 47 N	180 W – 178 E	Pacific Ocean, Southern Ocean and Indian Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Chondrocladia (Chondrocladia) concrescens* (Schmidt, 1880)	200–8,660 m	24 S – 50 N	177 W – 167 E	Pacific Ocean, Sea of Okhotsk, Atlantic Ocean, Norwegian seas and Indian Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Chondrocladia (Chondrocladia) crinita* Ridley and Dendy, 1886	3,658–5,998 m	3–46 N	134–156 E	North and West Pacific Ocean

Class	Family	Species	Depth range	Latitudinal range	Longitudinal range	Distribution
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Chondrocladia (Chondrocladia) dichotoma* Lévi, 1964	3,310–6,282 m	1–48 N	77–169 E	North Pacific Ocean and Indian Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Chondrocladia (Chondrocladia) grandis* (Verrill, 1879)	30–3,948 m	70 S – 38 N	8 E – 1 W	N/NW/S Atlantic Ocean, Arctic Ocean, Southern Ocean, Sea of Okhotsk, Kuril Islands and Aleutian Islands
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Chondrocladia (Chondrocladia) koltuni* Vacelet, 2006	4,976–5,249 m	43–55 N	153–166 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Chondrocladia (Chondrocladia) aff. virgata*	5,191 m	43 N	151 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Cladorhiza sp. nov 1*	5,250–5,408 m	41 N	155 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Cladorhiza sp. nov 2*	4,976–4,980 m	47 N	150–151 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Cladorhiza aff. abyssicola*	7,077 m	45 N	152 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Cladorhiza bathycrinoides* Koltun, 1955	150–3,800 m	44–49 N	147–157 E	NW Pacific Ocean and Sea of Okhotsk
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Cladorhiza longipinna* Ridley and Dendy, 1886	3,000–6,282 m	14–48 N	143 E – 175 W	North Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Cladorhiza mirabilis* (Ridley and Dendy, 1886)	4,115–5,127 m	39 S – 42 N	151 E – 118 W	Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Cladorhiza rectangularis* Ridley and Dendy, 1887	3,325–6,065 m	7 S – 49 N	146 E – 152 W	Pacific Ocean

Class	Family	Species	Depth range	Latitudinal range	Longitudinal range	Distribution
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Cladorhiza septemdentalis* Koltun, 1970	4,891–7,295 m	25–46 N	143–153 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Koltunicladia flabelliformis* (Koltun, 1970)	5,390 m	44 N	170 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Lycopodina infundibulum f. orientalis* (Koltun, 1970)	2,665–5,450 m	38–44 N	146–149 E	NW Pacific Ocean
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Lycopodina occidentalis* (Lambe, 1893)	820–8,840 m	38–53 N	151 E – 130 W	North Pacific
Demospongiae Sollas, 1885	Cladorhizidae Dendy, 1922	*Lycopodina globularis* (Lévi, 1964)	3,570–5,400 m	9–46 N	150 E – 89 W	North Pacific Ocean
Demospongiae Sollas, 1885	Coelosphaeridae Dendy, 1922	*Forcepia (Leptolabis) uschakowi* (Burton, 1935)	34–2,358 m	43–51 N	146–157 E	NW Pacific Ocean, Sea of Japan and Bussol Strait
Demospongiae Sollas, 1885	Esperiopsidae Hentschel, 1923	*Esperiopsis plumosa* Tanita, 1965	150–6,860 m	34–48 N	127–153 E	NW Pacific and Sea of Japan
Demospongiae Sollas, 1885	Myxillidae Dendy, 1922	*Melonanchora tetradentifera* Koltun, 1970	4,45–3,352 m	46 N	147–152 E	Sea of Okhotsk, Bussol Strait and NW Pacific
Demospongiae Sollas, 1885	Phellodermidae van Soest and Hajdu, 2002	*Echinostylinos mycaloides* Koltun, 1970	2,265–3,351 m	44–48 N	149–150 E	NW Pacific and Sea of Okhotsk
Demospongiae Sollas, 1885	Polymastiidae Gray, 1867	*Polymastia pacifica* Koltun, 1966	3,940–6,065 m	34–56 N	156 E – 132 W	North Pacific Ocean
Demospongiae Sollas, 1885	Polymastiidae Gray, 1867	*Sphaerotylus sp. 1*	5,418–5,419 m	43 N	157 E	
Demospongiae Sollas, 1885	Suberitidae Schmidt, 1870	*Suberites sp. 1*	2,350–3,366 m	46–48 N	149–151 E	

Class	Family	Species	Depth range	Latitudinal range	Longitudinal range	Distribution
Demospongiae Sollas, 1885	Tedaniidae Ridley and Dendy, 1886	*Tedania (Tedania) sp. 1*	3,351–3,352 m	46 N	147 E	
Demospongiae Sollas, 1885	Vulcanellidae Cárdenas, Xavier, Reveillaud, Schander and Rapp, 2011	*Poecillastra japonica* (Thiele, 1898)	47–2,440 m	36–54 N	151 E – 129 W	North Pacific Ocean
Hexactinellida Schmidt, 1870	Aphrocallistidae Gray, 1867	*Aphrocallistidae sp. 1*	3,300–3,301 m	46 N	151 E	Sea of Okhotsk
Hexactinellida Schmidt, 1870	Aphrocallistidae Gray, 1867	*Aphrocallistidae sp. 2*	3,300–3,301 m	46 N	151 E	Sea of Okhotsk
Hexactinellida Schmidt, 1870	Euplectellidae Gray, 1867	*Holascus undulatus* Schulze, 1899	2,868–6,328 m	45–55 N	155 E – 136 W	North Pacific
Hexactinellida Schmidt, 1870	Euplectellidae Gray, 1867	*Ijimaiella beringiana* Tabachnick, 2002	6,272–6,282 m	55 N	167 E	Aleutian Islands
Hexactinellida Schmidt, 1870	Euretidae Zittel, 1877	*Eurete irregular* Okada, 1932	1,676–4,798 m	45–48 N	145–174 E	Sea of Okhotsk, Bussol Strait and NW Pacific
Hexactinellida Schmidt, 1870	Euretidae Zittel, 1877	*Pinulasma fistulosum* Reiswig and Stone, 2013	2,084 m	51 N	179 E	Aleutian islands
Hexactinellida Schmidt, 1870	Farreidae Gray, 1872	*Farrea sp. 1*	4,859–5,419 m	40–46 N	150–157 E	NW Pacific Ocean
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Corynonema) populiferum harpagonis* Koltun 1967	3,400 m	45 N	156 E	Sea of Okhotsk
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Cyliconema) apertum* Schulze, 1886	320–6,235 m	44S–51 N	92E–175 W	Pacific and Indian Oceans
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Cyliconema) apertum simplex* Koltun, 1967	1,699–3,964 m	44–59 N	145–174 E	NW Pacific, Bering Sea, Bussol Strait and Sea of Okhotsk

Class	Family	Species	Depth range	Latitudinal range	Longitudinal range	Distribution
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Cyliconema) hozawai vicarium* Koltun, 1967	3,920–3,964 m	55–59 N	169–174 E	Bering Sea
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Cyliconema) tenerum vitiazi* Koltun, 1967	3,812 m	53 N	172 E	Bering Sea
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Onconema) obtusum* Lendenfeld, 1915	4,346–5,258 m	0–43 N	151 E – 117 W	North Pacific
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Oonema) robustum* Schulze, 1886	3,347–4,140 m	35–48 N	150–157 E	Sea of Okhotsk and NW Pacific
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Paradisconema) sp. nov 1*	2,350–3,303 m	46 N	151 E	Sea of Okhotsk
Hexactinellida Schmidt, 1870	Hyalonematidae Gray, 1857	*Hyalonema (Prionema) aff. agujanum* Lendenfeld, 1915	5,229 m	43 N	151 E	NW Pacific
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Acanthascus profundum* Koltun, 1967	342–2,440 m	36–55 N	164 E – 121 W	North Pacific Ocean
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Bathydorus echinus* Koltun, 1967	2,440–3,353 m	46–61 N	147 E, 167–164 W	North Pacific Ocean, Bering Sea and Sea of Okhotsk
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Bathydorus fimbriatus* Schulze, 1886	2,167–6,135 m	35–46 N	149 E – 177 W	North Pacific Ocean
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Bathydorus laevis pseudospinosus* Tabachnick and Menshenina, 2013	2,167–3,940 m	1–41 N	153 E – 80 W	North Pacific Ocean

Class	Family	Species	Depth range	Latitudinal range	Longitudinal range	Distribution
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Caulophacus (Caulodiscus) lotifolium* Ijima, 1903	3,299–6,710 m	38–48 N	146–178 E	NW Pacific Ocean and Sea of Okhotsk
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Caulophacus (Caulophacus) elegans* Schulze, 1886	3,680–4,202 m	35–58 N	157–177 E	NW Pacific Ocean
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Caulophacus (Caulophacus) schulzei* Wilson, 1904	2,350–3,366 m	46–47 N	147–151 E	Sea of Okhotsk
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Caulophacus (Caulophacus) schulzei hyperboreus* Koltun, 1967	3,932–3,400 m	46–57 N	150–175 E	Sea of Okhotsk and Bering Sea
Hexactinellida Schmidt, 1870	Rossellidae Schulze, 1885	*Sympagella cantharellus* (Lendenfeld, 1915)	4,063–5,045 m	5 S– 45 N	156 E – 82 W	Pacific Ocean

Table 3. Latitudinal bands detailing numbers of species found in each five degree interval in the NW Pacific deep-sea. Information on the number of unique stations sampled (unique latitude and longitude), longitudinal range and sampled depth range is given.

Latitudinal band	Total Porifera	Demospongiae	Hexactinellida	Calcarea	Unique sampling stations	Longitudinal range (°)	Depth range (m)
40–45°N	31	22	8	1	60	38.67	7,136
45–50°N	50	36	14	0	91	23.89	6,806
50–55°N	8	3	5	0	7	22.34	4,212
55–60°N	10	1	9	0	13	18.97	1,854

sampling stations, it potentially could be found to be nearly as rich in species. However, the second-richest latitudinal band has an additional 15° longitude of sampling (over 60% more longitude than the richest latitudinal band), which would require additional sampling to be comparable in terms of sampling intensity. In the two most northerly latitudinal bands, very few stations with samples have been recorded, and this is further impacted by the rapid reduction in deep sea and longitudinal range availability at these high latitudes. Despite limited sampling, many species have been found at these higher latitudes, and hypothetically, these latitudinal bands could be as rich as or richer in species than latitudes further south, if sampled comparably. Both hexactinellid and demosponge species are most speciose in the richest latitudinal band (45–50°N); however, hexactinellids also have many species found in the furthest southerly and northerly latitudinal bands. Demosponges are at their most diverse at the two most southerly latitudinal sectors of the NW Pacific Ocean. Results indicate that demosponge species dominate the two southerly latitudinal bands (both have over 70% of all species found), whereas hexactinellids dominate diversity in the two northerly latitudinal bands in the NW Pacific Ocean (90% species representation at 55–60°N).

In the NW Pacific Ocean, sponge species were distributed from 2,084–9,301 m, utilising both older records from previous expeditions, and newer records from the four recent Russian-German expedition (Downey and Janussen 2015; Downey et al. 2018; refer to Chapter 1). Nearly 80% (55 spp.) of sponge species in the NW Pacific are found to be stenobathic, distributed in only one depth zone, whereas over 20% (15 spp.) are eurybathic, found in two or more depth zones (Table 4). Nearly 60% of all species are restricted to the abyss, whereas over 15% are restricted to the lower bathyal, and 4% restricted to hadal depths. Abyssal depths are found to be the richest in terms of species, with close to 80% (56 spp., 34 demosponges, 21 hexactinellids, and 1 calcareous sponge) of all deep-sea species distributed in this broad depth zone. Twenty-species are distributed in the lower bathyal (13 demosponges and seven hexactinellids), and thirteen are known from hadal depths (nine demosponges and four hexactinellids). At each greater depth zone, there is a slight increase in the proportion of demosponge species, although only from 61 to 69%. Eighty-five percent (39 spp.) of demosponge species are restricted to a particular depth zone, with the remainder found to be eurybathic. Whereas, 65% (15 spp.)

Table 4. Depth ranges of all species found in the NW Pacific, with defined depth ranges for each depth zone.

	Total	Demospongiae	Hexactinellida	Calcarea
Stenobathic zones				
Lower bathyal (2,000–3,000 m)	11	9	2	0
Abyssal (3,000–6,000 m)	41	27	13	1
Hadal (6,000 m +)	3	3	0	0
Eurybathic zones				
Lower bathyal-Abyssal (2000–6,000 m)	5	1	4	0
Lower bathyal-Abyssal-Hadal (2,000–6,000 m +)	4	3	1	0
Abyssal and Hadal (3,000 m +)	6	3	3	0

*Depth ranges are only considered in the NW Pacific

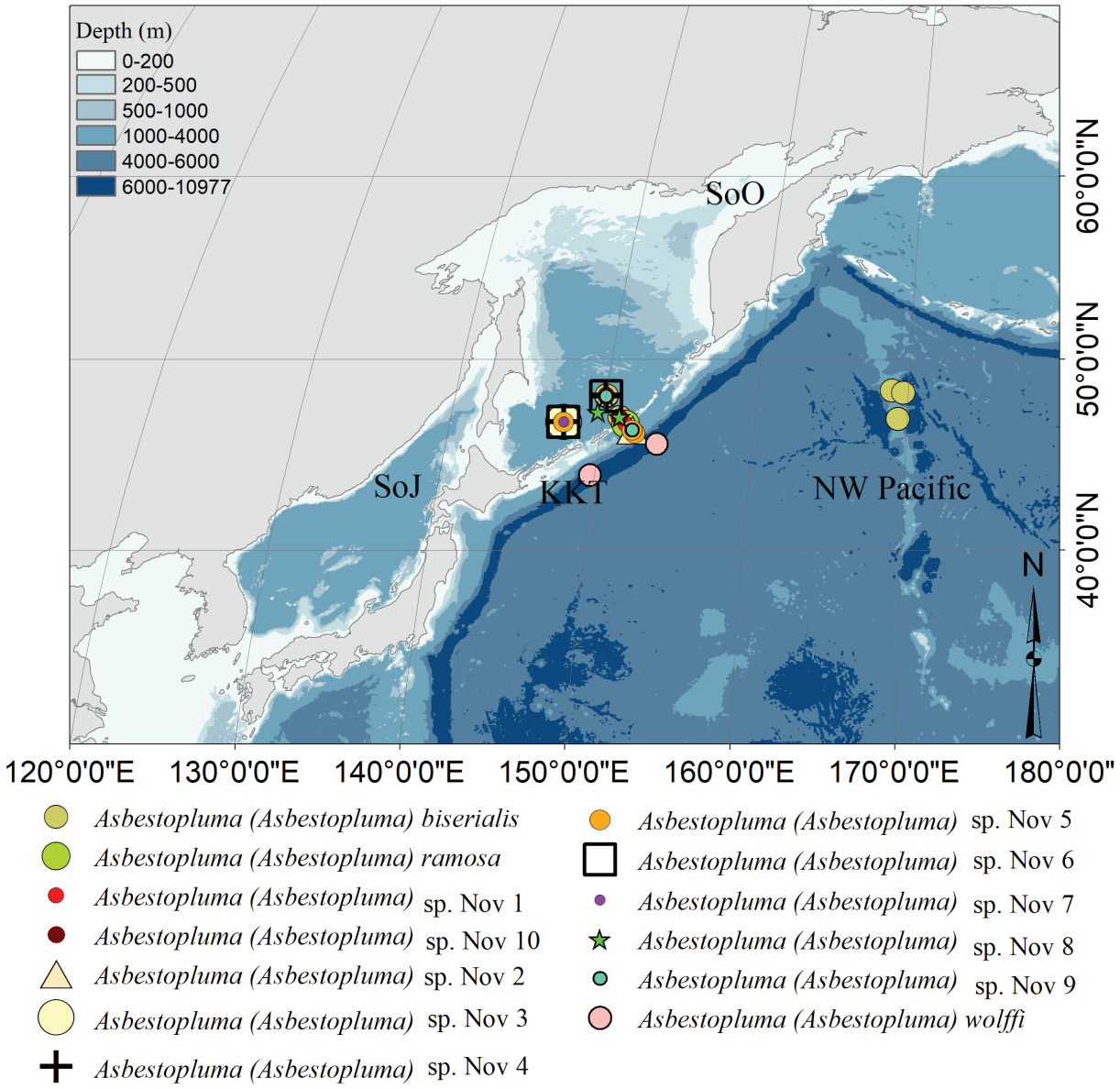
of hexactinellids are restricted to one depth zone, with a third of species found distributed in multiple depth zones.

4. 2. Biogeographic Patterns

Demosponges are the most diverse in terms of represented families, genera and species in the NW Pacific Ocean, and carnivorous sponges (Cladorhizidae family) are dominant parts of the deep-sea assemblage, represented in six genera (Table 2). The genus *Asbestopluma* (A.) is particularly species-rich in this region, comprising of 13 species, with many of them new to science. The majority of these species (13 spp.) are likely to be endemic to this region, with many only found at one or two stations, and most species found in the Sea of Okhotsk and the Kuril-Kamchatka ridge and trench (Downey and Janussen 2015; Downey et al. 2018). Unusually, A. (A.) *biserialis* (Ridley and Dendy 1886) does have a much broader range in the NW Pacific compared to most other species of this genus (Map 1). One other species, A. (A.) *ramosa* Koltun, 1958, is also found to be distributed throughout the North Pacific Ocean and have much broader known depth ranges as well (Table 2).

Chondrocladia (*Chondrocladia*) is another species rich genus found within the NW Pacific Ocean, represented by at least eight species, with many other specimens not yet fully identified (Table 2). However, so far, only three spp. are likely to be endemic, including one new to science species, with the remainder of species found to be distributed broadly in the Pacific Ocean and for one species, globally (Map 2; Table 2). Half of the species within this genus have broad ranges in the NW Pacific, which include C. (C.) *clavata* Ridley and Dendy, 1886, C. (C.) *dichotoma* Lévi, 1964, C. (C.) *concrescens* (Schmidt, 1880), and C. (C.) *koltuni* Vacelet, 2006. *Chondrocladia* species are not found to be distributed in the Kuril Basin of the Sea of Okhotsk.

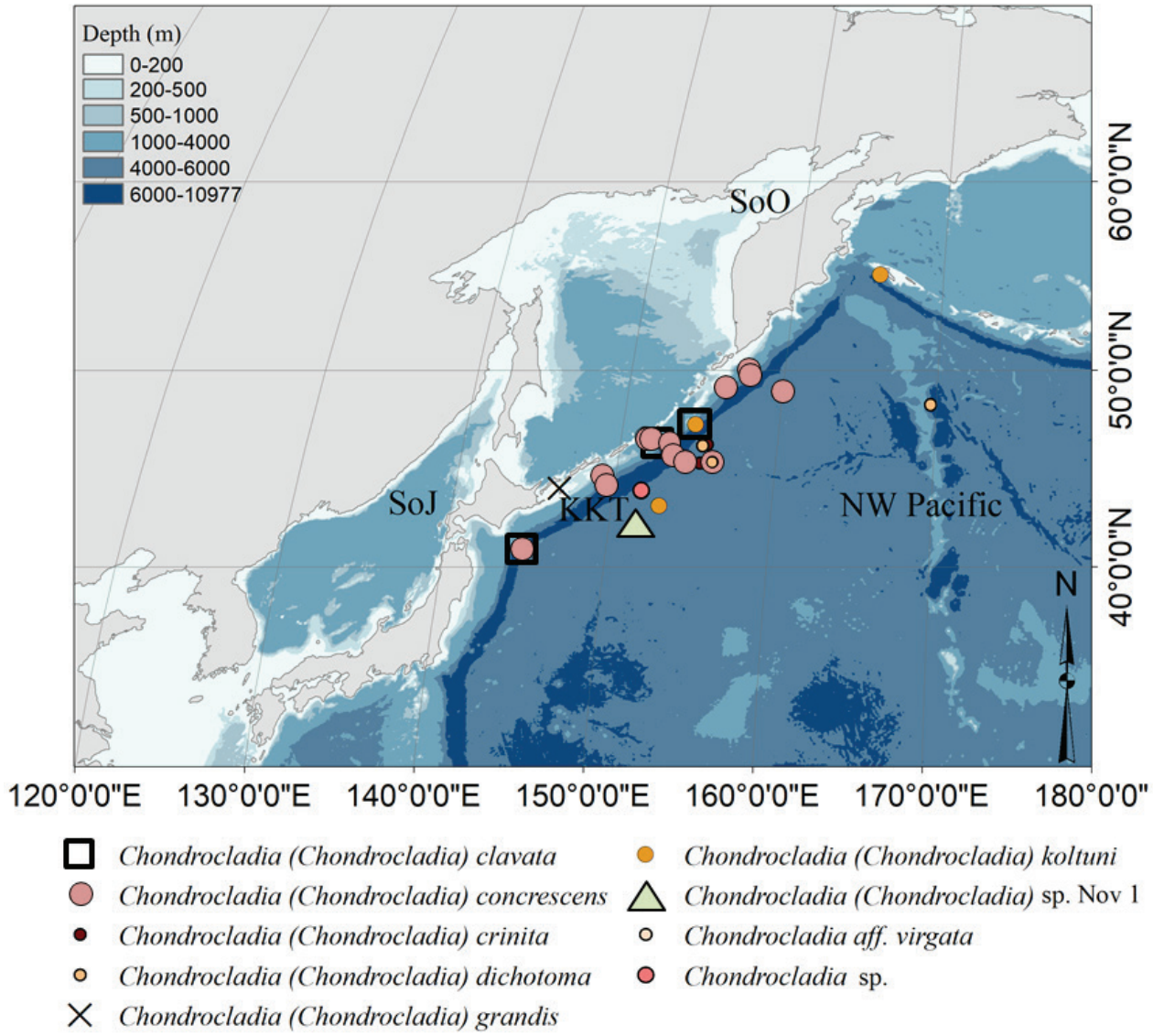
Cladorhiza is another species-rich genus within the Cladorhizidae family, comprising of eight spp. in the deep NW Pacific Ocean (Table 2). Half of these species are likely to be endemic in this region, with two of these species new to science. Three species are found more broadly in the



Map 1. Distribution of *Asbestopluma* species from the NW Pacific (Cladorhizidae family).

Pacific Ocean, *C. mirabilis* (Ridley and Dendy, 1886) and *C. rectangularis* Ridley and Dendy, 1887, with *C. longipinna* Ridley and Dendy, 1886 distributed only in the North Pacific (Map 3). Endemic *C. bathycrinoides* Koltun, 1955 is found to have a broad distribution in the Sea of Okhotsk and the Kuril-Kamchatka ridge, whereas broadly distributed *C. longipinna* is only found in the NW Pacific abyssal plains. Similar to *Chondrocladia*, most *Cladorhiza* species are not found to be distributed in the Kuril Basin of the Sea of Okhotsk.

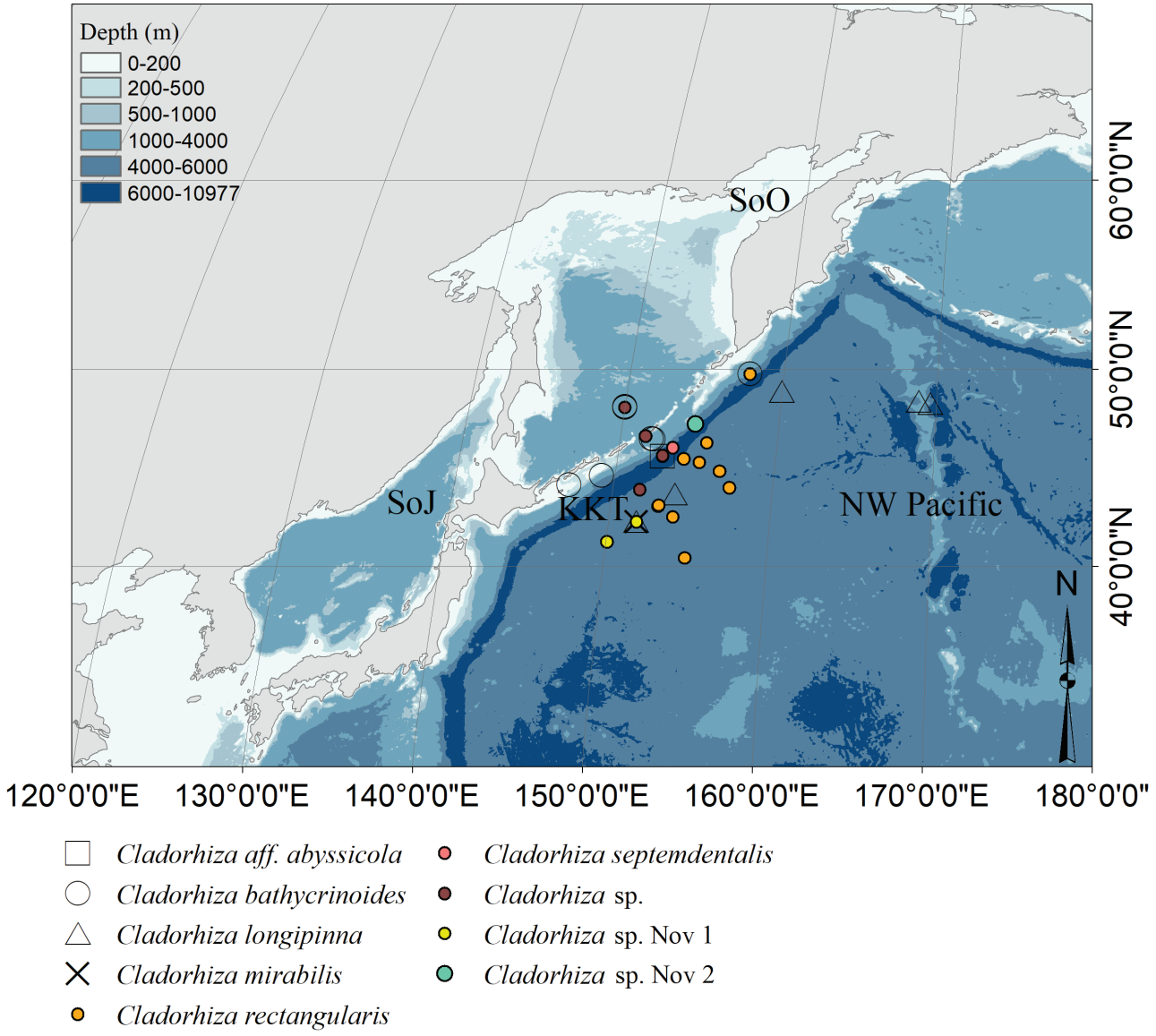
All remaining genera within the Cladorhizidae family, *Abyssocladia* Lévi, 1964, *Lycopodina* Lundbeck, 1905 and *Koltunicladia*, are found to be species-poor (Table 2). Apart from the genus *Lycopodina*, which is broadly distributed within the NW Pacific and the North Pacific generally, all other species are found to be endemic and restricted in distribution (Map 4). *K. flabelliformis* (Koltun, 1970) has only been found on the Emperor Seamounts, and the two species of *Abyssocladia* are restricted to either the NW Pacific abyssal



Map 2. Distribution of *Chondrocladia* species from the NW Pacific (Cladorhizidae family).

plain or the Bussol Strait. Many new specimens from the Cladorhizidae family have been found in the Kuril-Kamchatka Trench, including an *Asbestopluma* (A.) recorded from the depth of 9,013 m. Very few cladorhizid sponges have so far been found close to the Aleutian Trench and Bering Sea; however, with increased sampling, it is likely that this species-rich family is found throughout the NW Pacific Ocean.

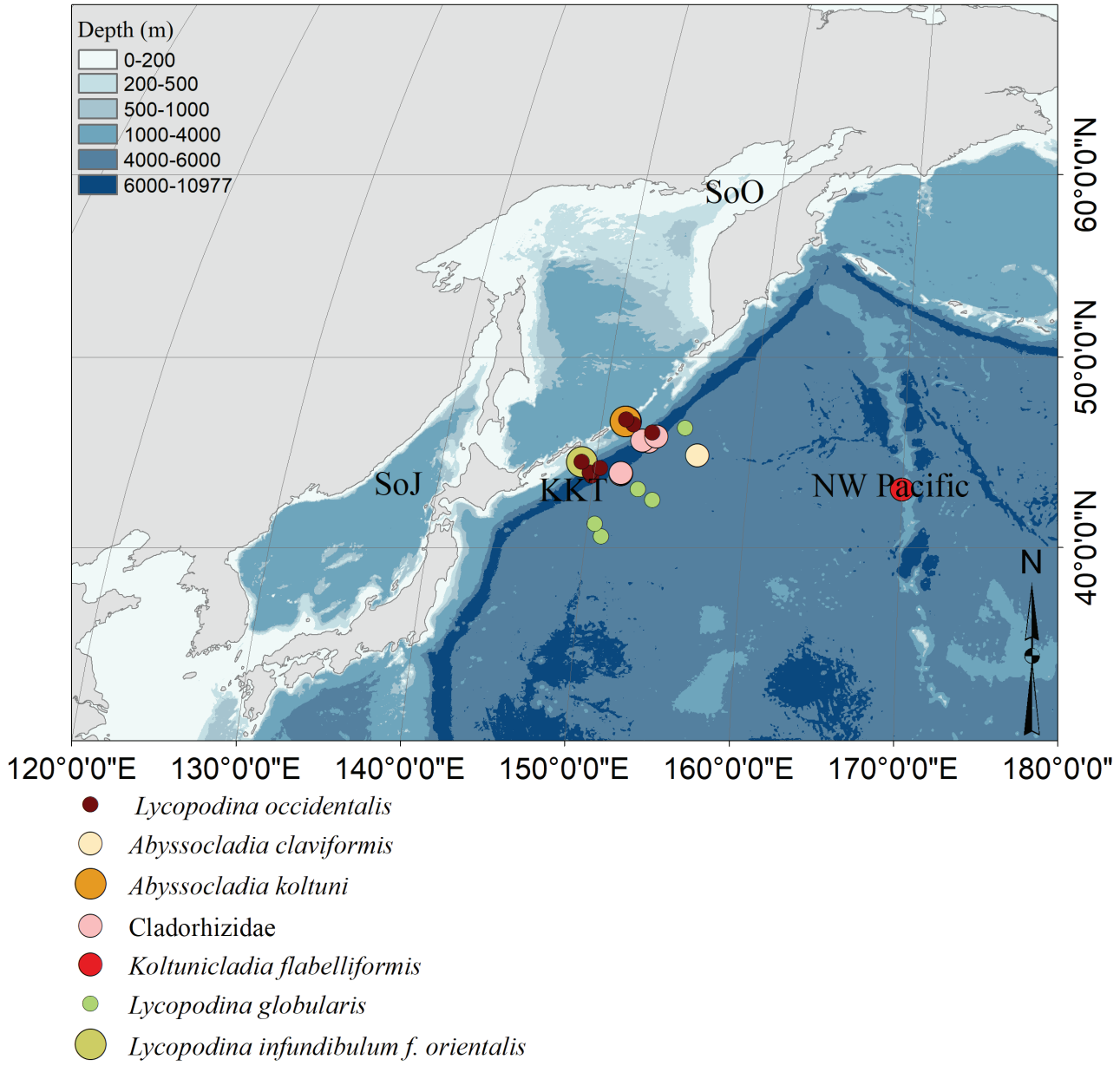
Seven demosponge species were found from six other families (Acarnidae, Dendy, 1922, Coelosphaeridae Dendy, 1922, Esperiopsidae Hentschel, 1923, Myxillidae Dendy, 1922, Phellodermidae van Soest and Hajdu, 2002, and Tedaniidae Ridley and Dendy, 1886), in the Poecilosclerida Topsent, 1928 Order in the NW Pacific Ocean (Table 2). All known species are endemic to the NW Pacific, apart from *Cornulum clathriata* (Koltun, 1955), which is found distributed in the North Pacific. More than half of these species have distributions in the semi-enclosed Sea of Okhotsk, whereas the remainder are distributed on the southerly edge of the Kuril Islands or on the abyssal plain (Map 5).



Map 3. Distribution of *Cladorhiza* species from the NW Pacific (Cladorhizidae family).

All remaining demosponge species (4 spp.) are found within either the Tetractinellida Marshall, 1876, Polymastiida Morrow and Cárdenas, 2015 or Suberitida Chombard and Boury-Esnault, 1999 orders (Table 2). None of these species are known to be endemic to the region, with *Poecillastra japonica* (Thiele, 1898), *Polymastia pacifica* Koltun, 1966, and *Cornulum clathriata* (Koltun, 1955) known to be broadly distributed in the North Pacific Ocean (Map 6). However, the remaining species have not been identified to the species level, and so these species could be endemic, with many restricted in distribution within the Sea of Okhotsk and the Bussol Strait.

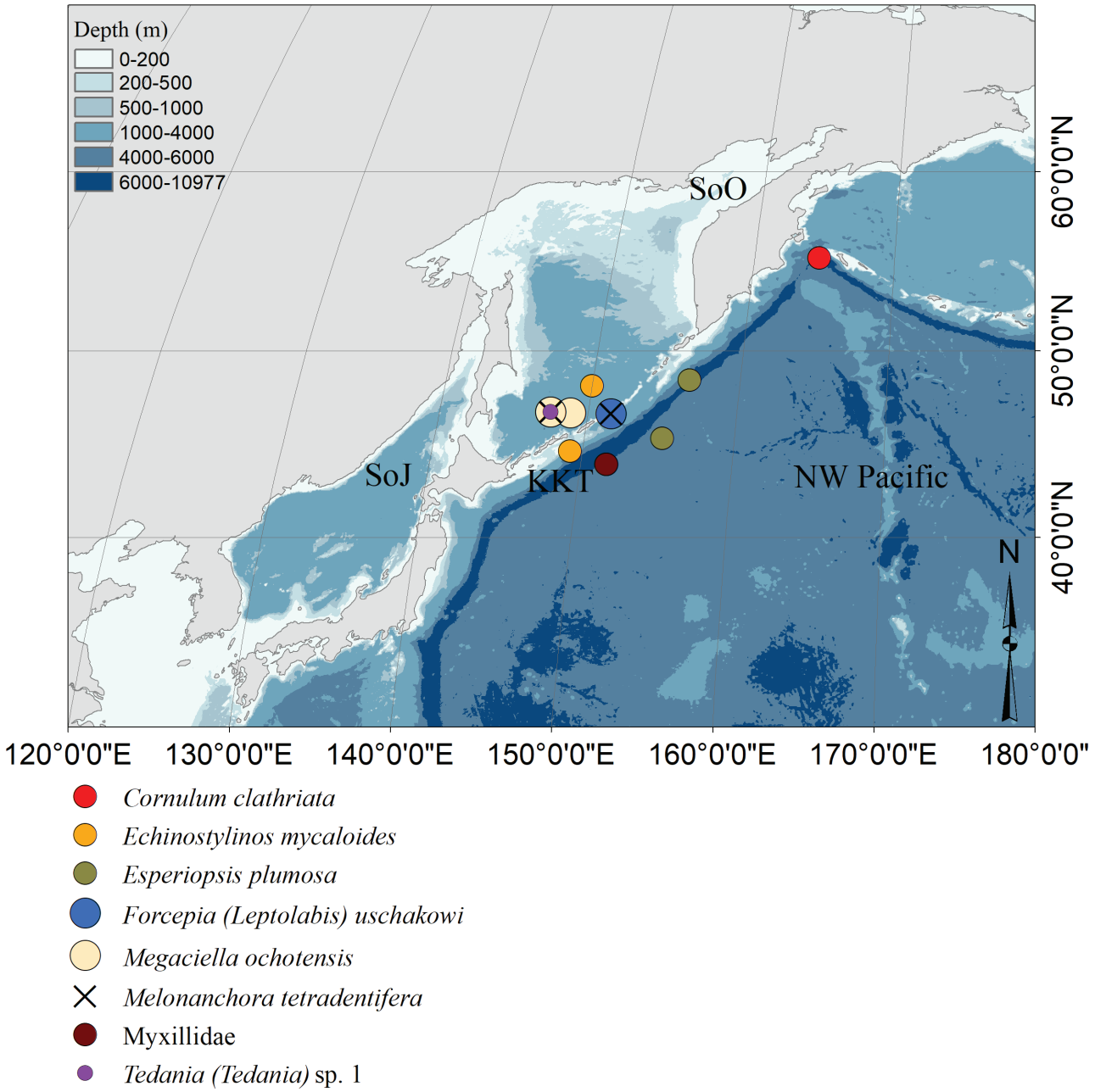
Overall, NW Pacific hexactinellids are not rich in genera or species, compared to demosponges; however, the genus *Hyalonema*, within the order Amphidiscosida Schrammen, 1924, has recorded eight species and one subspecies within this deep-sea region (Table 2). At least six of these species (including the subspecies)



Map 4. Distribution of remaining species from the Cladorhizidae family in the NW Pacific.

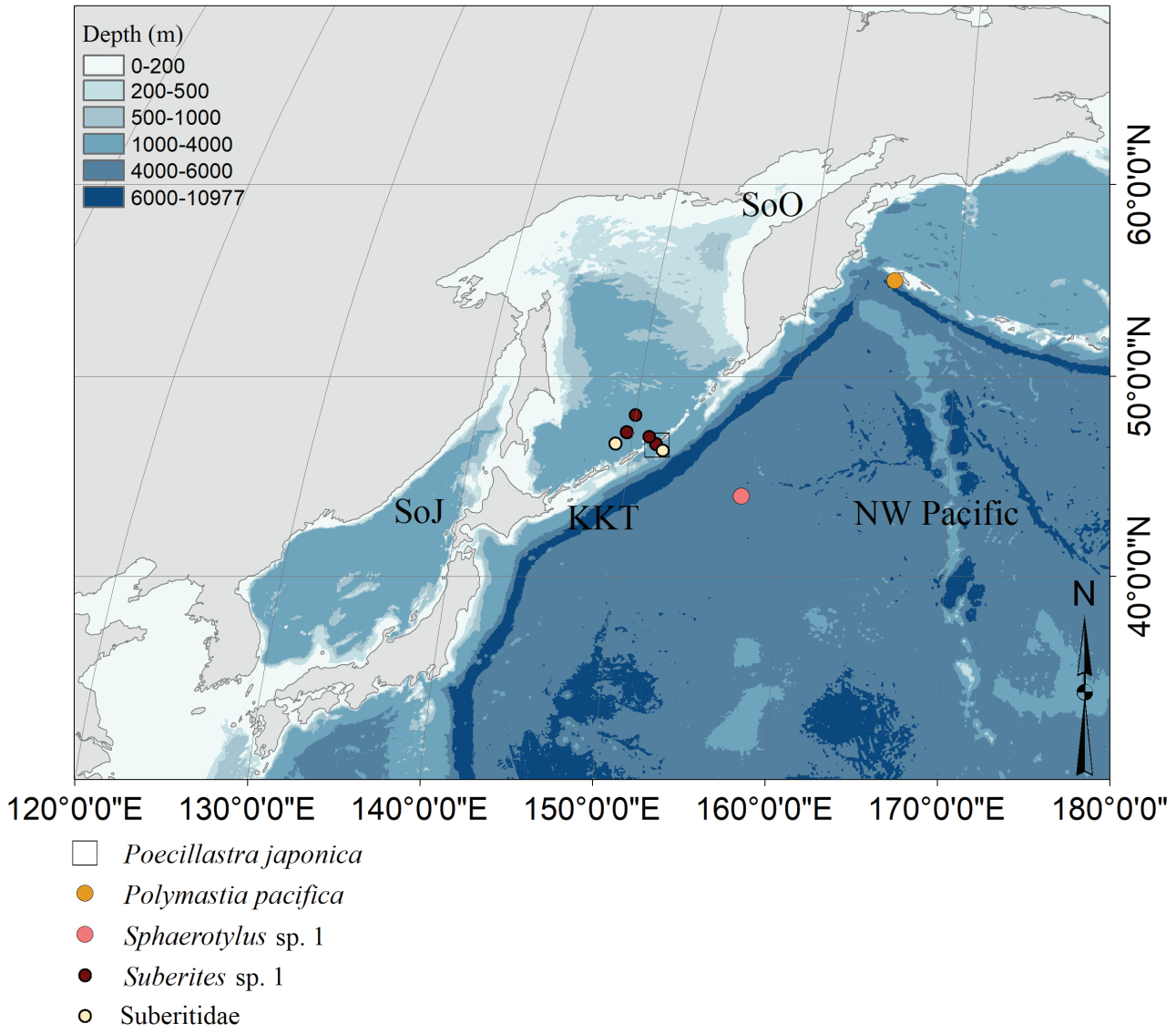
are likely be endemic to this region and have generally restricted distributions, like the, as yet unrecognised, subspecies, *H. (C.) hozawai vicarium* Koltun, 1967, which is only distributed in the Bering Sea (Map 7). *H. (C.) apertum simplex* Koltun, 1967 appears to be distributed broadly in the NW Pacific, being found at both the semi-enclosed Sea of Okhotsk and the Bering Sea; however, interestingly *H. (C.) apertum* Schulze, 1886 is distributed throughout the Pacific and Indian oceans, but is not known within the semi-enclosed seas of this region. *H. (Onconema) obtusum* Lendenfeld, 1915 is known to be distributed broadly in the North Pacific Ocean.

Within the Hexactinellida Schmidt, 1870 order Lyssacinosida Zittel, 1877, two families, the Rossellidae Schulze, 1885 and the Euplectellidae Gray, 1867 are represented within the NW Pacific (Table 2). In these two families, ten species



Map 5. Distribution of remaining demosponge species from the Poecilosclerida order.

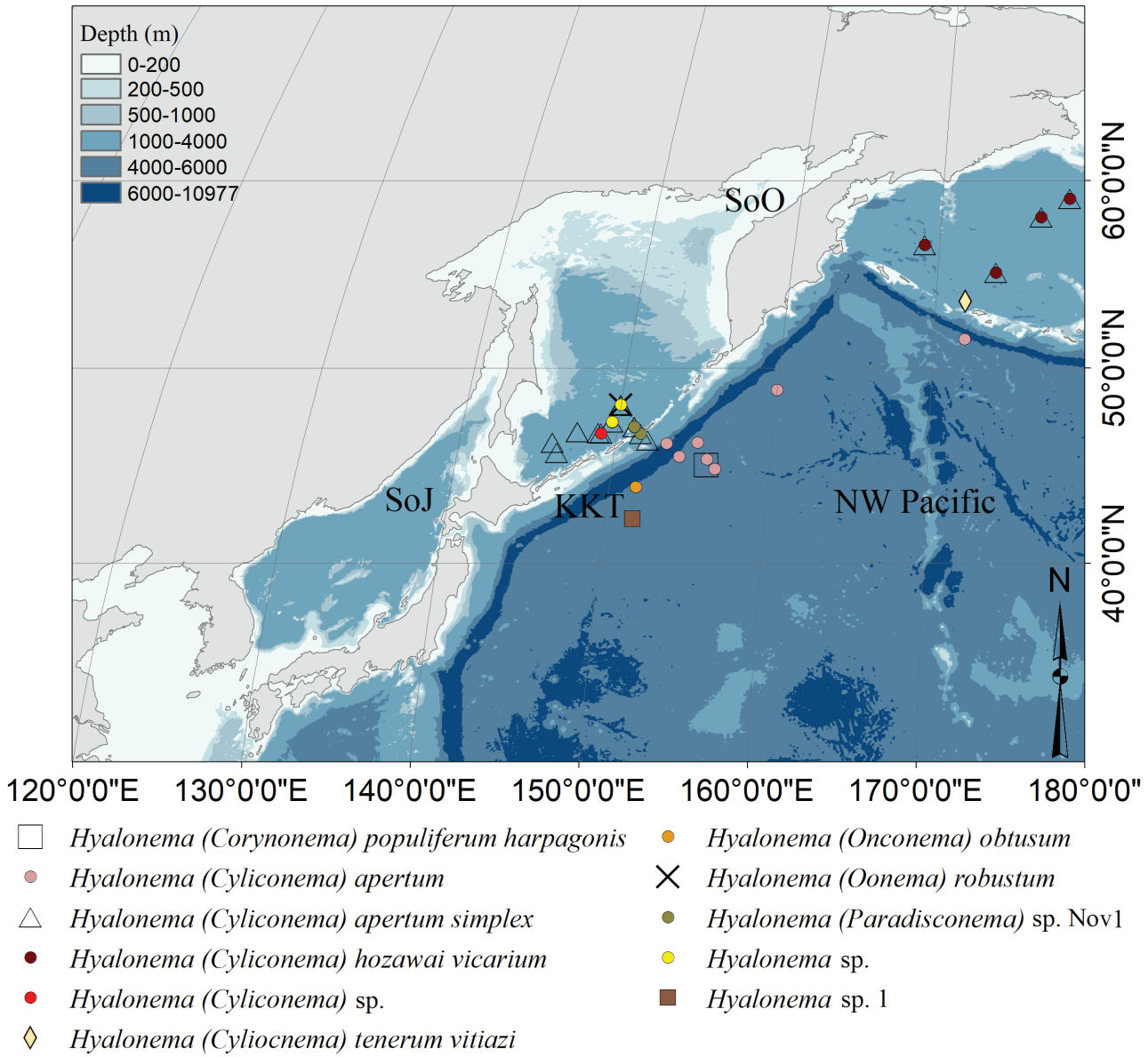
and one subspecies in six genera have been found. The most species rich of these genera, is *Caulophacus* Schulze, 1886, with three species and one subspecies represented. All of these *Caulophacus* species and subspecies are likely endemic to this region. All other species, apart from *Ijimaiella beringiana* Tabachnick, 2002, are found to be broadly distributed throughout the North Pacific, with *Sympagella cantharellus* (Lendenfeld, 1915) distributed throughout the Pacific Ocean (Map 8). Most of these species are found to have broad distributions throughout the NW Pacific, including some of the endemic species. Interestingly, *C. (Caulophacus) schulzei* Wilson, 1904 appears to be distributed only in the Sea of Okhotsk and Bussol Strait, whereas, *C. (C.) schulzei hyperboreus* Koltun, 1967 is distributed both within the semi-enclosed Sea



Map 6. Distribution of demosponges from the Polymastiida, Suberitida, and Tetractinellida orders.

of Okhotsk and Bering Sea. *I. beringiana* is only found in the Bering Sea and *Holascus undulatus* Schulze, 1899 is the only hexactinellid known from the Emperor Seamounts.

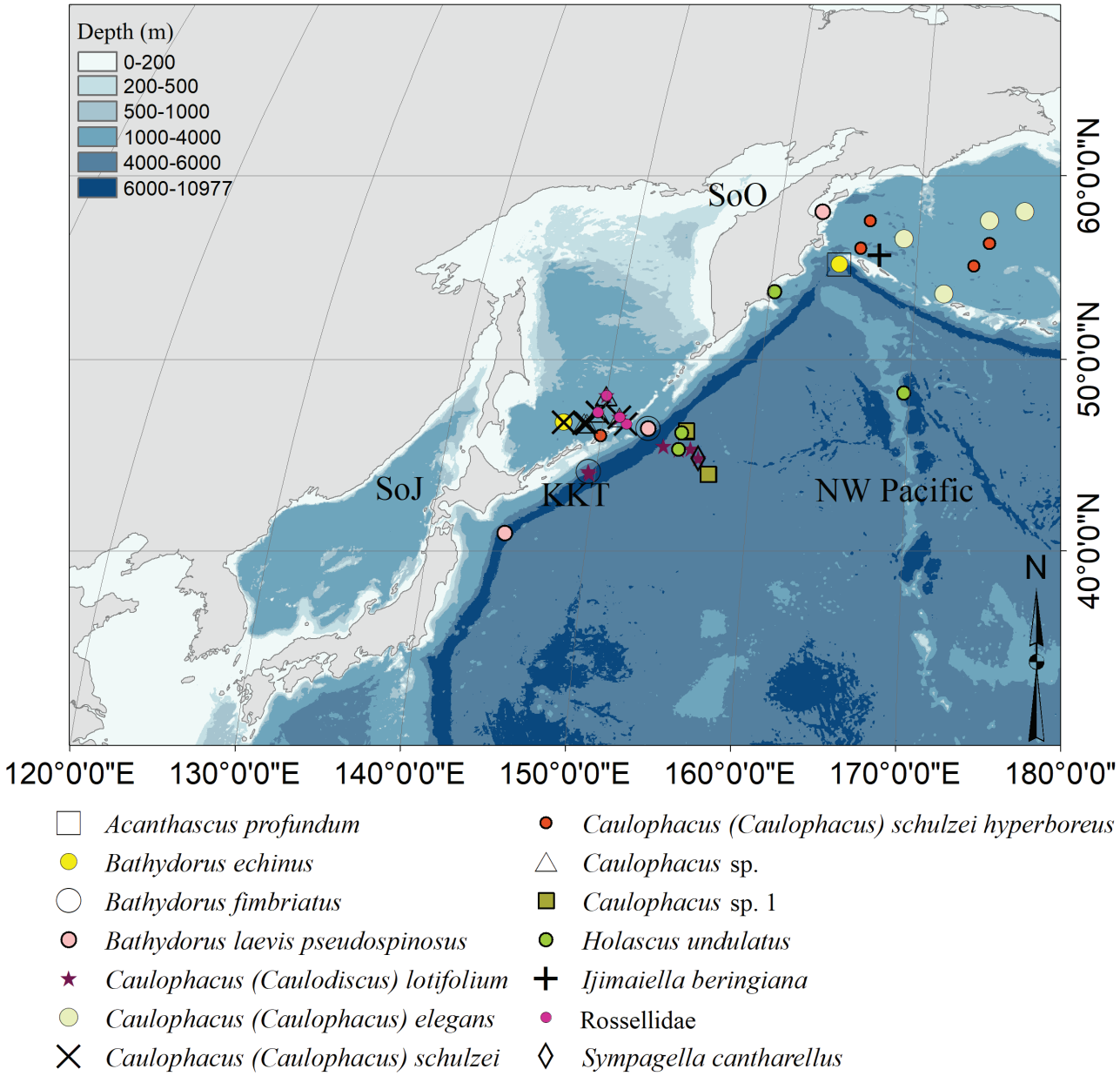
The final Hexactinellida order of Sceptrulophora Mehl, 1992, is comprised of three families, Euretidae Zittel, 1877, Aphrocallistidae Gray, 1867, and Farreidae Gray, 1872 in the NW Pacific (Table 2). These families comprise of at least four genera, and five species. Due to lower levels of taxonomic identification in this order, only two of the species are so far known to be endemic in the NW Pacific Ocean, and it is unclear if the remainder are endemic or of broadly distributed fauna. Endemic *Pinulasma fistulosum* Reiswig and Stone, 2013 is only found within the Bering Sea, whereas *Eurete iregulare* Okada, 1932 is found to be broadly distributed in both the Sea of Okhotsk, the Bussol Strait and the Bering Sea (Map 9). All representatives of the *Farrea* Bowerbank, 1862 genus are found to be broadly distributed only on the abyssal plain, and specimens of the Aphrocallistidae family were



Map 7. Distribution of *Hyalonema* species from the NW Pacific (Amphidiscosida order).

only found in the Kuril Basin of the Okhotsk Sea, with no known representatives from other parts of the deep NW Pacific.

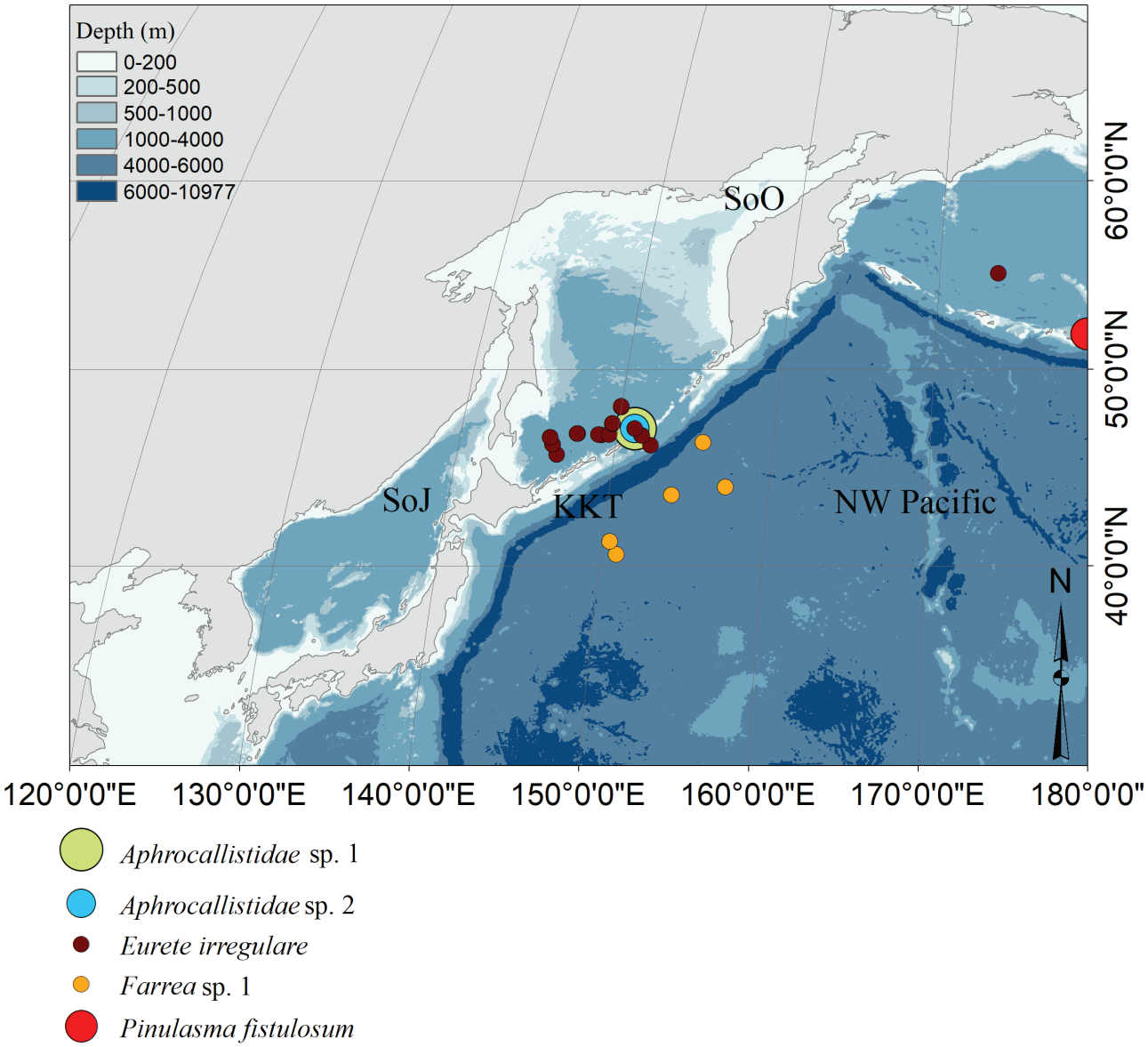
Close to 60% of all deep-sea species found in this region (40 spp.) are likely to be endemic to the NW Pacific Ocean (Table 2). Seventy-percent of these endemic species are demosponges (28 spp.), mainly found within the Cladorhizidae family, and 30% are hexactinellids (12 spp.), with most of these found within the Hyalonematidae family. Within the NW Pacific, three sponge genera are found to be monotypic (only having one species known to that genus), two are hexactinellid genera: *Pinulasma* Reiswig and Stone, 2013, *Ijimaiella* Tabachnick, 2002, and one demosponge genus *Koltunicladia*. This is greater than 10% of all genera known from depths greater than 2,000 m in the NW Pacific. With high levels of both genera and species endemism, this region is found to be faunistically distinct for deep-sea sponges. At least half of endemic



Map 8. Distribution of hexactinellid species from the NW Pacific (Lyssacionosida order).

sponge fauna appear to be restricted to the semi-enclosed Bering Sea and Sea of Okhotsk, with the remainder distributed in either the NW Pacific abyssal plain, the Bussol Strait, the Kuril-Kamchatka Trench, or the Emperor Seamounts.

Strong faunal connections are still found with sponge fauna in the North Pacific Ocean, with close to 20% (13 spp.) of species known to have this broad distribution, split generally evenly between both demosponges and hexactinellids, but dominated by the Rossellidae and Cladorhizidae families (Table 2). Weaker connections are seen within the entire Pacific Ocean, with less than 10% of NW Pacific species (five spp.) having this distribution, and these are dominated by four species in the Cladorhizidae family, and hexactinellid *S. cantharellus*. Very weak connections are seen globally; with only two *Chondrocladia* species found globally. Nine species morphotypes have



Map 9. Distribution of hexactinellid species from the NW Pacific (Sceptrulophora order).

unknown distributions due to the low level of identification, and this information could in the future aid our understanding of biogeographic patterns in the NW Pacific deep-sea fauna.

Previous studies have indicated that eurybathy is a relatively common distribution characteristic in the deep NW Pacific (Downey and Janussen 2015; Downey et al. 2018). Eurybathy appeared to be far more common for species found in the broad NW abyssal plains compared to the semi-enclosed Sea of Okhotsk (Downey et al. 2018). These differences appear to be due to the strongly eurybathic demosponges in the abyssal plain, compared to the more stenobathic species in the Sea of Okhotsk. Hexactinellids found in both the Sea of Okhotsk and the NW Pacific abyssal plains appear to have similar numbers of species with eurybathic ranges. However, newer analysis indicates that less than a quarter of species (15 spp.) throughout the NW Pacific have eurybathic characteristics, which are

represented roughly equally by demosponges and hexactinellids (Table 4). The most common restricted distribution was the abyss, with more than half of species (41 spp.) found only in this depth zone, and more than two-thirds of these represented by demosponges. Demosponges are more likely to be found in a restricted depth zone (39 spp., c. 85%), compared to hexactinellids (15 spp., c. 65%) in the NW Pacific.

5. Discussion

The deep NW Pacific sponge fauna was first sampled over a century ago (Okada 1932); however, it was systematically investigated during the 1940s to the 1960s during several campaigns from the RV *Vitiaz* (Koltun 1955a, 1955b, 1958, 1959, 1962, 1966, 1967, 1970). Until the most recent Russian-German expeditions, only 33 species and one subspecies, were known from this region. This figure has now more than doubled to 70 species morphotypes, two subspecies, with a high-likelihood of increased species numbers from the Sea of Japan and the Kuril-Kamchatka Trench, which have yet to be fully identified (Table 2). The number of genera known to this entire region has increased by a third from these recent expeditions (10 additional genera). The KuramBio (Kuril–Kamchatka Biodiversity Studies) expedition to the Kuril-Kamchatka abyssal plain found an additional eight species and two new genera (Downey and Janussen, 2015). During the SokhoBio (Sea of Okhotsk Biodiversity Studies) expedition, new specimens close to tripled the number of known species for this region and increased the number of genera by c. 50% (six new genera to region) (Downey et al. 2018). Only five sponge specimens were collected from stations deeper than 2,000 m during the 2010 SoJaBio (Sea of Japan Biodiversity Studies), and these are yet to be investigated, but are believed to represent one hexactinellid morphotype. No known sponges have been previously found below 2,000 m in the Sea of Japan (OBIS 2019), and so these would be the first sponges from this region. Thirteen species were previously known from the Kuril-Kamchatka Trench, and with an additional 87 sponge specimens from KuramBio II in 2016, it is likely that many new species will be described from this region. This expedition also collected specimens of both demosponges and hexactinellids at deeper depths than ever before, with one hexactinellid found at a depth of 9,301 m, and one demosponge at 9,013 m, several hundred metres deeper than the previous global records of depth for sponges (Koltun 1959). Early Russian expeditions also explored the Bering Sea, and so far 15 spp. are known from this and later expeditions (Koltun 1967; Reiswig and Stone 2013; OBIS 2019); and in the Emperor Seamounts, five spp. are known as well from earlier Russian expeditions (Koltun 1959, 1962, 1970). A new expedition in 2019 to the Emperor Seamounts (Nintoku Seamount) has recorded many species from depths of 2,100-2,400 m that are not known from previous expeditions in the NW Pacific Ocean, with several morphotypes noted from the families of Farreidae, Euplectellidae (particularly the genus *Walteria* Schulze, 1886), Rossellidae and some encrusting demosponges (pers. com L. Watling, August 2019) (Figure 2). These initial results indicate that this seamount ridge has families, genera, and species that are unusual compared to the rest of the NW Pacific deep-sea region.

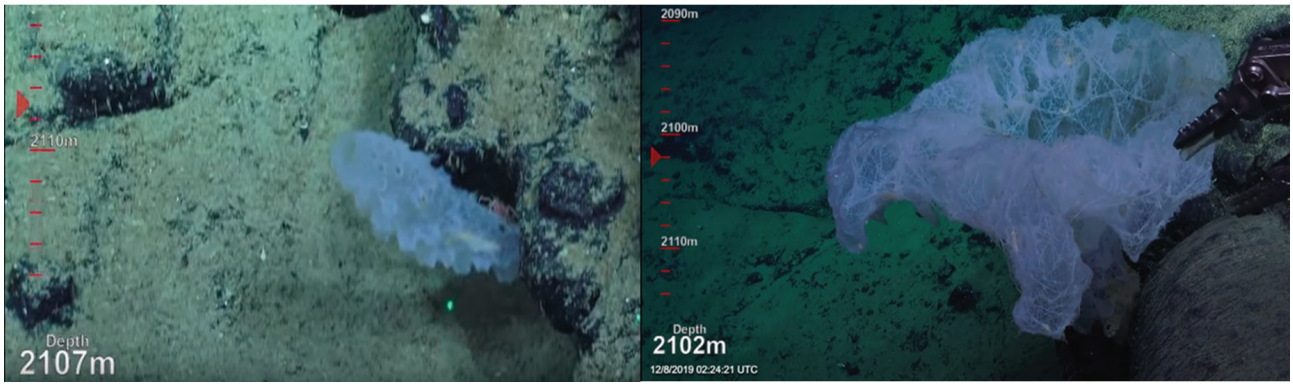


Figure 2. Examples of two hexactinellids sponges from the deep Emperor Seamounts (2019), Nintoku Seamount. Schmidt Ocean Institute. Les Watling.

Currently, over 20% (14 spp.) of species collected by these new Russian-German expeditions are new to science, which is similar to other deep–sea expeditions, such as the ANDEEP I–III (Janussen and Tendal 2007), and the abyssal Clarion Clipperton Zone in the mid–Pacific (Kersken et al., 2017), which both found 20–33% of species were new to science. However, with many specimens not fully identified, this is likely to increase substantially, indicating that the deep NW Pacific Ocean is likely richer in species but also limited in terms of sampling.

More than half of sponge species found on the Kuril-Kamchatka abyssal plain, and nearly two-thirds of species from the Sea of Okhotsk, appear to be geographically limited, only being found at one station (Downey and Janussen 2015; Downey et al. 2018). Close to 60% of species have apparent restricted geographical ranges and are represented by few specimens (Table 2). This is a known characteristic of deep-sea fauna, with many species either found in few samples, or found as singletons, indicating a low population density (Carney 1997; Ebbe et al. 2010; Hardy et al. 2015; Costello and Chaudhary 2017; Danovaro et al. 2017). Sponge growth and reproductive regimes in the deep sea are not well known (Hogg et al. 2010); however, it is likely that most sponges reproduce both sexually by releasing larvae and asexually by budding and fragmentation episodically. As reproduction is likely seasonal and recruitment episodic, these small, patchily rich areas of sponge singletons, could be due to rare reproductive events.

As well as a low population density, localised habitat features could be driving habitat-specific rarity (Ramirez-Llodra et al. 2010). The deep seafloor is formed of hundreds of millions of kilometres of continental slope and abyssal plain; however, small geological features within these are varied, such as seamounts, trenches, and ridges, which are common in the NW Pacific Ocean, and could be driving localised habitat specific rarity, potentially seen in a number of sponge species, such as *K. flabelliformis*, *H. (C.) ternerum vitiazi* Koltun, 1967, and *S. cantharellus*. Sponges tend to be more abundant and diverse on harder substrates, particularly seamounts, canyon heads and walls, ridges, and banks (Ramirez-Llodra et al. 2010; van Soest et al. 2012). The diversity of hard habitats in the NW Pacific could explain some of the localised higher diversity and/or abundance observed closer to the Kuril Islands ridge, trench and on the Emperor Seamounts (Table 2). These

regions also tend to be areas of localised upwelling, generating greater food availability for sponges in these regions (Ramirez-Llodra et al. 2010), which is potentially another factor determining the greater numbers of sponges found at some stations in the Sea of Okhotsk and around the Kuril-Kamchatka ridge and trench. These unique abiotic attributes and biotic processes have likely helped to create varied levels of patchy sponge presence and diversity across the NW Pacific region.

Demosponges dominate the deep NW Pacific region, accounting for two-thirds (46 spp.) of all species currently found (Table 2). Many of these newly added species were found in both the Sea of Okhotsk, as well as several from the Kuril-Kamchatka abyssal plain (Downey and Janussen 2015; Downey et al. 2018). Cladorhizid sponges dominate the faunal composition in the NW Pacific region, accounting for more than three quarters (35 spp.) of known demosponge species, and accounting for more than a third (6) of all demosponge genera. Cladorhizid sponges are typical deep-sea sponge fauna, having likely evolved carnivory in the food–poor depths of the ocean (Vacelet and Boury–Esnault 1995). More than 10% (20 spp.) of globally described cladorhizids (173 spp., WORMS 2019) are found from this region, and with the addition of new species in the future (currently 13 new spp. and 2 spp. aff.), this will increase. Currently, two-thirds of cladorhizid species (23 spp.) are endemic to the deep NW Pacific Ocean. This region contains 100% of *Koltunicladia* species (1 sp.), 43% of all *Asbestopluma* (A.) species (13 spp.), 22% of all *Chondrocladia* (C.) species (3 spp.), 18% of all *Cladorhiza* species (8 spp.), 10% of all *Lycopodina* species (3 spp.), and 8% of all *Abyssocladia* species (2 spp.). It is likely that with an increase in deep-sea exploration of the North Pacific, and identification of new specimens from the Kuril-Kamchatka Trench, that many more new cladorhizid species and genera will be found in the NW Pacific, which could have been an important region for the evolution of this family, potentially due to the variety of deep-sea habitats and numerous currents and upwelling areas (Lundsten et al. 2014; Downey and Janussen 2015).

Glass sponges (Hexactinellida) are not as rich as demosponges at the species (23), genera (10) or family (6) level in the deep NW Pacific (Table 2). However, glass sponges outweigh demosponges in abundance, accounting for nearly 60% of all specimens found in this region (Table 1), and were found to be particularly rich in the Sea of Okhotsk, accounting for three-quarters of all specimens found (Downey et al. 2018). Many species of hexactinellid, including *Hyalonema*, *Caulophacus*, *Eurete* Semper, 1868 and *Bathydorus* are found across many stations (Maps 7–9), highlighting their broad distributions across the NW Pacific (Table 2). Nine species morphotypes of hexactinellids were found in the Kuril Basin of the Sea of Okhotsk, indicating the richness of hexactinellids in this semi-enclosed deep-sea region (Downey et al. 2018). Hexactinellid species richness also occurs in the Bering Sea (12 spp.), the Kuril-Kamchatka abyssal plain (8 spp. and 1 subsp.), and the Kuril-Kamchatka Trench (6 spp.) (Table 2). Hexactinellid diversity is found to be at its least in the Bussol Strait (4 spp.) and the Emperor Seamounts (1 spp.). However, with a new expedition to the Emperor Seamounts, it is likely that hexactinellid richness will increase (pers. com L. Watling, August 2019). Hexactinellid species account for a third (23 spp.) of known species

in this deep-sea region (Table 2). The SokhoBio expedition has added six new hexactinellid species to the deep Sea of Okhotsk, Bussol Strait and NW Pacific fauna, which has nearly doubled the number of previously known hexactinellid species and added in one new genus (*Bathydorus*) to this region. One new to science species has been found: *Hyalonema (Paradisconema)* sp. Nov. 1. Hexactinellid abundance is exceptional in the Sea of Okhotsk, which is found to be at least fourteen orders of magnitude greater than the adjacent Kuril–Kamchatka region (Downey et al. 2018). Most hexactinellid families and genera found in the NW Pacific are found globally in all deep-sea environments (Tabachnick 1994), and the results from these studies indicate the presence of both new species, high levels of abundance, and the broad distributions of many hexactinellid species.

A hypothesised poleward decrease in diversity of deep benthic communities has been proposed, although it remains controversial (Gray 2001; Ramirez-Llodra et al. 2010). Latitudinal bands were compared within this study region, and superficially, diversity does appear to be greater at the southerly sector of the NW Pacific (Table 3). However, large differences in depth range, longitudinal range and sampling intensity, make it difficult to discern if there was a real decrease in diversity with increased latitude. Areas of semi-enclosed seas, such as the Sea of Okhotsk, regional diversity is found to be relatively high (Downey and Janussen 2015; Downey et al. 2018), compared to the adjacent Kuril-Kamchatka abyssal plain, and this high level of richness and diversity of species is likely influencing this poleward trend in reduced diversity above 50°N. What could be detected in this latitudinal analysis was a decrease in demosponge species and an associated increase of hexactinellids with increasing latitude. Hexactinellids are known to be more abundant and diverse in the high latitudes of the North and NE Pacific (Beulieu 2001; Leys et al. 2004; Reiswig 2014), which could be influencing this pattern. This is also found in the high latitudes of the Southern Ocean, with hexactinellids often found in greater numbers due to likely higher levels of dissolved silica, upwelling bottom waters, reduced runoff, and highly seasonable food availability (Downey et al. 2012).

Energy availability (Woolley et al. 2016) and major ocean currents (Lembke–Jene et al. 2017) could partly explain the variations observed in diversity and abundance throughout the NW Pacific Ocean. Large sectors of the NW Pacific Ocean are in areas of upwelling, such as the Sea of Okhotsk, the Kuril-Kamchatka Trench, Kamchatka Peninsula, Sea of Japan, and the Bering Sea (Zhabin et al. 2017), which increases the amount of nutrients available for a diverse range of species to thrive in these regions. Results from the Sea of Okhotsk indicate that sponges in this region are generally richer and more abundant than other areas sampled (Downey et al. 2018). The Sea of Okhotsk is a highly productive region (Sorokin and Sorokin 1999, Arzhanova and Zubarevich 1997, Radchenko et al. 2010, Sahling et al. 2003), and is located within a high carbon import and export latitude (Hays and Morley 2004). High levels of productivity are likely to be important in not only maintaining the high numbers of species in the Sea of Okhotsk, but also in the remarkable abundance of specimens found, which were at least eight orders of magnitude greater than the

adjacent Kuril–Kamchatka region (e.g. Downey and Janussen 2015; Downey et al. 2018). Major currents that flow in and out of this region could also explain differences in faunal abundance and composition. The East Kamchatka Current, Soya Warm Current, and Kuroshio Current are warmer, saline, nutrient poor currents, whereas the East Sakhalin Current and Oyashio Current are colder, denser, less saline, nutrient and oxygen–rich currents (Lembke–Jene et al. 2017). Food-rich and highly oxygenated currents flow into NE sector of the Kuril Basin, the Bering Sea, and the northern sector of the Emperor Seamounts, which could partly explain why we find more sponge species and greater abundance in many of these regions.

The source-sink hypothesis predicts that abyssal species distributions are sinks regulated by source populations in bathyal regions (Rex et al. 2005). However, sponge species depth distributions (abyss and shallower depth zones within their entire distribution: 17 spp.) are not common in this region (Table 4), with only a quarter of species with this distribution. Therefore, the source-sink hypothesis does not explain much of abyssal species distributions in the NW Pacific Ocean. A recent study using global data, found that it is unlikely that abyssal faunal populations are sustained only by larvae from bathyal and shelf populations, and that in productive regions, such as the Sea of Okhotsk, Bering Sea, and Emperor Seamounts, reproduction is local, and could actually be important in sustaining smaller populations in less productive regions of the deep sea (Hardy et al., 2015), such as the adjacent Kuril-Kamchatka abyssal plain. Results indicate that there is strong relationship between abyssal and hadal depths, with two-thirds (6 spp.) of species in the hadal, also found in the abyss in the NW Pacific (Table 4). A transition zone between the abyss and hadal has been indicated in previous studies (Belyaev 1966, 1989; Kamenskaya 1981, 1995; Jamieson et al. 2011), and could be due to abyssal populations sustaining hadal depths. However, a third of species in the hadal are not known from any other depth, and thus, hadal regions could be geological features that have evolved their own self-sustaining populations in the NW Pacific Ocean (Ramirez-Llodra et al. 2010).

In the NW Pacific Ocean, emergence and submergence processes are important to consider in understanding the evolution of deep-sea fauna in semi-enclosed seas, such as the Sea of Okhotsk, which has only limited deep-sea straits allowing access of species between this region and adjacent deep-sea regions (e.g. Brown and Thatje 2014), and the Bering Sea, which has multiple deep-sea straits. In the Bering Sea, two hexactinellid species (*Acanthascus profundum* Koltun, 1967 and *H. (C.) apertum simplex*) could be classed as pseudo-abyssal, as they are found to be deeper in the Bering Sea than elsewhere in their distribution. Two other species, demosponge *P. pacifica*, and hexactinellid *C. (C.) elegans*, are potentially undergoing emergence, as they are found to be shallower in the Bering Sea than elsewhere in their range. The Sea of Okhotsk is connected to the Kuril–Kamchatka abyssal plain through the Krusenstern Strait (1,920 m) and the Bussol Strait (2,318 m) (Radchenko et al. 2010). Analysis of the Sea of Okhotsk sponges indicates that six demosponge species are undergoing submergence, which indicates they could be classed as 'pseudo-abyssal', such as *Megaciella ochotensis* (Koltun, 1959) and *Forcepia uschakowi*

(Burton, 1935), whereas one hexactinellid species, *C. (C.) lotifolium* Ijima, 1903, could be undergoing emergence from this typically deeper abyssal and hadal ranged species (Downey et al. 2018). These results suggest that some Sea of Okhotsk and Bering Sea sponges are undergoing submergence from bathyal populations within and outside the Sea of Okhotsk, allowing the development of 'pseudo-abyssal' species, as well as emergent fauna from deeper distributed species, and therefore deep-sea straits could have been key in connecting these sponge communities. The lower proportion of submergent, pseudo-abyssal fauna in the Bering Sea could be due to limited sampling, but also the greater numbers of deep-sea connections to the NW Pacific abyssal plain enabling improved connectivity. However, the presence of a small number of eurybathic sponge species both within and outside of the Sea of Okhotsk and Bering Sea could indicate that emergence and submergence processes are important in understanding some of the sponge distributions in the semi-enclosed seas of the NW Pacific Ocean.

Utilising all depth information from the NW Pacific deep sea, stenobathy is found to be a common characteristic, with more than three-quarters (55 spp.) of sponges in this sector found with this trait (Table 4). Demosponges are more likely to have restricted depth distributions (39 spp., about 85%), compared to hexactinellids (15 spp., c. 65%) in the NW Pacific. Diversity in species is found to be greatest in the NW Pacific abyss, with 56 spp. found in this depth zone, compared to 20 spp. in the lower bathyal, and 13 spp. in the hadal. A known large-scale diversity pattern of deep-sea benthic communities is a unimodal relationship between diversity and depth, which peaks at intermediate depths (2,000–3,000 m) (Gray 2001). This study found the abyss to be richer in species than the lower bathyal; however, only sponges with deeper depths were analysed, and so a re-analysis of sponges found at shallower depths is needed to confirm these findings. However, abyssal depths could still be found to be richer in the NW Pacific, as there are a number of semi-enclosed basins, seamounts, and ridges at this depth range, which all have unique oceanographic features that could be enabling this abyssal diversity (Ramirez-Llodra et al. 2010). Stenobathy could be also be an artefact of sampling at a limited depth range, or it could be driven by absence of substrate, reduced food-supply at greater depths, and greater distances from deeper or shallower sites, such as in the broad abyssal plain in the NW Pacific. Less common, broader depth ranges found in both demosponges and hexactinellids are potentially driven by their ability to construct root tufts and reproduce both sexually and asexually (Tabachnick 1994), enabling them to colonise a broader range of deep-sea environments in the NW Pacific.

The deep NW Pacific is found to be a distinct biogeographic region, as it is overwhelmingly endemic, both in terms of sponge species and in terms of genera, which had been previously proposed by Menzies et al. (1973). However, the presence of large-scale oceanographic features, such as the similar levels of moderate particulate flux and the dominance of sub-Polar Gyre currents, have made a greater number of researchers to propose a single North Pacific biogeographic region (Vinogradova 1959, 1997; Kussakin and Mezhov 1979; Belyaev 1989; Watling et al. 2013). It is likely that smaller differences

generated by localised currents, and geological features (seamounts, trenches, ridges, and semi-enclosed basins), are far more important in the evolution of NW Pacific deep-sea sponge fauna (McClain and Mincks Hardy 2010), and these smaller features are likely important in the adjacent NE Pacific. The apparent richness of fauna surrounding the Kuril Islands, has led other researchers to hypothesise that this region could have been a recent centre of diversification for North Pacific boreal fauna (Kussakin and Mezhov 1979). So far, 15% of species found in the Kuril-Kamchatka Trench are endemic; however, the majority of samples have not been fully identified, and so these lower levels of endemism are likely to increase. Previously, exploration of trenches in the North Pacific found high numbers of endemic species, c. 40–50%, which led researchers to propose a distinct Aleutian-Japan biogeographic hadal province (Belyaev 1989; Vinogradova 1997). New species found around the Emperor Seamounts, which have not yet been found in the NW Pacific (Figure 2), indicate that seamounts are also likely to have distinct sponge communities in the NW Pacific, potentially being more faunistically connected to Hawaiian seamount chain, and they could also be a barrier between the NW Pacific and NE Pacific abyssal sponge fauna.

Moderate abyssal faunal connectivity is found between the NW Pacific region and other sectors of the Pacific Ocean (18 spp.), and this faunal connection is stronger with the rest of North Pacific (Table 2). Several species, which are new to this region, including *Lycopodina globularis* (Lévi, 1964), *Chondrocladia* (C.) *koltuni* Vacelet, 2006, and *Cladorhiza mirabilis* (Ridley and Dendy, 1886), highlight this faunal connection, as they were previously only known from the N and NE Pacific abyss (Lévi 1964; Koltun 1970; Vacelet 2006). The deep-sea Aleutian Island Archipelago sponge fauna, distributed both in the Bering Sea and abyssal North Pacific, has previously found to have strong taxonomic affinities with the Sea of Okhotsk sponge fauna (30% of species in common) (Stone et al. 2011). In this study, at least 12 spp. and 2 sub. spp. are found to be distributed in the Bering Sea/Aleutian Island area, as well as elsewhere in the NW Pacific. The majority of these species are hexactinellids, which could have come from the North Pacific Bering Sea region, which appears to be richer in glass sponges from latitudinal analysis in this study, and could have been distributed via the anticlockwise currents associated with the sub-Polar Gyre, to the Kamchatka Peninsula, the Sea of Okhotsk and the remainder of the region. Most deep-sea sponges are likely to be hermaphrodites, reproducing both sexually and asexually, and likely producing lecithotrophic (non-feeding) larvae. In one sponge study, researchers found high levels of genetic variability within populations, which indicated contributions from both highly dispersed sexually produced larvae and asexually produced budding/fragmentation (Maldonado and Uriz 1999). Despite vast distances and depths, some sponge species in the deep sea are likely connected through long-distance sexual and asexual dispersal through currents, across broad, often fragmented, distributions.

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CHAPTER 3

CNIDARIA AND CTENOPHORA

REVIEW OF DEEP-SEA CNIDARIA AND CTENOPHORA FAUNA IN THE NW PACIFIC OCEAN

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1. Introduction

The marine region encompassed between 40°N and 60°N and 120°E to 180°E contains a large area of the NW Pacific Ocean, including the northern half of the Sea of Japan, the Sea of Okhotsk, the southwestern part of the Bering Sea, and the Pacific Ocean, as well as the Kamchatka Peninsula, the Kuril Islands and the northern Japanese Islands. Much of this marine region is deep sea (>200 m in depth). Economically, the region is among the most productive marine fisheries regions in the world, including not only open-water fisheries but also commercially important crab fisheries (Spiridonov 2005). Despite its obvious importance to the global fishery, research on many marine taxa in the region is lacking, due to the relative remoteness of the region as well as other logistical issues such as severe weather. The lack of data and research in the region thus hampers our knowledge of many marine taxa, making conservation and protection planning difficult.

In this chapter, we will examine the state of knowledge in the NW Pacific Ocean for two phyla of marine invertebrates, the Cnidaria and Ctenophora, at depths below 2,000 m, in the lower bathyal (2,000–3,000 m), abyssal (3,000–6,000 m) and hadal (>6,000 m) zones. These two phyla are among the most ancient of metazoans (Simion et al. 2017), and are often grouped together as "coelenterates", although the scientific validity of such a group has now been debunked (e.g. Whelan et al. 2015; Simion et al. 2017; Nielsen 2019). Although superficially similar morphologically, this similarity is only at the macromorphological level, with both groups being often fragile and gelatinous. For example, ctenophores have rotational symmetry while cnidarians have diverse symmetries (including bilateral and radial symmetry). In all probability, the Cnidaria and Ctenophora are sister groups that evolved independently from the last common ancestor of Eumetazoa (Nielsen 2019).

Cnidaria (Figure 1) include the various corals, true jellyfish, and related animals, and can be broadly split into three major groupings; 1) the class Anthozoa, primarily benthic corals and allies, 2) the subphylum Medusozoa of true jellyfish (classes Scyphozoa, Cubozoa, Staurozoa) and hydrozoans (class Hydrozoa), and the classes 3) Myxozoa and Polypodiozoa, marine parasites. Cnidaria can be united by cnidocytes ("polar capsules" in Myxozoa), which are specialized cells used for prey capture, defense, and/or attachment. Many Cnidaria have asexual and sexual life-history stages, with two basic body forms, benthic polyps with a single oral opening facing upwards, and a planktonic medusa with the oral opening facing downwards. Around these oral openings, tentacles are aligned in various arrangements.

Cnidarians are common components of the deep-sea plankton and benthos (e.g. Lindsay and Hunt 1999; Cairns 2007; Dautova 2018a,b), and can often be considered as ecosystem engineers, providing habitat for other marine organisms (Ohtsuka et al. 2009; DiCamillo et al. 2013). As such, their diversity, abundance, and distribution in the water column and on the seafloor are important datasets in establishing conservation and protection planning. Deep-sea Cnidaria contain some of the most well-known and spectacular organisms from these ecosystems, including examples such as *Pandea*

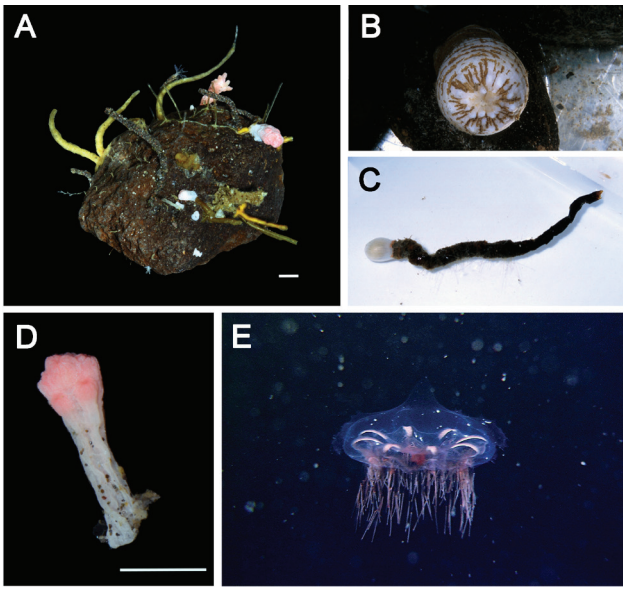


Figure 1. Some Cnidaria and Ctenophora species observed in the deep sea of the NW Pacific. (A) Stone with numerous benthic animals, including light pink alcyonarians, dark brown polychaete tubes, and light brown broken-off hydrozoan colony (?) from station 8–5 EBS, depth 2,327-2,330 m. Scale = 5 mm. (B) Actinarian *Hormathia spinosa* from station XR-10 off Kushiro, depth 5,509-5,561 m. (C) Actinarian *Galatheanthemum* sp. from station XR-12 off Kushiro, depth 5,471-5,514 m. (D) Octocoral *Aspera rosea* from station 8-4 EBS, depth 2,333-2,336 m. Scale = 5 mm. (E) *Halicreas minimum* from 1,043 m in Sagami Bay, Japan; this species has also been reported from >2,000 m within the study area of the NW Pacific. Images A and D by Anna Lavrentieva, B and C by Kensuke Yanagi, and E by Dhugal Lindsay.

rubra, a hydrozoan anthomedusan species that illustrates the run-on effect that ocean acidification can be expected to have on deep-pelagic ecosystems (Lindsay et al. 2008), as well as the huge, red, tentacle-less "fingerfoot medusa" *Tiburonia granrojo* (Matsumoto et al. 2003), *Epizoanthus* zoantharian species symbiotic with hermit crabs (Muirhead et al. 1986; Ryland and Ward 2016; Kise et al. 2019), and the enigmatic *Relicanthus* anemone, a sea anemone with unusual phylogenetic placement (Rodriguez et al. 2014; Xiao et al. 2019).

Ctenophores are also common components of the deep-sea plankton, sometimes being almost as abundant as cnidarians (e.g. Fig. 7 in Lindsay et al. 2000), with members of the benthic ctenophoran order Platyctenida commonly observed as epibionts on other benthic deep-sea animals (DJL, pers. obs.).

2. Objectives

The main objective of this chapter is to provide an overview of the state of current knowledge of the phyla Cnidaria and Ctenophora at depths below 2,000 m in the NW Pacific by examining records and occurrences from the Ocean Biogeographic Information System (OBIS) database combined with additional records from the literature and unpublished data.

3. Materials and Methods

In this review of knowledge of the Cnidaria and Ctenophora of the NW Pacific, we searched for records and occurrence data for each phylum in the Ocean Biogeographic Information System (OBIS 2020) on January 4, 2020. We limited our data search to depths below 2,000 m, and within 40°N to 60°N and 120°E to 180°E. Resulting datasets were downloaded, and assessed by taxonomic experts of each group (Anthozoa: JDR, KY, Medusozoa + Ctenophora: DJL). The OBIS Cnidaria dataset initially included 184 occurrence records, while that of the Ctenophora included three occurrence records. We subsequently re-

moved eight records from the Cnidaria dataset as the species identities and depths were clearly erroneous, and corrected the taxonomic nomenclature of several other records. We also added Actiniaria records from two research cruises that were not previously published; the Japan Agency for Marine Science and Technology's (JAMSTEC) KH01-2 cruise by the RV *Hakuho-Maru* in October to November 2001 around Chishima and the Japan Trench (n=38), and the KT08-27 cruise by the RV *Tansei-Maru* in October 2008 off the Sanriku Coast of northeastern Honshu, Japan (n=5) (both datasets and identifications from KY). We additionally added Octocorallia occurrence records (n=21) from Dautova (2018a) and Hydrozoa and Scyphozoa occurrence records (n=16) from Naumov (1971). After these checks, edits, and additions, the Cnidaria dataset contained 256 records, while the Ctenophora record numbers remained unchanged. Taxonomy of both phyla followed the World Register of Marine Species (WoRMS 2020). It should be noted that the higher taxonomy of the phylum Ctenophora is in desperate need of revision (e.g. Podar et al. 2001; Lindsay and Miyake 2007). Datasets are available as Supplemental Material 1.

We then examined the datasets in detail, and assessed 1) numbers of species (counting only records identified to species), 2) numbers of records by lowest taxonomic rank, 3) numbers of species for each larger taxonomic grouping (class/subclass/order), 4) numbers of records by depths, and 5) numbers of records reported by year. After this, we then reviewed and discussed the state of knowledge for both phyla in the NW Pacific Ocean, and propose ways forward to broaden our knowledge of these taxa in the deep sea of this region.

4. Results

Images of some Cnidaria and Ctenophora species observed in the deep sea of the NW Pacific are shown in Figure 1.

4.1 Cnidaria

Within Cnidaria, of 256 records and occurrences, 86 were for planktonic taxa (=33.6% of Cnidaria records), and 166 (=64.8%) were for benthic anthozoan taxa. Four records (=1.6%) were only noted as "Cnidaria" and could not be placed into either group. No Myxozoa or Polypodiozoa were reported. Within the non-Anthozoan cnidarians, there were 28 Scyphozoa (=10.9% of Cnidaria, 32.6% of Medusozoa), 58 Hydrozoa (=22.6%, 67.4%, respectively), and no Staurozoa or Cubozoa. Within Anthozoa, there were 28 Octocorallia (=10.9% of Cnidaria, 16.9% of Anthozoa), seven Scleractinia (=2.7%, 4.2%), and 83 Actiniaria (=32.3%, 50.0%), with an additional 48 records for "Anthozoa" only (=18.7%, 28.9%).

By lowest taxonomic rank, four records were to phylum (=Cnidaria; 1.6% of Cnidaria), 92 to class (=35.9%), one to subclass (=0.4%), 19 to order (=7.4%), 13 to superfamily (=5.1%), 12 to family (=4.7%), 29 to genus (=11.3%), and 86 to species (=33.6%). The 86 species records consisted of 23 different species: eight Hydrozoa, one Scyphozoa and 14 Anthozoa (eight Actiniaria, five Octocorallia, and one Scleractinia). By numbers of records, the anemone *Edwardsia sojabio* Sanamyan N. & Sanamyan K., 2013 was by far the most common, with 33 occurrences, followed by the octocoral *Radicipes sakhalinensis* Dautova, 2018 (n=9), the hydrozoans *Operculariella angelikae* Stepanjants, 2012 (n=7), *Botrynema brucei* Browne, 1908

(n=5), the anemone *Hormathia spinosa* (Hertwig, 1882) (n=5), the hydrozoans *Halicreas minimum* Fewkes, 1882 (n=3), and *Pantachogon haeckeli* Maas, 1893 (n=3), the scleractinian *Fungiacyathus* (*Bathyactis*) *marenzelleri* (Vaughan, 1906) (n=3), the scyphozoan *Atolla wyvillei* Haeckel, 1880 (n=2), the octocoral *Aspera rosea* Dautova, 2018 (n=2), and the actiniarian *Bathydactylus kroghi* Carlgren, 1956 (n=2, tentative identification). All other species only occurred once in our dataset.

By depth, there were nine records from >6,000 m, 90 from 5,000 to 6,000 m, 29 from 4,000 to 5,000 m, 73 from 3,000 to 4,000 m, and 55 from 2,000 to 3,000 m (Figure 3). The deepest records were for the hydrozoan *Pectis profundicola* (Naumov, 1971) between 6,800 to 8,700 m (Naumov 1971), an unidentified Anthozoa from 7,366 m, the actiniarians *Bathydactylus kroghi* from 7,141 m, and *Sicyonis* sp. (tentative identification), *Galatheanthemum* sp. and *Mesomyaria* sp. E from 7,139 m, as well as an unidentified Cnidaria at 6,985 m.

By year, the earliest records of Cnidaria within the region were from 1906 (specimens now housed in the Smithsonian, USNM), but these were removed from our dataset as described in the methods due to their capture depths being inferred as being at the seafloor, presumably during their import into the OBIS dataset, even though they were obviously from the pelagic zone closer to the surface (DJL, pers. obs.). Thus, subsequently, the next records were from 1966 (Naumov 1971) and 1981, while the large majority of Cnidaria records from the region were from 2000 or later, from only two cruises by K. Yanagi in 2001 and 2008 and a few publications, namely Brandt et al. (2013), Sanamyan and Sanamyan (2013), Stepanjants (2013), Trebukhova et al. (2013), Brandt et al. (2015), Fischer and Brandt (2015), Schwabe et al. (2015), and Dautova (2018a,b).

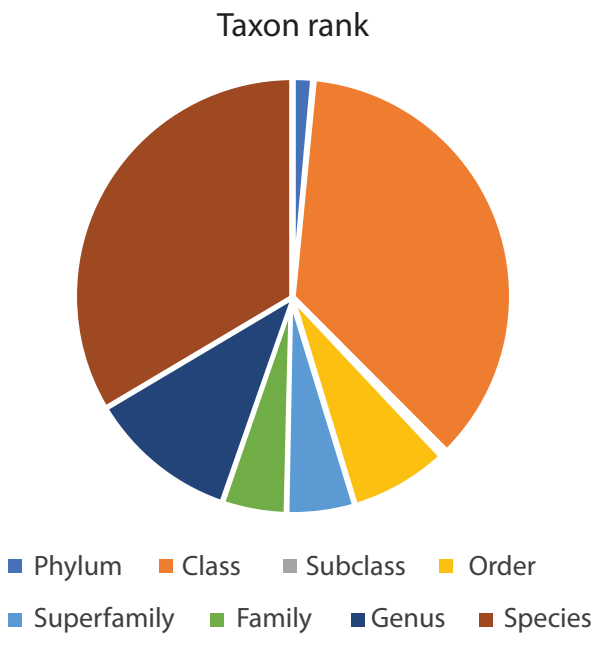


Figure 2. Records from the NW Pacific below 2,000 m of Cnidaria and Ctenophora by lowest taxonomic rank of identification (total n=256).

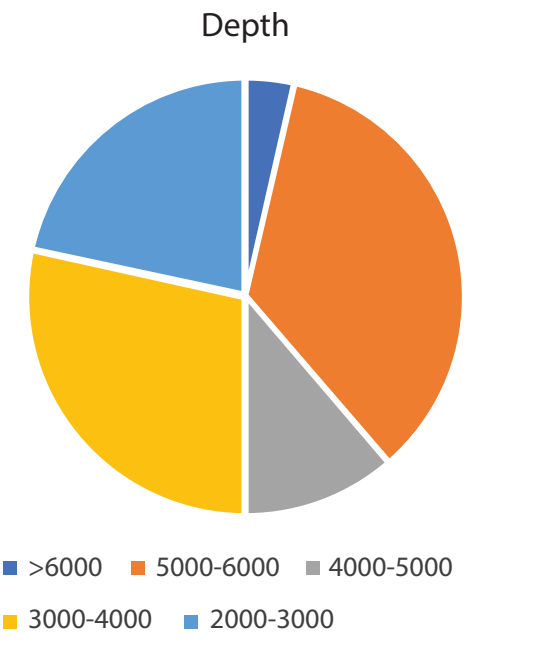


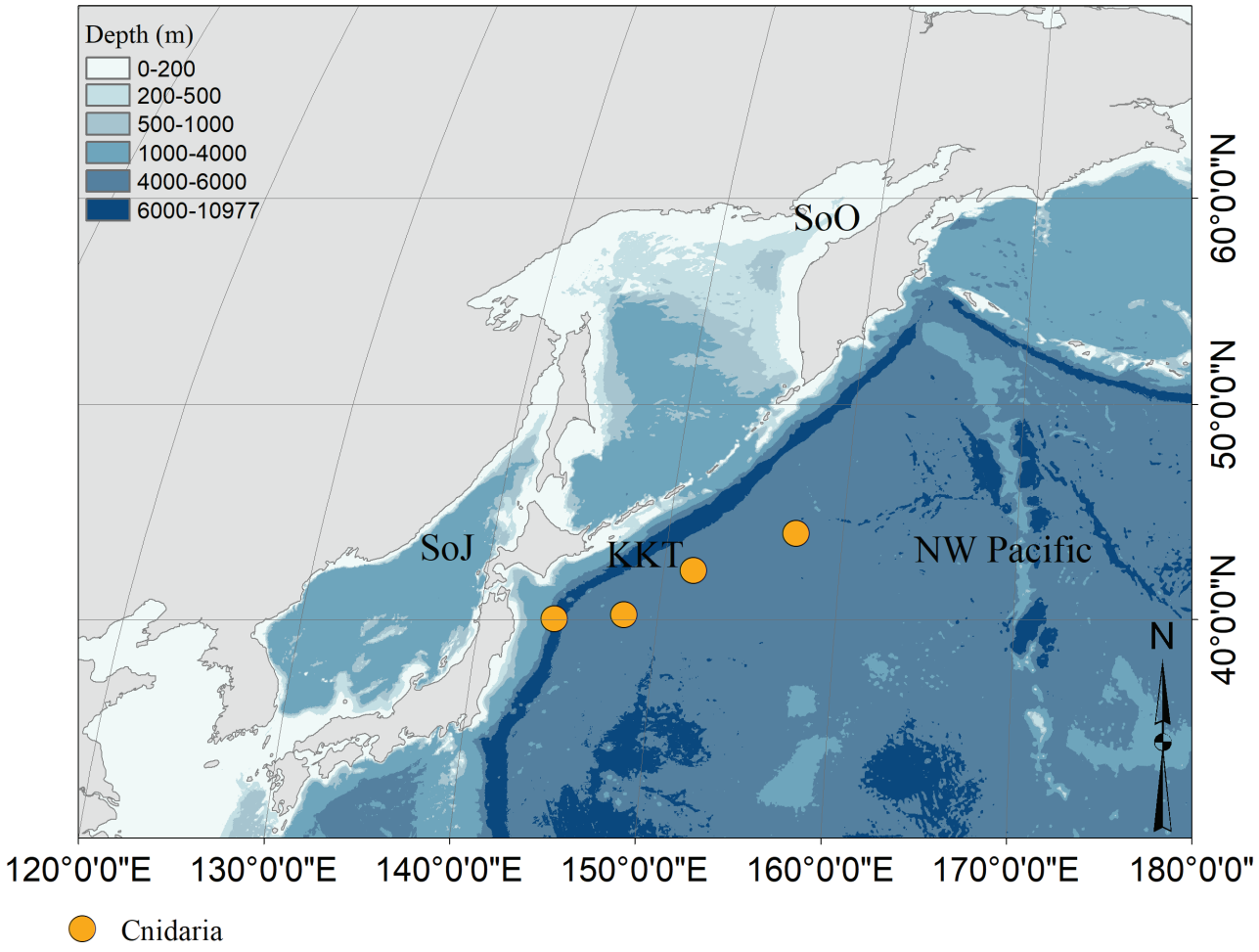
Figure 3. Records from the NW Pacific below 2,000 m of Cnidaria and Ctenophora by depth in m (total n=256).

4.2 Ctenophora

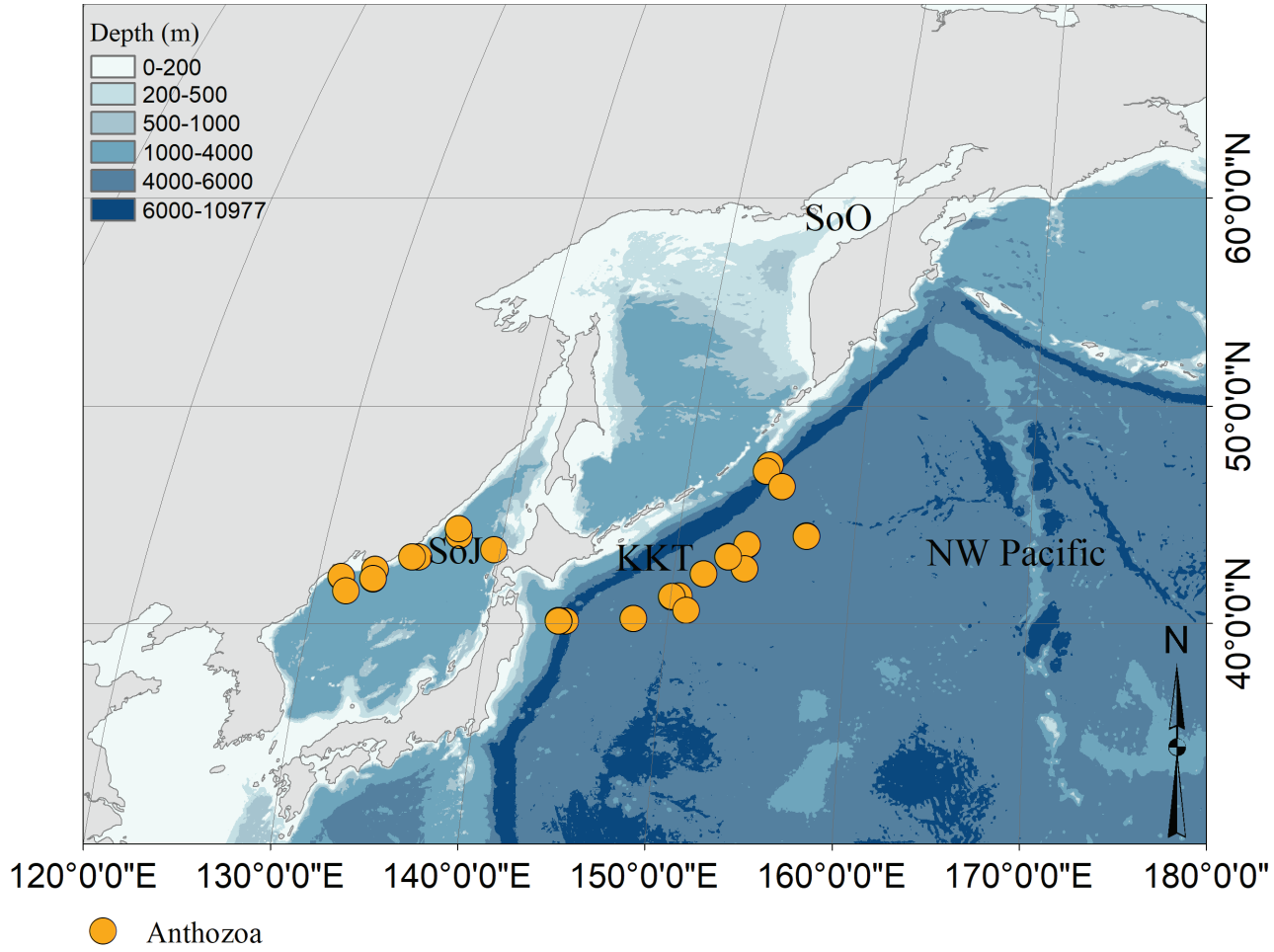
Within Ctenophora, there were only three records from the entire marine region, all of which were only identified to phylum level. Thus, there is no information on orders or numbers of species present. These three records were from depths of 4,859 to 5,379 m. The three records were all recorded from 2012 and reported in two papers; Brandt et al. (2015) and Fischer and Brandt (2015). Figure 11F in Brandt et al (2015), includes a photograph of a ctenophore of the Class Lobata (St. 11–9, 5,362 m depth) which, although not included in the original OBIS-derived data, would make this a fourth record for Ctenophora at abyssal depths in the study area.

4.3 Distributional patterns

Although distribution maps for various taxonomic groupings of cnidarians have been provided in this chapter (Maps 1–11), we consider the state of knowledge to still be too nascent to make serious hypotheses on distributional patterns of Cnidaria or Ctenophora in the NW Pacific.



Map 1. Map of occurrence records of phylum Cnidaria from the NW Pacific below 2,000 m. Note these records are for occurrences not identified to any taxonomic level below Cnidaria.

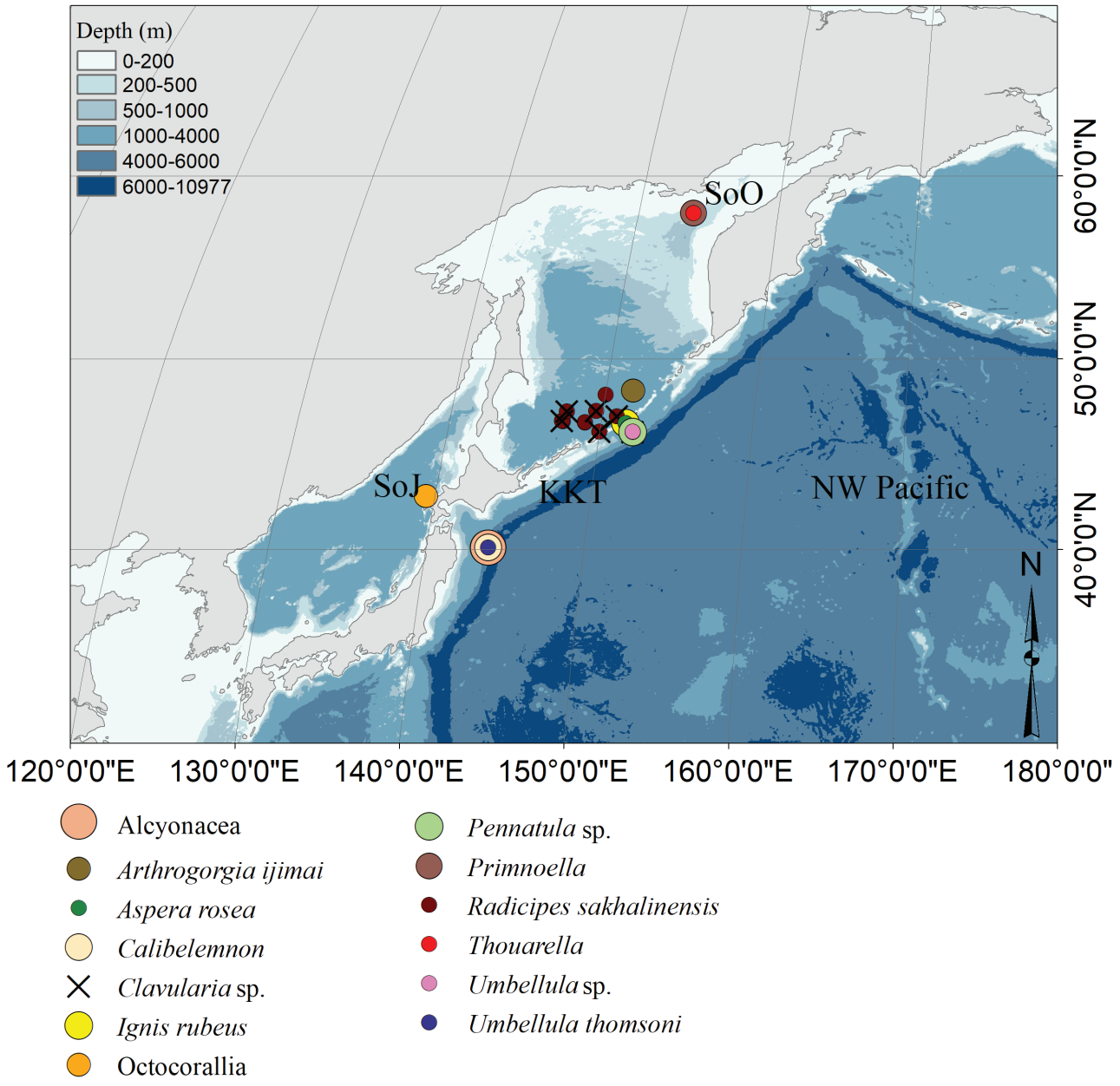


Map 2. Map of occurrence records of class Anthozoa from the NW Pacific below 2,000 m. Note these records are for occurrences not identified to any taxonomic level below Anthozoa.

5. Discussion

The area examined in this paper between 40°N to 60°N and 120°E to 180°E covers over nine million square kilometers of the Earth's surface, with the majority being marine. Of this marine area, a large portion is below 2,000 m in depth (e.g. see maps 1–11), and thus it is easy to state that the deep-sea area we examined in this study is vast. Despite this, records indicate less than 250 records of cnidarians, and only three records of ctenophores from this region. These records are almost completely from within the last 20 years. It is not an overstatement to say that research on these basal metazoan groups is almost completely lacking for the region, and that this research is in its infancy.

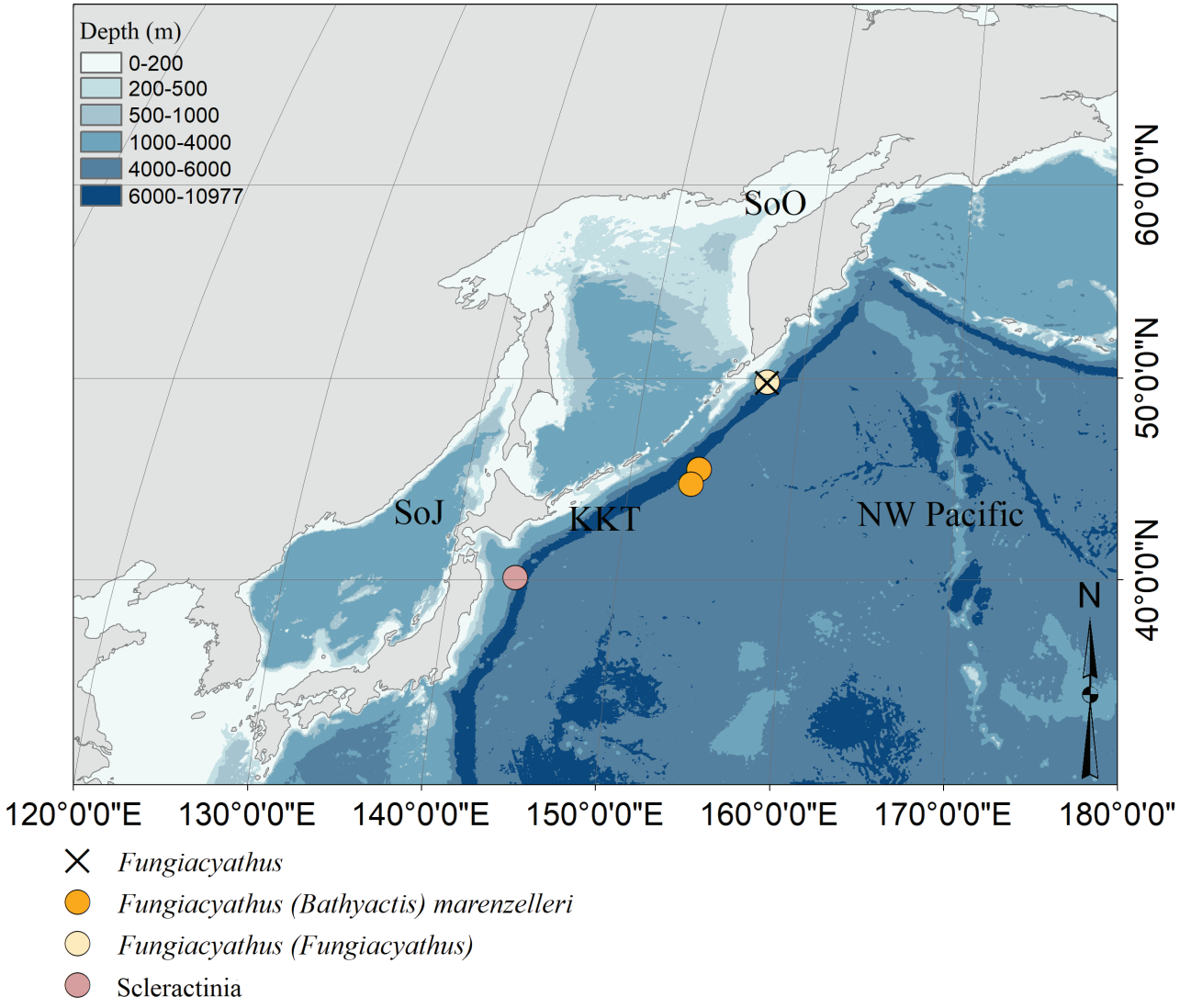
Within the region examined in this study, there are undoubtedly more specimens and records than we have reported here. For example, other planktonic Cnidaria records from the NW Pacific include those from four deep dives by the Mir submersibles in the Kurile-Kamtchatka Trench that were analyzed by Vinogradov and Shushkina (2002), but the majority of the pelagic cnidarian



Map 3. Map of occurrence records of subclass Octocorallia from the NW Pacific below 2,000 m.

taxa reported below 2,000 m depth were unidentifiable to species level, with the exception of *Pantachogon haeckeli* Maas, 1893 (reported as >2,500 m depth) and *Botrynema brucei* Browne, 1908 (deepest record at 3,400 m depth). Even generic identifications in Vinogradov and Shushkina (2002) were marked with question marks (e.g. *Poralia*?, *Turritopsis*?) or were for genera that have never previously been reported from depths below 2,000 m (e.g. *Colobonema*), illustrating the lack of information in general on bathyal and abyssal gelatinous zooplankton (Vinogradov and Shushkina 2002). These records have not been included in the dataset of the current study.

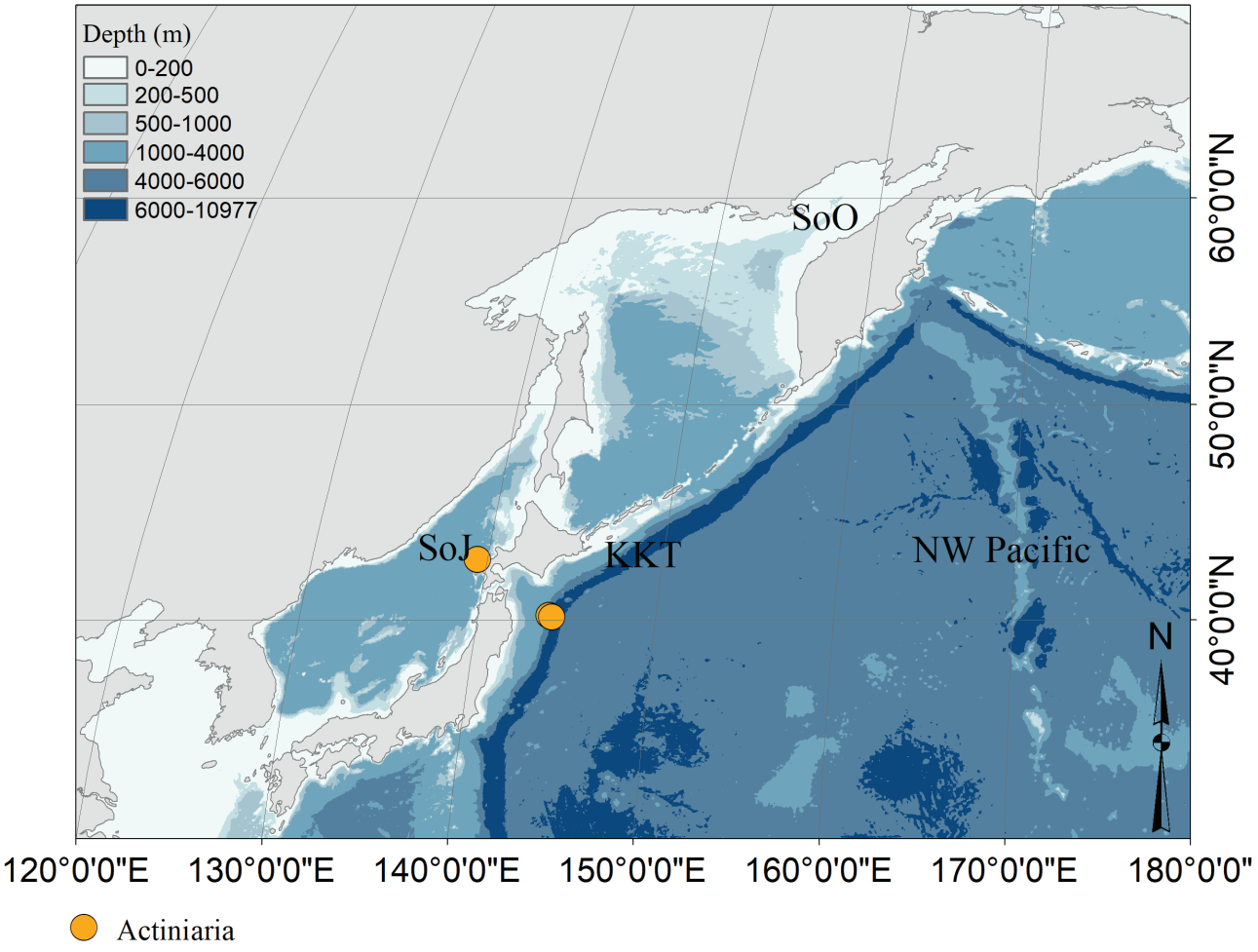
As well, Brandt et al. (2018) reported that there were 43 Cnidaria specimens collected in the



Map 4. Map of occurrence records of order Scleractinia from the NW Pacific below 2,000 m.

2015 SokhoBio Expedition in the Sea of Okhotsk, but asides from 21 records mentioned in Dautova (2018a) already included in our current dataset, we could not find detailed information on these specimens.

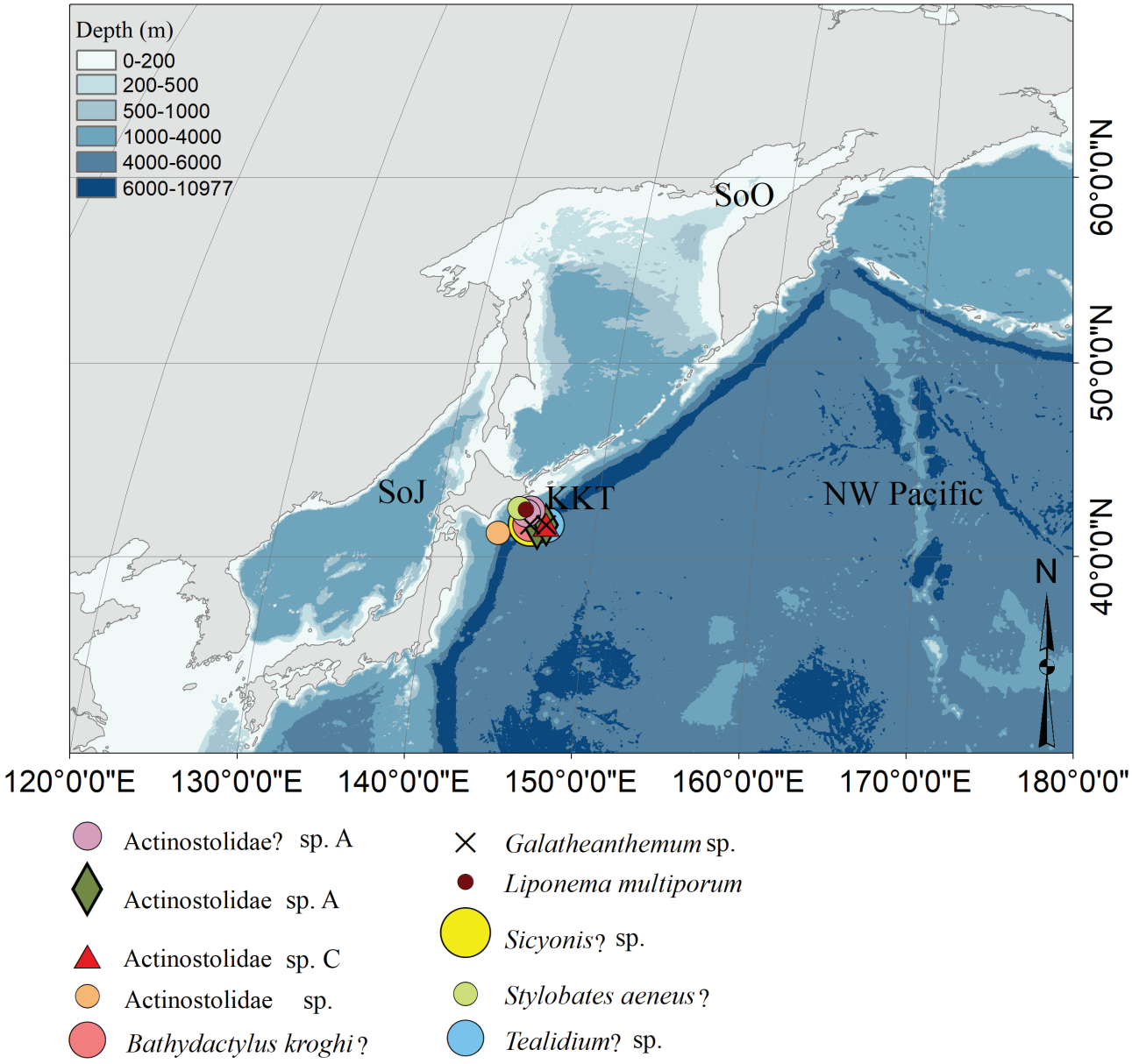
It is well known that the marine environment becomes more similar with surrounding regions as depth increases (Vecchione et al. 2015), and looking at the deepest records worldwide of various cnidarian and ctenophore taxa may provide a guideline for what species we may expect to find in future surveys of the NW Pacific. According to Malyutin (2015), the deep-sea coral communities of the Aleutian Islands, the eastern Bering Sea and the Gulf of Alaska (northeastern Pacific) are similar to the coral communities of the NW Pacific. All the occurrence records in Malyutin's 2015 paper had depths shallower than 1,000 m. Although we might expect similar trends at deeper depths, the investigation of additional deep-water communities in those areas is crucial to further corroborate such prediction.



Map 5. Map of occurrence records of order Actiniaria from the NW Pacific below 2,000 m. Note these records are for occurrences not identified to any taxonomic level below Actiniaria.

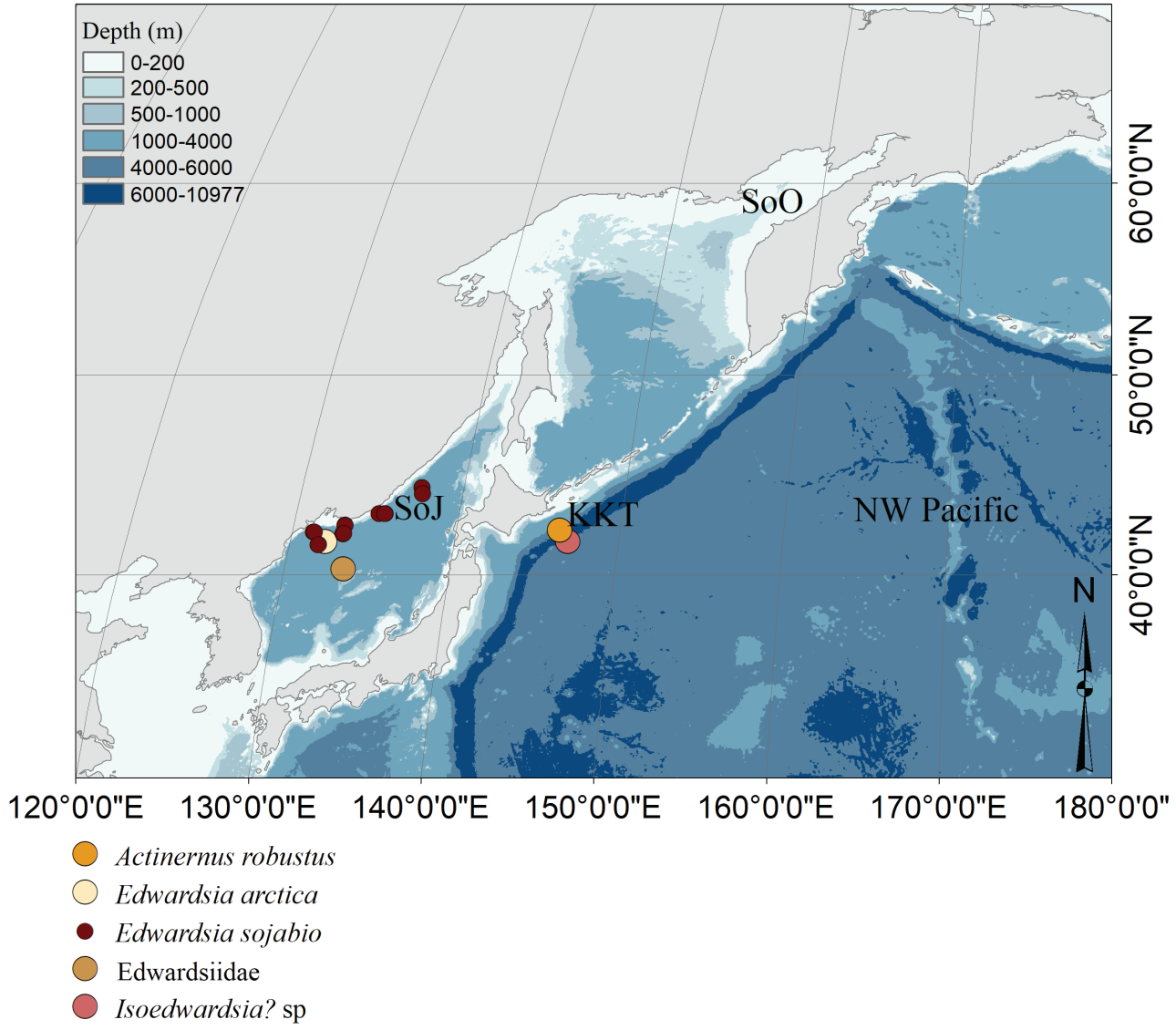
For example, for Anthozoa, there are records of the orders Actiniaria (sea anemones), Scleractinia (hard corals), and the subclass Octocorallia (soft corals, sea pens) from the NW Pacific area examined in this study. However, from the presence and depths of anthozoans from other regions, we may also expect to find the subclass Ceriantharia (deepest report of *Cerianthus valdiviae* Carlgren, 1912, from 5,248 m, Indian Ocean south of Sumatra, OBIS dataset), and the orders Corallimorpharia (*Corallimorphus* sp. reported from 5,274 m, South Orkney Islands, USNM catalogue number 61003), Zoantharia (*Abyssoanthus convallis*, 5,362 m, Japan Trench, Reimer & Sinniger 2010), and Antipatharia (*Stichopathes variabilis* van Pesch, 1914, 7,000 m, Sunda Trench, ZMUC Gal-II-1248) within the NW Pacific.

Similarly, regarding planktonic data, the class Staurozoa has been reported down to 2,694 m (*Lucernaria janetae* Collins & Daly, 2005, East Pacific Rise). The deepest record for a cnidarian is currently a small red rhopalonematid hydromedusa (DJL, pers. obs.), observed at 9,970 m depth in the Mariana Trench by a drop camera (Gallo et al. 2015). The deepest scyphozoan record is for an ulmarid medusa at 8,200 m depth



Map 6. Map of occurrence records of actiniarian superfamilies Actinostoloidea and Actinioidea and the family Galatheanthemidae from the NW Pacific below 2,000 m.

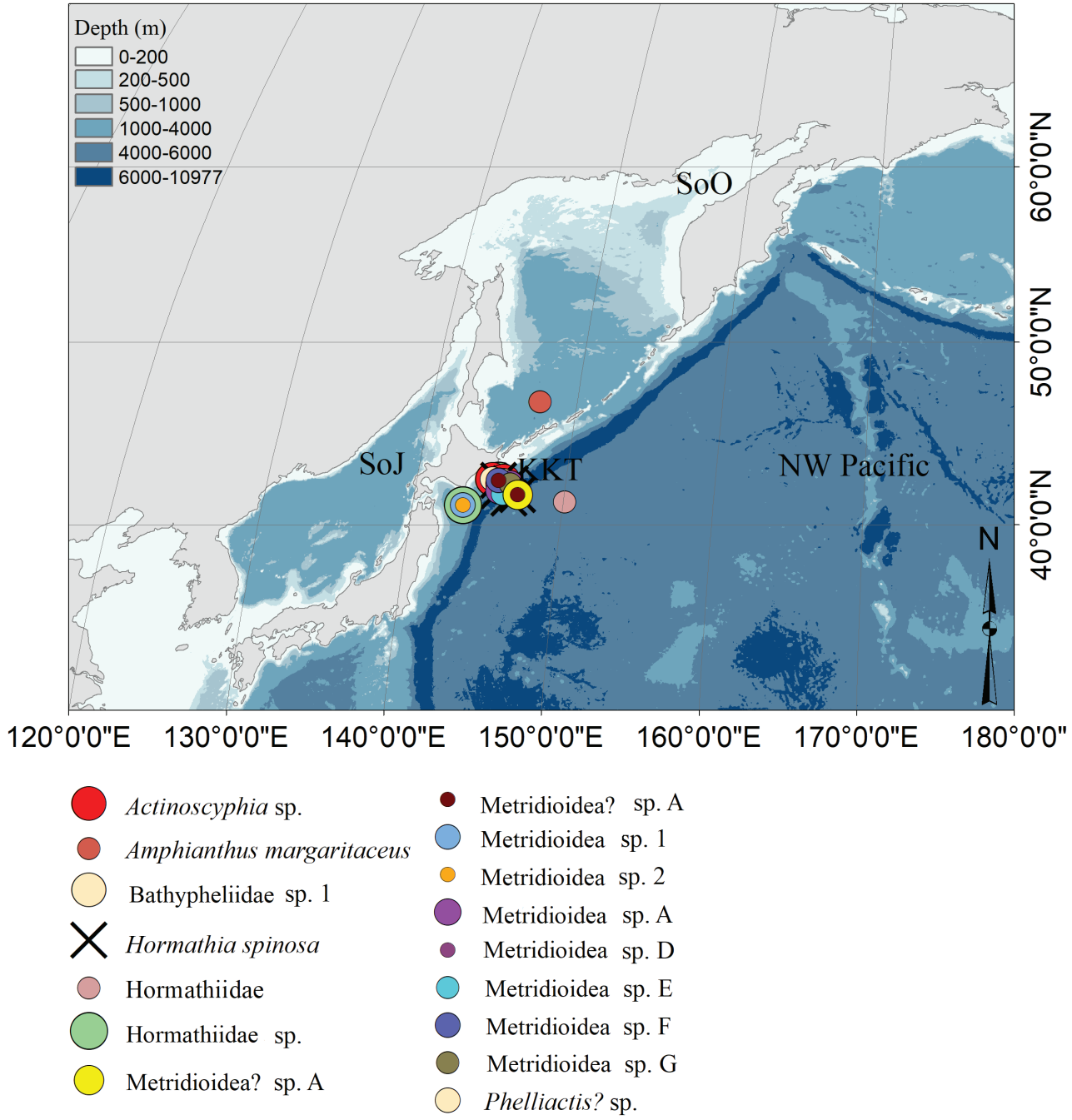
in the New Britain Trench (Gallo et al. 2015), identified at the time as tentatively belonging to the subfamily Poraliinae but now believed to warrant the erection of a new subfamily to contain it (DJL, pers. obs. based on new material collected in 2019 in the Gulf of Alaska). The deepest record for a ctenophore is 7,217 m depth in the Ryukyu Trench, for an enigmatic tentaculate ctenophore that anchors itself to the sediment by two filaments, while trailing two tentacles that lack tentillae (Lindsay and Miyake 2007). On the other hand, the cnidarian classes Cubozoa, Myxozoa, and Polypodiozoa have not been reported from depths of >2,000 m worldwide, and thus we would not expect them to be present in the NW Pacific.



Map 7. Map of occurrence records of actiniarian suborder Anenthemonae from the NW Pacific below 2,000 m.

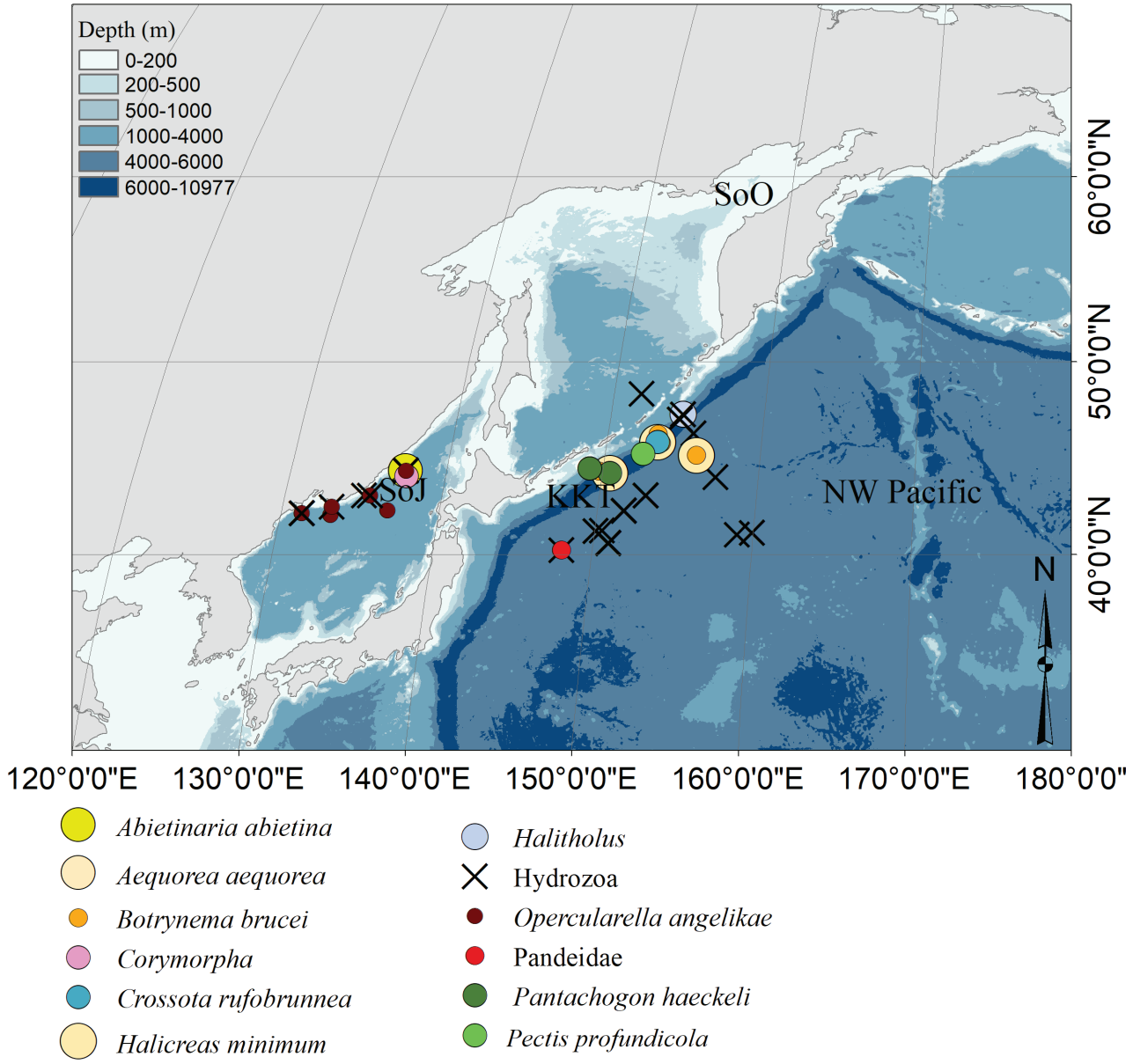
Another way to predict more about the deep-sea Cnidaria and Ctenophora fauna of the NW Pacific would be to examine occurrence records and information from neighboring regions that are more well examined. For example, the waters around Japan have long been surveyed and there are comparatively many more records, other data, and specimens from the deep sea of this area (e.g. Kitamura et al. 2008a, b). There are also deep-sea records of anthozoans to the east from the Aleutian Islands of Alaska (e.g. Cairns 1994; Heifetz et al. 2005; Herrera et al. 2010; Cairns 2011; Cairns and Lindner 2011; Thoma 2013; Stone and Cairns 2017).

From marine regions to the south of the current area of interest, there are many additional Cnidaria and Ctenophora records. For benthos, in the western Pacific, Williams (2011) reported the octocoral sea pen genera *Gyrophyllum* at depths ≥2,000 m, and *Protoptilum* and *Scleroptilum* at depths ≥4,000 m. Among gorgonians, *Swiftia pacifica* (Nutting, 1912) is a western Pacific bathyal species which



Map 8. Map of occurrence records of actiniarian superfamily Metridioidea from the NW Pacific below 2,000 m.

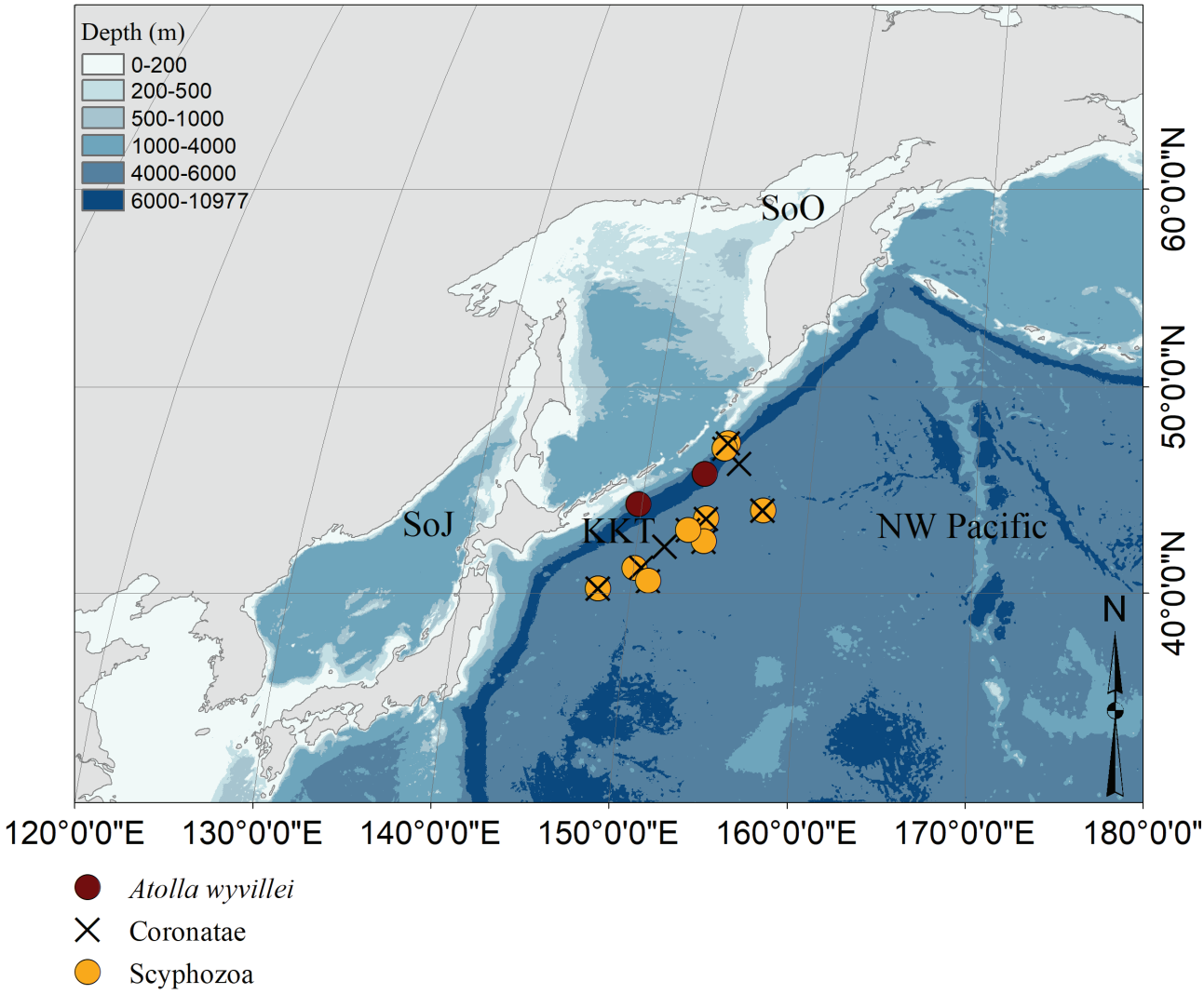
has been found at depths ≥2,000 m (Horvath 2019). Similarly, Imahara (1996) noted the gorgonian *Bathygorgia profunda* Wright, 1885 from 4,200 m, and the sea pen *Kophobelemnon stelliferum* (Müller, 1776) from down to 3,650 m in Sagami Bay. Additionally, from older records, Kölliker (1880) reported two more sea pen species from the deep sea of the North Pacific Ocean; an *Umbellula* (Gray, 1870) species from approximately 3,750 m, and *Scleroptilum grandiflorum* Kölliker, 1880 from approximately 4,200 m. Among other anthozoans, two species of the deep-sea zoantharian genus *Abyssoanthus* (Reimer & Fujiwara in Reimer, Sinniger, Fujiwara, Hirano & Maruyama, 2007) are known from the Japan Trench (5,347–5,360 m; Reimer and



Map 9. Map of occurrence records of class Hydrozoa from the NW Pacific below 2,000 m.

Sinniger 2010) and the Nankai Trough (3,259 m; Reimer et al. 2007), respectively.

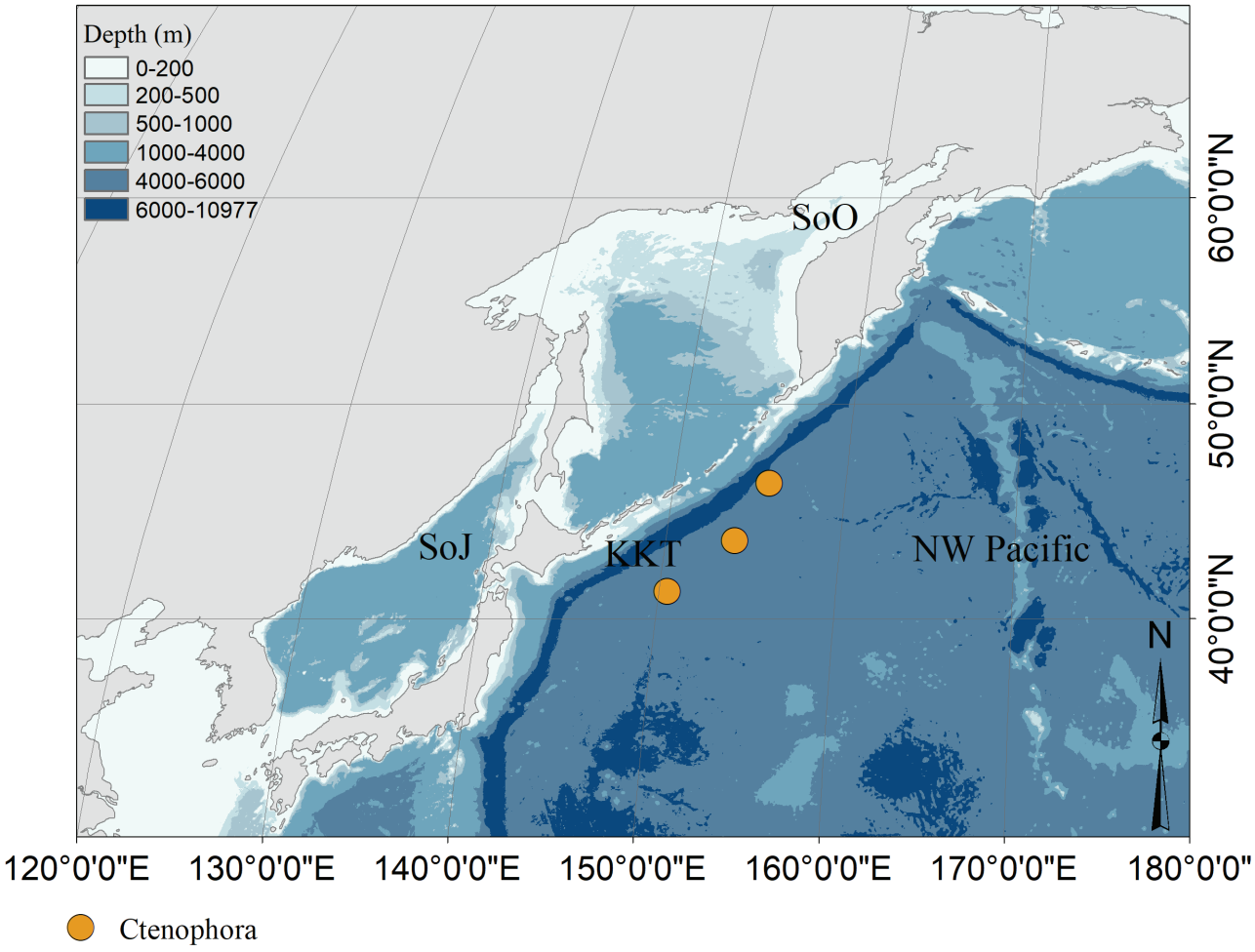
Regarding planktonic species, between 2,000-4,000 m depths in the Japan Trench, Lindsay (2005) reported the occurrence of unidentified narcomedusan species belong to the genera *Solmissus* (Haeckel, 1879) and *Aegina* (Haeckel, 1879). The most commonly observed medusa was *Botrynema brucei* Browne, 1908, which was most abundant in the 2,000-2,500 m layer but occurred down to 3,500 m depth (Lindsay 2005). The *Bathocyroe* (Madin & Harbison, 1978) species observed below 4,000 m depth was also most abundant in the 2,000-2,500 m depth layer (Lindsay 2005). The only other pelagic cnidarians identified to species level by Lindsay (2005) were: the trachymedusae *Halicreas minimum* Fewkes, 1882 (2,439 m depth) and *Crossota* aff. *millsae* (3,668 m depth); the physonect siphonophores



Map 10. Map of occurrence records of class Scyphozoa from the NW Pacific below 2,000 m.

Marrus antarcticus pacificus Stepanjants, 1967 [=*Marrus orthocanna* (Kramp, 1942)] (2,869 m depth) and *Tottonia contorta* Margulis, 1976 (=*Apolemia* sp.) (2,810 m depth); and the ulmarid scyphomedusa *Poralia rufescens* Vanhöffen, 1902 (2,522 m depth). An extremely large (ca. 80 cm diameter) Aulacoctenid cydippid ctenophore was observed at 3,562 m depth (Lindsay 2005).

However, even in surrounding regions, some taxa still display an apparent lack of data. For example, very little information has been published on the abyssal planktonic cnidarian and ctenophoran fauna of the entire NW Pacific Ocean with the notable exceptions of several works by Naumov and Lindsay (e.g. Naumov 1971; Lindsay 2005). Lindsay (2005) recorded a coronate medusa belonging to the genus *Periphylla* (F. Müller, 1861) at 6,464 m depth in the Japan Trench, though they were hesitant to identify it as the species *Periphylla periphylla* (Péron & Lesueur, 1810) due to the spiralling morphology and white colour of the tentacles. Below 4,000 m depth, Lindsay (2005) recorded an undescribed lobate



Map 11. Map of occurrence records of class Ctenophora from the NW Pacific below 2,000 m.

ctenophore species belonging to the genus *Bathocyroe*, as well as at least two species of physonect siphonophores (as "Agalmidae"), four species of hydroidomedusae (non-Narcomedusan), one "cydippid" ctenophore species and one other lobate ctenophore species.

Formal taxonomic species descriptions can help collate past data, and thus provide important information. This can be clearly seen for the sea anemone species *Edwardsia sojabio*, which is by far the species with the most numerous numbers of records for both phyla examined here, directly as a result of its formal species description (Sanamyan and Sanamyan 2013). Similarly, the octocorals *I. rubeus*, *A. rosea*, and *R. sakhalinensis* were recently described from specimens collected in 2015 (Dautova 2018a), greatly increased our knowledge of deep-sea octocorals in the region, increasing the numbers of records by four times (7 to 28 records). Species descriptions by their nature will provide taxa identified to the species level, something that is sorely lacking from our current understanding of the gelatinous fauna of the NW Pacific. Similarly, the previously unpublished data from two cruises newly reported in this paper (KH01-2, KT08-27 datasets) almost doubled the amount

of sea anemone data available, increasing the number of records of Actiniaria from 43 to 85. Thus, it can be easily concluded that even single studies can greatly increase our knowledge on Cnidaria and Ctenophora in the NW Pacific given the current state of our understanding.

Due to the paucity of data, conclusions on the patterns of distribution within the NW Pacific remain to be made. For example, there are almost no data for many Cnidaria or Ctenophora taxa for the deep sea below 2,000 m in the northern Japan Sea (e.g. Maps 4-14). Examining data from further south, a high diversity of deep-sea ctenophores has been reported on the Pacific side of the Japanese archipelago (Lindsay and Hunt 2005), while only the beroid ctenophore *Beroe abyssicola* Mortensen, 1927, the "cydippid" ctenophore *Euplokamis* sp. and the lobate ctenophore *Bolinopsis infundibulum* F.O. Müller, 1776 have been recorded in the deep Japan Sea at the present time, albeit above 1,000 m depth (Lindsay & Hunt 2005). As the water mass in the deep Japan Sea (Japan Sea Proper Water) remains homogeneous below the thermocline, with extremely low temperatures, the above three ctenophore taxa can be inferred to be secondary deep-sea species that have invaded the deep Japan Sea to take advantage of the niche space made available by primary deep-sea taxa not being able to survive at such temperature-pressure combinations (Lindsay & Hunt 2005). The Ctenophora of the deep NW Pacific Ocean would be expected to contain both primary and secondary deep-sea forms. Future work should not only focus on the NW Pacific, but particularly on areas shown by this review to be neglected thus far.

Conclusions

Due to the lack of Cnidaria and Ctenophora data in the NW Pacific, it is far too premature to make any conclusions on abundances, total diversity, endemicity, or ecology of the various cnidarian and ctenophore species in the region. One positive aspect that can be discerned from the general lack of Cnidaria and Ctenophora deep-sea data from the NW Pacific is that any future surveys or research on the region will almost assuredly gather important new information.

Although many oceanographic cruises and research expeditions have been undertaken over the last two centuries with the aim of exploring the marine diversity of the NW Pacific and Far East, such as the Pacific expedition led by Mortensen in 1914 and the Galathea Expedition organized by the Zoological Museum University of Copenhagen (ZMUC), most of these expeditions were further south from the NW Pacific region between 40°N and 60°N and 120°E to 180°E examined in the current paper. Expeditions and cruises make the collection of a variety of marine invertebrates possible, which are then deposited in museums and research institutes. However, even with extensive and massive sampling campaigns, the identification of material, especially at the species level, is often hampered by a lack of taxonomic specialists. Thus, we strongly recommend future research cruises investigating the deep sea of the NW Pacific involve relevant Cnidaria and Ctenophora taxonomy experts to help increase the current paucity of data for these two phyla (as seen in the 2015 SokhoBio survey; Brandt et al. 2018; Dautova 2018a). Due to the

extreme fragility of many taxa within these two gelatinous phyla, future surveys should include a crewed submersible or remotely-operated vehicle in order to collect both in-situ photographic and video records and the physical specimens needed for a complete morphological and molecular characterization of the fauna. Once this high-quality baseline data has been collected and vetted by taxonomic experts it will become possible for future surveys to be carried out at lower cost using such tools as towed cameras and environmental DNA probing, but our present state of knowledge about these taxa in the study area prohibits such approaches at the present time.

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CHAPTER 4
BRACHIOPODA

A REVIEW ON DEEP-SEA BRACHIOPOD *PELAGODISCUS ATLANTICUS* (KING, 1868) FOUND ALONG THE NW PACIFIC

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1. Introduction

The brachiopods or lamp shells are a diverse group of exclusively marine invertebrates. Their bodies are enclosed in two bilaterally symmetrical valves. The ventral (pedicle) valve is usually larger than the dorsal (brachial) valve. The shell morphology, and its various skeleton structures, and its soft body impression, are well preserved in fossil states and allow tracing of the evolution of these animals. Brachiopods are known from the early Cambrian with the greatest diversity found during the Palaeozoic. The modern brachiopods comprise only 5% of the total number of species that ever existed on Earth (Carlson 2016).

The brachiopods have a pelago-benthic life cycle with larval or juvenile planktonic and benthic adult stages (Lüter 2007; Kuzmina et al. 2019). Most brachiopods are epifaunal animals with a few exceptions. The adults attach to the substrate with a pedicle, which can regulate the position of the shell relative to water currents or may cement with their ventral valves. All brachiopods are filter feeding animals and filter using a special tentacle-organ, the lophophore. The lophophore is "a tentaculated extension of the mesosoma (and its cavity, the mesocoelom) that embraces the mouth but not anus" (Hyman 1959; Emig 1976). The presence of lophophore characterizes Lophophorata, a group that includes Bryozoa, Phoronida and Brachiopoda. In brachiopods, the lophophores may vary from the simple ring shape (trocholophous) to the curved shape consisting of three arms (plectolophous) (Emig 1992; Kuzmina and Temereva 2019). The brachiopod lophophores are located within the mantle cavity, a space between the valves. Tentacles are covered by ciliary bands that create the water currents.

The phylum Brachiopoda Duméril, 1805 consists of three subphyla: Linguliformea Williams, Carlson, Brunton, Holmer & Popov, 1996, Craniiformea Popov, Basset, Holmer & Laurie, 1993, and Rhynchonelliformea Williams, Carlson, Brunton, Holmer & Popov, 1996. The shell linguliforms is organophosphatic and lacks articulatory structures. The linguliforms have a U-shaped gut with an anus that is located anterior on the right side. Recent linguliforms are represented in only two families, Lingulidae Menke, 1828, and Discinidae Gray, 1840, which strongly differ in their biology and the morphology of their shells and soft bodies (Emig 1997). The lingulides are infaunal, they have a long muscle pedicle and burrow into soft sediments. The discinides are epifaunal and live on hard substrates usually fixed by a short muscle pedicle.

The craniiforms is a minor group of brachiopods and comprise only one class with a recent family Craniidae Menke, 1828, with three extant genera. All craniiforms have organocalcitic shell without articulatory structures. The gut is open with the anus located in the posterior midline of the body. Recent craniiforms lack the pedicle to cement themselves to substrate by the ventral valve (Williams et al. 1997).

The rhynchonelliforms are the most advanced group of brachiopods. This subphylum includes five classes but only the class Rhynchonellata Williams, Carlson, Brunton, Holmer & Popov, 1996, retains extant species, which includes three orders: Rhynchonellida Kuhn, 1949, Thecideida Elliot, 1958, and Terebratulida Waagen, 1883.

The rhynchonelliform shell is calcitic and has well-developed articulation structures and the calcitic lophophore supports the brachidium. The gut of the recent rhynchonelliforms is blind, so the fecal pellets are eliminated through the mouth (Williams et al. 1997).

Recent brachiopods are found in all seas and oceans from the Arctic to the Southern Oceans (Zezina 2008). The north subtropical and tropical zones contain the largest number of species. Each of these zones includes almost a third of the entire fauna of extant brachiopods (see table 6 in Zezina 2008). The rhynchonelliforms include a large number of endemic species, while the recent linguliforms lack endemic species (Richardson 1997). This is due to the presence of planktotrophic stages of linguliformes that can float up to six weeks (Chuang 1959; Paine 1963), while the craniiform and rhynchonelliform larvae swim for only 4 days.

The extant brachiopods occur in all depths from littoral to abyssal except ultra-abyssal (Bitner et al. 2013). However, most of the recent brachiopods prefer to live on the seaward edge of the shelf and the upper part of the slope, which can be explained by the following factors (Zezina 2008):

1. In their evolution, the rhynchonelliforms adapted to digest finely suspended material with the formation of a minimal amount of metabolic waste products, which led to the loss of the hindgut and the acquisition of blindly closed alimentary tract. However, at the boundary of the Mesozoic and Cenozoic, the plankton composition changed with the advent of new components, the so-called shelly phytoplankton. This food was unavailable for rhynchonelliforms because they were not able to remove numerous planktonic shells through the hindgut. Rhynchonelliforms are forced to occupy the edge of the shelf and the upper part of the slope below the photic zone and adapted to feeding on the products of decay of dead plankton. Linguliforms preserved their entire alimentary tract and, thus, they are tolerant to this factor and occupy the upper sublittoral photic zone. However, craniiforms with open guts prefer to live outside the phytal zone like rhynchonelliforms.

2. Because animals and macrophytes live together in the upper sublittoral, competition for the place of settlement in this zone is very strong. So, the region below the phytal zone is more favourable for brachiopods.

3. The rapid currents near the edge of the shelf make the sediment coarser, which is suitable for the majority of brachiopods.

2. Objectives

The current chapter is a review of published data on deep-sea brachiopod *Pelagodiscus atlanticus* (King 1868) found during four Russian-German deep-sea expeditions in the NW Pacific Ocean.

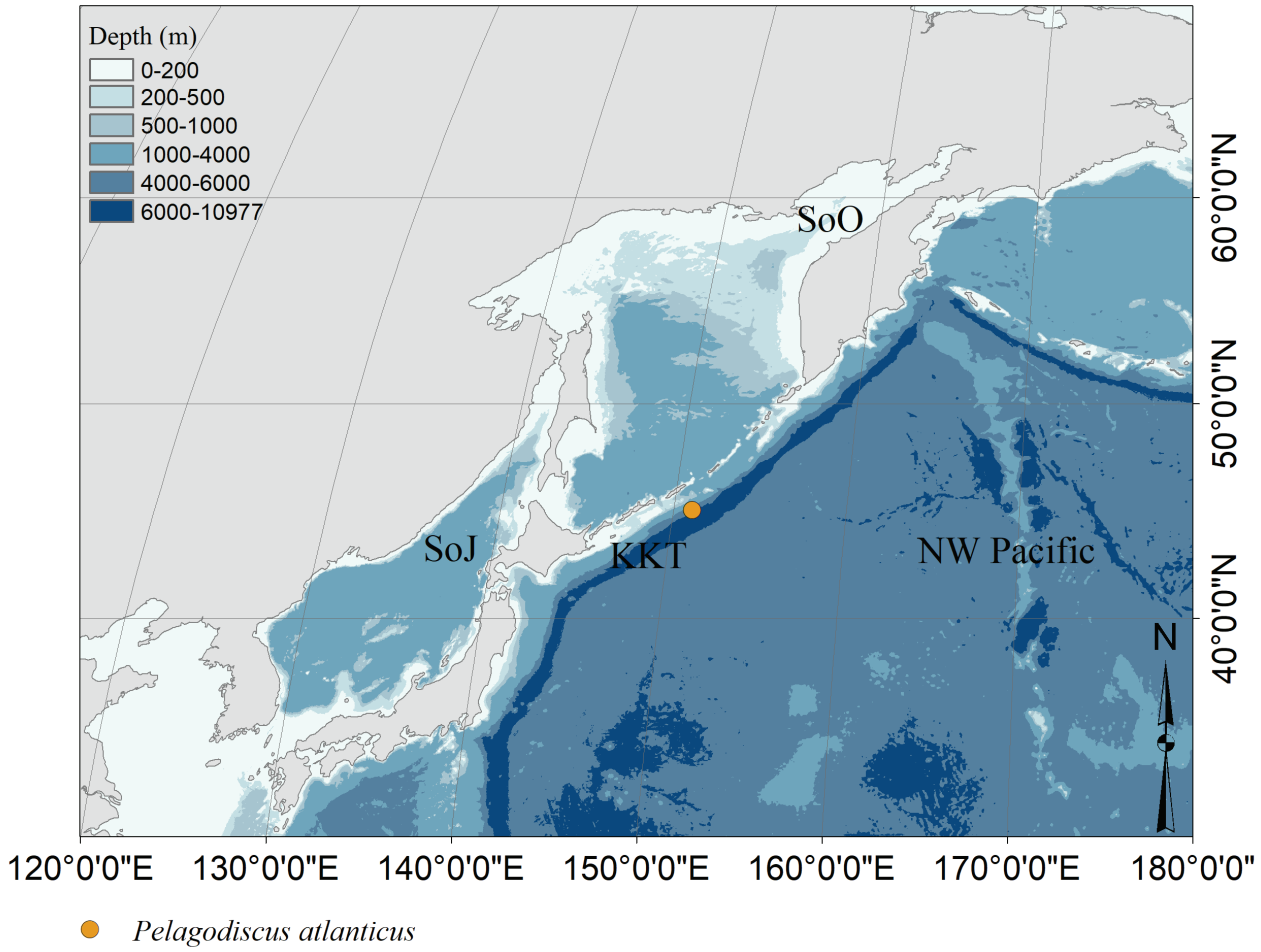
3. Material and Methods

Two specimens of *P. atlanticus* were collected in the Kuril-Kamchatka Trench (45° 12 02'N, 151° 60 08'E) during the German-Russian expedition Kurambio II on RV *Sonne* (16 August 2016–26

September 2016) (Map 1). Specimens were obtained at 5,571.6 m depth using the Agassiz Trawl at station number SO-250-86.

3.1. Microscopy

Two whole specimens with diameters of dorsal valves 4.0 and 4.2 mm, respectively, were fixed in 2.5% glutaraldehyde in filtered sea water. After fixation, the specimens were rinsed in 0.1 M phosphate buffer. Fixed animals were photographed in the laboratory using a Leica MZ6 stereomicroscope (Leica Microsystems GmbH, Wetzlar, Germany) equipped with a digital camera. After post-fixation, specimens were placed in a 1% osmium tetroxide in phosphate buffer for 30 min at 20°C, the specimens were rinsed in distilled water, dehydrated in ethanol and isopropanol, and embedded in Spurr Resin (Epoxy Embedding MediumKit, Fluka, Switzerland). Semi-thin and ultra-thin sections were prepared with a diamond knife on a Leica UC5 ultratome (Leica Microsystems GmbH, Wetzlar, Germany). Specimens were cut serially; ultrathin sections were taken every 10 µm. Semi-thin sections were stained with methylene blue and examined and photographed with a Zeiss Axioplan 2 imaging photomicroscope. Ultrathin sections were stained with uranyl acetate and lead citrate, and were examined with a Jeol Jem 100 V and Jeol-1,011 80 kV transmission electron microscopes (JEOL Ltd., Tokyo, Japan).



Map 1. Distribution of *Pelagodiscus atlanticus*.

3.2. Micro-CT (Micro-computed tomography)

X-ray imaging of whole specimens embedded in Spurr Resin was performed with a SkyScan 1172 micro-CT scanner (Bruker) at the Laboratory of Natural Resources, Geological Faculty, Moscow State University. The specimens were scanned at a resolution of 1.68 μm, with a rotation step of 0.3°, without a filter, and at current conditions of 40 kV and 250 mA. The 3D reconstruction was obtained using the program NRecon. CTan and CTvol software were used for data processing.

4. Results

P. atlanticus is a small deep-water representative of family Discinidae, a linguliform brachiopod. Its soft body is enclosed by dorsal and ventral chitinophosphatic valves, which are very small and thin (Figure 1). The dorsal valve (about 4 mm in diameter) is much larger than the ventral valve (about 3 mm in diameter). The valves grow holoperipherally, so the apex (first-formed region) is near the center of the valve (Figure 1a). The body wall forms mantle folds that line the inner surface of both valves. Marginal long and short setae emerge from the edge of both mantles. The short muscle pedicle attaches the ventral valve to the hard substrate (Figure 1c) (Kuzmina and Temereva 2019). *P. atlanticus* has a small simple horseshoe-shaped lophophore with two arms directed posteriorly (Figure 1b) (Kuzmina and Temereva 2019). The lophophoral arms are located symmetrically about the mouth. The basal part of the lophophore is attached to the anterior body wall. The distal portions of the arms are separated from the body wall and are raised into the mantle cavity. The arms are fringed with a double row of tentacles. Two coelomic canals, large and small, extend inside each arm of the lophophore. Hydrostatic pressure in the large coelomic canals supports the arms of lophophore. The small canals connect with the coelomic

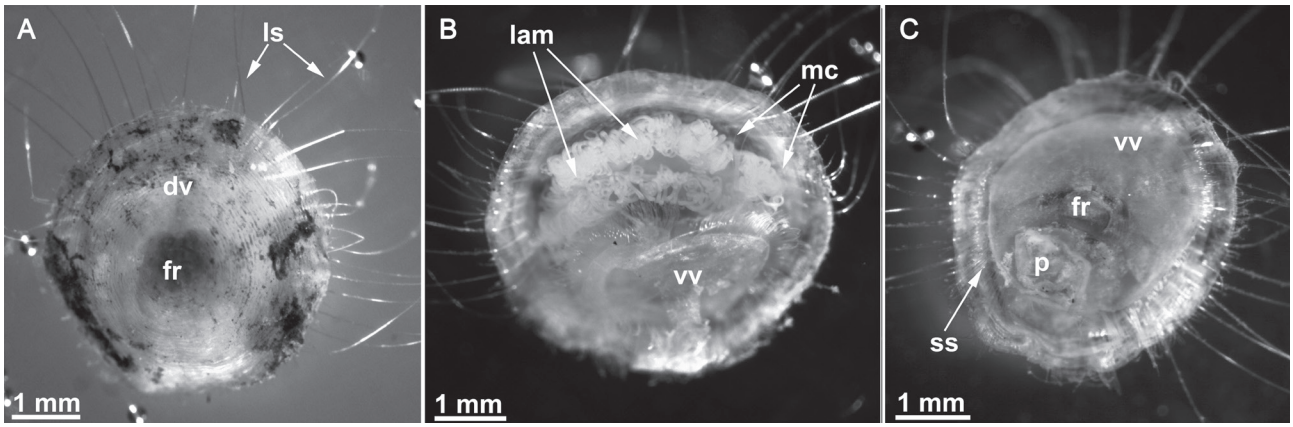


Figure 1. Dorsal and ventral chitinophosphatic valves of deep-water of *Pelagodiscus atlanticus* (Kuzmina and Temereva, 2019). (A) Dorsal view of the fixed animal: the dorsal valve (*dv*) with long setae (*ls*) is visible. (B) Ventral view of the fixed animal: the ventral valve (*vv*) is partly open, and the mantle cavity (*mc*) contains two lophophoral arms (lam). (C) View of the ventral valve (*vv*) with short setae (*ss*) and a round pedicle (*p*). first-formed region of the shell.

canals of tentacles and perform transport functions. The lophophore of *P. atlanticus* was regarded as a modified zygolophous type and, apparently, demonstrated the distinct part of the lophophore evolution of brachiopods (Kuzmina and Temereva 2019). This simple form of the lophophore is a transition form in the ontogenesis of other representatives of discinides (Zezina 2015).

We studied the spermatogenesis and ultrastructure of sperm in *P. atlanticus* (Temereva and Kuzmina 2018). The spermatozoon has a large acrosome, a small compact nucleus, eight mitochondria around the nucleus, two orthogonal centrioles, and a long tail. Comparative evaluation of all data on the structure of brachiopod spermatozoa indicates that *P. atlanticus* retains the most ancestral type of spermatozoon among all brachiopods.

5. Discussion

Thera are 63 species of deep-sea recent brachiopods that live at a depth of more than 2,000 meters and can be divided into two groups (Zezina 1989, 1994). The first group contains eurybathic species, the second is exclusively deep-sea animals (Zezina 1994). The most deep-sea species of recent brachiopods is *P. atltanicus*, whose empty shells were found at a depth of 7,460-7,600 meters in the Romanche Fracture Zone (Zezina 1994). This species is eurybathic with a range of depths for live specimens from 336-5,530 meters and is also the deepest among recent brachiopods (Zezina 1994; Emig 1997). On the marginal ridge of the Kuril-Kamchatka Trench, the density of this species is about 12 individuals per square meter (Zezina 1981). Stones of various diameters (Foster 1974), shells of brachiopods and molluscs (Cooper 1975), bones of whales and manganese nodules (Zezina 1981) can serve as a substrate for the attachment of this species in the deep sea.

Deep-water conditions are unfavourable for brachiopods, leading to dwarfism, paedomorphosis, and homeomorphy (Zezina 2008; Bitner et al. 2013). Thus, the small size of the shell and the underdeveloped simple lophophore of *P. atlanticus* are interpreted as paedomorphic features (Zezina 2015), which is characteristic of the deep-sea brachiopod fauna (Zezina 1994, 2015; Bitner et al. 2013). A large number of mitochondria in the spermatozoon of *P. atlanticus* may also be considered as an adaptation for deep-water occurrence in this species since spermatozoon needs a lot of energy for external fertilization at extreme depths (Temereva and Kuzmina 2018).

Acknowledgements

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CHAPTER 5
ENTOPROCTA

A REVIEW ON THE BIOGEOGRAPHY OF THE DEEP-SEA ENTOPROCTA ALONG THE NW PACIFIC

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1. Introduction

Entoprocta, or Kamptozoa, is a phylum of invertebrate animals including about 200 species. Entoprocts are solitary or colonial animals living as epibionts of different animals (sponges, cnidarians, polychaetes, sipunculans, echiurids, bryozoans, echinoderms, and hemichordates) or as foulers of various substrates (stones, algae, mollusk shells, arthropod cuticle, tunic of ascidians) (Nielsen 1964, 2008, Soule and Soule 1965, Borisanova 2018). Two species of Entoprocta were found in fresh water (Leidy 1851, Wood 2005), all the others are marine animals. The majority of species live in the shelf zone, most often at shallow depths down to several tens of meters. Only one colonial species, *Barentsia gracilis* (Sars, 1835), and six solitary species of genus *Loxosomella* Mortensen, 1911 were described from the deep-sea floor (Borisanova 2018, Borisanova and Chernyshev 2019). All deep-sea *Loxosomella* species were described in recent years, and all of them were found in NW Pacific.

2. Objectives

This chapter represents a brief review of the biogeography of the deep-sea Entoprocta found during Russian-German deep-sea expeditions in the NW Pacific.

3. Material and Methods

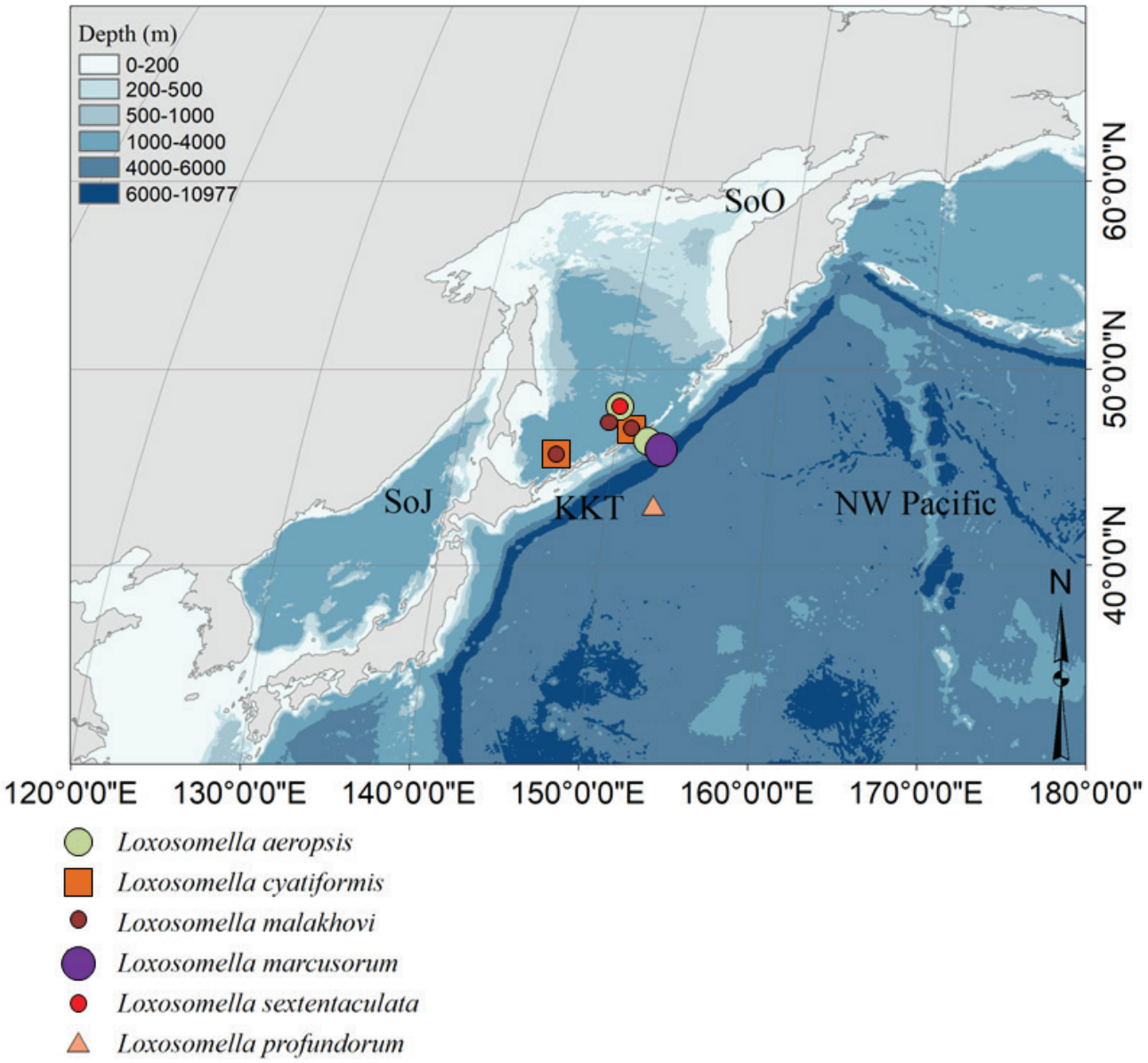
Six deep-sea species of the genus *Loxosomella* (family Loxosomatidae Hincks, 1880) were found in the NW Pacific region during three German–Russian deep-sea expeditions (Map 1).

Loxosomella profundorum Borisanova, Chernyshev, Neretina & Stupnikova, 2015, was collected during the German–Russian deep-sea expedition KuramBio aboard RV *Sonne* to the abyssal plain adjacent to the Kuril-Kamchatka Trench in the summer of 2012; *Loxosomella marcusorum* Borisanova, Chernyshev, 2019 was collected during the German–Russian deep-sea expedition KuramBio II aboard the RV *Sonne* to the Kuril-Kamchatka Trench region in August–September 2016; *Loxosomella aeropsis* Borisanova, Chernyshev & Ekimova, 2018, *L. cyatiformis* Borisanova, Chernyshev & Ekimova, 2018, *L. malakhovi* Borisanova, Chernyshev & Ekimova, 2018, *L. sextentaculata* Borisanova, Chernyshev & Ekimova, 2018 were collected during the German-Russian deep-sea expedition SokhoBio aboard RV *Akademik Lavrentyev* to the Kuril Basin of the Sea of Okhotsk, Bussol Strait, and the adjacent open Pacific abyssal area in July - August 2015. Five species were found in abyssal area (*L. aeropsis*, *L. cyatiformis*, *L. malakhovi*, *L. profundorum*, *L. sextentaculata*) at depths ranging from 3,206 to 5,223 m, one species in hadal zone at depth 6,202-6,204 m (*L. marcusorum*) (Table 1). The samples containing entoprocts were collected with a box corer (BC) (*L. malakhovi*) or dredged with a modified camera-epibenthic sledge (EBS) (*L. cyatiformis*, *L. malakhovi*, *L. profundorum*), and Agassiz trawl (AGT) (*L. aeropsis*, *L. marcusorum*, *L. sextentaculata*).

All species were fixed in 95% ethanol (for light microscopy, scanning electron microscopy, and for molecular analyses). Several specimens of two species (*L. aeropsis*, *L. malakhovi*) were also fixed in 4% paraformaldehyde solution in 0.1 M phosphate-buffered saline (for confocal laser scanning microscopy).

Table 1. List of deep-sea loxosomatid entoprocts from the NW Pacific.

Species	Point of species detection	Coordinates	Depth, (m)	Locality	Host species	References
Loxosomella profundorum		43.029667 N 152.976833 E	5,222–5,223	NW Pacific, east of the Kuril Islands	Corallimorpharia Carlgren, 1943	Borisanova et al. 2015
Loxosomella aeropsis	1	48.05 N 150.005 E	3,348	Kuril Basin, Sea of Okhotsk	*Aeropsis fulva* (Agassiz, 1898) (Aeropsidae Lambert, 1896, Echinoidea)	Borisanova et al. 2018
	2	46.261667 N 152.051667 E	3,580	Open Pacific abyssal area between the Bussol Strait and the Kuril-Kamchatka Trench.		
Loxosomella cyatiformis	1	45.588333 N 146.411667 E	3,206	Kuril Basin, Sea of Okhotsk	*Catillopecten squamiformis* (Bernard, 1978) (Propeamussiidae Abbott, 1954, Bivalvia)	Borisanova et al. 2018
	2	46.91 N 151.088333 E	3,296			
Loxosomella malakhovi	1	45.625 N 146.373333 E	3,216	Kuril Basin, Sea of Okhotsk	*Aglaophamus* sp. (Nephtyidae Grube, 1850, Polychaeta)	Borisanova et al. 2018
	2	46.91 N 151.088333 E	3,296			
	3	46.95 N 151.083333 E	3,300			
	4	48.09 N 150.026667 E	3,347			
	5	47.203332 N 149.611666 E	3,366			
Loxosomella sextentaculata		48.05 N 150.005 E	3,348	Kuril Basin, Sea of Okhotsk	*Laonice* sp. (Spionidae Grube, 1850, Polychaeta)	Borisanova et al. 2018
Loxosomella marcusorum	1	45.942883 N 152.904267 E	6,201.7	Kuril-Kamchatka Trench	*Thalassema* sp. (Thallassematidae Forbes & Goodsir, 1841 (Echiura)	Borisanova and Chernyshev 2019
	2	45.943117 N 152.904183 E	6,203.9			



Map 1. Distribution of Entoprocta species in the NW Pacific.

4. Results

The brief descriptions of the deep-sea entoproct species of the NW Pacific are given below. The main morphological characteristics are listed in Table 2.

***Loxosomella cyatiformis* Borisanova, Chernyshev, Ekimova, 2018**

(Figure 1A)

Loxosomella cyatiformis was found in the Kuril Basin of the Sea of Okhotsk, at depths 3,206 m and 3,296 m. Specimens were found living on scallop valves. *L. cyatiformis* is a medium-sized species. The total body length is from 383 μm to 596 μm. The stalk is longer than the calyx. Foot is absent in adults. Calyx bears 14 tentacles. One unpaired papilla is present on the abfrontal side of calyx. Stomach is triangular. Buds originate from the latero-frontal areas located at the lower

Table 2. Main morphological characteristics of deep-sea Entoprocta.

Species	Average body length, µm	Tentacle number	Sensitive papilla	Shape of stomach	Foot	Budding area
Loxosomella cyatiformis	498	14	One unpaired	triangular	No	latero-frontal, lower level of stomach
Loxosomella malakhovi	190	8	No	roundish	No; stalk ends with concaved disk	frontal, middle level of stomach
Loxosomella sextentaculata	834	6	No	roundish	Present	latero-frontal, upper level of stomach
Loxosomella aeropsis	558	9–10	No	roundish or slightly triangular	No	latero-frontal, middle level of stomach
Loxosomella profundorum	3,200	10–12	1 pair	heart-shaped	No	latero-frontal, upper level of stomach
Loxosomella marcusorum	596	10–12	No	roundish-triangular	No; stalk ends with star-shape plate	latero-frontal, bottom of stomach

level of the stomach. Full-developed buds with a conspicuous foot. Species was collected in late July–early August 2015, and some specimens were found with developing embryos, up to seven embryos in the calyx.

Loxosomella malakhovi Borisanova, Chernyshev, Ekimova, 2018

(Figure 1B, 1C)

Loxosomella malakhovi was found in the Kuril Basin of the Sea of Okhotsk, at depths 3,216–3,366 m. Specimens were attached to the gills of parapodia of nephtyid polychaetes. *L. malakhovi* is a small-sized species. The total body length is from 160 µm to 225 µm. The stalk is very short. Foot is reduced, and the stalk is ended with a roundish concaved disk which grasps part of the host tissue. The calyx bears eight tentacles. Sensitive papillae are not found. The stomach is roundish. Buds originate from the frontal area located at the middle level of the stomach. Full-developed buds with a prominent foot. Specimens were collected from mid-July to early August 2015, and many specimens were found with developing embryos, usually with two large embryos in the calyx.

Loxosomella sextentaculata Borisanova, Chernyshev, Ekimova, 2018

(Figure 1D)

Loxosomella sextentaculata was found in the Kuril Basin of the Sea of Okhotsk, at a depth of 3,348 m. Specimens were found attached to parapodia of spionid polychaetes. *L. sextentaculata* is a large-sized species. The total body length is from 705 µm to 938 µm. The stalk is long, and ends with a large foot. Calyx bears six tentacles. Sensitive papillae are not found. The stomach is roundish. Buds originate from the latero-frontal areas located at the upper level of the stomach. Full-developed buds were not observed. Species was collected in late July 2015, and no embryos were observed.

***Loxosomella aeropsis* Borisanova, Chernyshev, Ekimova, 2018**

(Figure 1E, 1F)

Specimens of *Loxosomella aeropsis* were collected in the Kuril Basin of the Sea of Okhotsk at a depth of 3,348 m and in open Pacific abyssal area between the Bussol Strait and the Kuril-Kamchatka Trench at a depth of 3,580 m. Specimens were found living attached to the anterior spines of sea urchins. *L. aeropsis* is a medium-sized species. Total body length is from 417 μm to 925 μm, the stalk is longer than the calyx. The foot is absent in adults. Calyx bears 10 or, more rarely, nine tentacles. Sensitive papillae are not found. The stomach is roundish or slightly triangular. Buds originate from the latero-frontal areas located at the middle level of stomach. Full-developed buds bear eight tentacles and have a short foot. Species was collected in late July 2015, and no embryos were observed in the calyxes of any specimens.

***Loxosomella profundorum* Borisanova, Chernyshev, Neretina and Stupnikova, 2015**

(Figure 1G, 1H)

Loxosomella profundorum was found in the abyssal plain adjacent to the Kuril-Kamchatka Trench, at depths of 5,222–5,223 m. Specimens were attached to the oral disc of the corallimorpharian polyp. *L. profundorum* is one of the largest species among entoprocts. The total body length is from 1.3 mm to 4 mm, the stalk is long, up to 3.5 mm. Foot is reduced in adults. Calyx bears 10–12 tentacles. One pair of sensitive papillae is present. Stomach is heart-shaped. Buds originate from the latero-frontal areas located at the upper level of the stomach. Full-developed buds were not observed. Species was collected in mid-August 2012, and no embryos were observed.

***Loxosomella marcusorum* Borisanova, Chernyshev, 2019**

(Figure 1I)

Loxosomella marcusorum was found in the Kuril-Kamchatka Trench, in the hadal zone, at depths of 6,202-6,204 m. *L. marcusorum* is an epibiont of echiurids. It is a medium-sized species. Total body length is from 449 μm to 685 μm, the stalk is shorter than the calyx. Foot is absent, the stalk is ended with an expanded star-shaped plate immersed in the host body. Calyx bears 10–12 tentacles. Sensitive papillae were not found. Stomach is roundish-triangular. Buds originate from the latero-frontal areas located at lower level of stomach. Full-developed buds were not observed. The species was collected in late August 2016, and many specimens had embryos developing in the calyx, usually with four embryos at a time.

5. Discussion

Eight new species of Entoprocta were found in the NW Pacific region during three deep-sea expeditions in recent years: *Loxosomella aeropsis*, *L. cyatiformis*, *L. malakhovi*, *L. marcusorum*, *L. profundorum*, *L. sextentaculata*, and two species, that have not yet been described (one species is an epibiont of polychaetes from the family Scalibregmatidae Malmgren, 1867, another species is associated with Sipuncula (Borisanova et al. 2018)). The discovery of eight new species in three expeditions suggests that the biodiversity of Entoprocta in the abyssal and hadal zone may be quite high in this region, and future investigations will contribute to our knowledge of the deep-sea entoproct species diversity.

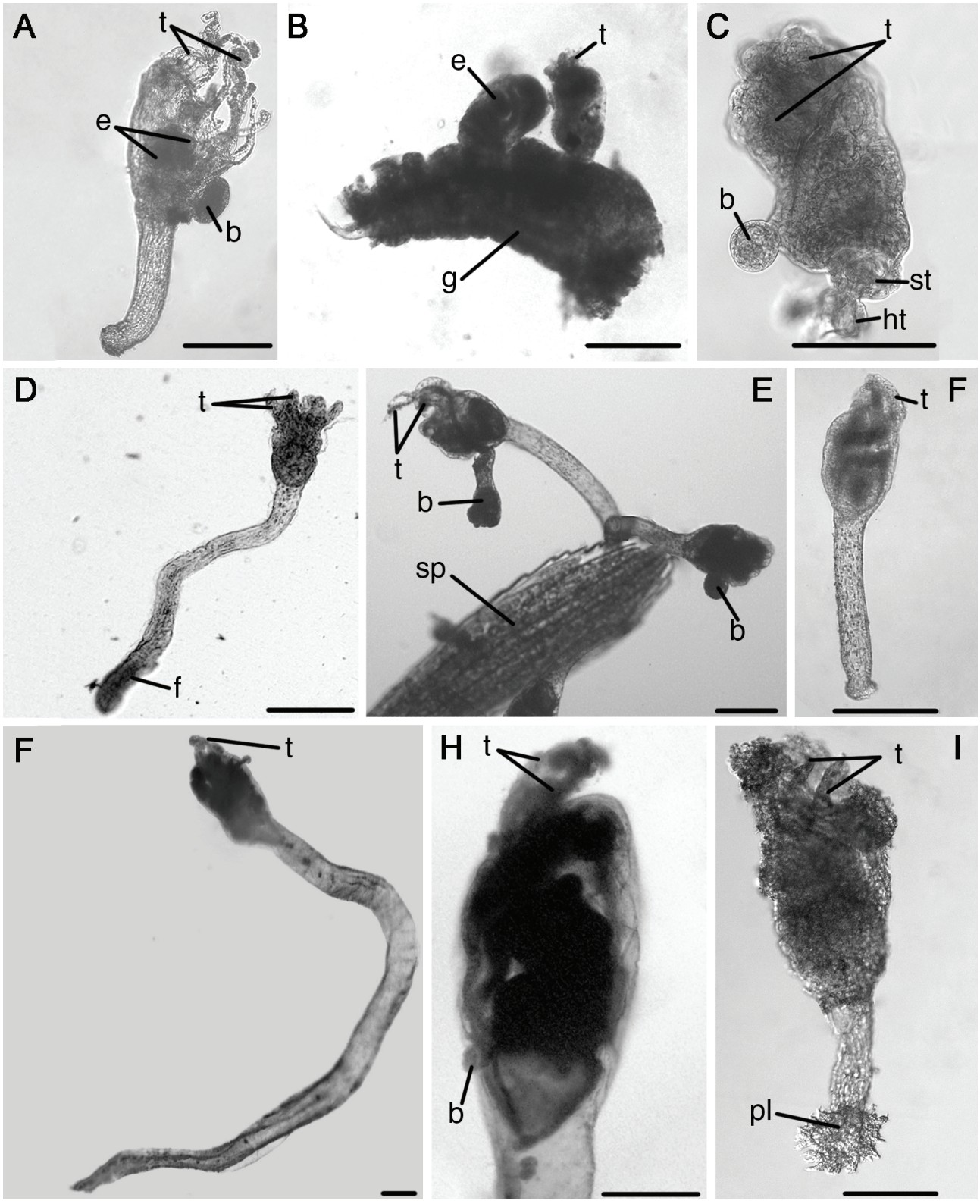


Figure 1. Deep-sea entoprocts of the NW Pacific. (A) *Loxosomella cyatiformes*, lateral view, (B, C) *Loxosomella malakhovi:* (B) two specimens on a gill of parapodia, (C) specimen with a bud, lateral view, (D) *Loxosomella sex-tentaculata,* frontal view, (E, F) *Loxosomella aeropsis:* (E) two specimens on a spine of sea urchin, (F) lateral view of specimen, (G, H) *Loxosomella profundorum:* (G) frontal view of specimen, (H) lateral view of calyx with a bud, (I) *Loxosomella marcusorum*, lateral view. Abbreviations: b, bud; e, embryo; f, foot; g, gill of parapodia; ht, host tissue; pl, star-shaped plate; sp, spine of sea urchin; st, stalk; t, tentacles. Scale bars: (A, B, D–I) 200 μm, (C) 100 μm.

Deep-sea Entoprocta are associated with different deep-sea animals, including those that are not characteristic for shallow-water entoproct species: corallimorpharians, sea urchins, and bivalve molluscs. The new symbiotic associations in the abyssal zone could have evolved due to the shortage of firm substrata and the low density of benthic animals, which results in an extremely limited choice of available hosts for epibiotic species. Although five species (*Loxosomella malakhovi*, *L. marcusorum*, *L. sextentaculata*, and two undescribed *Loxosomella* species) were found in association with annelids, the most typical hosts for Entoprocta (Nielsen 1964, Borisanova 2018).

Molecular genetics analysis of four species of deep-sea Entoprocta indicates that these species are not close to each other and cluster with different species of shallow-water entoprocts from different habitats. *L. cyatiformis* forms a single clade with *L. vancouverensis* Rundell & Leander, 2012 from the western coast of the Pacific Ocean (Vancouver Island in British Columbia, Canada). *L. malakhovi* clustered together with *L. varians* Nielsen, 1964 which was found in the Atlantic Ocean, and *L. murmanica* (Nilus 1909) which was found in the Atlantic, Antarctic and Arctic Ocean, but not in the Pacific (Nielsen 1989, Emschermann 1993). *L. aeropsis* forms a sister clade to *L. malakhovi*, *L. murmanica*, and *L. varians*. *L. profundorum* is genetically different from all solitary entoproct species and forms a sister clade to all Loxosomatidae.

Acknowledgements

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CHAPTER 6

NEMERTEA

A REVIEW ON DEEP-SEA BENTHIC NEMERTEANS ALONG THE NW PACIFIC

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1. Introduction

Nemertea is a phylum of the invertebrates known as nemerteans, or ribbon worms, which includes about 1300 valid species (Kajihara et al. 2009). These worms are found from the supralittoral to the abyssal zone on different bottoms, including silt, sand, algae, sponges, and dead corrals. Nemerteans are predators and scavengers feeding on small crustaceans, annelids, and molluscs. About 50 species are symbionts of decapods, barnacles, bivalve mollusks, ascidians, star-fishes, sea urchins, sea anemones, and echiurids. Most of the bathypelagic nemerteans (about 100 species) known to date are commonly found within a depth range of a few hundred to a few thousand meters, reaching their highest abundance at 600–3,000 m. To date, 22 species of fresh-water nemerteans and 13 species of land nemerteans living have been described (Gibson 1995; Sundberg and Gibson 2008).

Available information on deep-sea benthic nemerteans is even less compared to the shallower waters. By 2013, only seven of the described species of benthic nemerteans have been collected from depths exceeding 2,000 m, with none truly abyssal among them. In the last five years, we have had the opportunity to create a diverse and abundant collection of benthic nemerteans from abyssal and hadal depths. The data obtained indicate a high species diversity of benthic nemerteans inhabiting depths greater than 3,000 m. Nine species of the abyssal, pseudoabyssal and hadal nemerteans have been described quite recently (Chernyshev 2013; Chernyshev et al. 2015; Chernyshev and Polyakova 2018a; Chernyshev and Polyakova 2018b, Chernyshev and Polyakova 2019).

2. Objectives

The present chapter summarizes published data on deep-sea benthic nemerteans found during four Russian-German deep-sea expeditions in the NW Pacific.

3. Material and Methods

During four Russian-German deep-sea expeditions (SoJaBio 2010, KuramBioI 2012, SokhoBio 2015, and KuramBioII 2016) benthic nemerteans were collected at depths from 470 to 9,577 m. Specimens were sampled using a camera epibenthic sledge (EBS), Agassiz trawl (AGT), and giant box-corer (BK). We divided the collected nemerteans into two groups. The first one included nemerteans studied live and fixed for both morphological (in 4% paraform) and genetic (in 96% ethanol) analyses. Due to the rapid technique for examination of the internal structure using confocal laser scanning microscopy, the taxonomic affiliation of these nemerteans was determined, and some specimens were identified to the genus or species level. However, these nemerteans in each sample were represented by one, rarely two specimens. The second group includes individuals collected using EBS and fixed in chilled (–20°C) 96% ethanol and kept in a –20°C freezer. They are of little use for morphological studies, and thus their systematic position has not been determined as accurately as for individuals studied live.

Deep-sea benthic nemerteans are frequently found damaged in hydrobiological samples: in most cases, with the epidermis and the posterior or anterior parts of the body missing, making them unsuitable

for description. Most of collected specimens could be identified down to the family or order level only. Animals collected using EBS are best preserved for genetic studies (Chernyshev and Polyakova 2018a), but a quick fixation in cold 95% ethanol makes specimen less suitable for histological studies; a fixation in formol does not allow genetic analysis of material. The optimum way is fixation of a largest portion of living nemertean's body in 4% formalin for morphological investigation and a small portion in 95% ethanol for genetic studies. This approach was applied in description of the first abyssal heteronemertean *Sonnenemertes cantelli* (Chernyshev et al. 2015).

4. Results

In samples from the abyssal and hadal zones, a vast majority of nemerteans belonged to four groups: (1) carininid palaeonemerteans (Carininidae); (2) tubulanid palaeonemerteans (Tubulanidae s. str.); (3) heteronemerteans; (4) eumonostiliferous hoplonemerteans. Archinemerteans (cephalotrichid palaeonemerteans) and reptantian hoplonemerteans occurred much more rarely; carinomid palaeonemerteans and cratenemertid hoplonemerteans were not found in the samples from the abyssal and hadal zones (Chernyshev 2013, 2017; Chernyshev and Polyakova 2018a, Chernyshev and Polyakova 2018b, 2019; Chernyshev et al. 2015) (Figure 1 and Map 1). Deep-sea palaeonemerteans are represented by new species from known genera (*Carinina*, *Cephalothrix*, and *Tubulanus* s.l.).

All deep-sea *Carinina* collected in the NW Pacific form a highly supported clade, which is sister group to a clade of the shallow-water species (Chernyshev and Polyakova 2019). The most basal position in this clade is occupied by Carininidae KuramBio II 103, collected in the Kuril-Kamchatka Trench at a depth of 9,301 m. A preliminary study of the internal structure of some of the hadal carininids showed their structure typical of Carininidae: they had intraepidermal lateral nerve cords, well-developed inner circular musculature of the body wall, rhynchocoel wall with thick circular muscle layer, and inner position of the lateral blood vessels. A distinguishing feature of the collected deep-sea *Carinina* (except for Carininidae KuramBio II 103) is that they had relatively large body sizes (with the length of the anterior fragment of the body being 4–5 cm; the total body length was apparently 1.5–2 times larger). It should specially be noted that, according to DNA analysis, the specimens collected at the hadal stations, did not belong to the same species as those collected at abyssal depths in the Kuril-Kamchatka Trench, near the Kuril Islands, and from the abyssal plain near the Kuril-Kamchatka Trench.

Cephalothrix iwatai Chernyshev, 2013 (Figure 1a) is a single known deep-sea archinemertean and obviously common species in depth of 1,500–3,300 m in the Sea of Japan (Chernyshev 2013). Most nemerteans of genus *Cephalothrix* occur in the intertidal zone; whereas, only few have been found in depths from 20 to 40 m. In the Sea of Japan, several shallow-water *Cephalothrix* species have been recorded, but they all differ from *C. iwatai* and do not live in soft bottoms. Other deep-sea species for the Sea of Japan, *Micrura bathyalis* Chernyshev, 2013 from depths 2,670–3,426 m, is closely related to the sublittoral *Cerebratulus* species. The lack of typical abyssal species of nemerteans in the deep Sea of Japan is connected with isolation of this basin from the Pacific abyssal depths.

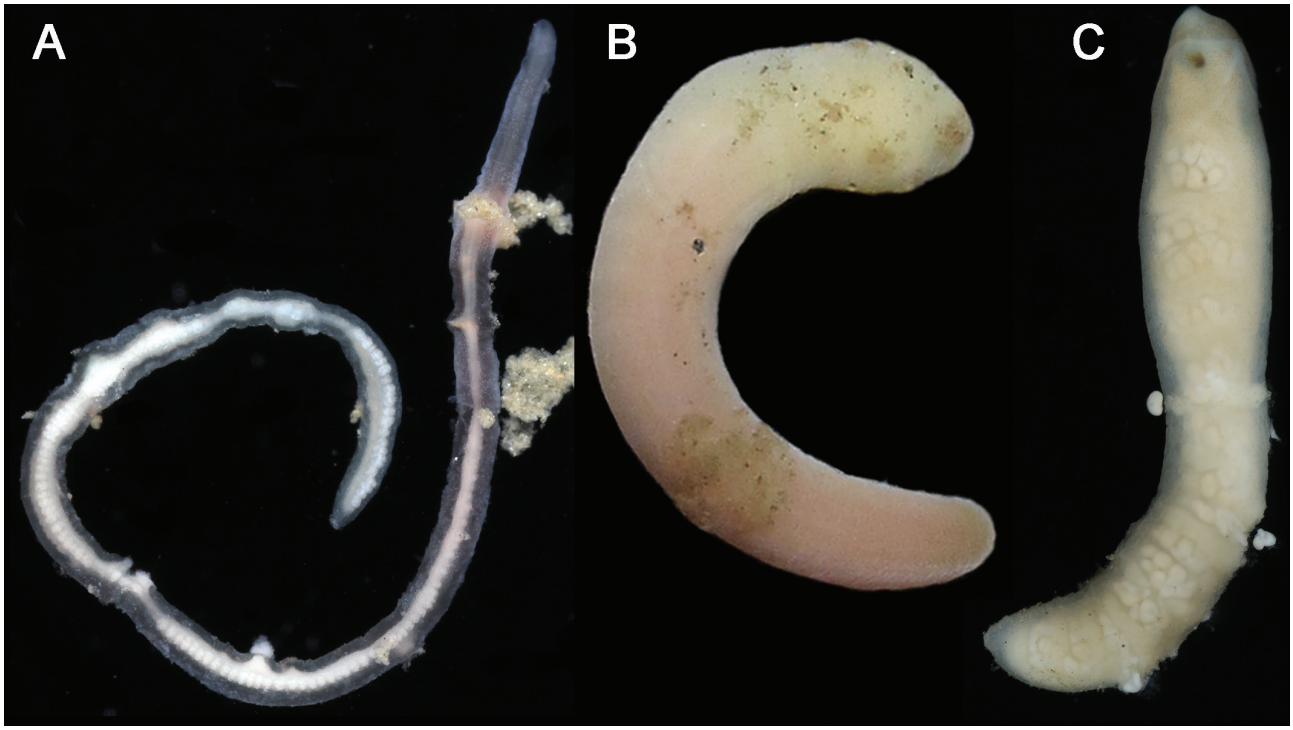
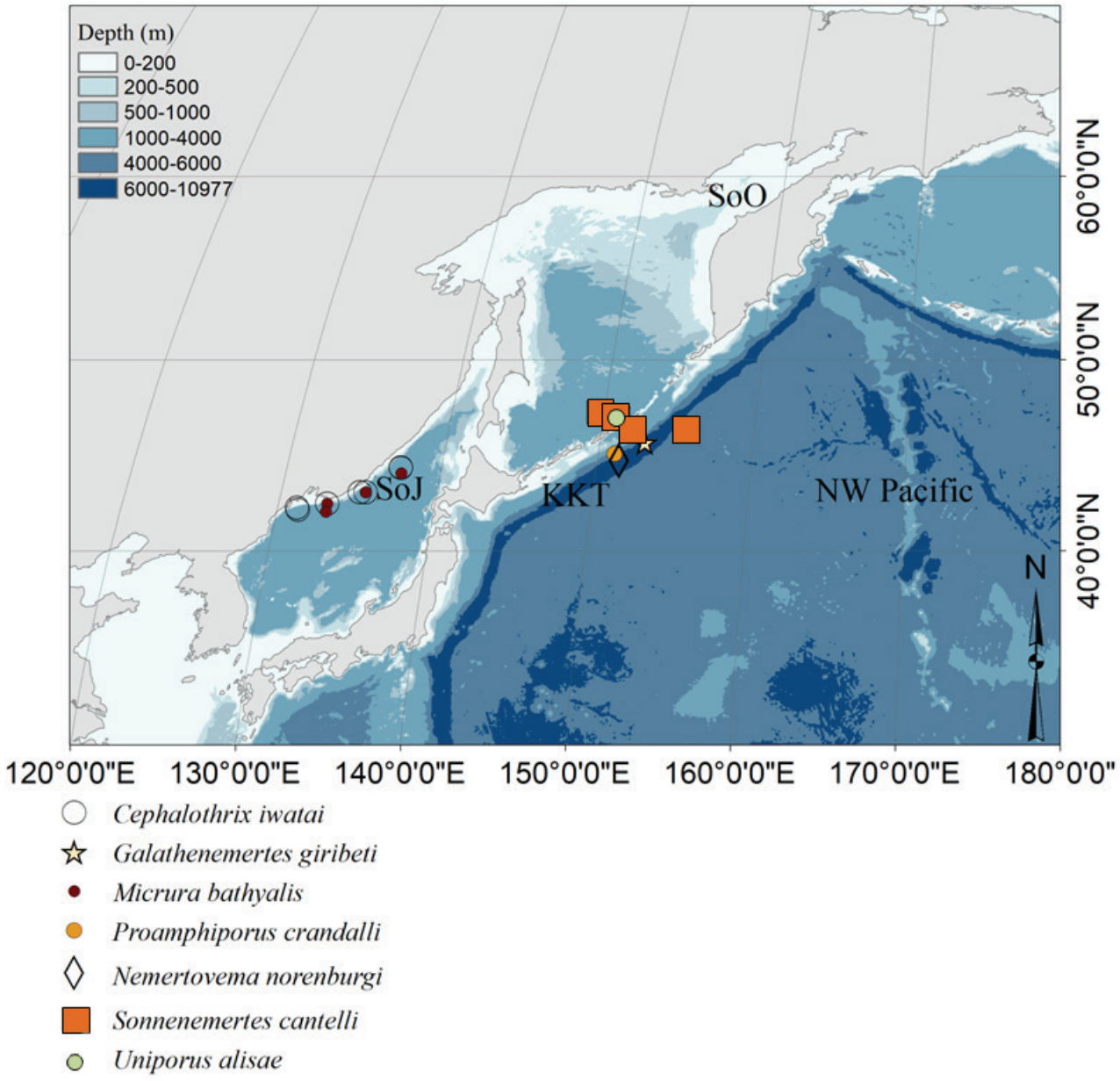


Figure 1. NW Pacific nemerteans. (A) *Cephalothrix iwatai*; (B) *Sonnenemertes cantelli*; (C) *Proamphiporus crandalli*.

Basal heteronemertean *Sonnenemertes cantelli* Chernyshev, Abukawa and Kajihara, 2015 (Figure 1b) was collected in samples from four stations in the Sea of Okhotsk and on both sides of the Kuril-Kamchatka Trench. *Sonnenemertes cantelli* has not been found in samples from depths shallower than 3,000 m and deeper than 6,000 m. For this reason, the species can be considered a marker of abyssal fauna. Our records of *S. cantelli*, originally described from a single abyssal station adjacent to the Kuril-Kamchatka Trench (Chernyshev et al. 2015) and reported from the Sea of Okhotsk (Chernyshev and Polyakova 2018b), further support relationships between the abyssal fauna of the Kuril Basin and parts of the NW Pacific fauna via straits between the Kuril Islands. *Sonnenemertes cantelli* apparently feeds on small sipunculid worms (Chernyshev and Polyakova 2018b).

Abyssal *Proamphiporus crandalli* Chernyshev and Polyakova, 2019 (Figure 1c) found in the Kuril-Kamchatka Trench from depth of 5,496 m is very similar in external traits and internal morphology to *Amphiporus rectangulus* Strand et al., 2014, described from the coastal waters of Norway from a depth of 220 m. Deep-sea benthic nemerteans do not have any specific color pattern, and live worms are unicoloured: mostly in whitish, pinkish, yellowish or, rarely, reddish tones. It is noteworthy that *P. crandalli* is the only abyssal nemertean with specific color pattern on the head, much resembling that in *A. rectangulus*.

Uniporus alisae Chernyshev and Polyakova, 2018 collected in the Sea of Okhotsk from depth of 3,301 m is morphologically close to *Uniporus hyalinus* Brinkmann, 1914–1915 described from the bathyal (depth 1,000–1,200 m) of the Norwegian



Map 1. Distribution of NW Pacific nemertean species.

Sea. Externally both species are very similar and have gelatinous translucent body.

The *Nemertovema* is a single known hadal genus with two described species: *Nevertovema hadalis* Chernyshev and Polyakova, 2018, collected in the Puerto Rico Trench from a depth of 8336–8,339 m (Chernyshev and Polyakova 2018a), and *Nemertovema norenburgi* Chernyshev and Polyakova, 2019, found in the Kuril-Kamchatka Trench from depths of 8,220 and 8,271 m (Chernyshev and Polyakova 2019). The pairwise COI-gene sequence distances between *N. hadalis* and *N. norenburgi* are 8.1–8.5%, which seems unusual because of the huge geographic gap between the Puerto Rico Trench and the NW Pacific localities. For comparison, the *p*-distances between COI-gene sequences of the sympatric cryptic species of the shallow water nemerteans are 8–14%.

Galathenemertes giribeti Chernyshev and Polyakova, 2019, found in the tube of sea anemone *Galatheanthemum* sp. in the Kuril-Kamchatka Trench from depth of 7,256 m, is the deepest known symbiotic nemertean and the second known species associated with Actinia. This species is closely related to ascidian-associated nemertean *Gononemertes parasita* Bergendal, 1900 (Chernyshev and Polyakova 2019). Deep-sea symbiotic nemerteans comprise species from the genera *Ovicides* and *Gononemertes* s.l. At least four undescribed species of *Gononemertes*-like nemerteans have been obtained from the peribranchial cavity of deep-sea carnivorous ascidians of the genus *Culeolus* (Herdman, 1881): (1) "*Gononemertes*" sp.1 from *Culeolus nadejdi* found in the Sea of Okhotsk (depth 1,040–1,050 m) (Sanamyan 1992); (2) "*Gononemertes*" sp. 2 from *Culeolus* sp. found in the abyssal plain adjacent to the Kuril–Kamchatka Trench (depth 4,869 m) (Chernyshev et al. 2015); (3) "*Gononemertes*" sp. 3 from *Culeolus* sp. found in the Kuril Basin of the Sea of Okhotsk (depths 3,301-3,347 m) (Chernyshev and Polyakova 2018b); (4) "*Gononemertes*" sp. 4 from *Culeolus barryi*, off the coast of California (depth 1,200 m) (Sanamyan et al. 2018). The phylogenetic analysis has confirmed the previously stated assumption that deep-sea *Gononemertes*-like nemerteans associated with *Culeolus* cannot be attributed to the genus *Gononemertes* with the type species *G. parasita* associated with the shallow-water ascidian *Phallusia* (Chernyshev and Polyakova 2018b).

5. Discussion

The taxonomic diversity of the abyssal and hadal nemerteans is quite high, though sequences have been obtained for less than a third of the species collected during deep-sea expeditions in the NW Pacific. Of particular interest is the finding of genetically close species (*Nemertovema hadalis* and *N. norenburgi*) in the Puerto Rico and Kuril-Kamchatka Trenches, which may indicate the relationships in the hadal nemertean fauna from different regions of the World Ocean. Among the deep-sea heteronemerteans and hoplonemerteans, species that could not be assigned to any of the known genera seem to be predominant. The genetic and morphological similarity between *Amphiporus rectangulus* and *Proamphiporus crandalli* is the first proven case of close phylogenetic relationships between sublittoral and real abyssal nemertean species (Chernyshev and Polyakova 2019).

The species diversity of nemerteans in the samples from the abyssal zone is usually quite high (about 50–60 species in the NW Pacific Ocean); however, in the Sea of Japan only two nemertean species, *Cephalothrix iwatai* (Chernyshev, 2013) and *Micrura bathyalis*, were found at a depth of over 3 km. With the rare exceptions, abyssal and hadal nemerteans are genetically well distinguished from shallow-water species. The *p*-distances between the COI sequences of the *C. iwatai* and shallow-water *Cephalothrix* sp. 4 TCH-2015 from northeast Pacific are 6.4–6.5%, indicating their close relationship. Accordingly, this fact indicates that *C. iwatai* is a 'young' eurybathic species.

Another interesting finding of our research was the different species compositions of nemerteans in the abyssal and hadal zones of the Kuril-Kamchatka Trench and adjacent abyssal depths. Moreover, we found no species present in the samples from both the abyssal and ba-

thyal zones. The exceptions were *Cephalothrix iwatai* and *Micrura bathyalis*, but it should be taken into account that both species live in the Sea of Japan, which lacks real abyssal fauna (Andriashev 1979). Apparently, among nemerteans eurybathic species with a wide range of habitat depths are not as common. There is no doubt that the abyssal and hadal zones of the World Oceans are inhabited by a large number of species and genera of nemerteans new to science.

Acknowledgements

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CHAPTER 7

SOLENOGASTRES

DIVERSITY AND DISTRIBUTION OF SOLNOGASTRES (MOLLUSCA) ALONG THE NW PACIFIC

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1. Introduction

Solenogastres (= Neomeniomorpha) are exclusively marine, vermiform molluscs. Together with Caudofoveata (= Chaetodermomorpha), they form the clade Aplacophora, a name referring to their body, which lacks a shell. Solenogastres is a comparatively species poor and understudied class of Mollusca with currently 293 described species organized in 24 families and four orders. Most Solenogastres are minute and reach only a few millimeters in body length and are thus usually collected with sampling gear designed for benthic meiofauna (only few giant species reach exceptional body lengths of up to 30 cm, and can be retrieved through macrobenthic sampling).

In Solenogastres, the molluscan foot is reduced to a narrow ciliary gliding sole, usually visible as a fine median line running along the ventral side of the animal and they lack a head shield (both characters help to distinguish them from equally worm-shaped Caudofoveates). Aragonitic sclerites protrude from the chitinous cuticle surrounding the entire body. These sclerites (comprising the so-called scleritome) are highly diverse, ranging from solid or hollow needles to solid scale-like elements. Depending on the composition of the scleritome, Solenogastres often appear smooth and shiny, shaggy, or very spiny. Together with the organization and histology of the digestive and reproductive system, the scleritome serves as one of the main taxonomic characters required to differentiate and identify solenogaster species. Most scientific work conducted on this group focuses on traditional taxonomy, but recent phylogenomic studies have begun investigating internal evolutionary relationships and rendered several parts of the current classificatory system (i.e. the order Cavibelonia Salvini-Plawen, 1978) paraphyletic (Kocot et al. 2019). Solenogastres systematics will thus likely receive major revisions in the near future.

1.1. Biology and Ecology

Solenogastres are commonly found among benthic fauna, even though they are seldom encountered in high individual numbers. They prey on marine invertebrates, mainly cnidarians (preferably hydrozoans) and polychaetes.

Little is known about the biology and ecology of Solenogastres, and observations are restricted to a few well-studied taxa. They are hermaphrodites and after copulation most species are assumed to deposit small batches of fertilized eggs from which lecitotrophic swimming larvae hatch (Todt and Wanninger 2013). A few species of Solenogastres brood and retain the encapsulated larvae within their pallial cavity until juveniles emerge, altogether suggesting limited dispersal abilities (Todt and Kocot 2014).

1.2. Habitat

Solenogastres inhabit a wide range of sediments from coarse shell gravel and volcanic sands to fine, silty sediments. Several species have been found living epizoically on cnidarians (Figure 1) or in association with sponges (Kocot et al. 2019).

While a few species can be collected in knee-deep waters of the shallow intertidal zone, the lower continental shelf is currently assumed to harbor the highest species diversity (Todt 2013).

The solenogaster fauna of the world's vast abyssal plains and the hadal zone of oceanic trenches still remain largely unexplored.



Figure 1. Dondersiidae sp. SB-2 (Pholidoskepia), from the Kuril Basin of the Sea of Okhotsk. Found wrapped around a cnidarian. Head to the right. Scale bar: 1 mm.

1.3. Geographical Distribution

Solenogastres are known from all oceans, sampled from the Arctic to the Antarctic. Most taxonomic work has focused on historical samples from Antarctica (see monographs by Salvini-Plawen 1978a; 1978b) and the North Atlantic along the western European coast, thus the majority of species has been described from these regions. To date, out of 293 recognized solenogaster species on a global-scale, 56 species are known from the entire Pacific Ocean and only 17 have been recorded from the NW Pacific. They occur mostly in the shallow bathyal around the Japanese coast (11 species, 27-600 m), the Sea of Japan (one species, 200-600 m), the Sea of Okhotsk (2 species, 200-400 m), and the Bering Sea (1 species, 880 m) (García-Álvarez and Salvini-Plawen 2007; Sirenko 2013).

2. Objectives

The present chapter aims to compile the current knowledge on the diversity and distribution of Solenogastres in the investigated area of the NW Pacific, recorded from the deep sea below 2,000 m. Based on this data, we explore putative patterns of species richness and distribution comparing the open NW Pacific and the semi-isolated adjacent Sea of Okhotsk.

3. Material and Methods

3.1. Coverage Area:

The KuramBio I and II (Kuril-Kamchatka Biodiversity Studies I and II, see Brandt et al. 2015, 2020) and SokhoBio (Sea of Okhotsk Biodiversity Studies, Brandt et al. 2018) Expeditions between 2012 and 2016 explored the benthic deep-sea fauna of the open NW Pacific and its adjacent regions. Solenogastres were collected during these expeditions using Agassiz trawls and epibenthic sledges. Overall, the investigated area ranges from 120-180°E and 40-60°N. It partially covers the open NW Pacific abyssal plain and the semi-isolated Kuril Basin of the Sea of Okhotsk, which is connected to the open NW Pacific via two deep straits. East of the Kuril Islands, the Kuril-Kamchatka Trench extends southwards reaching hadal depths of almost 9,600 m.

3.2. Depth Gradient

We have compiled data on Solenogastres occurring in the coverage area from bathyal (2,000-3,000 m), upper (3,000-4,000 m) and lower abyssal (4,000-6,000 m), and hadal depths (6,000 m and below).

3.3. Latitudinal Gradient

This chapter covers the deep-sea Solenogastres found in the temperate open NW Pacific and the Sea of Okhotsk with a latitudinal gradient of 40-60°N. Sampling sites correspond to the stations investigated during the recent KuramBio I (2012) and II (2016) (Brandt et al. 2015, 2020) and the SokhoBio (2015) (Brandt et al. 2018) expeditions.

4. Results

4.1. Richness Patterns

Prior to this recent expedition series to the deep NW Pacific no Solenogastres were described from the investigated area of the NW Pacific below 2,000 m. However, these expeditions revealed a unique solenogaster diversity: 66 candidate species were collected between the Kuril Basin of the Sea of Okhotsk, the open NW Pacific Plain, and the Japanese and Kuril-Kamchatka Trench, spanning a depth range from 3,000 to more than 9,500 m (see Bergmeier et al. 2017, 2020; Ostermair et al. 2018).

Following the currently recognized classificatory system of Solenogastres (García-Álvarez and Salvini-Plawen 2007), these 66 species cover all four traditional solenogaster orders and represent at least 10 families (see the Species Check-List in Chapter 1, Table 1). The two orders Cavibelonia Salvini-Plawen, 1978 and Pholidoskepia Salvini-Plawen, 1978 constitute in mostly equal parts for 98% of all collected Solenogastres in the area, and are both distributed from the upper abyssal down to the hadal zone. These two most common groups can be usually differentiated directly in the field under a stereomicroscope, as Cavibelonia are in general characterized by a spinier and rough appearance due to a scleritome largely composed of needle shaped elements, whereas Pholidoskepia are rather smooth and shiny, predominantly covered in scale-like elements).

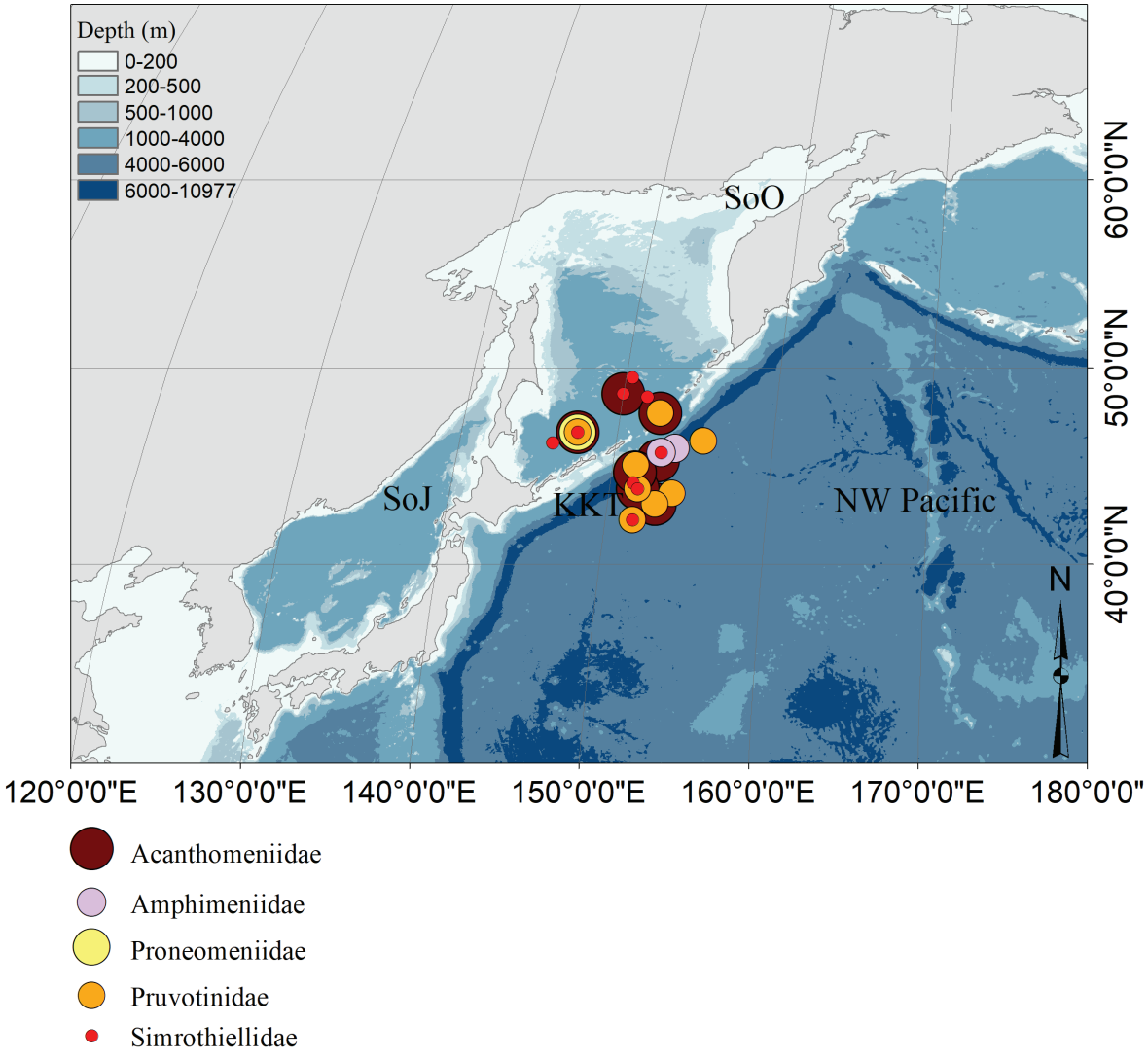
The five cavibelonian families are represented by 44 species, and while species of Acanthomeniidae, Amphimeniidae, Pruvotinidae, and Simrothiellidae all have been reported from the abyssal zone before (in the Atlantic, Indian, South Pacific and Southern Ocean), abyssal Proneomeniidae are currently only known from the NW Pacific (Map 1). Three families of Pholidoskepia (20 species) are present in the investigated regions and are among the first records of this order below 2,500 m (Map 2), apart for a single dondersiid species from the abyssal Atlantic (Cobo et al. 2020).

The remaining orders Neomeniamorpha and Sterrofustia are both rare and only account for one (Neomeniamorpha) and two (Sterrofustia) species, and while neomeniamorph Solenogastres are known from the bathyal NW Pacific, Sterrofustia have only been found once outside of the Southern Ocean before.

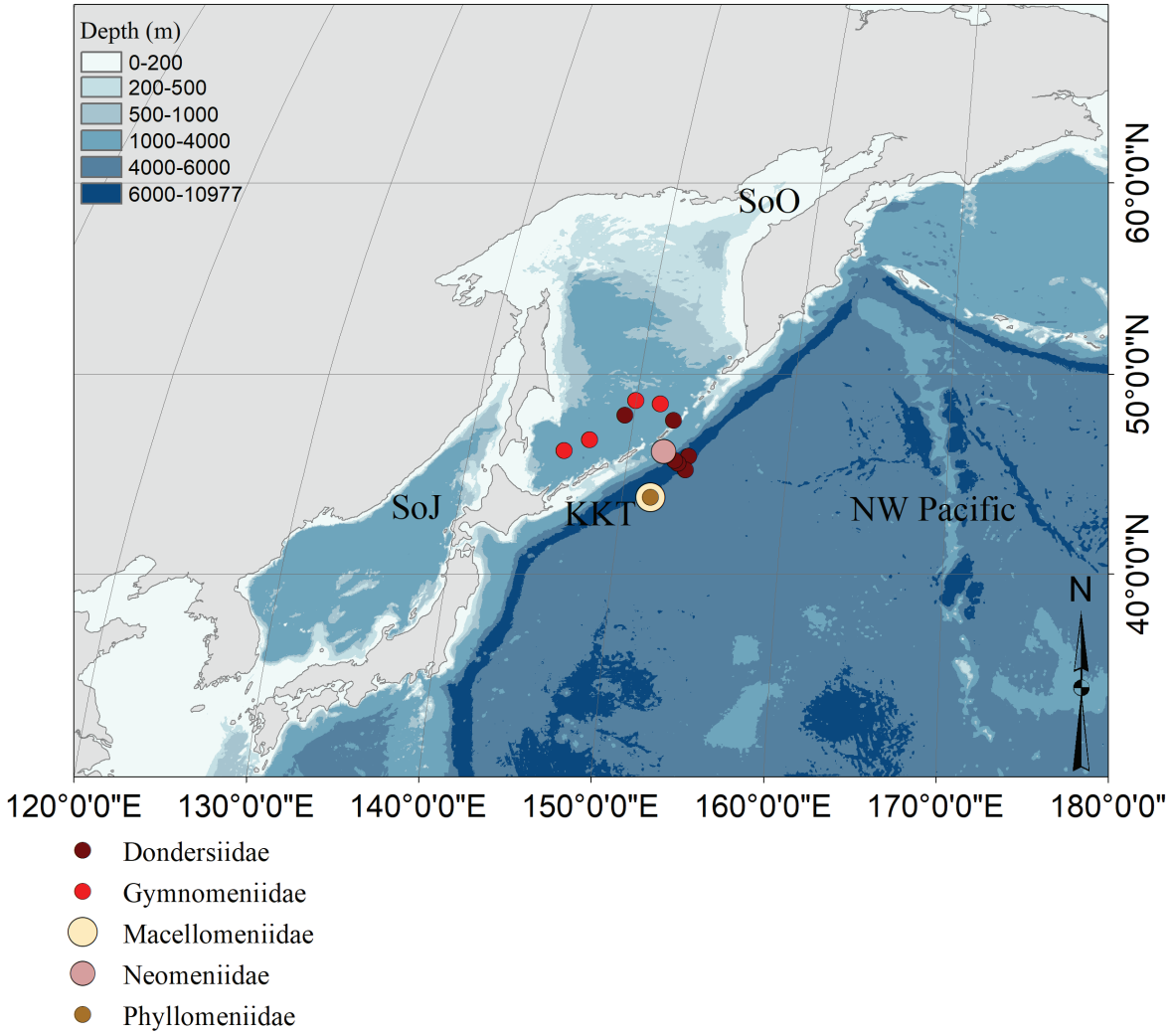
Species diversity varies along a depth gradient: 15 species are present in the upper abyss (3,000-4,000 m), 43 species in the lower abyssal (4,000-6,000 m), and 11 species in the hadal zone (6,000-9,577 m). Most of the upper abyssal species are recorded at around 3,300 m throughout the Kuril Basin in the Sea of Okhotsk (12 species) and the Bussol Strait (3 species) between the Sea of Okhotsk and the open sea (Table 1, Map 3 and 4). Nevertheless, the lower diversity of Solenogastres in the semi-isolated Kuril Basin when compared to the open NW Pacific plain might be a result of

Table 1. Species numbers (on familial level) in the investigated Northwest Pacific regions.

Family	Kuril Basin, Sea of Okhotsk (ca. 3,300 m)	Slopes and bottom of the Kuril-Kamchatka-Trench (ca. 5,200-9,577 m)	Open Northwest Pacific (abyssal plain) (ca. 4,800-5,400 m)
Acanthomeniidae	2	4	8
Amphimeniidae	-	2	-
Proneomeniidae	1	-	2
Pruvotinidae	1	2	6
Simrothiellidae	1	2	12
Dondersiidae	4	4	6
Gymnomeniidae	1	-	3
Macellomeniidae	-	-	1
Neomeniidae	-	-	1
Phyllomeniidae	-	-	1



Map 1. Records of cavibelonian solenogaster families (Acanthomeniidae, Amphimeniidae, Pruvotinidae, and Simrothiellidae) in the Northwest Pacific.



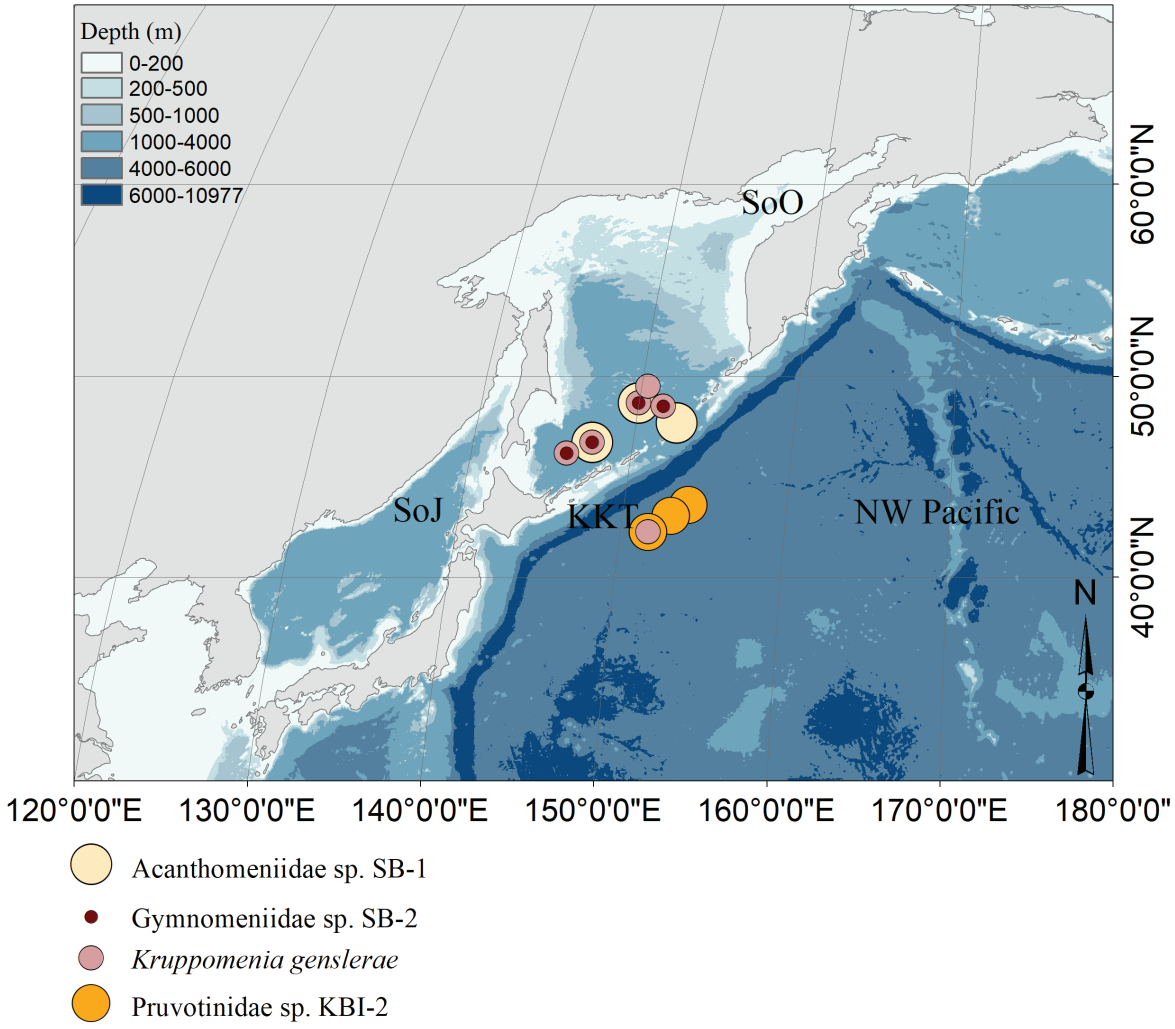
Map 2. Records of pholidoskepian (Dondersiidae, Gymnomeniidae, Macellomeniidae), neomeniomorph (Neomeniidae), and sterrofustian (Phyllomeniidae) solenogaster families.

oxygen-depleted bottom waters, formed during interglacial periods (Liu et al. 2006). 41 species are currently known from the open NW Pacific and its abyssal plain, while the slopes of the Kuril-Kamchatka Trench harbor nine species (5,200-7,200 m). Overall six species were sampled at four localities along the bottom of the trench, for the first time demonstrating the presence of Solenogastres in the hadal zone of oceanic trenches.

4.2. Biogeographic Patterns

Overall, the known solenogaster fauna of the abyssal and hadal zone of the NW Pacific is characterized by a high rate of singletons (i.e. species collected as single individuals only). Currently, within the investigated region, 45 out 66 species are collected only as singletons, and eight additional species were found only at a single location. This suggests that they might generally occur at low densities and/or with patchy distribution and consequently render potential hypotheses on their biogeographic and bathymetric distributions difficult based on the current state of knowledge.

Out of 10 families, four (Acanthomeniidae, Pruvotinidae, Simrothiellidae, Dondersiidae) are



Map 3. Distribution of dondersiid species recorded at three or more localities in the Sea of Okhotsk.

widely distributed across the Sea of Okhotsk, the Kuril-Kamchatka Trench and the open NW Pacific. Two families (Proneomeniidae, Gymnomeniidae) are present on both sides of the Kuril-Kamchatka Trench (albeit not recorded from the slopes or bottom), and four have only been recorded with restricted distribution, e.g. the large-sized Amphimeniidae (Figure 2) are currently only known from the lower slope and bottom of the Kuril-Kamchatka Trench (Table 1, Map 1 and 2).



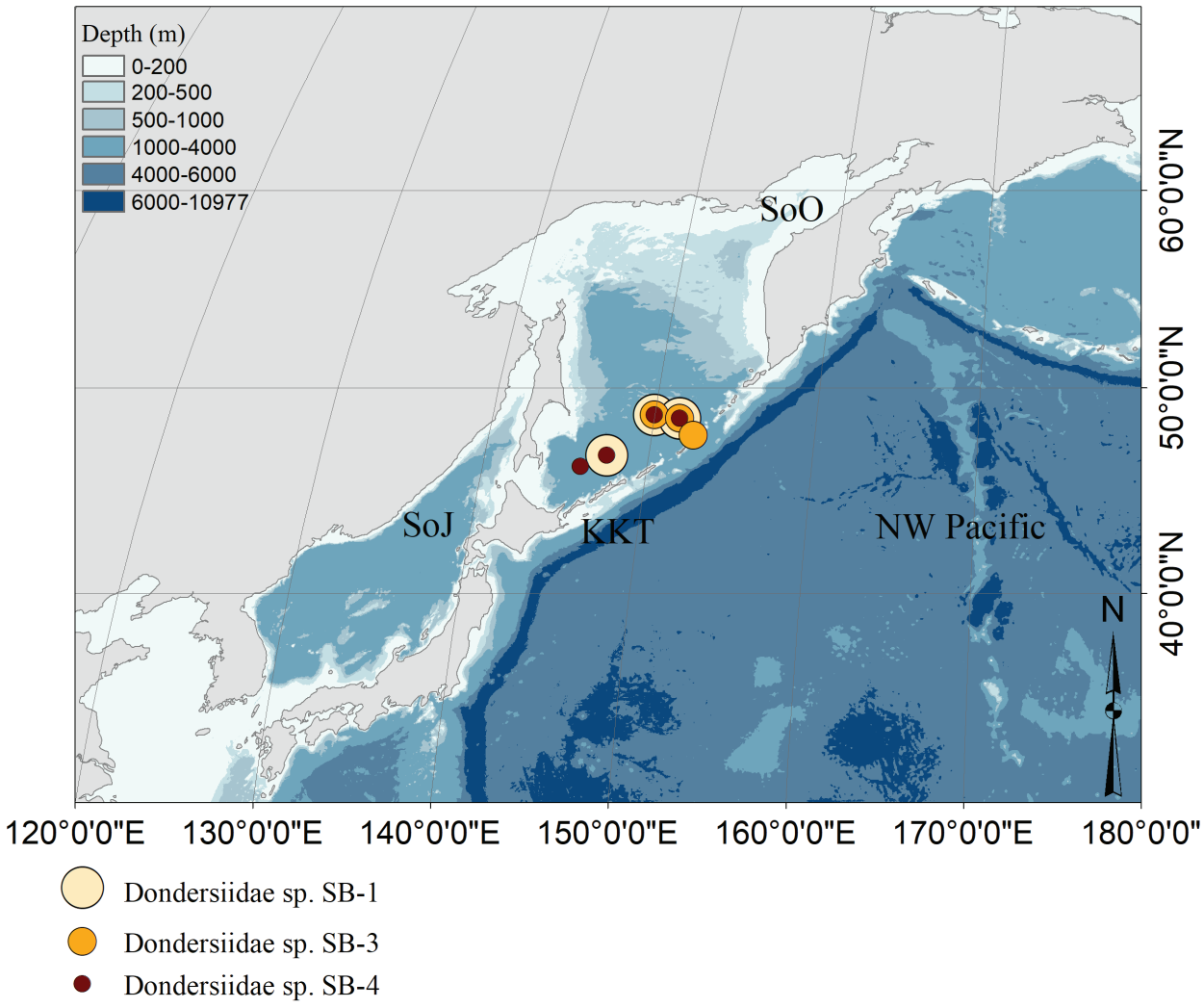
Figure 2. A large-sized Amphimeniidae sp.2 (Cavibelonia), found between 7,100 and 8,200 m at the bottom of the Kuril-Kamchatka Trench. Head to the left. Scale bar: 1 cm.

In the Sea of Okhotsk, 55% of the species are comparatively common, i.e. present at three or more localities (Map 3 and 4). Dondersiidae sp. SB-4 (Figure 3) is one of three common dondersiid

species in the Kuril Basin (Map 3), and accounts for 40% of the local solenogaster fauna. The families Acanthomeniidae, Gymnomeniidae, and Simrothiellidae are each represented by single species, albeit collected at several locations within the Kuril Basin (Map 4). 98% of species from the NW Pacific abyssal plain are highly restricted in their occurrence, and only a single species (Pruvotinidae sp.KBI-2) was found at three different localities, all in close vicinity (Map 4).

Overall there is only little faunal overlap on species level between the Sea of Okhotsk and the open NW Pacific: *Kruppomenia genslerae* Ostermair, Brandt, Haszprunar, Jörger & Bergmeier, 2018 (Figure 4) is so far the only solenogaster species reported from both sides of the Kuril-Kamchatka Trench (Map 4), as confirmed via molecular barcoding, suggesting a connection between the abyssal NW Pacific Plain and the semi-isolated Kuril Basin of the Sea of Okhotsk.

Most deep-sea Solenogastres known from the NW Pacific all show restricted depth ranges of max. 1,800 m. However, Acanthomeniidae sp. 6 exhibits an astonishing vertical distribution of more than 6,000 m, as conspecifity between five individuals recorded from the bottom of the



Map 4. Distribution of pholidoskepian (Gymnomeniidae sp.SB-2) and cavibelonian solenogaster species recorded at three or more localities in the Northwest Pacific.

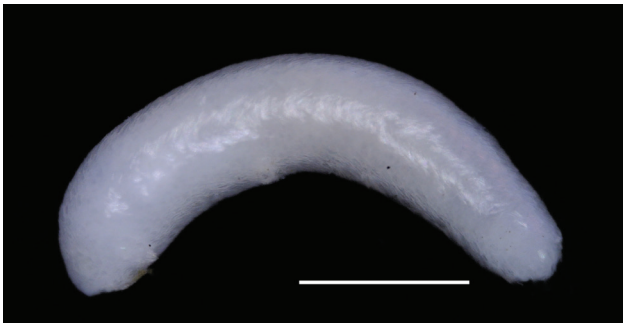


Figure 3. Dondersiidae sp.SB-4 (Pholidoskepia), a common species found in the Sea of Okhotsk. Note the shiny, smooth appearance due to the flatly arranged scales. Head to the left. Scale bar: 1 mm.



Figure 4. Holotype of *Kruppomenia genslerae* Ostermair, Brandt, Haszprunar, Jörger & Bergmeier, 2018 (Cavibelonia). Note the spiny outer appearance (needle-like, püreojectinv spicules). Head to the left. Scale bar: 1 mm.

Kuril-Kamchatka Trench and a single individual from the Sea of Okhotsk was confirmed via molecular barcoding (Bergmeier et al., in press).

5. Discussion

Within the last couple of years, the number of deep-sea species of Solenogastres (below 2,000 m) recorded from the NW Pacific has risen from zero to 66 candidate species, with the majority new to science and still pending formal descriptions.

It is generally assumed that solenogaster diversity is the highest on the continental shelf (Todt 2013) and decreases with increasing depth, which is a general trend in benthic deep-sea diversity (Rex et al. 1990). The comparably high number of abyssal species in the NW Pacific is most likely result from sampling bias, as the solenogaster fauna of the adjacent bathyal zone currently remains largely unexplored.

The currently known species recorded in the NW Pacific and summarized in this chapter present only a fraction of the actual diversity of deep-sea Solenogastres in the region, and we expect them to continuously rise with increasing sampling efforts.

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CHAPTER 8

BIVALVIA

SPECIES COMPOSITION AND RICHNESS OF BIVALVE FAUNA ALONG THE NW PACIFIC

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1. Introduction

Bivalve mollusks occur from the intertidal zone to the greatest depths of the World Ocean (Filatova 1968, 1971; Knudsen 1970; Scarlato 1981; Belyaev 1989; Coan et al. 2000; Jamieson 2015). Along with peracarid crustaceans, polychaetes and echinoderms, they are the most common and widespread animals in the abyssal zone and have played a key role as a model group in deep-sea biology research (Filatova 1958, 1971, 1976, 1982; Knudsen 1970; Brandt et al. 2005, 2007; Allen 2008; Tittensor et al. 2011). Bivalves are also found in the hadal zone of all investigated deep-water trenches at all depths down to the maximum depth in the Mariana Trench (Filatova 1960; Knudsen 1970; Belyaev and Mironov 1977; Filatova and Schileyko 1985; Belyaev 1989; Ramirez-Llodra et al. 2010; Jamieson 2015; Kamenev 2019). In the hadal zone, they are one of the richest groups of animals, after polychaetes and isopods, in terms of the number of species (Jamieson 2015), and rank second to holothurians in terms of average abundance on the bottom of various trenches, forming sometimes populations with very high densities (Zenkevitch et al. 1955; Filatova 1971; Belyaev 1989). Bivalves are currently one of the best-known animal groups in the northern Pacific (Scarlato 1981; Higo et al. 1999; Coan et al. 2000; Okutani 2000). However, the species composition and distribution of bivalves in the NW Pacific (north of 40°N) at depths in excess of 2,000 m remain insufficiently studied thus far. The NW Pacific is one of the most productive regions of the Pacific Ocean (Sokolova 1981) with high diversity of its benthic fauna (Zenkevitch and Filatova 1958; Filatova 1960, 1968; Belyaev 1989). In this regard, the study of the composition and distribution patterns of the deep-sea fauna in this region of the Pacific Ocean is of particular interest.

The investigated region of the NW Pacific includes several deep-water ecosystems that are connected with one another to a varying degree: deep-sea basins (maximum depths greater than 3,000 m) in the Sea of Japan, the Sea of Okhotsk, and the Bering Sea; oceanic slopes of the Kuril, Commander, and Aleutian Islands, as well as eastern coast of Kamchatka Peninsula (2,000-6,000 m); abyssal oceanic plain (5,000-6,000 m) adjacent to the Kuril-Kamchatka and Aleutian trenches; the northernmost part of the Japan Trench, the Kuril-Kamchatka Trench, and the deepest western part of the Aleutian Trench (depths in excess of 6,000 m). These deep-sea regions differ in the time of origin, geomorphology, depth, hydrological and hydrochemical regimes, bottom sediment structure, and consequently, the habitat conditions of benthic animals. In addition, they differ in the state of study of the deep-sea bivalve fauna.

1.1. Sea of Japan

The Sea of Japan with a maximum depth of 3,670 m (Mel'nichenko 2007), unlike other marginal seas of the NW Pacific, is rather isolated and communicates with the neighboring seas and the Pacific Ocean only via shallow straits (15-130 m deep) (Tada 1994; Tyler 2002; Kitamura et al. 2011). The deep-sea basin of the Sea of Japan includes 3 basins: Tsushima, Central, and Honshu. The Central Basin located north of the 40°N latitude is the largest. Its area is approximately equal to the total area of other deep-sea basins of this sea. The bottom of the

Central Basin is an almost flattened slightly sloping plain. The depths of the bottom gradually increase from west to east from 3,200 to 3,450-3,650 m. The maximum depth, which is the greatest for the Sea of Japan, reaches 3,670 m. On the plain surface of the hollow, there are several underwater elevations, which are mainly located in the western and northern parts of the basin. The maximum depths of the elevations are 1,064-1,326 m (Mel'nichenko 2007).

The first data on the quantitative and bathymetric distribution patterns of dominant species of macrobenthos, including several species of bivalves, in the bathyal and abyssal zones of the Sea of Japan appeared in works of Derjugin (1939) and Derjugin and Somova (1941). Only after the expeditions of the P. P. Shirshov Institute of Oceanology of the Russian Academy of Sciences (Moscow) (IO RAS) (1950, 1972, 1976) undertaken to study the deep-sea bottom fauna of the Sea of Japan, a number of papers dealing with quantitative distribution of macrobenthos in the bathyal and abyssal zones of that sea was published (Mokyevsky 1954; Zenkevitch and Filatova 1958; Zenkevitch 1963; Levenstein and Pasternak 1973, 1976; Pasternak and Levenstein 1978). A total of four species of bivalves were recorded in the Sea of Japan at depths below 2,000 m. Later, Scarlato (1981) examined the bivalves of the Zoological Institute of the Russian Academy of Sciences (Saint-Petersburg) collected in the NW Pacific over 150 years and gave descriptions and illustrations of 279 species and subspecies, of which 6 species were found in the Sea of Japan at depths in excess of 2,000 m. This monograph has long been the most complete Russian-language source of information on the deep-water bivalve fauna of the Sea of Japan. Japanese malacologists also described several species found at the bathyal slope of the Sea of Japan (Kuroda 1929; Okutani and Izumidate 1992) and published surveys of the bivalve fauna of Japan with brief notes on the finding of some species in the deep Sea of Japan (Habe 1977; Higo et al. 1999; Okutani 2000; Okutani and Saito 2014, 2017). During the period from 1972 to 2010, the IO RAS and A.V. Zhirmunsky Institute of Marine Biology of the Far Eastern Branch of the Russian Academy of Sciences (Vladivostok) organized five expeditions (4 expeditions of the IO RAS and SoJaBio (Sea of Japan Biodiversity Studies) Russian-German expedition on the RV *Akademik M.A. Lavrentyev*), which investigated the bottom fauna in the bathyal and abyssal zones of the Sea of Japan. As a result of examination of this extensive material, the most complete data were obtained on the composition and distributions of bivalves in deep-water basins of the Sea of Japan at depths of 465-3,435 m (Kamenev 2013).

1.2. Sea of Okhotsk

The Sea of Okhotsk is a deep-water sea (maximum depth 3,374 m) separated from the Pacific Ocean by a chain of the Kuril Islands (Udintsev 1981). The Pacific waters enter the sea through 17 straits between the Kuril Islands; the Bussol Strait (maximum width 83.3 km; maximum depth 2,318 m) and the Kruzenstern Strait (maximum width 66.7 km; maximum depth 1,920 m) (Glukhovsky et al. 1998) are the widest and deepest. The south-eastern part of the Sea of Okhotsk adjacent to the Kuril Islands is the deepest. The Kuril Basin bounded by the 3,000 m isobath is located here (Ushakov 1953; Glukhovsky et al. 1998). The Kuril Basin narrows in the east and gradually passes into a narrow depression. The abyssal zone

(depths in excess of 3,000 m) occupies 123,400 km^2, 7.7% of the total area of the sea (Glukhovsky et al. 1998). The northern, continental side of the basin is relatively sloping (5°). The south-eastern slope on the side of the Kuril Islands is steep (20-25°). The floor of the basin has gently sloping, flat or slightly undulating valleys in the west, which gradually give way to flat, horizontal valleys in the east. The sea floor is covered with thick finely-grained sediments, the bulk of which are diatom remains (Tsoy 2007, 2011).

As a result of extensive biological investigations during the last 70 years, the bivalve fauna of the subtidal and bathyal zones of the Sea of Okhotsk, which occupy 92.3% of the sea floor area, is fairly well known (Scarlato 1981; Kamenev 1996, 2002, 2008, 2009; Kamenev and Nadtochy 1998, 1999, 2000; Kamenev et al. 2001; Kamenev and Nekrasov 2012; Kharlamenko et al. 2016). Nevertheless, despite the intensive investigations of the deep-sea fauna of the NW Pacific and the Russian Pacific seas, very little was known about the species composition of bivalves that inhabit the abyssal zone of the Sea of Okhotsk (Ushakov 1953; Savilov 1961; Scarlato 1981).

Benthic animals from the abyssal zone of the Sea of Okhotsk were sampled, for the first time, by an expedition with the RV *Albatross* (1906), which made 1 haul at a depth of 3,375 m (Ushakov 1953). Later, in the course of intensive hydrological and hydrobiological investigations in the Sea of Okhotsk, an expedition on the RV *Gagara* (1932) collected one more sample from the bottom of the Kuril Basin from 3,350 m depth using a dredge (Ushakov 1953). In both deep-sea samples, a rich benthic fauna was found that contained many taxonomic groups, with the exception of live bivalves. Moreover, an integrated Kuril-Sakhalin expedition on the RV *Toporok* (1947-1949) investigated the fish fauna and valuable invertebrates off the southern Kuril Islands and the southern part of Sakhalin Island and collected one trawl sample from the 2,850 m depth in the south-western Sea of Okhotsk. In the subsequent years (1949–1990), the IO RAS expeditions have conducted only four deep-sea stations (RV *Vityaz*, cruise no. 2, 1949) in the Kuril Basin of the Sea of Okhotsk at depths below 2,900 m, including altogether seven samples. The bivalves from the samples were not identified to species. Ushakov (1953) and Savilov (1961) who reviewed the results of all investigations of benthic animals of the Sea of Okhotsk listed only specimens of the genera *Thyasira* and *Cardiomya* among the bivalve fauna of the sea floor of the Kuril Basin. Later, Scarlato (1972) described a new bivalve species *Cardiomya filatovae* Scarlato, 1972 on the basis of an empty shell that was found in a deep-water sample collected by the *Gagara* expedition in the Kuril Basin of the Sea of Okhotsk. Thus, only 10 samples were collected in the abyssal zone of the Sea of Okhotsk during all the years of investigations. *Cardiomya filatovae* and a small number of specimens of the genus *Thyasira* were found in the samples, the rest of the bivalve material remained unidentified.

In 2015, a SokhoBio (Sea of Okhotsk Biodiversity Studies) Russian-German expedition on the RV *Akademik M.A. Lavrentyev* investigated the benthic fauna of abyssal depths (greater than 3,000 m) in the Kuril Basin of the Sea of Okhotsk and collected macrobenthos in the deepest Bussol Strait, which connects the Sea of Okhotsk and the Pacific Ocean, as well as at abyssal depths of the Pacific slope of the Kuril Islands

that is adjacent to the strait. Investigation of the materials collected by the SokhoBio expedition and two Russian expeditions (RV *Toporok*, 1948; RV *Vityaz*, 1949) from the bottom of the Kuril Basin of the Sea of Okhotsk (2,850–3,366 m depth) revealed a rich fauna of bivalves including 25 species (Kamenev 2018c).

1.3. Bering Sea

Deep-sea Commander, Aleutian, and Bowers basins of the Bering Sea with a maximum depth of about 4,300 m are located in its western part and are least isolated from the Pacific Ocean (Belous and Svarichevsky 2007). The Bering Sea communicates with the Pacific Ocean through the wide and deep Kamchatka Strait (depth about 4,500 m) and the Blizhniy Strait and numerous relatively shallow straits between the Aleutian Islands.

The benthic fauna at depths of more than 2,000 m in the western Bering Sea was explored by an expedition with the RV *Dalnevostochnik* (1932) and four expeditions of the IO RAS (RV *Vityaz*, 1950, 1951, 1952; RV *Akademik Mstislav Keldysh*, 1990) (Scarlato 1981; Monin 1983). As a result of these expeditions, extensive material of benthic animals, including bivalves, was collected from depths of more than 2,000 m. However, most of the material of bivalves is not yet examined. To date, only 14 species of bivalves are listed for the deep-water bivalve fauna of the western Bering Sea (Scarlato 1981; Filatova and Schileyko 1984; Krylova 1997; Kamenev 2014, 2018a, b, 2019). However, according to preliminary data (Kamenev, unpublished data), a much richer bivalve fauna occurs in the western part of the Bering Sea at depths greater than 2,000 m.

1.4. Abyssal plain of the NW Pacific and the Kuril-Kamchatka and Aleutian trenches

The first studies of the bivalve fauna of the abyssal plain of the central and NW Pacific were performed based on examination of collections made by the famous round-the-world expedition of HMS *Challenger* in 1872–1876 (Smith 1885). Unfortunately, all samples of benthic animals in the NW Pacific were collected by this expedition from south of 40°N. Intensive studies of the deep-sea fauna of the NW Pacific north of 40°N were begun in 1949 by expeditions of the IO RAS. During the period from 1949 to 1990, the IO RAS organized 13 expeditions, which explored the benthic fauna of the abyssal plain of the NW Pacific Ocean, and the Kuril-Kamchatka and Aleutian trenches. These expeditions collected tremendous material of benthic animals of different taxonomic groups from the entire region. As a result of examination of this material, a large number of new species of bivalves found in the abyssal and hadal zones of the NW Pacific were described, and the distribution of many species in the Pacific was investigated (Filatova 1958, 1960, 1971, 1976; Ivanova 1977; Filatova and Schileyko 1984, 1985; Krylova 1993, 1995, 1997). However, Russian scientists concentrated primarily on the study of benthic animals collected in oceanic trenches, and hence, much of the material sampled from the Pacific abyssal plain remained unexamined.

The Kuril-Kamchatka and Aleutian trenches are narrow V-shaped depressions of the oceanic floor along the Kuril and respectively Aleutian chains of islands, which are separated by a relatively small area of the ocean floor with depths of less than 6,000 m off the south-eastern coast of Kamchatka.

The Kuril-Kamchatka Trench with a maximum depth of 9,600 m (Vasiliev et al. 1978; Kamenev 2019) is among 9 deepest trenches of our planet (Belyaev 1989). The shallower Aleutian Trench (maximum depth 7,822 m) is one of the longest (3,700 km) (Jamieson 2015). The fauna of the Kuril-Kamchatka and Aleutian trenches was explored almost exclusively by expeditions of the RV *Vityaz* (1949-1969). Only one quantitative sample was taken from the bottom of the eastern part of the Aleutian Trench in 1970 by the U.S. RV *Thomas Washington* (Belyaev 1989). On the whole, during all the years of study, 26 trawl hauls were made and five quantitative samples were collected using an Okean grab in the Kuril-Kamchatka Trench; eight trawl hauls and five quantitative samples, one of which was taken with a box-corer, in the Aleutian Trench.

During deep-sea research expeditions, a very rich material of bivalves was collected in the Kuril-Kamchatka and Aleutian trenches. No less than 18 species of bivalves were found in the hadal zone of the Kuril-Kamchatka Trench, which was much better studied, compared to the Aleutian Trench (Belyaev 1989); 11 of them were described as new to science. In the Aleutian Trench, only 10 species were recorded, three species remained unidentified (Filatova 1971, 1976; Ivanova 1977; Filatova and Schileyko, 1984, 1985; Belyaev 1989; Krylova 1993, 1997; Kamenev 2018a, 2019).

Likewise, Japanese researchers were conducting intensive studies of the deep-sea bivalve fauna in the NW Pacific. However, most of their research was performed in the Pacific Ocean south of the 40°N latitude. Okutani (1974) listed 44 species of bivalves found around Japan at depths greater than 2,000 m. Later, after studying the abyssal plain and oceanic trenches in this NW Pacific region, the list was extended significantly (Okutani and Kawamura 2002; Sasaki et al. 2005; Okutani et al. 2009).

In recent years, two joint German-Russian expeditions KuramBio (Kuril-Kamchatka Biodiversity Studies) (2012) and KuramBio II (2016) performed complex studies of the benthic fauna of the Pacific abyssal plain adjacent to the Kuril-Kamchatka Trench and the hadal zone of the Kuril-Kamchatka Trench (Brandt and Malyutina 2015; Brandt et al. 2019). After examination of the materials of these expeditions, as well as some of the materials collected by previous expeditions of the IO RAS, nine new species were described and bivalve species composition and distribution in these regions were investigated (Kamenev 2014, 2015, 2018a, b, 2019; Krylova et al. 2015). Moreover, Japanese researchers described 9 species found in the abyssal and hadal zones of the Japan Trench north of 40°N and in the southernmost part of the Kuril-Kamchatka Trench (Okutani and Fujiwara 2005; Sasaki et al. 2005; Okutani et al. 2009). As a result of these studies, data on the species richness of the deep-sea bivalve fauna of the NW Pacific are extended significantly.

2. Objectives

The main objectives of this work are (1) to investigate the species composition and richness of bivalve fauna of the deep NW Pacific areas (north of 40°N) at depths in excess of 2,000 m; (2) to analyze the geographic distribution of species founded in these areas; (3) to study the change in the species composition and richness of bivalves in relation to depth.

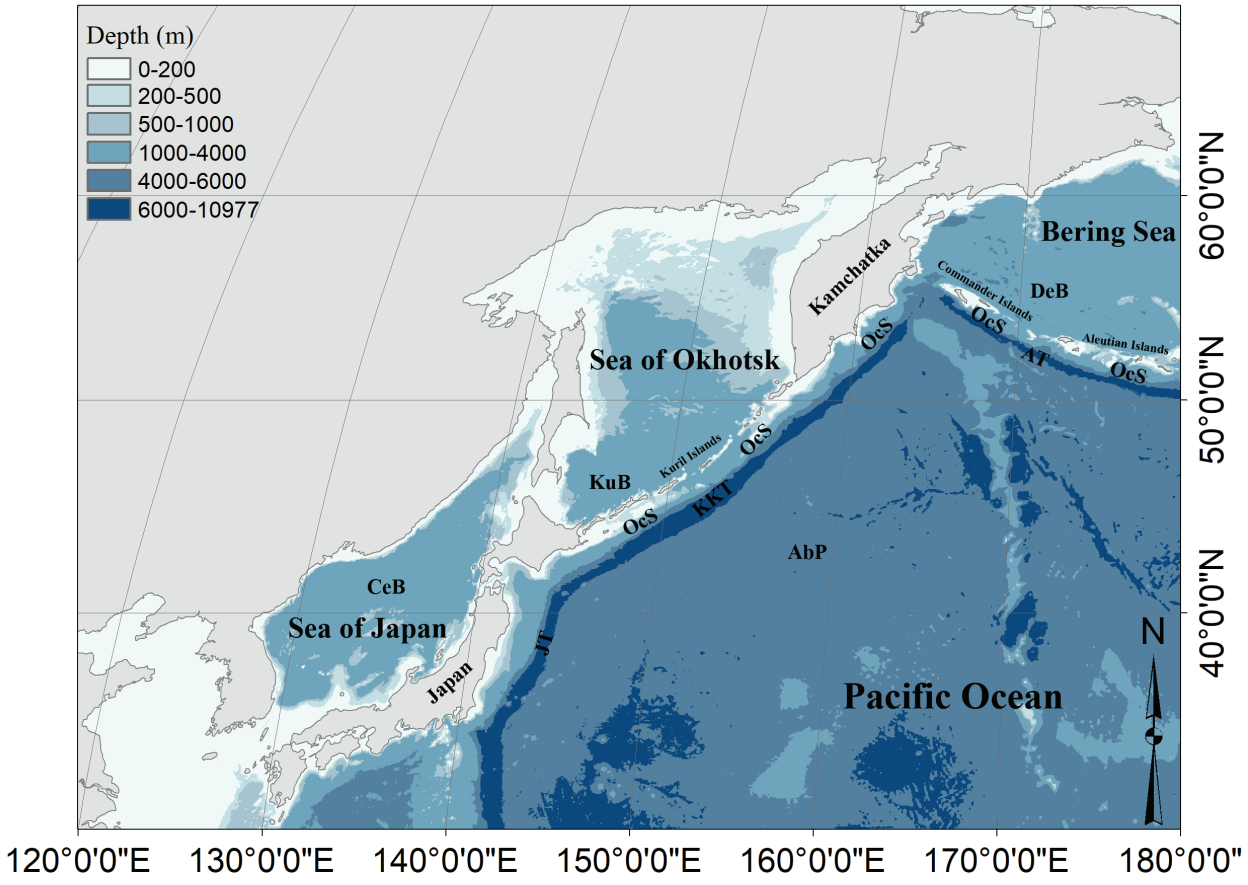
3. Material and Methods

For this study I designated 8 deep-sea areas within the NW Pacific, differing in the time of origin, geomorphology, depth, hydrological and hydrochemical regimes, bottom sediment structure: the Central Basin of the Sea of Japan; the Kuril Basin of the Sea of Okhotsk; the Commander, Aleutian, and Bowers basins of the Bering Sea; oceanic slopes of the Kuril, Commander, and Aleutian Islands, as well as the eastern coast of Kamchatka Peninsula; the abyssal oceanic plain adjacent to the Kuril-Kamchatka and Aleutian trenches; the northernmost part of the Japan Trench; the Kuril-Kamchatka Trench; the western part of the Aleutian Trench (Map 1). For the analysis of species composition and distribution of bivalve molluscs in these areas I used all available data from relevant literature sources (Table 1).

4. Results

4.1. Composition of the bivalve fauna of deep NW Pacific areas

To date, 123 species (including morphospecies) that belong to 56 genera and 23 families have been recorded for the NW Pacific north of 40°N at depths greater than 2,000 m (Table 1, Figures 1



Map 1. Deep NW Pacific areas (north of 40°N): CeB – Central Basin of the Sea of Japan; KuB – Kuril Basin of the Sea of Okhotsk; DeB – deep-sea Commander, Aleutian, and Bowers basins of the Bering Sea; OcS – oceanic slopes of the Kuril, Commander, Aleutian Islands, and eastern coast of Kamchatka Peninsula; JT – Japan Trench; KKT – Kuril-Kamchatka Trench; AT – Aleutian Trench; AbP – abyssal plain of the Pacific Ocean.

Table 1. List of species and the depth range (in meters) of finding of bivalves recorded at depths greater than 2000 m in different deep NW Pacific areas (north of 40°N) and in eastern Pacific.

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
Nuculidae Gray, 1824	*Nucula profundorum* Smith, 1885					4,861-5,406				734-4,134	Coan et al. 2000; Coan and Valentich-Scott 2012; Kamenev 2015, 2019
Pristiglomidae Sanders and Allen, 1973	*Pristigloma* cf. *alba* Sanders and Allen, 1973					5,112-5,427					Kamenev 2015
	Setigloma japonica (Smith, 1885)					4,861-5,427				3,000-5,240	Schileyko 1983; Coan et al. 2000; Kamenev 2015
Nuculanidae H. Adams and A. Adams, 1858	*Ledellina convexirostrata* Filatova and Schileyko, 1984					4,861-5,427		6,441-6,710		4,860	Filatova and Schileyko 1984; Kamenev 2015, 2019
	Ledellina formabile Filatova and Schileyko, 1984			3,661-4,294						2,800	Filatova and Schileyko 1984; Kamenev 2019
	Microgloma sp.				3,342-3,432	4,861-5,427					Kamenev 2015
	Nuculana leonina (Dall, 1896)		307-2,850	2,622-3,034						1,690-2,500	Kamenev 2018c; Coan et al. 2000
	Parayoldiella ultraabyssalis (Filatova, 1971)							8,355-9,583			Filatova 1971; Filatova and Schileyko 1985; Belyaev 1989; Kamenev 2019

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Parayoldiella mediana (Filatova and Schileyko, 1984)							7,265-8,740			Filatova and Schileyko, 1984, 1985; Belyaev 1989; Kamenev 2015
	Poroleda extenuata (Dall, 1897)		2,850		2,992-3,432					2,000-2,900	Coan et al. 2000; Kamenev 2018c
	Robaia robai (Kuroda, 1929)	83-2,900									Scarlato 1981; Okutani 2000; Kamenev 2013
Bathyspinulidae Coan and Scott, 1997	*Bathyspinula calcarella* (Dall, 1908)				5,220-5,572	4,861-5,752		6,000-6,860	6296-6328	4,200-5,830	Filatova 1958, 1976; Filatova and Schileyko 1984; Belyaev 1989; Coan et al. 2000; Coan and Valentich-Scott 2012; Kamenev 2019
	Bathyspinula calcar (Dall, 1908)					5,379-5,743				4,000-5,000	Filatova 1958; Coan et al. 2000; Coan and Valentich-Scott 2012; Kamenev 2015
	Bathyspinula vityazi (Filatova, 1964)						6,475-7,587	6,435-9,335	6,965-7,250		Filatova 1964, 1971, 1976; Belyaev 1989; Kamenev 2019
Malletiidae H. Adams and A. Adams, 1858	*Katadesmia vincula* (Dall, 1908)		3,206-3,366	1,490-4,382	1,260-5,572	4,861-5,427	7,320	6,400-7,256	6,856-7,250	590-3,585	Coan et al. 2000; Okutani and Fujiwara 2005; Coan and Valentich-Scott 2012; Kamenev 2015, 2018c, 2019

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
Neilonellidae Schileyko, 1989	*Neilonella politissima* Okutani and Kawamura, 2002					4,861-5,787					Kamenev 2015, 2019
	Neilonella profunda Okutani and Fujiwara, 2005						7,320				Okutani and Fujiwara 2005
	Neilonella sp. 1					5,216-5,427					Kamenev 2015
	Neilonella sp. 2				4,679-5,572	4,861-5,752		6,047-6,561			Kamenev 2015, 2019
	Neilonella sp. 3							7,055-7,256	7,246		Belyaev 1989; Kamenev 2019
	Neilonella sp. 4							7,055-8,740			Kamenev, 2019
Siliculidae Allen and Sanders, 1973	*Silicula beringiana* Kamenev, 2014			4,89-4,811	4,890-4,984						Kamenev 2014
	Silicula okutanii Kamenev, 2014				5,013-5,572	5,101-5,497		6,441-6,561			Kamenev 2014, 2015, 2018c, 2019
Tindariidae Verrill and Bush, 1897	*Tindaria antarctica* Thiele and Jaeckel, 1931				5,220-5,572	4,861-5,427		6,441-6,561			Kamenev 2015, 2019
	Tindaria sp. 1					4,861-5,352					Kamenev 2015, 2019
	Tindaria sp. 2				4,679-5,572	4,861-5,427					Kamenev 2015, 2018c, 2019
	Tindaria sp. 3					4,861-5,427					Kamenev 2015, 2019
	Tindaria sp. 4					4,861-5,427					Kamenev 2015

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Tindaria sp. 5					4,977–4,998					Kamenev, 2015
	Tindaria sp. 6		2,327–3,366								Kamenev 2018c
	Tindaria sp. 7							6,441–6,561	6,296–7,286		Belyaev 1989; Kamenev 2019
Yoldiidae Dall, 1908	*Megayoldia* sp.		2,850								Kamenev 2018c
	Yoldiella derjugini Scarlato, 1981	22–2,520								520–800	Scarlato 1981; Coan et al. 2000; Kamenev 2013
	Yoldiella cf. *jeffreysi* (Hidalgo, 1877)					4,861–5,497					Kamenev 2015, 2019
	Yoldiella kaikonis Okutani & Fujiwara, 2005						7,299–7,333				Okutani and Fujiwara 2005
	Yoldiella olutoroensis Scarlato, 1981			3,000							Scarlato 1981
	Yoldiella orbicularis Scarlato, 1981	53–2,300									Scarlato 1981; Kamenev 2013
	Yoldiella sp. 1		3,206–3,307		3,342–3,432						Kamenev 2018c
	Yoldiella sp. 2							6,441–7,256			Kamenev 2019
Mytilidae Rafinesque, 1815	*Dacrydium rostriferum* Bernard, 1978		3,206–3,366	3,313–4,294	4,679–5,013	4,690–5,787		6,090–6,561		2,350–2,870	Coan et al. 2000; Kamenev 2015, 2018c, 2019
	Dacrydium vitreum (Møller, 1842)	40–3,347		500–3,170						depth not specified	Scarlato 1981; Coan et al. 2000; Kamenev 2013

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
Arcidae Lamarck, 1809	*Bathyarca imitata* (Smith, 1885)		3,206-3,307			4,861-5,497				1,463-4,000	Coan et al. 2000; Coan and Valentich-Scott 2012; Kamenev 2015, 2018c, 2019
	Bentharca asperula (Dall, 1881					4,861-5,223				3,100-4,900	Coan et al, 2000; Coan and Valentich-Scott 2012; Kamenev 2007, 2015
Pectinidae Rafinesque, 1815	*Delectopecten vancouverensis* (Whiteaves, 1893)	730-3,435								27-4,100	Scarlato 1981; Coan et al. 2000; Coan and Valentich-Scott 2012; Kamenev 2013
	Hyalopecten abyssalis Kamenev, 2018					4,550-5,020					Kamenev 2018a
	Hyalopecten kurilensis Kamenev, 2018					4,995-5,045					Kamenev 2018a
	Hyalopecten vityazi Kamenev, 2018							6,090-8,100	6,410-7,246		Kamenev 2018a, 2019
Propeamussiidae Abbott, 1954	*Catillopecten brandtae* Kamenev, 2018					4,860-5,423					Kamenev 2015, 2018b
	Catillopecten malyutinae Kamenev, 2018					4,988-5,418		6,090-6,135		4,081	Kamenev 2015, 2018b, 2019
	Catillopecten natalyae Kamenev, 2018				3,342-3,432	5,112-5,497					Kamenev 2015, 2018b, 2019

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Catillopecten squamiformis (Bernard, 1978)		2,901-3,366	3,957-4,382	3,342-4,990	4,391-4,990				2,000-5,020	Coan et al. 2000; Kamenev 2015, 2018b, 2019
	Parvamussium pacificum Kamenev, 2018					4,860-5,497				5,180	Kamenev 2015, 2018b, 2019; P. Valentich-Scott, personal communication
Limidae Rafinesque, 1815	*Limatula* sp. 1				5,220-5,572	4,861-5,497					Kamenev 2015, 2019
	Limatula sp. 2					4,997-5,406					Kamenev 2015
Thyasiridae Dall, 1900	*Adontorhina cyclia* S.S. Berry, 1947		308-3,366		3,342-3,432					12-3,000	Kamenev 1995, 1996, 2013, 2018c; Coan et al. 2000; Coan and Valentich-Scott 2012
	Adontorhina sp. 1				4,679-5,013						Kamenev 2018c
	Axinodon sp. 2		1,694-3,366		4,679-5,013						Kamenev 2018c
	Axinopsida subquadrata (A. Adams, 1862)	5-2,550									Scarlato 1981; Kamenev 2013
	Axinulus sp. 1		3,342-3,432			4,861-5,787					Kamenev 2015, 2018c
	Axinulus sp. 2							9,301-9,583			Kamenev 2019
	Axinulus sp. 3				5,220-5,572			6,047-6,221			Kamenev 2019
	Axinulus sp. 4								6,460-7,285		Belyaev 1989

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Axinulus hadalis (Okutani, Fujikura and Kojima, 1999)						6,326-7,434				Okutani et al. 1999; Sasaki et al. 2005
	Channelaxinus excavata (Dall, 1901)		2,901-3,218	2,359						800-2,520	Kamenev 2018c; Coan et al. 2000; Coan and Valentich-Scott 2012
	"*Genaxinus*" sp. 1				5,220-5,572	5,101-5,752		6,047-9,583			Kamenev 2019
	"*Genaxinus*" sp. 2				5,220-5,572	5,726-5,752		6,441-7,256			Kamenev 2019
	Mendicula sp. 1		1,694-3,366		3,342-5,572	4,861-5,787		6,047-7,256			Kamenev 2015, 2018c, 2019
	Mendicula sp. 2		2,327-3,366		3,342-5,572	4,997-5,752		6,047-6,221			Kamenev 2015, 2018c, 2019
	Mendicula sp. 3		1,694-3,366		3,342-3,432						Kamenev 2018c
	Parathyasira sp. 1		3,206-3,366		3,342-5,013	4,977-5,406					Kamenev 2015, 2018c
	Parathyasira sp. 2				4,679-5,013	5,217-5,406					Kamenev 2015, 2018c
	Parathyasira sp. 3							6,047-6,561			Kamenev 2019
	Thyasira kaireiae (Okutani, Fujikura and Kojima, 1999)						5,791-6,390				Okutani et al. 1999; Sasaki et al. 2005
	Thyasira sp. 1					4,861-5,787					Kamenev 2015

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Thyasira sp. 2	900-3,102									Kamenev 2013
	Thyasiridae gen. sp.							7,055-8,740			Kamenev 2019
Tellinidae Blainville, 1814	*Macoma shiashkotanika* (Scarlato, 1981)				465-4,984						Kamenev and Nadtochy 1999; Kamenev 2018c
Montacutidae Clark, 1855	Montacutidae gen. sp.					5,101-5,497		6,441-6,561			Kamenev 2015, 2019
	Mysella sp.		1,694-3,351								Kamenev 2018c
	Syssitomya cf. *pourtalesiana* Oliver, 2012					5,347-5,427					Kamenev 2015
Vesicomyidae Dall and Simpson, 1901	*Abyssogena phaseoliformis* (Métivier, Okutani & Ohta, 1986)						5,400-6,400	4,700-6,200	4,550-6,400	4,190-4,982	Métivier et al. 1986; Fujikura et al. 2002; Kojima et al. 2004; Sasaki 2005; Okutani et al. 2009; Krylova et al. 2010
	Calyptogena extenta (Krylova & Moskalev, 1996)							3,512		3,000-4,445	Okutani et al. 2009; Coan and Valentich-Scott 2012
	Calyptogena sp.				4,819						Okutani et al. 2009
	Ectenagena laubieri kurilensis (Okutani & Kato, 2009)				3,512-3,560						Okutani et al. 2009

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Isorropodon fossajaponicum (Okutani, Fujikura and Kojima, 2000)						6,248-6,809				Okutani et al. 2000; Fujikara et al. 2002; Sasaki et al. 2005
	"*Vesicomya*" *filatovae* Krylova and Kamenev, 2015					4,861-5,497					Kamenev 2015, 2019; Krylova et al. 2015
	Vesicomya pacifica (Smith, 1885)		3,299-3,366	3,957-3,978	3,342-5,572	4,861-5,787				1,200-6,200	Coan et al. 2000; Coan and Valentich-Scott 2012; Kamenev 2015, 2018c, 2019; Krylova et al. 2015, 2018
	Vesicomya profundi Filatova, 1971							6,047-9,050	7,246		Filatov, 1971; Belyaev 1989; Krylova et al. 2015, 2018; Kamenev 2019
	Vesicomya sergeevi Filatova, 1971							6,090-9,530			Filatova 1971; Belyaev 1989; Krylova et al. 2015, 2018; Kamenev 2019
Xylophagidae Purchon, 1941	*Xylophaga* sp. 1					5,216-5,223					Kamenev 2015
	Xylophaga sp. 2					5,347-5,379					Kamenev 2015
	Xylophaga sp. 3					5,217-5,243					Kamenev 2015
	Xylophaga sp. 4					5,217-5,243					Kamenev 2015

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Xylophaga sp. 5					5,347–5,352					Kamenev 2015
Protocuspidariidae Scarlato and Starobogatov, 1983	*Protocuspidaria* sp.					5,236–5,406					Kamenev 2015
Cuspidariidae Dall, 1886	*Bathyneaera hadalis* (Knudsen, 1970)			3,957–3,978		4,418–5,752		6,047–8,740			Krylova 1993, 1997; Kamenev 2015, 2019
	Cardiomya behringensis (Leche, 1883)	31–2,900									Scarlato 1981; Kamenev 2013
	Cardiomya filatovae Scarlato, 1972		3,299–3,366	3,260–3,875	3,880–3,900						Scarlato 1972, 1981; Krylova 1997; Kamenev 2018c
	Cardiomya sp. 1				3,342–3,432						Kamenev 2018c
	Cardiomya sp. 2		3,351–3,353								Kamenev 2018c
	Cuspidaria cf. *abyssopacifica* Okutani, 1975		3,299–3,353		3,342–3,432						Kamenev 2018c
	Cuspidaria cf. *arcoida* (Okutani and Kawamura, 2002)					5,112–5,130					Kamenev 2015
	Cuspidaria buccina Bernard, 1989					5,112–5,130				3,585	Coan et al., 2000; Kamenev 2015
	Cuspidaria sp. 1					5,101–5,497					Kamenev 2019
	Cuspidaria sp. 2		3,206–3,307								Kamenev 2018c

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Cuspidaria sp. 3		3,305-3,366								Kamenev 2018c
	Cuspidaria sp. 4				2,430-2,670						Krylova 1997
	Cuspidaria sp. 5			3,875							Krylova 1997; Coan et al. 2000;
	Myonera garretti Dall, 1908		3,299-3,366	3,260-4,294						1,645-4,294	Krylova 1997; Coan et al. 2000; Coan and Valentich-Scott 2012; Kamenev 2018c
	Myonera paucistriata Dall, 1886					4,550-5,427				1,000-3,806	Krylova 1997; Coan et al. 2000; Kamenev 2015
	Octoporia sp.					5,379-5,427					Kamenev 2015
	Rengea murrayi (Smith, 1885)					4,861-5,427					Kamenev 2015
	Rhinoclama filatovae (Bernard, 1979)					4,550-5,497				3,315-5,140	Krylova 1997; Coan et al. 2000; Kamenev 2015, 2019
Poromyidae Dall, 1886	*Cetoconcha* sp.				3,342-3,432	5,236-5,379					Kamenev 2015, 2018c
	Poromya sp.					5,347-5,352					Kamenev 2015
Lyonsiellidae Dall, 1895	*Dallicordia* cf. *alaskana* (Dall, 1895)					5,347-5,352				450-3,570	Coan et al. 2000; Coan and Valentich-Scott 2012
	Policordia extenta Ivanova, 1977							8,185-8,400			Ivanova 1977; Belyaev 1989; Kamenev 2019

Family	Species	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northern-most part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench	Eastern Pacific	References
	Policordia laevigata Ivanova, 1977							8,185–8,740			Ivanova 1977; Belyaev 1989; Kamenev 2019
	Policordia maculata Ivanova, 1977							9,000–9,050			Ivanova 1977; Belyaev 1989; Kamenev 2019
	Policordia ovata Ivanova, 1977								5,740	6,040	Ivanova 1977
	Policordia rectangulata Ivanova, 1977							8,175–9,583			Ivanova 1977; Belyaev 1989; Kamenev 2019
	Policordia sp. 1		3,206–3,366								Kamenev 2018c
	Policordia sp. 2							6,047–6,221			Kamenev 2019

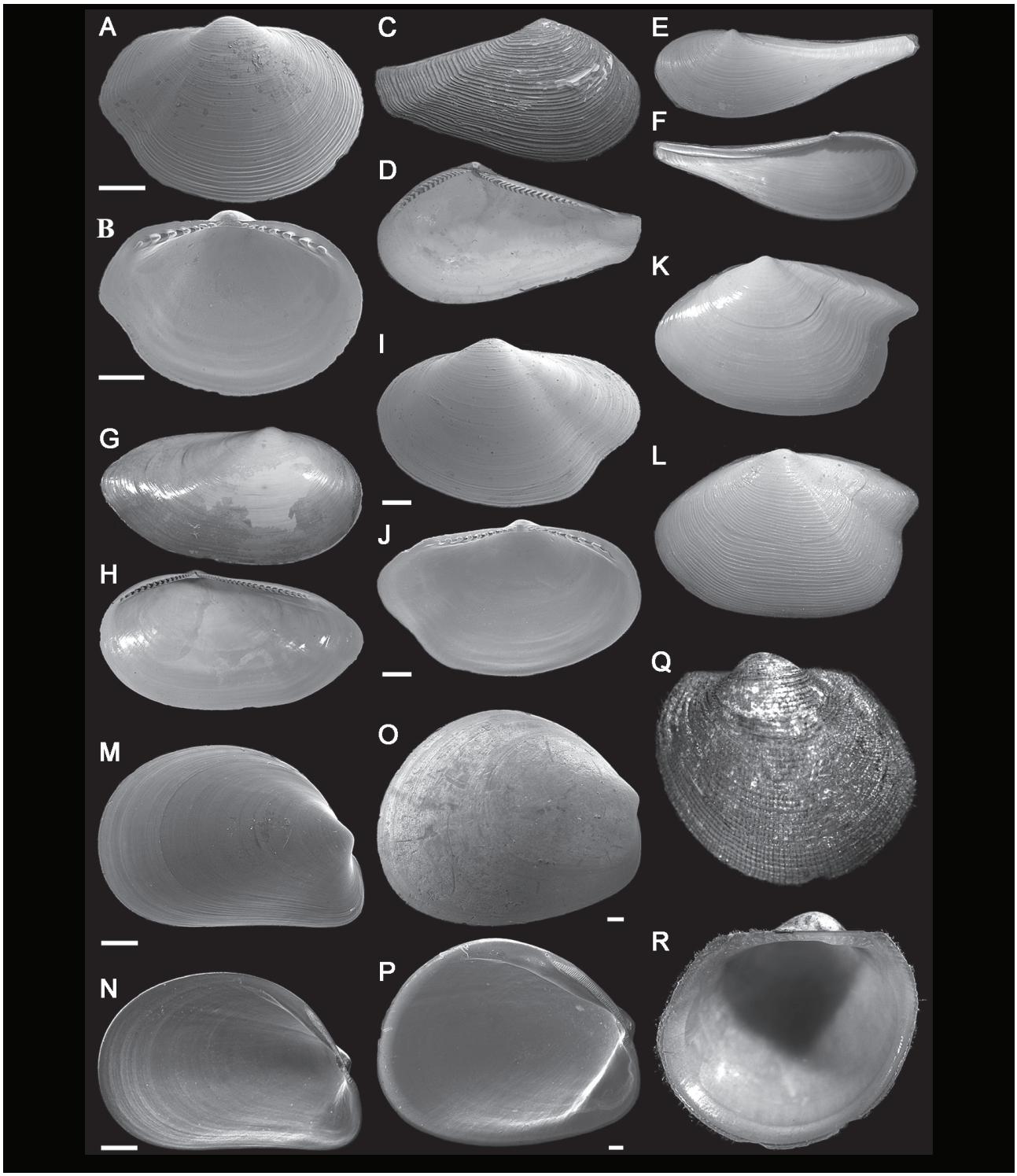


Figure 1. Widely distributed deep-sea bivalve species of the North Pacific: (A–B) *Ledellina convexirostrata*, Kuril-Kamchatka Trench, 6,551–6,560 m; (C–D) *Nuculana leonina*, Bering Sea, 2,622–3,034 m, 23.6 mm shell length; (E–F) *Poroleda extenuata*, Kuril Islands, Pacific Ocean, 3,342–3,432 m, 24.0 mm shell length; (G–H) *Katadesmia vincula*, Sea of Okhotsk, 3,351–3,353 m, 14.9 mm shell length; (I–J) *Parayoldiella ultraabyssalis*, Kuril-Kamchatka Trench, 9,294–9,431 m; (K) *Bathyspinula calcarella*, abyssal plain adjacent to Kuril-Kamchatka Trench, Pacific Ocean, 5,417–5,422 m, 15.4 mm shell length; (L) *Bathyspinula vityazi*, Kuril-Kamchatka Trench, 7,955–8,015 m, 15.0 mm shell length; (M–N) *Dacrydium rostriferum*, abyssal plain adjacent to Kuril-Kamchatka Trench, Pacific Ocean, 5,290–5,427 m; (O–P) *Dacrydium vitreum*, Sea of Japan, 970–1,075 m; (Q–R) *Bathyarca imitata*, Sea of Okhotsk, 3,305–3,307 m, 6.8 mm shell length. Scale bars: (A–B, I–J, M–N) = 500 μm; (O–P) = 200 μm.

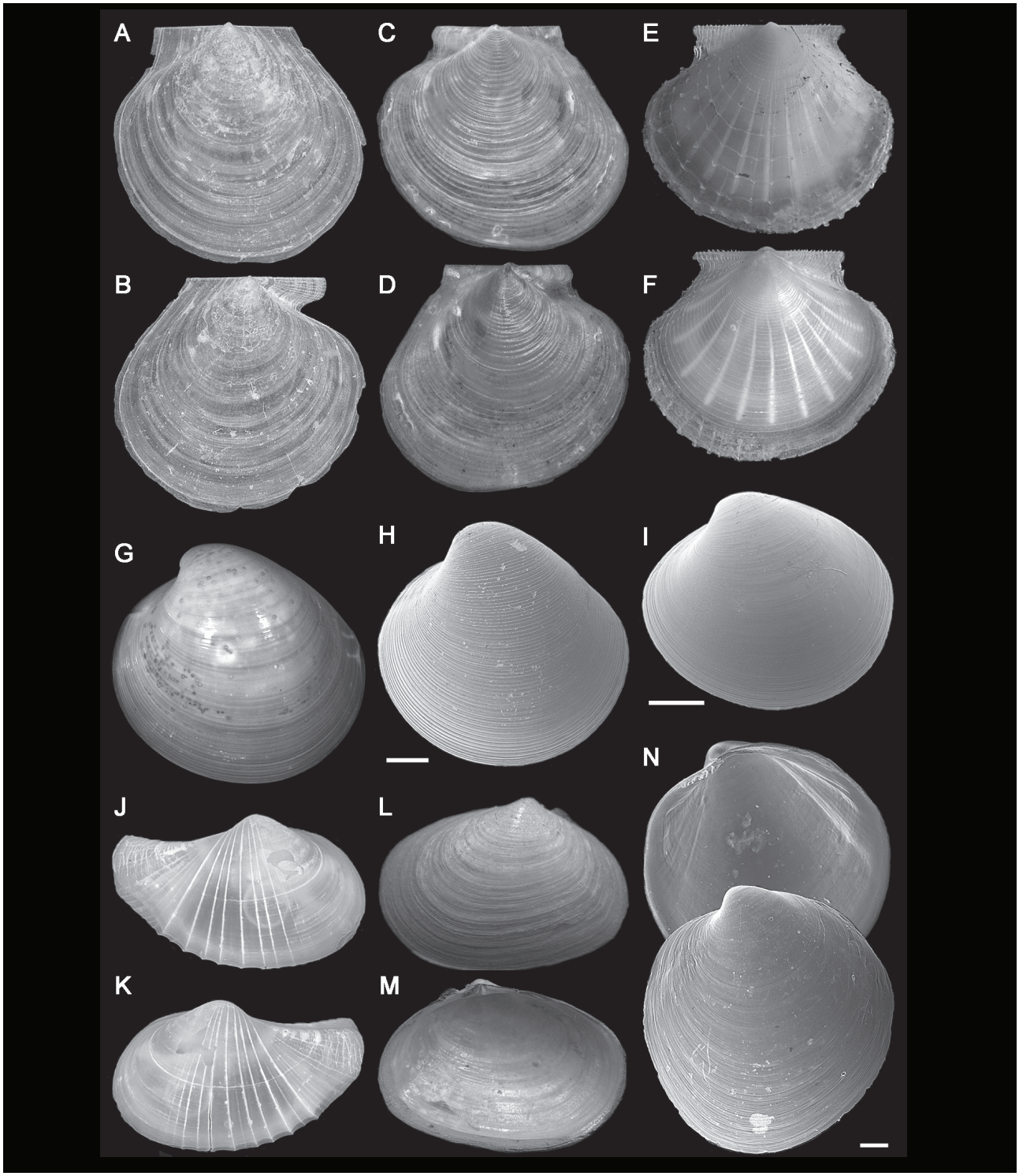


Figure 2. Widely distributed deep-sea bivalve species of the North Pacific: (A–B) *Delectopecten vancouverensis*, Sea of Japan, 2,700–3,100 m, 15.7 mm shell length; (C–D) *Catillopecten squamiformis*, Bering Sea, 3,957–3,978 m, 10.1.mm shell length; (E–F) *Parvamussium pacificum*, abyssal plain adjacent to Kuril-Kamchatka Trench, Pacific Ocean, 5,398–5,389 m, 8.5 mm shell length; (G) *Vesicomya pacifica*, Sea of Okhotsk, 3,351–3,353 m, 5.2 mm shell length; (H) *Vesicomya profundi*, Kuril-Kamchatka Trench, 8,240–8,345 m; (I) *Vesicomya sergeevi*, Kuril-Kamchatka Trench, 9,170–9,335 m; (J–K) *Bathyneaera hadalis*, Kuril-Kamchatka Trench, 8,740–8,735 m, 10.0 mm shell length; (L–M) *Macoma shiashkotanika*, Bering Island, Commander Islands, Bering Sea, 1,490 m, 9.3 mm shell length; (N) *Adontorhina cyclia,* Sea of Japan, 970–1,075 m, Scale bars: (H) = 500 μm; (I) = 1 mm; (N) = 200 μm.

and 2). About one third of them (39 species, 31.7%) belong to the subclass Protobranchia. Out of the 123 species, 68 species (55.3%) were identified to the species level. Other 55 species (44.7%) need additional research, and very probably, most of them are new to science. The richest families in terms of number of species were the Thyasiridae (22 species) and Cuspidaridae (18 species). Other families were represented by no more than nine species, and four families (Nuculidae, Malletidae, Tellinidae, and Protocuspidariidae) were represented by merely one species. The abyssal plain adjacent to the Kuril-Kamchatka and Aleutian trenches had the greatest number of species (60) among all the deep NW Pacific areas studied (Table 2). In deep-sea basins of the Sea of Japan, Sea of Okhotsk, and Bering Sea, the richest bivalve fauna was recorded for the Kuril Basin in the Sea of Okhotsk. The smallest number of species (8) at depths of more than 2,000 m was found in the Sea of Japan. Almost four times more species were found in the hadal zone (at depths greater than 6,000 m) of the Kuril-Kamchatka Trench than in the hadal zone of the Aleutian Trench. At the present time, the bivalve fauna of the Kuril-Kamchatka Trench is the richest, after the bivalve fauna of the abyssal plain, in number of species among the deep NW Pacific areas compared.

4.2. Geographic distribution of species

On the whole, almost half of the 68 identified species (29 species, 42.6%) are widespread in the northern Pacific and were recorded in the eastern Pacific off the coasts of America. In its turn, out of the remaining 39 species, most species (23) are widespread in the NW Pacific. These species were found in the shelf, bathyal, and abyssal zones of the NW Pacific marginal seas or in different areas of the vast abyssal plain adjacent to the Kuril-Kamchatka and Aleutian trenches. Likewise, a considerable part of hadal species was found in more than one trench of the NW Pacific. It should be noted that a significant part of morphospecies is also widespread in this Pacific region. Now, merely 15 identified species were recorded only in one of the deep NW Pacific areas compared and can be considered endemic to the areas. Almost all species are fairly widespread in their areas and some of them form extensive populations and occur in large numbers. Thus, *Robaia robai* (Kuroda, 1929) and *Yoldiella orbicularis* Scarlato, 1981 are widespread only in the Sea of Japan, while *Parayoldiella ultraabyssalis* (Filatova, 1971), *Vesicomya sergeevi* Filatova, 1971,

Table 2. The number of bivalve families, genera, and species recorded at depths greater than 2,000 m in different deep-sea areas of the NW Pacific (north of 40°N).

Taxon	Sea of Japan	Sea of Okhotsk	Bering Sea	Oceanic slopes of the Kuril, Commander, and Aleutian islands	Oceanic plain	Northernmost part of the Japan Trench	Kuril-Kamchatka Trench	Western part of the Aleutian Trench
Family	6	12	9	15	22	6	15	8
Genus	7	21	13	24	37	8	22	9
Species	8	26	14	34	60	8	35	10

Policordia laevigata Ivanova, 1977, and *Policordia rectangulata* Ivanova, 1977 occur widely in the hadal zone of the Kuril-Kamchatka Trench, where *P. ultraabyssalis* and *V. sergeevi* are the dominant species of macrobenthos on the lower slopes and bottom of the trench, forming very abundant populations. Out of all identified species, only four (*Yoldiella olutoriensis* Scarlato, 1981, *Policordia extenta* Ivanova, 1977, *Policordia maculata* Ivanova, 1977, and *Hyalopecten kurilensis* Kamenev, 2018) were described from specimens found only in one sample. This, in part, may be due to that the deep-sea area of finding of species is poorly studied. For example, *Y. olutoriensis* was found in a very poorly studied deep-sea basin of the Bering Sea. It is also possible that the species are in the category of rare species and may be found in other Pacific regions after more intensive studies in the NW Pacific. For example, *H. kurilensis* was so far found only in one sample collected from the abyssal plain adjacent to the Kuril-Kamchatka Trench.

4.3. Vertical distribution of species

The analyzed deep NW Pacific areas included partially or fully three vertical zones of the World Ocean: the lower bathyal zone (2,000-2,999 m); the abyssal zone (3,000-5,999 m); almost the entire hadal zone (6,000-9,600 m). Analysis of the bivalve species richness within 1,000 m depth ranges showed that the number of species and, correspondingly, genera and families markedly increases with increasing depth from 2,000 to 5,999 m (Table 3). The greatest number of species (60) was found in the lower abyssal zone at depths of 5,000-5,999 m, on the oceanic plain adjacent to the trenches. At depths of more than 6,000 m, in the hadal zone of the trenches, the bivalve species richness sharply decreases with depth, reaching the minimum (8 species) at the maximum depth (more than 9,000 m). In the hadal zone of the NW Pacific region studied, the highest number of species (38 species) was found in its uppermost depth range (6,000-6,999 m). The proportion of members of the subclass Protobranchia in the bivalve fauna of the hadal zone increases to 39.5%, compared to the species-richest abyssal depth range of 5,000-5,999 m where it is 30%.

A small portion of all deep-sea species of the NW Pacific (28 species, 22.8%) were not encountered at depths greater than 4,000 m and occurred in the subtidal, bathyal, and upper abyssal zones.

Table 3. The vertical distribution of the number of bivalve families, genera, and species recorded at depths of more than 3,000 m in the NW Pacific (north of 40°N).

Taxon	Depth range (m)							
	2,000-2,999	3,000-3,999	4,000-4,999	5,000-5,999	6,000-6,999	7,000-7,999	8,000-8,999	9,000+
Family	12	16	18	22	15	10	8	5
Genus	20	30	33	41	21	13	9	6
Species	24	41	47	60	38	18	13	8

Most of these relatively shallow-water species were recorded in deep-sea basins of the NW Pacific marginal seas. Only a small portion of these species was found on the oceanic slopes of the Japanese, Kuril, and Aleutian Islands and eastern Kamchatka Peninsula. Most species (69 species, 56.1%) were only recorded at depths of more than 4,000 m in the lower abyssal zone and in the hadal zone. About one third of them (22 species, 31.9%) were exclusively found in the hadal zone of the Japan, Kuril-Kamchatka, and Aleutian trenches at depths of more than 6,000 m. Hence, at the present time, they can be considered endemic to this zone.

For most of deep-sea bivalve species found in the studied NW Pacific region, the vertical distribution range does not exceed 3,000 m. Only 17 species (13.8%) were found in the depth range greater than 3,000 m. For 10 out of the 17 species (*Katadesmia vincula* (Dall, 1908), *Silicula beringiana* Kamenev, 2014, *Dacrydium rostriferum* Bernard, 1978, *Delectopecten vancouverensis* (Whiteaves, 1893), "*Genaxinus*" sp. 1, *Macoma shiashkotanika* (Scarlato, 1981), *Vesicomya pacifica* (Smith 1885), *Bathyneaera hadalis* (Knudsen, 1970), *Myonera paucistriata* Dall, 1886, *Dallicordia alaskana* (Dall 1895)), the vertical distribution range exceeds 4,000 m. All the species are widespread in the northern Pacific, except *Silicula beringiana* Kamenev, 2014, which was predominantly recorded in the Bering Sea.

5. Discussion

The first surveys of the species richness of the deep-sea bivalve fauna of the World Ocean (Clarke 1962; Knudsen 1970), as well as the Pacific (Filatova 1968) listed only 6 species for the NW Pacific north of the 40°N latitude at depths of more than 2,000 m. This is not surprising because these studies reported results obtained from the very first deep-sea expeditions, and a significant portion of bivalve materials collected north of 40°N by mainly Russian researchers was to be examined (Filatova 1968). Subsequent analogous reviews of the deep-sea bivalve species composition of the NW Pacific south of 40°N, already listed no less than 50 species found off Japan at depths below 2,000 m (Okutani 1974, 1975). In the following years, Russian and Japanese researchers described a large number of new species of bivalves found in the Sea of Japan, the Sea of Okhotsk, and the Bering Sea, as well as in the abyssal and hadal zones of the Pacific. As a result, the list of species inhabiting depths of more than 2,000 m to the north of 40°N was extended to 42 species (Filatova 1971, 1976; Scarlato 1972, 1981; Ivanova 1977; Filatova and Schileyko 1984, 1985; Belyaev 1989; Krylova 1993, 1997; Kamenev and Nadtochy 1999; Okutani et al. 1999, 2009; Okutani and Fujiwara 2005; Sasaki et al. 2005).

In recent years, examination of materials collected by Russian-German (2010 and 2015) and German-Russian (2012 and 2016) expeditions in the deep-sea basins of the Sea of Japan and the Sea of Okhotsk, as well as on the abyssal plain adjacent to the Kuril-Kamchatka Trench and in the hadal zone of the trench down to its maximum depth made a significant contribution deep-sea bivalve fauna research (Kamenev 2013, 2014, 2015, 2018a, b, c, 2019; Krylova et al. 2015). Thus, all these studies in the NW Pacific north of the 40°N latitude revealed a very rich and diverse deep-sea bivalve fauna (123 species). For comparison,

Knudsen (1970) listed 193 species belonging to 20 families for the deep-sea bivalve fauna of the whole World Ocean. Taking into account more recent data, Allen (2008) listed 14 living bivalve families present at the 5,000 m depth in the Atlantic, while in the studied Pacific region members of 22 bivalve families were recorded for the abyssal plain (5,000-6,000 m). As an example, we also note that in such a large region as Great Australian Bight (southern coast of Australia) merely 43 species of bivalves from 18 families were recorded at depths of 200 to 5,000 m (MacIntosh et al. 2018). In reality, the deep-sea bivalve fauna of the NW Pacific is even richer, and further research will significantly increase the number of species inhabiting depths below 2,000 m. To date, fairly well-studied bivalve faunas are those of the deep-sea basin of the Sea of Japan, the bottom of the Kuril Basin (depths of more than 3,000 m) of the Sea of Okhotsk, the oceanic abyssal plain near the Kuril-Kamchatka Trench, and the Kuril-Kamchatka Trench. So far, the rich faunas of the lower slopes of the Kuril Basin (2,000-3,000 m) in the Sea of Okhotsk, oceanic slopes (2,000-5,000 m) of the Kuril, Commander, Aleutian Islands, and eastern Kamchatka, deep-sea basins of the Bering Sea (2,000-4,000 m), and the hadal zone of the Aleutian Trench are still very poorly studied (Scarlato 1981; Kamenev 2018c). As an example, according to preliminary data, the deep-sea fauna of the Bering Sea harbors no less than 40 species (Kamenev, unpublished results), while only at two stations performed on the oceanic slope of the Kuril Islands 23 species of bivalves were found at depths of 3,000-5,000 m (Kamenev 2018c).

The high species richness and diversity of the deep-sea bivalve fauna of this northern Pacific region are probably due to the abundant organic matter fluxes to the bottom. Many researchers showed that one of the main factors limiting the diversity and abundance of deep-sea fauna is food availability to bottom animals (Rex et al. 2005; Rex and Etter 2010). The NW Pacific is one of the most productive regions of the World Ocean with high level of primary production in the marginal seas and around the Kuril-Kamchatka Trench (Sokolova 1976, 1981). Hence, organic matter abundantly supplied to the bottom creates favorable feeding conditions for the diverse and plentiful bottom fauna in the abyssal and hadal zones of this Pacific region (Filatova 1960, 1968; Belyaev and Mironov 1977; Belyaev 1989).

The deep-sea fauna of the Sea of Japan is the poorest (in number of species) among all deep NW Pacific areas. Only three species were recorded at maximum depths (more than 3,000 m) of that sea. No characteristic species of the Pacific abyssal zone were found in the deep-sea basins of the Sea of Japan. The deep-water bivalve fauna of the Sea of Japan is an impoverished shelf fauna comprised of eurybathic species that extend from the shelf to the bathyal and abyssal zones. Most of them have a wide geographic distribution. The lack of typical abyssal species of bivalves in the deep Sea of Japan is probably connected with the isolation of this body of water from the Pacific abyssal depths (Kamenev 2013).

In the Sea of Okhotsk, only the fauna of the bottom of the Kuril Basin at depths below 3,000 m was studied in detail (Kamenev 2018c). In contrast to the Sea of Japan, in the abyssal zone of the Sea of Okhotsk there is a species-rich fauna of bivalves with many Pacific eurybathic

bathyal-abyssal species, which could penetrate into the Sea of Okhotsk through deep-sea straits between the Kuril Islands.

The greatest number of species was recorded for the abyssal plan adjacent to the trenches. Most species were found in this region during the KuramBio German-Russian expedition (2012). This expedition sampled many small species with a fragile shell which were difficult to collect in previous expeditions using such sampling gear as trawls and dredges. Knudsen (1970) noted that "there is little doubt; however, that the abyssal zone harbors numerous minute species which, owing to too crude sampling methods, have remained unknown". The finding of these minute species much increased the bivalve species richness of this region (Kamenev 2015). A rich, in number of species, fauna was also recorded for the Kuril-Kamchatka Trench. The bottom fauna of this trench is the best studied as a result of numerous expeditions of Russian researchers (Belyaev 1989). Nevertheless, using modern sampling methods and gear, studies of the KuramBio II German-Russian expedition (2016) significantly increased data on the bivalve species richness of this trench owing to the finding of minute species (Kamenev 2019).

The relatively low species richness of the deep-sea bivalve fauna of the Bering Sea, oceanic slopes of the Kuril, Commander and Aleutian Islands, and the eastern coast of Kamchatka, as well as the Aleutian Trench, are exclusively connected with insufficient study of these deep-sea regions. Overall, about half of species comprising the deep-sea fauna of this NW Pacific region were not determined to the species level. Many of the species will probably be described as new to science and the systematic position of many will be ascertained as a result of further research.

Allen (2008) noted that in the abyssal zone there is a large increase in the number of deposit feeding species to which protobranchs belong. In the Atlantic Ocean, at depths greater than 4,500 m, the proportion of protobranch species is 57.3%. In the studied sector of the NW Pacific, at similar abyssal depths (5,000-5,999 m), the proportion of protobranch species is almost two times lower (30%) than in the Atlantic and increases to 39.5% in the hadal zone at depths of more than 6,000 m. The relatively low share of protobranch species in the abyssal and hadal zones of this region is probably connected with recent records of many species of the Pectinidae, Propeamussidae, Thyasiridae, Vesicomyidae, Cuspidariidae, and Lyonsiellidae. More than half of deep-sea species (64 species, 52%) of this NW Pacific region belong to these families. The richest, in number of species, families were the Cuspidariidae and Thyasiridae, with thyasirids being the least studied (77.3% of the total number of species of this family were not identified to species level). Previously, this family was only represented by a few species in the NW Pacific deep-sea fauna (Scarlato 1981; Belyaev 1989; Sasaki et al. 2005). Only recent studies using epibenthic sledge have allowed collecting a large number of minute thyasirids having a very fragile shell, which is easily destroyed by sampling with trawls and dredges (Kamenev 2015, 2018c, 2019). In the Atlantic Ocean, this family is also the richest in number of deep-sea species, of which a great many remain to be described (Allen 2008). An important contribution to the knowledge of the

species richness of the family Vesicomyidae was made by Japanese researchers who found many specialized species in chemosynthesis-based biological communities in this region (Sasaki et al. 2005).

With increase in depth, the number of species increases, reaching the maximum at 5,000-5,999 m depth. Such a change in the bivalve species richness in the depth range of 2,000-5,999 m primarily reflects the level of knowledge of faunas of different deep-sea regions of the NW Pacific. The least studied regions such as the slopes of the Kuril Basin, oceanic slopes of the Kuril, Commander and Aleutian Islands, and Kamchatka, as well as the deep-sea basins of the Bering Sea have depths of 2,000 to 5,000 m. Preliminary researches revealed a very rich bivalve fauna in these vast regions (Kamenev 2018c; unpublished results). Thorough studies of these deep NW Pacific regions will increase the number of bivalve species and, correspondingly, change the picture of the vertical distribution of species in the whole region. At the 5,000-5,999 m depth, there is a relatively well-studied vast area of the oceanic abyssal plain near the trenches. Therefore, to date the richest bivalve fauna is known at these depths. Many researchers have also shown that the ecosystem of the abyssal plain of the World Ocean is one of the richest and diverse on the planet (Etter and Mullineaux 2001; Snelgrove and Smith 2002; Stuart et al. 2003). It is very likely that this vast plain is the species-richest among all deep NW Pacific regions to the north of 40°N. Depths of greater than 6,000 m correspond to the hadal zone of oceanic trenches, in which the bottom fauna becomes much impoverished with increasing depth (Belyaev 1989; Jamiesson 2015). Future detailed studies of the bottom fauna of the Aleutian Trench will probably change the species ratio within different depth ranges of the hadal zone of the region of the NW Pacific but will not influence the general pattern of vertical distribution of species at depths below 6,000 m.

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CHAPTER 9

SIPUNCULA

A REVIEW ON BIOGEOGRAPHY OF THE DEEP-SEA SIPUNCULA ALONG THE NW PACIFIC

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1. Introduction

Sipunculans are a well-separated monophyletic group of marine coelomic worms with a small number of external characters (Cutler 1994; Rice 1993). These non-segmented worms have a sac-like trunk and a retractable introvert. Their taxonomic rank is still controversial, and recent phylogenomic analyses recognized Sipuncula as an early branch within the annelid radiation (Weigert et al. 2014, 2016).

From the other side, sipunculans occur widely along oceans, from polar to the tropical seas. Their bathymetric range is also extensive from the intertidal flats down to the abyssal depth. The world's deep-sea sipunculan fauna has been studied insufficiently. The most recent revision listed only 22 species of sipunculans from depths greater than 500 m (Saiz et al. 2018). This also largely applies to the NW Pacific (NWP) (Maiorova and Adrianov 2017). Most of the available collections, including those from the Kuril–Kamchatka Trench (KKT) area, were made by trawling during a series of expeditions on the renowned RV *Vityaz* in the 1950s–1960s (Murina 1957, 1958, 1961, 1964, 1971). Only five records of sipunculans had been sampled from depths exceeding 2,000 m before the RV *Vityaz* expeditions. Among these are *Nephasoma* (*Nephasoma*) *flagriferum* (Selenka 1885) was sampled by *Challenger* in 1875, two records were sampled by the *Siboga* Expedition in the Indo-Malayan Archipelago (Sluiter 1902) and the eurybathic N. (N.). *eremita* (Sars, 1851) was obtained by RV *Gagara* in the Bering Sea at the depth of 3,867 m (Makarov 1950).

Recently, more species were collected by several further expeditions, with the most extensive collections made during scientific cruises of several Russian and German research vessels in the NWP (Maiorova and Adrianov 2013, 2015, 2017, 2018). The greatest contribution to the description of museum material and the inventory of the NWP sipunculan fauna was made by V.V. Murina, who published a reasonably detailed key to sipunculans of the arctic and boreal waters of Eurasia (Murina 1977). All data on the world's sipunculan fauna available at that time were reviewed by Stephen and Edmonds (1972) who recognized 320 sipunculan species. Despite the efforts of researchers, detailed descriptions of live worms are absent because of the poor condition of the bottom-trawl material. Moreover, the degree of intactness and the quality of the preserved material do not allow genetic methods to be used for ascertaining the taxonomic status of some closely related species, which is important in the case of the variability of many morphological characters even within one species. Many revisions of the individual taxa of sipunculans undertaken in the 1980s have substantially hampered the use of the previously published taxonomic keys (Cutler and Cutler 1982, 1985, 1986; Cutler et al. 1983). In 1994, Cutler published a new overall review of this group and a new key to sipunculans of the world, in which he reduced many species, among them those described by Fisher, Murina and Sato from the North Pacific, to synonymy and the total number of species from 320 to roughly 150 (Cutler 1994). Unfortunately, this very valuable and important book lacks illustrations of most species, thus hindering its use as a field guide. Nevertheless, well-illustrated papers on the sipunculan fauna of some areas of the western Pacific

appeared later, which substantially helped the identification of common species of sipunculans (Adrianov and Maiorova 2010; Morozov and Adrianov 2002; Cutler 1994; Cutler et al. 2004; Maiorova and Adrianov 2013, 2015; Pagola-Carte and Saiz-Salinas 2000). In recent years, interest in the NWP sipunculan fauna has increased in connection with a series of deep-sea expeditions that have been conducted in this region using state-of-the-art technology for the collection of biological material, including underwater robotic vehicles (Adrianov et al. 2013, 2016). These investigations showed that even at relatively low species richness, the sipunculans are an abundant group of deep-sea benthos in all seas of the Russian Far East, including abyssal and ultra-abyssal depths (Maiorova and Adrianov 2013, 2015, 2018). Analysis of previously published, museum and our own material from deep-water samples showed that 11 valid species of sipunculans are reliable records from depths below 2,000 m in the NWP. Some species were also known from less deep waters of the Pacific Ocean.

Several species have only been reported from their type localities. Some of these have been synonymized with other, more widespread, species or are now regarded *Incertae sedis* or *species inquirenda* (Cutler 1994). The majority of sipunculan species have large reported distribution ranges. This view of generally wide geographic distributions is supported by the presence of free-swimming and long-lived planktotrophic larvae able to travel huge distances via oceanic currents and could have allowed some sipunculan species to colonize the entire depth range from the intertidal zone to the abyssal plains and deep-sea trenches (Hall and Scheltema 1975). Recently, molecular data has challenged the notion of widely distributed sipunculan species by revealing significant genetic differences among geographically separated populations, leading to the detection of "cryptic" (i.e., morphologically unrecognizable but genetically distinct) or "pseudo-cryptic" (i.e., morphologically and genetically distinct but lumped together in the taxonomic literature) species (Schulze et al. 2019). These include *Apionsoma misakianum* Ikeda, 1904 (see Staton and Rice 1999), *Sipunculus nudus* Linnaeus, 1766 (see Kawauchi and Giribet 2014), *Phascolosoma perlucens* Baird, 1868 (see Kawauchi and Giribet 2010), *Phascolosoma agassizii* Keferstein, 1866 (see Schulze *et al.* 2012, Johnson *et al.* 2016, Johnson and Schulze 2016), *Themiste pyroides* (Chamberlin, 1919) (see Schulze *et al.* 2012), and *Thysanocarida nigra* (Ikeda, 1904) (see Schulze *et al.* 2012). Species newly recognized on a molecular level are not formally described yet. The populations of previously largely synonymized sipunculans *G. (Golfingia). margaritacea* (Sars, 1851), *N. (N). minutum* (Keferstein, 1862) and *N. (N.) diaphanes* (Gerould 1913), as well as some others, can also be revised in future.

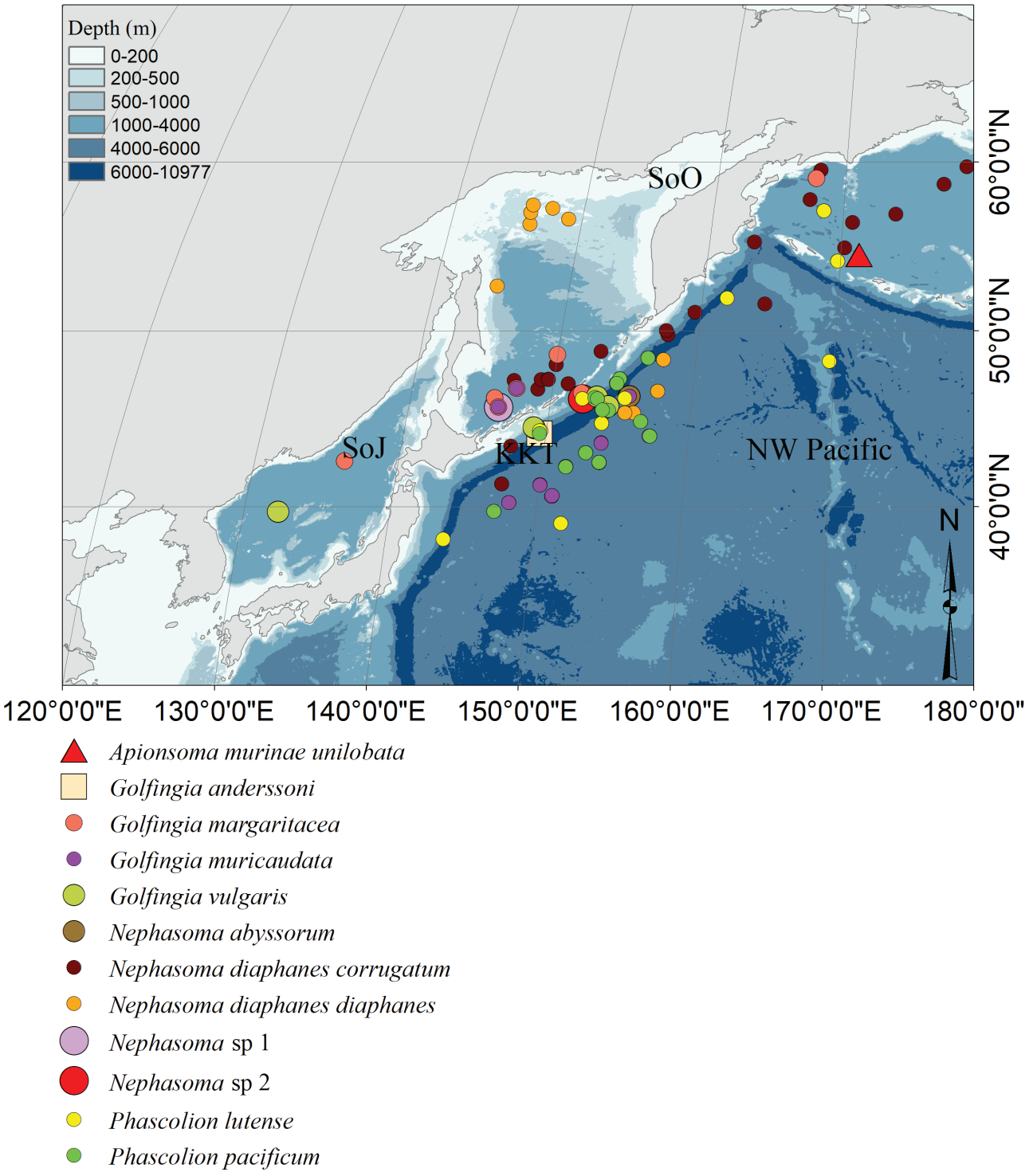
2. Objectives

In this chapter we are providing a review of the biogeography of the deep-sea Sipuncula of the NW Pacific Ocean (NWP).

3. Material and Methods

The data used herein represents a final compilation of all the works published previously

by Murina (1964, 1971, 1977) and Maiorova and Adrianov (2013, 2015, 2017, 2018) on the Sipuncula group. Distribution of all sipunculan species recorded in the NWP at a depth below 2,000 m from 40 to 60°N and between 120 and 180°E are displayed in Map 1.



Map 1. Distribution of deep-sea sipunculans in NWP.

4. Results

4.1. Family Golfingiidae Stephen & Edmonds, 1972

Genus *Golfingia* Lankester, 1885

***Golfingia (Golfingia) anderssoni* (Théel, 1911)**
(Figure 1 A)

Diagnosis. Medium sized sipunculans (trunk no longer than 85 mm). Only juveniles may have hooks on introvert. Tentacular crown around mouth with an array of digitiform tentacles. External midregion of trunk wall smooth with minute papillae. Worms have a caudal appendage and distinctive wart-like papillae covering an area about 65-90% of the distance toward the posterior end of the trunk. In this they are strikingly similar to N. (N.) *flagriferum*. Nephridia opening anterior to the anus.

Biogeographical remarks. Most species of subgenus *Golfingia* inhabit cold waters at depths of 2-6,800 m. Exceptions are also known, so *G. (Spinata) pectinatoides* Cutler & Cutler, 1979 lives in tropical coral sands in the Indo-West Pacific (IWP). A similar habitat is occupied by *G. (G.) vulgaris herdmani* (Shipley, 1903) in shallow Indian Ocean waters and around Australia, as well as some populations of *G. (G.) elongata* (Keferstein, 1862) are recorded in intertidal warm-temperate waters. Two endemic species are scattered over the NW Atlantic (*G. (G.) iniqua* (Sluiter, 1912)) and South Africa (*G. (G.) capensis* (Teuscher, 1874)). Two species described by Murina based on single records come from East Africa (*G. (G.) mirabilis* Murina, 1969)) and the NW Pacific (*G. (G.) birsteini* Murina, 1973)) (Murina 1969, 1973).

The deep-water species, *G. (G.) anderssoni* commonly occur in the Atlantic and Pacific oceans. This species has been collected from almost all Antarctic waters except the Bellingshausen and Amundsen Seas and the distribution of the species is mainly restricted to the southern hemisphere at depths of 75-1,880 m (Cutler 1994; Saiz Salinas 1995). Although some other isolated records exist and in NWP, it is found in the Philippine Sea (3,150 m) and near KKT at depths of 5,739 and 6,135 m. This species belongs to the large sipunculan family Golfingiidae, which has many cold deep-water representatives in the world oceans (Murina 1975; Cutler 1994; Saiz Salinas 2014, 2018). Presence of a long caudal appendage may be a physiological pre-adaptation to the deep-water habitat.

***Golfingia (Golfingia) margaritacea* (Sars, 1851)**
(Figure 1 B)

Diagnosis. Medium sized smooth-skinned sipunculans, commonly 30-90 mm long, but may be up to 150 mm long. Small hooks have been seen only in a few small shallow-water individuals and juveniles. The number of unpigmented tentacles (15-30) varies with the size of the worm. The contractile vessel without swellings and branches, but may have villi in some shallow-water populations.

Biogeographical remarks. This very widely distributed species is found in the Atlantic, Arctic, Southern and Pacific oceans. The species is unknown from the Indian Ocean and Mediterranean Sea. In the Sea of Okhotsk, this species is the most abundant found and has a high biomass (Maiorova and Adrianov 2013). In the Sea of Japan, this species was previously known from the Tatar Strait and Sakhalin Island,

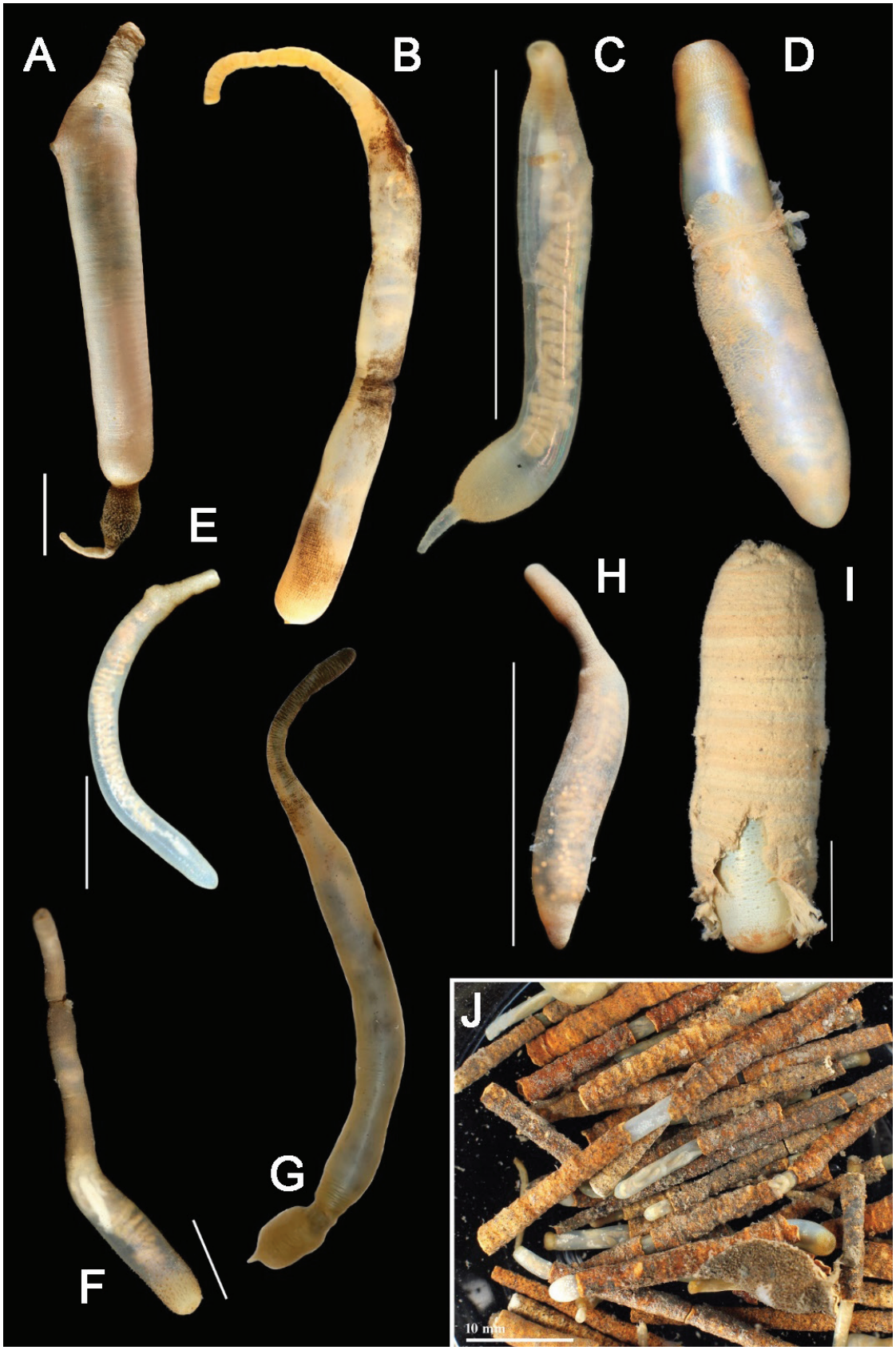


Figure 1. (A) *Golfingia anderssoni* Bar, 10 mm., (B) *Golfingia margaritacea margaritacea* Bar, 10 mm., (C) *Golfingia muricaudata* Bar, 10 mm., (D) *Nephasoma abyssorum abyssorum* Bar, 10 mm., (E) *Nephasoma diaphanes diaphanes* Bar, 10 mm., (F) *Nephasoma diaphanes corrugatum* Bar, 10 mm., (G) *Nephasoma* sp1 Bar, 10 mm., (H) *Nephasoma* sp2 Bar, 10 mm., (I) *Phascolion lutense* Bar, 10 mm, (J) *Phascolion pacificum* Bar, 10 mm.

north to Tsushima Strait in the south, alongside the Korean, Japanese and Russian coasta as well as in the middle part of the Sea of Japan. The depth range is 1–5,300 m, but most specimens have been collected from depths of less than 300 m (see Cutler 1994). Furthermore *G. (G.) margaritacea* has a confusing nomenclatural history after Cutler and Cutler (1987) synonymized several varieties, forms, or subspecies to only two subspecies. Now rather abundant populations of *G. (G.) margaritacea* across the world oceans, are representing a suitable material for exploring further the cosmopolitan concept on sipunculans.

***Golfingia (Golfingia) muricaudata* (Southern, 1913)**

(Figure 1 C)

Diagnosis. Small- to medium-sized elongated, cylindrical, with nipple-like tail, worms (up to 70 mm in length). Tentacular crown with an array of 8–10 short transparent non-pigmented tentacles, arranged in a single row around the mouth. Two reddish eyespots visible. Anterior introvert with highly packed large papillae. Small hooks (20 μm) observed only in juveniles. Papillae on trunk are randomly distributed, tail covered by minute tall papillae. The nerve cord ends anterior to the tail. Specimens from the Kuril Basin differ from specimens from the abyssal plain near the Kuril-Kamchatka Trench by the length of tail (8% vs 15%) (Maiorova and Adrianov 2015).

Biogeographical remarks. This mainly deep water species is found in the Atlantic, Indian and Pacific oceans. The depth range is 60–6,860 m, but most specimens have been collected from depths of more than 2,000 m (see Cutler 1994). In the North Pacific, it has been reported from British Columbia, around the Bering Sea, and from the Bering Sea to Japan (including the Kuril Basin of the Sea of Okhotsk) (Maiorova and Adrianov 2018). In the North Atlantic (near Ireland) and Southern Ocean (Bouvet Island), it occurs at depths of 150–1,081 m, while in the NW Pacific this species is noted at depths of 2,959–6,860 m (Murina 1964; Maiorova and Adrianov 2015).

***Golfingia (Golfingia) vulgaris vulgaris* (de Blainville, 1827)**

Diagnosis. Small- to medium-sized worms (very few exceed 30 mm in length). Tentacular crown around mouth with an array of digitiform tentacles, whose number and complexity increase with age within species of this genus. Hooks (up to 150 μm) irregularly arranged. Both ends of the trunk are distinct – dark brown or black and heavily papillated – while the mid-trunk is smooth and whitish. The nephridia open anterior to the anus. Although four retractors are the norm, worms with only three have been noted (Cutler et al. 1984 and own observation).

Biogeographical remarks. This aptly named cosmopolitan species is found in the NE Atlantic Ocean including Greenland, Scandinavia, and the British Isles, and into the Mediterranean, Adriatic, and Red seas; south to the Azores, Canary Islands, Cape Verde Islands, and West Africa; the Indian Ocean off South Africa and Zanzibar; the Pacific Ocean in the Kuril-Kamchatka Trench, Japan, Malaya, Singapore, and one record (Frank 1983) off British Columbia (the only one from the eastern Pacific). The depth range is 5-2,000 m, but specimens from depths greater than 500 m are rare (Cutler 1994). There is one very deep record: from 5,853 m in the KKT (Murina 1977).

Genus *Nephasoma* Pergament, 1940

***Nephasoma (Nephasoma) abyssorum abyssorum* (Koren and Danielssen, 1875)**

(Figure 1 D)

Diagnosis. Small- to medium-sized worms, with trunk 10–30 mm in length. Tentacular crown around mouth with one row of digitate tentacles. Dark hooks (50–150 μm) may be spirally arranged, or scattered at distal part of introvert. Two nephridia open at the level of the anus.

Biogeographical remarks. With nine species occurring at depths greater than 4,000 m and 21 at depths greater than 1,000 m, *Nephasoma* is clearly deep water genus. Of the six remaining intertidal and shelf species, three have been collected often (*N. (N.) minutum*, *N. (N.) rimicola* (Gibbs 1973), and *N. (N.) schuttei* (Augener, 1903)), with the remaining three only collected once. A few eurybathyal species fit both categories: *N. (Cutlerensis) rutilofuscum* (Fischer, 1916), 1–1,500 m; *N. pellucidum*, 1–1,600 m; *N. (N.) confusum* (Sluiter, 1902), 4–4,300 m; and *N. (N.) eremita* (Sars, 1851), 20–2,000 m (Cutler 1994).

The richest fauna of *Nephasoma* inhabit the Atlantic Ocean (16 species). Five species (*N. (N.) abyssorum abyssorum*, *N. (N.) capilleforme* (Murina, 1973), *N. (N.) diaphanes corrugatum* Cutler & Cutler, 1986, and *N. (N.) eremita*) live throughout the Atlantic and in the Pacific, and three (*N. (N.) confusum*, *N. (N.) diaphanes diaphanes* and *N. (N.) pellucidum pellucidum* (Keferstein 1865) are found in these two oceans plus the Indian Ocean (Murina 1977; Cutler 1994).

Of the 13 species living in the Pacific Ocean, two (*N. laetmophilum* (Fischer, 1952) *and N. vitjazi* (Murina 1964) are known only from the original descriptions (Fisher 1952; Murina 1964). Of the seven species that have been collected in the Indian Ocean, two (*N. filiforme* (Sluiter, 1902) and *N. tasmaniense* (Murina, 1964) are known only from the original descriptions (Sluiter 1902; Murina 1964). Ten *Nephasoma* species live in the Southern Ocean (Edmonds 1969; Saiz Salinas 1995, 2014; Cutler et al. 2001). The Arctic Ocean is only inhabited by five species of *Nephasoma*, but all are common in the North Atlantic and the North Pacific, and elsewhere as well (Pergament 1946; Murina 1977; Kędra and Murina 2007; Kędra and Włodarska-Kowalczuk 2008; Kędra et al. 2018).

The deep-water species *N. (N.) abyssorum abyssorum* is found in the NE Atlantic and Arctic oceans, and with single records in the SE and NW Atlantic. In the NW Pacific, and the Mediterranean Sea, it is found at bathyal to abyssal depths (500–5,300 m).

***Nephasoma (Nephasoma) diaphanes diaphanes* (Gerould, 1913)**

(Figure 1 E)

Diagnosis. Small-sized worms, with trunk 2–9 mm in length. Trunk whitish, opaque or golden brown, smooth, with hyaline cuticle and flattened papillae. Smooth thickened cuticular collar like pseudoshield encircle anterior trunk, and posterior pseudoshield surrounding posterior extremity of trunk. Tentacular crown composed of two primary tentacles and non-pigmented tentacular lobes around mouth present. Small scattered hooks (30–40 μm) on distal introvert. Cupola-shaped papillae located between hooks. Short nephridia open at anus level. This species often lives in foraminiferan

tests, small polychaete tubes, or scaphopod shells.

Distribution. Considered a cosmopolitan species in cold water, most often found at bathyal and abyssal depths (down to 6,860 m). In the NW Pacific the species occurs in the Kuril Basin and along the Pacific side of the Kuril Islands with high abundance at most localities.

Together with *G. (G.) margaritacea*, this species has a confusing taxonomic story after many species across the world ocean were transferred by Cutler and Cutler (1986) to *N. (N.) diaphanes*. Immature members of other species are easily mistaken for *N. (N.) diaphanes diaphenes*, so the literature has some unfortunate but unavoidable zoogeographical "noise".

***Nephasoma (Nephasoma) diaphanes corrugatum* (E. B. Cutler and N.J. Cutler, 1985)**
(Figure 1 F)

Diagnosis. Pear shaped to cylindrical; trunk usually 5–10 mm long (occasionally 20–30 mm). The skin is tan to grayish brown, translucent to opaque, with irregular, wavy, zigzag longitudinal epidermal ridges on the introvert base and the anterior part of the trunk. Often the papillae on the posterior end are darker than the surrounding skin. Hooks small (20–30 μm), scattered, pale, triangular hooks. The tentacular crown consists of six to eight short lobes plus two longer dorsal tentacles. This species often lives in foraminiferan tests, and small polychaete tubes.

Biogeographical remarks. Broad latitudinal range from the Atlantic and Pacific oceans, plus the Mediterranean and Red seas. Collected at depths ranging from 80 to 7,123 m, most occur >1,000 m. This species was found together with *N. (N.) d. diaphanes* along both slopes of the Kuril-Kamchatka Trench and adjacent abyssal (Maiorova and Adrianov 2015, 2015; Murina 1958).

***Nephasoma* sp1 in Maiorova and Adrianov, 2018**
(Figure 1 G)

Diagnosis. Medium-sized worms 80 mm in length. Tentacular crown is around mouth with 30 non-pigmented tentacles. Introvert behind tentacular apparatus is covered by irregular shaped oval papillae, hooks absent. Trunk whitish or yellowish, lustrous; flattened papillae randomly distributed; some areas covered with black particles. Nephridia open minute posterior to anus.

Biogeographical remarks. Known from a single locality in the Sea of Okhotsk at 3,200 m depth (site #11 of SokhoBio expedition).

***Nephasoma* sp2 in Maiorova and Adrianov, 2018**
(Figure 1 H)

Diagnosis. Small-sized worms, with pyriform trunk 9 mm in length. Trunk with irregular, zigzag, longitudinal epidermal ridges on introvert base, anterior and posterior parts of the trunk. Two tentacles and short nonpigmented tentacular lobes around mouth present. No hooks found behind tentacular apparatus, this area only covered with highly cuticularized tall papillae with radiating ridges in cortical layers of cuticle. Nephridia open minute anterior of anus level.

Biogeographical remarks. Known from single locality at the landward slope of KKT at 4,700 m depth.

Genus *Phascolion* Théel, 1875

Subgenus *Phascolion (Montuga)* Gibbs, 1985

Phascolion (Montuga) lutense Selenka, 1885

(Figure 1 I)

Diagnosis. Medium-sized worms (up 50 mm in length). Inhabitants tubes composed of sediment, mucous and own descended cuticle. Tentacular crown around mouth with only short non-pigmented folds (lobes). Hooks present in narrow zone behind the tentacles on distal part of introvert, but ill-defined in rough cuticle (50–70 μm in height). Dark cap on the front trunk end consists of densely arranged tall finger-shaped brownish papillae. The trunk is smooth with flat rounded or elliptical papillae without hardened edge randomly distributed around trunk (400 μm outer border, inner part 140 μm), but not holdfast papillae. Tall and brown papillae present at anterior and posterior ends of trunk. Body wall musculature continuous. Ventral nerve cord ends before posterior end (retractor roots origin) (3/4 of trunk length) separates into two fine branches. Single large left brown-purple nephridium opens at anus level and not attached to body wall. Retractor muscles originate at 95% to posterior end of trunk, fused in column with three or four separate unequal origins.

Biogeographical remarks. Together with *Nephasoma*, the genus *Phascolion* are amongst the most well distributed and most species-rich genera of sipunculans. With almost equal numbers of species (14 and 12, respectively), they inhabit both shelf waters (1–300 m) and deeper waters, *Phascolion* is the deep-water genus. Six species are known from both shelf and continental slope depths (300–3,000 m), including *P. (Isomya) hedraeum* Selenka & de Man, 1883 (7–4,600 m) and the eurytopic *P. (Phascolion) strombus strombus* (Montagu, 1804) (1–4,030 m). Six taxa are known only from slope and deeper waters (300–6,900 m), but only *P. (M.) lutense* and *P. (M.) pacificum* Murina, 1957, occur in significant numbers at abyssal depths (>4,000 m) as well as on the continental slope (Murina 1971, 1977). Three species of *Phascolion* have significant populations in all three of the world's oceans, *P. (I.) strombus strombus* being the most widely distributed and eurytopic. Two deep-water species, *P. (M.) lutense* and *P. (M.) pacificum*, are close seconds throughout the northern and southern Atlantic and Pacific. Aside from the three widespread eurytopic deep-water species noted above, the eastern half of the Pacific Ocean is almost devoid of *Phascolion*. A single specimen of *P. (P.) bogorovi* Murina, 1973, was collected from the Peru-Chile Trench, and is the only one known from this part of the ocean (Murina 1973).

The deep-water species *P. (M.) lutense* is common in the Atlantic, Indian and the Pacific oceans; found at depths from 1,800 to 6,860 m (Cutler 1994). In the NWP it was collected at depths ranging from 4,690 to 6,860 m (Murina 1961, 1969, 1971).

Phascolion (Montaga) pacificum Murina, 1957

(Figure 1 J)

Diagnosis. Small to medium-sized worms (5–25 mm in length). Tall conical brown papillae present at anterior and posterior ends of trunk. Introvert with dark conical papillae in proximal part. Often inhabit foraminifera tubes. Rounded or elliptical (holdfast) papillae with hardened edge randomly distributed over trunk (50–60 mm in diameter and 45–50 mm

in height). Tentacles present only as short non-pigmented folds around mouth. Hooks present (30–35 mm). Ventral nerve cord ends at the ¾ of trunk length. Single (left) medium sized brown-purple nephridium opens at the anus level. Retractor muscles originate at 95% to the posterior end of the trunk, fused in column with one, two or three separate unequal origins.

Biogeographical remarks. This species is described from both the Japanese and Kuril-Kamchatka Trench and is particularly distinguished from the only other representative of this subgenus *P. (M.) lutense* by the presence of holdfast papillae. This bathyal and abyssal species (300–6,860 m) is widespread in the NW and SW Pacific and also in the northeastern (up to 57°N), southeastern, and South Atlantic, and the sub-Antarctic Indian Ocean. The only records at lower latitudes are from the Peru-Chile Trench (5,760–6,860 m) and 28°N (1,760 m) in the eastern Atlantic (Cutler 1994; Murina 1957, 1961; Saiz Salinas 1993). Also recently described subspecies of *Phascolion (M.) pacificum denticulatum* Saiz et al., 2015) is recorded from shallow waters (15–20 m deep) off Malvan and Ratnagiri in India. This is the first record of any *Phascolion* species for all the Indian coasts (Saiz et al. 2015).

4.2. Family Phascolosomatidae Stephen & Edmonds, 1972

Genus *Apionsoma* Sluiter, 1902

***Apionsoma (Apionsoma) murinae murinae* (Cutler, 1969)**

Diagnosis. Small-sized sipunculans less than 10 mm in trunk length. Introvert 10–15 times longer than trunk. Hooks recurved and with series of basal spinelets, organized in rings Distinctive mammiform papillae at the posterior end of the trunk. Contractile vessel without true villi and any swellings. Spindle muscle attached posteriorly. A pair of unilobed nephridia.

Biogeographical remarks. Two of four valid species of *Apionsoma* species are deep water taxa (*A. (A.) murinae murinae* and *A. murinae bilobatae* (Cutler, 1969)) occur in the Atlantic and Pacific oceans at bathyal to abyssal depths (300–5,200 m). According to Murina (1964), in the Pacific, this species occurs in the Bering Sea and the Peru-Chile Trench, and in other deep waters of the southern Pacific. The second taxon is also found in the Mediterranean Sea and on both sides of the Indian Ocean at shallow to continental slope depths (200–1,200 m) (Cutler, 1994). The three remaining species (*A. (A.) misakianum* (Ikeda, 1904), *A. (A.) trichocephalus* Sluiter, 1902, and *A. (Edmondsius) pectinatum* (Keferstein, 1867)) are also widespread, but in shallow, warm waters. The first is known from the Indian Ocean and both sides of the Pacific, but only the western Atlantic, including the Gulf of Mexico. The second co-occurs in warm-water sandy habitats over most of this range plus the eastern Atlantic Ocean. The third is less common but circumtropical and has been collected on both sides of all three oceans (Cutler 1994).

5. Discussion

The most ubiquitous NWP sipunculan species is *N. (N.) diaphanes corrugatum*. Other widespread sipunculan species are *N. (N.) diaphanes diaphanes*, *G. (G.) muricaudata and P. (M.) lutense*. Also, *N. (N.) d. corrugatum* and *N. (N.) d.*

diaphanes comprise 30% and 25%, respectively, of the total records of sipunculans in the deep area of the NW Pacific. Both species are present along almost the entire Kuril-Kamchatka Trench, at the adjacent abyssal plain, in the Kuril Basin of the Sea of Okhotsk and the Bering Sea, and only in the Sea of Japan, they have not been recorded. Several other common species (*G. (G.) muricaudata*, *G. (G.) margariatcea margaritacea*, *P. (M.) lutense* and *P. (M.) pacificum*) were sampled from widely scattered locations with a high number of specimens per sample. The remaining species (*N. (N.) abyssorum*, *G. (G.) anderssoni*, *G. (G.) vulgaris vulgaris*, *Nephasoma* sp1, *Nephasoma* sp2 and *A. (A.) murinae murinae*) are represented by few specimens, and mostly from single locations. Concerning the vertical distribution, most specimens of *G. (G.) m. margaritacea* were found at depth range 1,700–3,990 m; other abundant deep-sea sipunculan species (*N. (N.) d. diaphanes*, *G. (G.) muricaudata*, *G. (G.) margaritacea*, *P. (M.) lutense* and *P. (M.) pacificum*) were found at abyssal depths up to 6,800 m. The most dense sipunculan populations (*N. (N.) d. corrugatum*, *P. (M.) lutense* and *P. (M.) pacificum*) were found at depths of 6,800 m on the eastern slope of KKT. The deepest record of sipunculans in the selected area belongs to *N.(N.) d. corrugatum* from 7,123 m in the KKT.

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CHAPTER 10

POLYCHAETA

A REVIEW ON THE DEEP-SEA BENTHIC POLYCHAETES ALONG THE NW PACIFIC

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1. Introduction

Generally, polychaetes are the most abundant and diverse invertebrate group in marine environments worldwide. They occur in all substrates from the intertidal to hadal depths, displaying a wide variety of life forms, and constitute an important food base for many other animals. Of the macrofaunal taxa, polychaetes are often known to be dominant in deep-sea environments, including hydrothermal vents and cold seeps (Hessler and Jumars 1974; Rouse and Pleijel 2001; Paterson et al. 2009; Reuscher et al. 2009; Kongsrud et al. 2017).

The deep-sea Japan Basin, with a maximum depth of around 3,700 m, is located in the north-western part of the Sea of Japan and is isolated from the adjacent deep-sea areas by shallow straits (La Perouse Strait and Tatarsky Strait) (Talley et al. 2004). The deep-sea fauna of the Sea of Japan is considered to be rather poor and composed of eurybathic species found in adjacent high-boreal regions (Derjugin 1939; Zenkevich 1963). The earliest investigations of the deep-sea fauna of the Sea of Japan found only eight polychaete species from depths of 1,000–3,900 m (Annenkova 1937, 1938), including the polynoid species *Harmothoe derjugini* (Annenkova, 1937), which was considered a truly endemic deep-sea species of the Sea of Japan (Mokievsky 1954). Later, Levenstein (1969) reviewed the data on deep-water polychaete fauna of the Pacific Ocean and listed about 25 polychaete species inhabiting depths greater than 2,000 m in the Sea of Japan.

The deep-water Kuril Basin, bounded by 3,000 m isobaths, is located in the deepest southwestern part of the Sea of Okhotsk, and is characterized by a low oxygen concentration. It is separated from the Pacific Ocean by the Kuril Island archipelago and is connected to the ocean through several straits of bathyal depths (Bussol Strait, max. depth of 2,318 m, and Kruzenstern Strait, max. depth of 1,920 m) (Zenkevitch 1963; Shuntov 2001; Tyler 2002). During the 20th century, in the course of extensive biological surveys, the polychaete fauna of the northern and central parts of the Sea of Okhotsk was relatively well studied (Ushakov, 1950, 1953), while the deepest southwestern part of the Sea of Okhotsk remained practically unstudied, since only five abyssal stations were sampled from the Kuril Basin. Among invertebrates collected from the abyssal depths of the Kuril Basin deeper 3,000 m only three polychaete species (*Notomastus latericeus* Sars, 1851 and *Maldane sarsi* Malmgren, 1865 considered to be eurybathic and distributed worldwide, and *Lumbrineris abyssicola* Uschakov, 1950 considered to be truly abyssal and endemic to the Sea of Okhotsk) were recorded (Uschakov, 1950, 1953).

The Kuril-Kamchatka Trench (KKT) extends from the southeast coast of Kamchatka to the Japan Trench, east of Hokkaido, and separates the abyssal seafloor of the NW Pacific Basin from the Kuril Islands slope and from the Kuril Basin in the Sea of Okhotsk. The abyssal KKT area is considered one of the most productive regions in the World Ocean (Sokolova 1976, 1981). The earliest investigations of benthic fauna of the KKT performed during six biological *Vityazs'* expeditions revealed high diversity and species richness of the deep-sea macrobenthos in the North Pacific (Levenstein 1961, 1969; Zenkevich 1963; Belyaev 1983; 1989). Polychaeta, Bivalvia and Isopoda were known to be dominant taxa in deep-sea samples (Hessler and Jumars 1974). For the Pacific Ocean,

Levenstein (1969) listed 204 bathyal and abyssal species of polychaetes, including 13 species from the KKT at depths of 5,070–9,950 m (RV *Vityaz* collections). But many samples collected by the RV *Vityaz* and other Russian research vessels are still unstudied and apparently many bathyal and abyssal polychaete species new to science remain undescribed (Kupriyanova et al. 2011).

2. Objectives

The present chapter summarizes published data on deep-sea benthic polychaetes found during the Russian-German deep-sea expeditions, and reviews literature data on polychaete species occurring deeper 2,000 m in the NW Pacific area.

3. Material and Methods

The four deep-sea areas of the NW Pacific: Sea of Japan, Sea of Okhotsk, abyssal plain adjacent to the Kuril-Kamchatka Trench (KKT area), and Kuril-Kamchatka Trench (KKT), were studied during the Russian-German and German-Russian sampling campaigns from 2010 to 2016. During the SoJaBio (Sea of Japan Biodiversity Studies) expedition 13 stations along four transects were taken in the northwestern sector of the Sea of Japan (Japan Basin) at depths of 455–3,666 m. During the SokhoBio (Sea of Okhotsk Biodiversity Studies) expedition eight stations were sampled across the Kuril Basin of the Sea of Okhotsk at depths of 1,676–3,366 m, one station in the Bussol Strait at depths of 2,327–2,358 m, and two stations at the western abyssal slope of the KKT at depths of 3,347–5,009 m. From the abyssal plain of the KKT area (4,830–5,780m) and from the abyssal and hadal depths of the KKT (5,120–9,584 m) twelve and eleven stations, respectively, were sampled during the expeditions KuramBio I and KuramBio II (Kuril-Kamchatka Biodiversity Studies).

Different types of modern gears were used during the expeditions: an epibenthic sledge (EBS), an Agassiz trawl (AGT), and a Box-Corer (BC, sampling area of 0.25 m^2). Sledge operation procedure is described in Brandt et al. (2019). On deck, the samples were washed with ice-cold water and sieved through 300-µm mesh screens. Samples from the first deployment of each station were fixed with pre-cooled 96% ethanol. Samples from the second deployment were fixed with 4% formaldehyde and later transferred to 75% ethanol. Collected samples were sorted either on board or later in the laboratory.

In this article, we also consider literature data on polychaete species occurring below 2,000 m in the NW Pacific area, limited between approximately 40 and 60 degrees North latitude and 120–180 degrees East longitude. The abyssal zone is generally defined as lying between 2,000 m and 6,000 m depth, and waters deeper than 6,000 m are treated as the hadal zone. Both zones are described mainly by their extremely uniform environmental conditions, as reflected in the distinct life forms inhabiting it.

4. Results

During the SoJaBio expedition more than 11300 polychaete specimens of 90 species belonging to 70 genera and 28 families were collected in the Japan Basin at depths of 470–3,431 m (Alalykina 2013). However, most specimens (5,406) and

species (84) were sampled from the shallow station positioned on the continental slope of the Japan Basin at depths of 450–550 m. Species richness and polychaete diversity rapidly decreased with depth. At depths between 1,000–1,500 m 36 species were found, between abyssal depths of 2,500–2,700 m 14 species, and at depths greater than 3,300 m only eight species were registered. In total, only 18 polychaete species (5,928 specimens) were accounted in depths below 2,000 m in the Japan Basin (see abb. X in Table 1, own data).

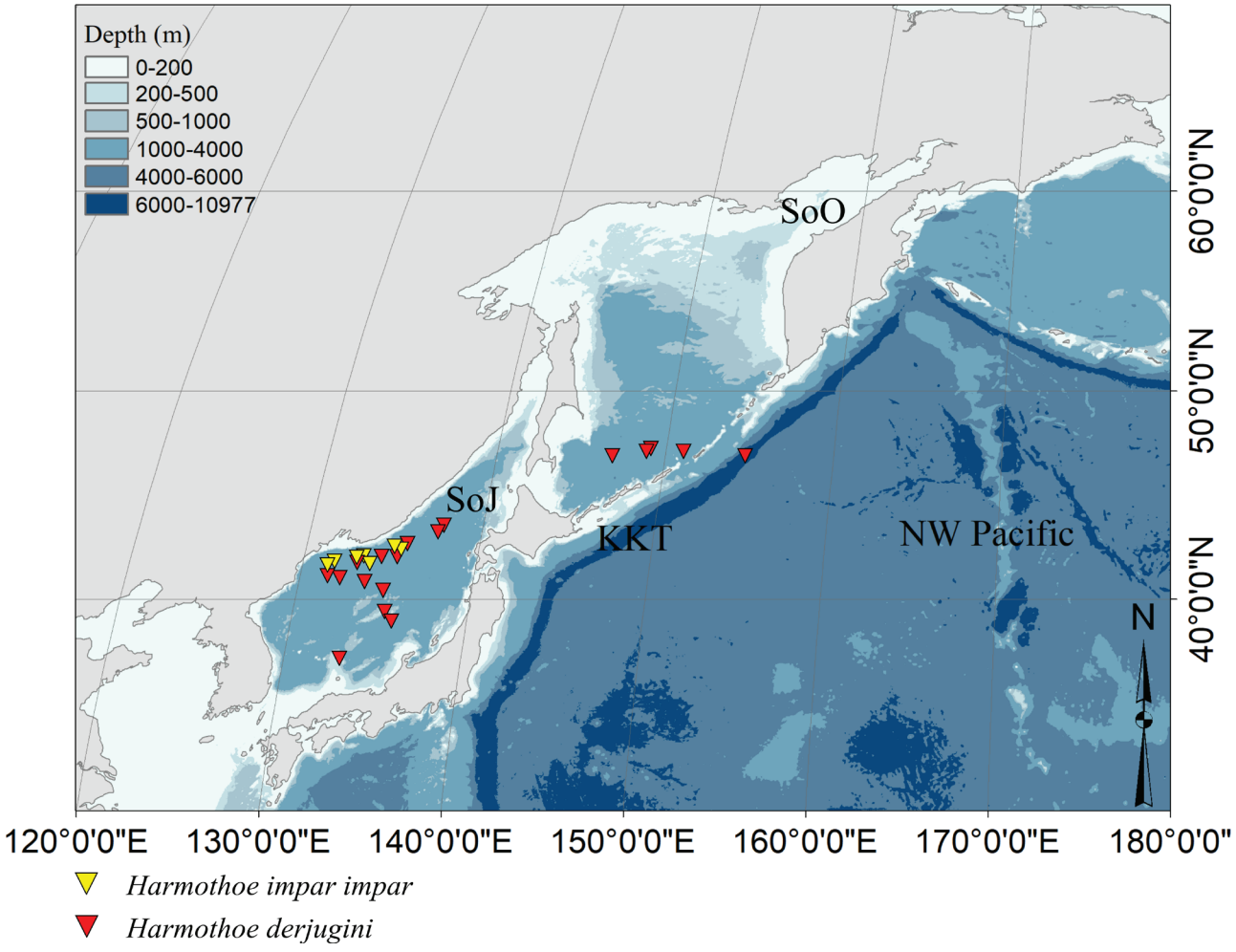
From abyssal depths (3,206–3,366 m) of the Kuril Basin more than 16,000 polychaete specimens of 157 species (123 genera, 47 families) were collected during the SokhoBio expedition. About 3,000 polychaetes specimens of 129 species (97 genera, 35 families) were sampled from the KuramBio I expedition in the oceanic abyssal plain adjacent to the Kuril-Kamchatka Trench at depths of 4,830–5,780 m. The abyssal and hadal depths of KKT were sampled during three expeditions: two SokhoBio stations (St. 9 and 10) at depths of 3,347–5,009 m; two KuramBio I stations (St. 3 and 4) at depths of 4,987–5,780 m; and eleven KuramBio II stations at depths of 5,120–9,584 m. A total of 22,900 polychaete specimens of 208 species (137 genera, 47 families) were collected from the KKT (see abb. X in Table 1, own data).

Presented results show that the biodiversity of the deep-sea polychaete fauna of the Kuril Basin is comparable to that in the KKT, as well as in the Pacific Ocean abyssal plain adjacent to the KKT, and higher than in the abyssal Japan Basin of the Sea of Japan.

The polychaete species composition changed within each area studied. The abyssal polychaete fauna of the Japan Basin is characterized by the dominance of spionid species *Laonice* sp. (45% of total abundance in terms of number of specimens), as well as the ampharetid species *Ampharete* sp.2, and polynoid species *Harmothoe derjugini* and *H. impar impar* (Johnston, 1839) were also well represented. For the sampled abyssal area of the Kuril Basin, the most abundant and common species were ampharetid species *Anobothrus sonne* Alalykina & Polyakova, 2019 (Figure 1E, F) and *Glyphanostomum* sp. nov.2, spionid *Prionospio* sp.1, pholoid *Pholoe minuta caeca* Uschakov, 1950, and sigalionid *Labioleanira okhotica* Alalykina, 2018 (Figure 1D, G) constituting more than 50% of the total polychaete abundance. In the investigated area of the Pacific abyssal plain, the most widely distributed and abundant species were fauveliopsid species *Laubieriopsis hartmanae* (Leventein, 1970), *Fauveliopsis levensteinae* Salazar-Vallejo, Zhadan & Rizzo, 2019, and *Travisia glandulosa* McIntosh, 1879 (Figure 1A–C). The species *T. glandulosa* together with *L. hartmanae*, *Notomastus latericeus*, and *Galathowenia* sp. have been found to be dominant in abyssal and hadal depths of the KKT. No clear species change was observed between abyssal and hadal stations within the KKT. The abyssal-hadal species *T. glandulosa* and *L. hartmanae* were abundant and widespread both at the abyssal and hadal depths of the KKT. In all the studied areas (Japan Basin, Kuril Basin, Pacific abyssal plain and KKT) the most speciose families were the Ampharetidae, Phyllodocidae, Polynoidae, and Sphaerodoridae. Most of these collected polychaete species are new to science.

A number of polychaete species (*i.e.*, *Melinnampharete eoa* Annenkova, 1937, *Notomastus latericeus*, *Apistobranchus* sp., *Chaetozone* sp.1,

and *Sphaerodorum* cf. *gracilis* (Rathke, 1843)) sampled deeper than 2,000 m, were widespread in the studied areas, inhabiting the deep Japan Basin, as well as the Kuril Basin, abyssal Pacific plain, and the KKT (Table 1). Among them, the polynoid species *Harmothoe derjugini* previously considered as endemic of the abyssal zone of the Sea of Japan was also recorded in the deep Kuril Basin (Alalykina 2018) and in the KKT at depths of 4,987–4,991 m (Alalykina 2015). In Map 1 the distribution patterns of two polynoid species, *H. derjugini* and *H. impar impar*, which are abundant and widely distributed in the abyss of the Sea of Japan are shown. More than half of the species found in the Kuril Basin occur on the Pacific slope of the KKT. The high number of fauveliopsid (*L. hartmanae* and *F. levensteinae*, see Map 2) and travisiid (different species of genus *Travisia*, see Map 3) records suggests that they can be regarded as common and widespread species in the North Pacific deep sea. Records of widespread and eurybathic species common to both the Kuril Basin and the Pacific slope of the KKT, and also the Japan Basin, confirm the relationship between the abyssal faunas of the studied areas of the NW Pacific. The existence of a transitional zone between the abyssal and hadal has already been suggested



Map 1. Distribution of NW Pacific polynoid species *Harmothoe derjugini* and *H. impar impar*.

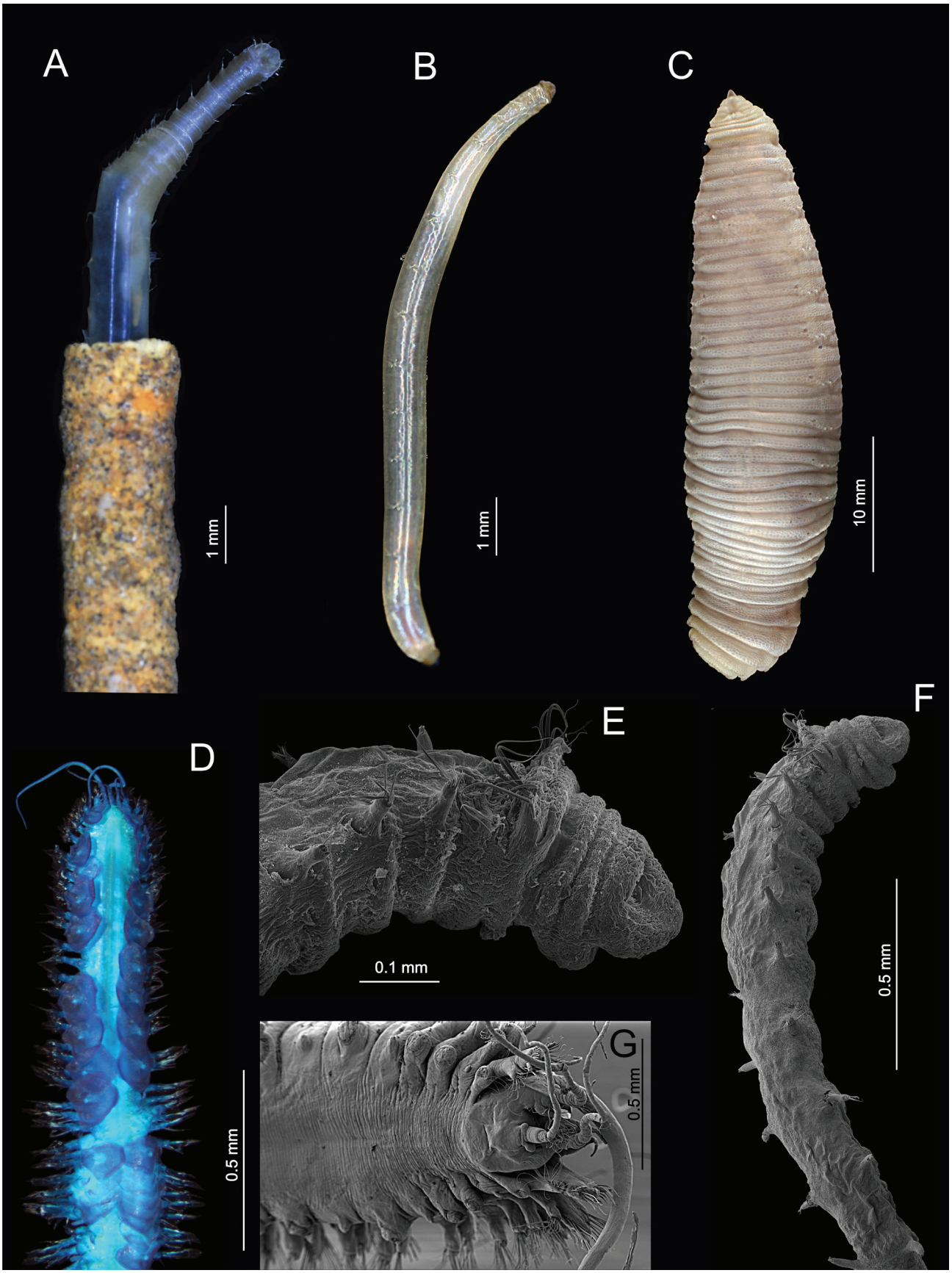


Figure 1. NW Pacific polychaetes: (A) *Fauveliopsis levensteinae* inhabiting the sand-agglutinating foraminiferan tube; (B) *Laubieriopsis hartmanae;* (C) *Travisia glandulosa;* (D, G) *Labioleanira okhotica;* (E, F) *Anobothrus sonne* (A–C: photo by A.S Maiorova).

Table 1. List of polychaetes recorded in the studied NW Pacific region at depths below 2,000 m (X – own data, L – literature records).

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Phyllodocidae							
Austrophyllum sphaerocephalum (Levenstein, 1961)		X	L		**X, L**	Kuril Basin of the Okhotsk Sea, Kuril-Kamchatka Trench, Bering Sea, Pacific; 2,440–4,130 m	Levenstein 1961; Uschakov 1972; Alalykina 2018
Eteone sp.				X			
Eteone vitiazi Uschakov, 1972				L		Japan (off east of Honshu), Pacific; 5,475 m	Uschakov 1972
Eulalia cf. *pacifica* (Imajima, 1964)		X		L		Kuril Basin of the Okhotsk Sea, off east of Japan, Pacific; 2,230–2,350 m	Uschakov 1972; Alalykina 2018
Eulalia gravieri Uschakov, 1972				L		Japan (off east of Honshu), off Kamchatka Peninsula, Pacific; 1,641–3,265 m	Uschakov 1972
Eulalia sp.		X			X		
Eumida cf. *angolensis* Böggemann, 2009		X				Angola Basin, Atlantic; 3,950–5,443 m	Böggemann 2009
Eumida nuchala (Uschakov, 1972)		X		L	**X**	Angola and Cape Basins, Atlantic; Japan (east of Honshu), Pacific; 3,704–5,475 m	Uschakov 1972; Böggemann 2009
Eumida sp.				X			
Lugia abyssicola Uschakov, 1972		X		L		South-Sandwich Trench, Antarctic; Japan (Hokkaido), California, Pacific; 4,200–5,475 m	Uschakov 1972; Levenstein 1975
Mystides caeca Langerhans, 1880		X				Off north Carolina, Angola,Cape and Guinea Basins, Atlantic; off California, Pacific; 102–5,496 m	Blake 1994a; Böggemann 2009
Mystides schoderae Uschakov, 1972				L		Japan (off Hokkaido), Pacific; 3,095–5,800 m	Uschakov 1972
Mystides sp.nov.		X		X	**X**		
Paranaitis bowersi (Benham, 1927)		X				Ross Sea, Antarctic; 219–1,837 m	Uschakov 1962; Kato and Pleijel 2003

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Paranaitis sp.					X		
Paranaitis uschakovi Eibye-Jacobsen, 1991		X				Japan (east of Honshu), Pacific; 45–598 m	Kato and Pleijel 2003
Protomystides levensteinae Uschakov, 1972		X		L		Kuril Basin of the Okhotsk Sea, Aleutian and Mariana Trenches, Pacific; 4,549–5,740 m	Uschakov 1972
Protomystides orientalis Uschakov, 1972		X			**X**	Japan (east of Honshu), north New Zealand, Pacific; 598–1,225 m	Uschakov 1972
Pseudomystides rarica (Uschakov, 1958)		X		X, L	**X, L**	South-Sandwich Trench, Atlantic; Japan (off Hokkaido), Bonin Islands, Kuril-Kamchatka Trench, Kermadec Trench, Pacific; 1,125–5,070 m	Uschakov 1972; Levenstein 1975
Pseudomystides sp.nov.		X					
Sige cf. *brunnea* (Fauchald, 1972)		X			**X**	North California, Pacific; 1,110–3,000 m	Blake 1994a; Pleijel 1990
Sige dogieli (Uschakov, 1953)		X			**X, L**	Kuril Basin of the Okhotsk Sea, off Tsugaru Strait, Kuril-Kamchatka Trench, Japan Trench, Pacific; 6,157–8,100 m	Uschakov 1972; Levenstein 1973; Pleijel 1990; Buzhinskaja 2013; Alalykina 2018
Sige sandwichensis (Uschakov, 1975)				L	**X**	South Sandwich Trench, South Atlantic Ocean; 5,078–7,218 m	Uschakov 1975; Pleijel 1990
Sige sigeformis (Annenkova, 1937)					**X**	Bering Sea, Japan Sea, Okhotsk Sea, Aleutian Trench, North Pacific; 443–7,185 m	Uschakov 1972; Levenstein 1973
Lopadorrhynchidae							
Maupasia coeca Viguier, 1886					**X**	Widespread; up to 2,000 m	Uschakov 1972
Pelagobia longicirrata Greeff, 1879		**X**		L	**X, L**	Widespread, bathypelagic	Uschakov 1972; Jirkov 2001
Alciopidae							
Krohnia excellata (Uschakov, 1955)			**L**	L		NW Pacific; up to 4,000 m	Uschakov 1957, 1972

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Lacydoniidae							
Lacydonia papillata Uschakov, 1958		**X**		X, L	**X, L**	Kuril Basin of the Okhotsk Sea, off Japan (east of Honshu), Kuril-Kamchatka Trench, Pacific; Angola and Guinea Basins, Atlantic; 3,352–5,690 m	Levenstein 1969; Uschakov 1972; Böggemann 2009; Alalykina 2018
Aphroditidae							
Aphrodita talpa Quatrefages, 1866	L		L			Pacific (Japan Sea, Okhotsk Sea, Bering Sea) and Indian Ocean; 0–2,995 m	Annenkova 1937; Levenstein 1961, 1969
Laetmonice japonica McIntosh, 1885		X			**L**	Off southern Japan, Kuril-Kamchatka Trench, Yellow Sea, Pacific; 42–2,900 m	Uschakov 1982; Imajima 2003
Laetmonice pellucida Moore, 1903				X	**X, L**	Bering Sea, Okhotsk Sea, Kuril-Kamchatka Trench, Pacific; 1,076–5,260 m	Uschakov 1950, 1982; Buzhinskaja 2013
Laetmonice wyvillei McIntosh, 1885				X, L	**X, L**	Widespread; 900–5,707 m	Uschakov 1952, 1982; Averincev 1972
Laetmonice sp.1		X					
Laetmonice sp.2		**X**					
Polynoidae							
Admetella longipedata (McIntosh, 1885)					**L**	Kuril-Kamchatka Trench, Japan Trench, Pacific; 400–6,860 m	Levenstein 1973; Uschakov 1982
Bathyeliasona abyssicola (Fauvel, 1913)		X	L			Atlantic (Bay of Biscay), Pacific (Bering Sea, Kuril Basin of the Okhotsk Sea, Aleutian Trench), Indian Ocean; 3,760–7,180 m	Levenstein 1961, 1971; Uschakov 1982; Alalykina 2018
Bathyeliasona kirkegaardi (Uschakov, 1971)				L		Pacific (Banda Sea, Aleutian and Kermadec Trenches), Indian Ocean; 5,525–7,246 m	Levenstein 1971, 1973; Uschakov 1982

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Bathyfauvelia affinis (Fauvel, 1914)		X		X, L	**X, L**	Arctic; Atlantic; Kuril-Kamchatka Trench, Pacific; 1,060–6,850 m	Levenstein 1981; Uschakov 1982
Bathyfauvelia sp.nov.		X					
Bathykermadeca hadalis (Kirkegaard, 1956)				L		Pacific (Japan Trench, Banda Sea, Kermadec Trench); 7,350–7,370 m	Levenstein 1982
Bathykurila zenkevitchi (Uschakov, 1955)					**L**	Kuril-Kamchatka Trench, Japan Trench, Pacific; 6,670–8,135 m	Levenstein 1971, 1973; Uschakov 1982
Bathypolaria carinata Levenstein, 1981		X		X	**X**	Canada Basin, Arctic; 2,750–3,920 m	Levenstein 1981; Jirkov 2001
Harmothoe cf. *rarispina* (M. Sars, 1861)		X				White Sea, Barents Sea, Arctic; Bering Sea, Okhotsk Sea, Japan Sea, Pacific; 5–2,358 m	Uschakov 1982; Jirkov 2001; Alalykina 2018
Harmothoe derjugini Annenkova, 1937	X, L	**X**		X	**X**	Japan Sea, Kuril Basin of the Okhotsk Sea, Kuril-Kamchatka Trench, NW Pacific; 2,500–4991 m	Sokolova 1982; Uschakov 1982; Alalykina 2013, 2015, 2018
Harmothoe impar impar (Johnston, 1839)	X, L					Arctic, NW Pacific; up to 2,990 m	Annenkova 1937; Levenstein 1969; Alalykina 2013
Harmothoe sp.	X						
Lagisca tenebricosa (Moore, 1910)			L			Bering Sea, Okhotsk Sea, NW Pacific; 1,733-2,172 m	Levenstein 1961
Lepidasthenia grimaldii (Marenzeller, 1892)				L	**L**	North Atlantic, NW Pacific; 400–5,700 m	Uschakov 1955, 1957, 1982
Macellicephala longipalpa Uschakov, 1957		X		X	**X**	Arctic, Pacific (Kuril-Kamchatka Trench); 120–4,991 m	Uschakov 1982; Jirkov 2001; Alalykina 2015, 2018
Macellicephala sp.1				X	**X**		
Macellicephala sp.2		X		X	**X**		
Macellicephala tricornis Levenstein, 1975				X	**X**	Antarctic Ocean, South Sandwich trench; 7,200–8,116 m	Levenstein 1975
Macellicephala violacea (Levinsen, 1887)		X		L	**X, L**	Widespread boreal; 46–8,400 m	Uschakov 1982; Jirkov 2001;Alalykina 2018

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Macellicephaloides grandicirra Uschakov, 1955					**L**	Kuril-Kamchatka Trench, Pacific; 8,100–9,000 m	Levenstein 1971; Uschakov 1982
Macellicephaloides sp.1				X	**X**		
Macellicephaloides sp.2				X	**X**		
Macellicephaloides uschakovi Levenstein, 1971					**L**	Kuril-Kamchatka Trench, Pacific; 8,120 m	Levenstein 1971; Uschakov 1982
Macellicephaloides verrucosa Uschakov, 1955					**L**	Kuril-Kamchatka Trench, Japan Trench, Pacific; 6150–8,015 m	Levenstein 1971; Uschakov 1982
Macellicephaloides vitiazi Uschakov, 1955					**L**	Kuril-Kamchatka Trench, Pacific; 7,000–8,430 m	Levenstein 1971; Uschakov 1982
Polaruschakov polaris (Uschakov, 1976)		X				Arctic; 730–2,245 m	Uschakov 1982; Jirkov 2001
Polaruschakov sp.				X	**X**		
Polynoidae Gen.sp.				X	**X**		
Sigalionidae							
Labioleanira okhotica Alalykina, 2018		X			**X**	Kuril Basin of the Okhotsk Sea, western slope of the Kuril-Kamchatka Trench, NW Pacific; 3,211–4,803 m	Alalykina 2018
Neoleanira areolata (McIntosh, 1885)			L			Bering Sea, Okhotsk Sea, NW Pacific; 110–4,811 m	Levenstein 1961, 1966
Neoleanira sp.				X	X		
Pholoidae							
Pholoe minuta caeca Uschakov, 1950		**X**			**X**	Okhotsk Sea, off Central Oregon, North Pacific; 1,250–2,000 m	Uschakov 1950; Fauchald and Hancock 1981
Chrysopetalidae							
Dysponetus cf. *caecus* (Langerhans, 1880)		X			**X**	Mediterranean, Angola Basin, East Atlantic; up to 5,000 m	Boggemann 2009; Watson et. al. 2014
Dysponetus gracilis Hartman, 1965		X			**X**	NW Atlantic; up to 2,800 m	Hartman 1965; Hartman and Fauchald 1971; Aguirrezabalaga et. al. 1999

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Dysponetus sp.				X			
Chrysopetalidae Gen.sp.				X	X		
Glyceridae							
Glycera cf. *onomichiensis* Izuka, 1912		X	L		**X**	Pacific; up to 3,940 m	Uschakov 1950; Levenstein 1966, 1969
Glycera sp.1		X		X	X		
Glycera sp.2					X		
Goniadidae							
Bathyglycinde lindbergi (Uschakov, 1955)		X	L		**X**	NW Pacific (Kuril Basin of the Okhotsk Sea, Bering Sea), Atlantic; 1,185–5,858 m	Levenstein 1961, 1966; Böggemann 2005; Alalykina 2018
Bathyglycinde sp.				X	**X**		
Goniada maculata Örsted, 1843	L		L			Widespread Boreal; up to 4,820 m	Annenkova 1937; Levenstein 1961, 1969
Goniada sp.		X			X		
Syllidae							
Amblyosyllis sp.				X			
Anguillosyllis cf. capensis Day, 1963		X		**X**	**X**	South Africa, Atlantic and Indian Ocean; Cape, Angola and Guinea Basins, Atlantic; Japan Sea, Kuril-Kamchatka Trench, Pacific; 183–5,655 m	Day 1963; Böggemann 2009; Alalykina 2013, 2015
Syllis alternata Moore, 1908	L					Japan Sea, California, Pacific; up to 2,520 m	Annenkova 1937; Levenstein 1969
Syllidae Gen.sp.		X					
Hesionidae							
Gyptis sp.		X		X	X		
Hesionidae Gen.sp.1		X		X	X		
Hesionidae Gen.sp.2		X		X	X		
Pilargidae							
Ancistrosyllis groenlandica McIntosh, 1878		X				Arctic, Atlantic, Eastern Pacific; 45–3,993 m	Blake 1994b; Böggemann 2009
Sigambra sp.1		X					
Sigambra sp.2	X						

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Nereididae							
Ceratonereis (Composetia) beringiana (Levenstein, 1961)			L			Bering Sea, Pacific; 2,995–4,382 m	Levenstein 1961, 1966; Khlebovich 1996
Ceratocephale loveni Malmgren, 1867		**X**	**L**	**X**	**X**	Kuril Basin of the Okhotsk Sea, Bering Sea, Japan Trench, Pacific; Atlantic; 102–6,700 m	Levenstein 1961, 1966; Jirkov 2001; Alalykina 2018
Nereis beringiana Levenstein, 1961					**X**	Bering Sea, Pacific; 510–4,930 m	Khlebovich 1996; Buzhinskaja 2013
Nephtyidae							
Aglaophamus malmgreni (Théel, 1879)	L		L			Bering Sea, Japan Sea, Pacific; Arctic; North Atlantic; up to 3,980 m	Annenkova 1937; Levenstein 1969
Aglaophamus sp.1		X			X		
Aglaophamus sp.2	X						
Nephtys brachycephala Moore, 1903			L			Bering Sea, Okhotsk Sea, North Pacific; 110–2,160 m	Levenstein 1961, 1966
Sphaerodoridae							
Clavodorum sp.1		X		X	**X**		
Clavodorum sp.2					X		
Ephesiella sp.		X			X		
Euritmia sp.		X					
Sphaerephesia lesliae Alalykina, 2015				X	**X**	Kuril-Kamchatka Trench and adjacent abyssal plain, NW Pacific; 5,216–5,429 m	Alalykina 2015
Sphaerephesia sp.1		X					
Sphaerephesia sp.2		X					
Sphaerodoridium sp.1		X		X	**X**		
Sphaerodoridium sp.2		X		X	**X**		
Sphaerodoridium sp.3		X		X			
Sphaerodoropsis sp.1				X	**X**		
Sphaerodoropsis sp.2		X			X		
Sphaerodoropsis sp.3		X			X		
Sphaerodoropsis sp.4		X			X		
Sphaerodorum sp.	X			X	**X**		

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Sphaerodoridae Gen.sp.	X						
Euphrosinidae							
Euphrosinopsis horsti Kudenov, 1993		X				Pacific Antarctic Ridge, Antarctic; 3,219–3,255 m	Kudenov 1993
Euphrosinella paucibranchiata (Hartman, 1960)				L		Pacific; 780–4,700 m	Kucheruk 1981
Euphrosine sp.				X	X		
Lumbrineridae							
Abyssoninoe abyssorum (McIntosh, 1885)		X				Orkney trench, Antarctic; Norway, Mediterranean, Atlantic; Peru-Chile Trench, Pacific; 274–6,000 m	Levenstein 1978; Frame 1992
Augeneria tentaculata Monro, 1930		X			**X**	Off South Orkney Islands, Antarctic; North Sea, Norwegian coast, Atlantic; Japan, Pacific; 80–2,350 m	Imajima and Higuchi 1975; Orensanz 1990
Eranno abyssicola (Uschakov, 1950)		X, L	L		**X**	Bering Sea, Okhotsk Sea, NW Pacific; 3,500–4,820 m	Uschakov 1950; Levenstein 1966, 1969; Alalykina 2018
Lumbrineris bistriata Levenstein, 1961			L			Bering Sea, NW Pacific; 3,260–4,382 m	Levenstein 1961, 1966
Lumbrineris japonica (Marenzeller, 1879)	L		L			Japan Sea, Bering Sea, Okhotsk Sea, NW Pacific; 2,359–3,500 m	Annenkova 1937; Levenstein 1961, 1969
Lumbrineris sp.1		X		X	**X**		
Lumbrineris sp.2					X		
Cenogenus cf. *antarctica* (Monro, 1930)		X			**X**	Antarctic; 365–3,747 m	Monro 1930; Frame 1992
Cenogenus sp.	X			X	**X**		
Paraninoe hartmanae Levenstein, 1977				L	**L**	Kuril-Kamchatka Trench, Japan Trench, Aleutian Trench, North Pacific; 6,156–8,100 m	Levenstein 1977
Lumbrineridae Gen. sp.		**X**					

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Onuphidae							
Anchinothria pycnobranchiata (McIntosh, 1885)			L			Bering Sea, Japan Trench, Aleutian Trench, Pacific; 3,042–5,020 m	Levenstein 1957, 1961; Kucheruk 1978, 1981
Hyalinoecia sp.		X			X		
Nothria abyssia Kucheruk, 1978				L		Antarctic, Pacific; 2,700–5,400 m	Kucheruk 1978
Nothria sp.				X	X		
Onuphis sp.				X	**X**		
Paradiopatra ehlersi (McIntosh, 1885)				L	**L**	Antarctic, Pacific (Japan Trench, Kuril-Kamchatka Trench); 3,200–6,350 m	Kucheruk 1978, 1981
Paradiopatra sp.		**X**		X	**X**		
Dorvilleidae							
Dorvillea sp.		X		X	X		
Ophryotrocha sp.		**X**			**X**		
Oenonidae							
Drilonereis zenkevitchi Levenstein, 1961			L			Bering Sea, NW Pacific; 2,995–3,260 m	Levenstein 1961, 1966
Drilonereis sp.		**X**					
Orbiniidae							
Berkeleyia sp.nov.		X			X		
Leitoscoloplos sp.		X		X	**X**		
Leodamas sp.		X					
Scoloplos sp.		**X**			**X**		
Spionidae							
Aonides sp.				X	**X**		
Laonice cf. *cirrata* (M.Sars, 1851)	X						
Laonice sp.		X		X	X		
Paraprionospio pinnata (Ehlers, 1901)	L					Cosmopolitan; up to 2,360 m	Annenkova 1937; Levenstein 1969
Prionospio sp.1		X		X	X		
Prionospio sp.2				X	X		
Polydora sp.	X						
Spiophanes sp.		X		X	X		
Spionidae Gen.sp.				X			

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Trochochaetidae							
Trochochaeta sp.nov.		**X**			**X**		
Apistobranchidae							
Apistobranchus sp.		**X**			**X**		
Chaetopteridae							
Phyllochaetopterus claparedii McIntosh, 1885			L			Bering Sea, Okhotsk Sea, Pacific; 14–3,730 m	Levenstein 1961, 1966
Spiochaetopterus typicus M Sars, 1856	L		L			Arctic, North pacific and Atlantic; up to 3,932 m	Annenkova 1937; Levenstein 1961, 1969
Spiochaetopterus sp.		**X**		**X**	**X**		
Paraonidae							
Aricidea (Acmira) finitima Strelzov, 1973				L		Japan (off east of Hokkaido), Pacific; 3,860 m	Strelzov 1973
Aricidea (Acmira) simplex Day, 1963			**L**	L	**L**	Japan Sea, Kuril-Kamchatka Trench, Bering Sea, Pacific; Antarctic; Atlantic; 35–5,540 m	Strelzov 1973
Aricidea (*Aricidea*) cf. *wassi* Pettibone, 1965		X				North Sea, Adriatic Sea, Atlantic; off California, Japan, Pacific; 15–1,480 m	Blake 1996; Strelzov 1973
Aricidea (*Strelzovia*) cf. *maialenae* Aguirrezabalaga & Gil, 2009		X			**X**	Capbreton Canyon, Bay of Biscay, NE Atlantic; 492–1,113 m	Aguirrezabalaga and Gil 2009
Aricidea (Strelzovia) facilis Strelzov, 1973				L		Pacific, Antarctic; 1,952–5,030 m	Strelzov 1973
Aricidea (*Strelzovia*) *pulchra* Strelzov, 1973		X		L	**L**	Pacific Ocean; 1,602–5,511 m	Strelzov 1973
Aricidea (Strelzovia) quadrilobata Webster & Benedict, 1887				L		Atlantic, Antarctic, Pacific; 22–5,680 m	Strelzov 1973
Aricidea (Strelzovia) ramosa Annenkova, 1934	L					Japan Sea, South California; up to 2,400 m	Annenkova 1937; Levenstein 1969
Aricidea sp.1				X	**X**		
Aricidea sp.2				X	**X**		
Aricidea sp.3				X	**X**		

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Aricidea sp.4				X	**X**		
Cirrophorus branchiatus Ehlers, 1908		X			L	Western Canada to southern California, Atlantic; Okhotsk Sea, Japan Sea, Kuril-Kamchatka Trench; up to 2,795 m	Strelzov 1973; Blake 1996
Cirrophorus sp.					X		
Levinsenia gracilis (Tauber, 1879)		X		X, L	**X, L**	Cosmopolitan, up to 3,800 m	Strelzov 1973; Blake 1996
Levinsenia oligobranchiata (Strelzov, 1973)				L	**L**	Western slope of the Kuril-Kamchatka Trench, NW Pacific; 3,388–3,860 m	Strelzov 1973
Paradoneis abranchiata Hartman, 1965				X, L	**X, L**	Atlantic, Pacific (Kuril-Kamchatka Trench); 1,500–4,860 m	Strelzov 1973
Paradoneis forticirrata (Strelzov, 1973)					**L**	California, Japan, Kuril-Kamchatka Trench, Pacific; 40–2,780 m	Strelzov 1973
Paraonides cf. *monilaris* Hartman & Fauchald, 1971		X			**X**	NW Atlantic; 2864–4,825 m	Hartman and Fauchald 1971
Sabidius cornatus (Hartman, 1965)		**X**			**L**	Atlantic, Pacific; 400–3,388 m	Hartman 1965; Strelzov 1973
Cirratulidae							
Aphelochaeta pacifica (Annenkova, 1937)	L					Japan Sea, Pacific; up to 2,900 m	Annenkova 1937; Levenstein 1969
Chaetozone cf. *setosa* Malmgren, 1867	X, L					Arctic, North pacific and Atlantic; up to 2,400 m	Annenkova 1937; Levenstein 1969
Chaetozone sp.1	X	**X**		X	X		
Chaetozone sp.2	X			X	X		
Chaetozone sp.3				X	X		
Cirratulus cirratus (O.F. Müller, 1776)	L					Japan Sea, Pacific; up to 2,900 m	Annenkova 1937
Cirratulidae Gen.sp.				X			
Cossuridae							
Cossura sp.		**X**		**X**	**X**		
Flabelligeridae							
Brada sp.1		X			X		
Brada sp.2		X			X		
Brada sp.3		X		X	**X**		

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Brada sp.4				X	**X**		
Brada sp.5				X	**X**		
Diplocirrus sp.1		X		X	X		
Diplocirrus sp.2		X		X	**X**		
Flabelligera affinis Sars, 1829	X						
Flabelligera sp.					X		
Pherusa plumosa (Müller, 1776)	L					Arctic, North Pacific, North Atlantic; up to 2,900 m	Annenkova 1937
Pherusa sp.1		X		X	X		
Pherusa sp.2					X		
Poeobius meseres Heath, 1930					**X**	Pacific Ocean; pelagic	Salazar-Vallejo 2008
Ilyphagus irenaia (Chamberlin, 1919)			L		L	Pacific; 1,580–3,280 m	Levenstein 1961, 1966
Flabelligeridae Gen. sp.				X			
Acrocirridae							
Acrocirrus sp.1		X		X	**X**		
Acrocirrus sp.2				X	X		
Chauvinelia arctica Averincev, 1980		X		X	**X**	Canadian Basin, Greenland Sea, Arctic; 2,300–3,380 m	Jirkov 2001; Salazar-Vallejo et. al. 2007
Flabelligella sp.				X	**X**		
Flabelligena sp.1		X		X	**X**		
Flabelligena sp.2				X	**X**		
Flabelligena sp.3				X	**X**		
Flabelligena sp.4					X		
Flabelliseta sp.		X			X		
Helmetophorus sp.				X	**X**		
Swima sp.				X	**X**		
Acrocirridae Gen.sp.				X	**X**		
Fauveliopsidae							
Laubieriopsis hartmanae (Levenstein, 1970)		X		**X, L**	**X, L**	Kuril Basin of the Okhotsk Sea, Japan, Kuril-Kamchatka and Peru-Chile Trenches, Pacific; 4,090–6,700 m	Levenstein 1970a; Petersen 2000; Alalykina 2018; Salazar-Vallejo et. al. 2019

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Fauveliopsis levensteinae Salazar-Vallejo, Zhadan & Rizzo, 2019		**X**		**X, L**	**X, L**	Kuril Basin of the Okhotsk Sea, from off Japan and Kamchatka Peninsula to Aleutian Islands, Pacific; 1,641–6,280 m	Alalykina 2018; Salazar-Vallejo et. al. 2019
Scalibregmatidae							
Asclerocheilus sp.		X			X		
Pseudoscalibregma parvum (Hansen, 1879)			L			Arctic; Bering Sea, Pacific; up to 3,680 m	Levenstein 1961, 1966
Pseudoscalibregma sp.1		X		X	**X**		
Pseudoscalibregma sp.2				X	**X**		
Scalibregma inflatum Rathke, 1843	X, L		L			Cosmopolitan; up to 4,400 m	Annenkova 1937; Levenstein 1961, 1969
Scalibregma sp.		**X**			**X**		
Opheliidae							
Ophelina sp.1		X		X	X		
Ophelina sp.2				X	X		
Travisiidae							
Travisia glandulosa McIntosh, 1879				X, L	**X, L**	Antarctic, Atlantic, Pacific (Japan Trench, Kuril-Kamchatka Trench, Aleutian Trench); 300–8,830 m	Levenstein 1970b, 1973; Dauvin and Bellan 1994
Travisia forbesii Johnston, 1840				L		Arctic, Atlantic, Pacific; 19–3,000 m	Levenstein 1970b; Dauvin and Bellan 1994
Travisia fusus (Chamberlin, 1919)				L		Pacific Ocean; 2915–7,587 m	Levenstein 1970b, 1973
Travisia cf. *profundi* Chamberlin, 1919			L	L	**X**	Bering Sea, Pacific; Atlantic; 975–7,290 m	Levenstein 1970b, 1973; Dauvin and Bellan 1994
Travisia pupa Moore, 1906			L		**L**	Bering Sea, Japan Trench, Kuril-Kamchatka Trench, North Pacific; 33–3,012 m	Levenstein 1970b, 1973; Dauvin and Bellan 1994
Travisia sp.1		X		X	**X**		
Travisia sp.2		**X**			**X**		

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Capitellidae							
Notomastus latericeus Sars, 1851	L	**X, L**	**L**	**X**	**X**	Cosmopolitan; up to 4,360 m	Uschakov 1950; Levenstein 1961, 1969; Alalykina 2018
Heteromastus sp.				X			
Capitella sp.		**X**			**X**		
Maldanidae							
Asychis ramosus Levenstein, 1961			**L**	L		NW Pacific; 2,416–3,680 m	Levenstein 1961, 1966
Axiothella sp.				X	**X**		
Clymenura sp.		X		X	**X**		
Lumbriclymene campanatula Detinova, 1984				L		Japan (off east of Honshu), Pacific; 3,042 m	Detinova 1984
Lumbriclymene sp.		X		X	**X**		
Lumbriclymenella brevis Detinova, 1984				L		NW Pacific; 5,210–6,531 m	Detinova 1984
Maldane sarsi Malmgren, 1865	L	**L**	**L**			Cosmopolitan; up to 4,391 m	Annenkova 1937; Uschakov 1953; Levenstein 1966, 1969
Maldane sp.		X		X	**X**		
Maldanella cf. *antarctica* McIntosh, 1885		L			**X, L**	Antarctic, North Pacific (Kuril Basin of the Okhotsk Sea, western slope of the Japan Trench and Kuril-Kamchatka Trench); 600–5,740 m	Detinova 1981, 1982
Maldanella japonica Detinova, 1982				L		NW Pacific; 5,502–6,480 m	Levenstein 1973; Detinova 1981, 1982
Maldanella parafibrillata Detinova, 1982			**L**	L	**X**	NW Pacific; 1,740–5,495 m	Levenstein 1961; Detinova 1982
Maldanella sp.					X		
Microclymene tricirrata Arwidsson, 1906			L			Bering Sea, Okhotsk Sea, NW Pacific; Atlantic; 270–4,400 m	Levenstein 1961, 1969
Nicomache sp.				X	**X**		
Notoproctus oculatus Arwidsson, 1906	L		L			NW Pacific, North Atlantic; up to 6,096 m	Annenkova 1937; Levenstein 1961, 1969

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Notoproctus sp.				X	**X**		
Petaloproctus sp.		X		X	X		
Petaloproctus tenuis (Théel, 1879)	L		L			Japan Sea, Okhotsk Sea, Bering Sea, NW Pacific; Arctic, North Atlantic; up to 4,465 m	Annenkova 1937; Levenstein 1961, 1969
Praxillella gracilis orientalis Zachs, 1933	L		L			Japan Sea, Okhotsk Sea, Bering Sea, NW Pacific; up to 2,460 m	Annenkova 1937; Levenstein 1961, 1969
Praxillella sp.		X		X	X		
Rhodine sp.		**X**					
Oweniidae							
Owenia fusiformis Delle Chiaje, 1844	L					Cosmopolitan, eurybathic	Annenkova 1937; Levenstein 1969
Galathowenia lobopygidiata (Uschakov, 1950)		X	L		**X**	Bering Sea, Okhotsk Sea, Pacific; 110–6,650 m	Uschakov 1950; Levenstein 1961, 1966
Galathowenia sp.				X	**X**		
Myriochele cf. *heeri* Malmgren, 1867		**X**		X	**X**	Cosmopolitan, eurybathic	Jirkov 2001
Sabellariidae							
Gesaia vityazia Kirtley, 1994					**X, L**	Kuril-Kamchatka Trench, Pacific; 5,970 m	Kirtley 1994
Sternaspidae							
Caulleryaspis cf. *nuda* Salazar-Vallejo & Buzhinskaja, 2013		X				Off Oregon, NE Pacific; 2,519 m	Salazar-Vallejo and Buzhinskaja 2013
Sternaspis annenkovae Salazar-Vallejo & Buzhinskaja, 2013			L		**X, L**	East off northern Kuril Islands, NW Pacific; 3,980–4,070 m	Levenstein 1961, 1966; Salazar-Vallejo and Buzhinskaja 2013
Sternaspis cf. *williamsae* Salazar-Vallejo & Buzhinskaja, 2013					X	Off Oregon to California, N Pacific; 1,000–2,800 m	Salazar-Vallejo and Buzhinskaja 2013
Sternaspis scutata (Ranzani, 1817)	L					Cosmopolitan, up to 4,418 m	Annenkova 1937; Levenstein 1969
Pectinariidae							
Pectinaria (Amphictene) moorei Annenkova, 1929	L					Japan Sea, Okhotsk Sea, Bering Sea, NW Pacific; up to 2,900 m	Annenkova 1937; Levenstein 1969

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Ampharetidae							
Abderos sp.					**X**	Central Weddell Sea, Antarctic; 1,582–3,404 m	Schüller and Jirkov 2013
Amage asiaticus Uschakov, 1955	L	**L**				Japan Sea, Okhotsk Sea, Bering Sea, NW Pacific; 28–4,382 m	Annenkova 1937; Levenstein 1961, 1966, 1969
Amage scutata Moore, 1923		X				California, Japan, Pacific; 73–1,229 m	Hilbig 2000; Imajima 2009
Amage sp.1				X	**X**		
Amage sp.2				X	**X**		
Amage sp.3					X		
Ampharete acutifrons (Grube, 1860)	L					Arctic, North Pacific and North Atlantic; up to 2,400 m	Annenkova 1937; Levenstein 1969
Ampharete arctica Malmgren, 1866	L					Japan sea, Bering Sea, NW Pacific; up to 5,270 m	Annenkova 1937; Levenstein 1969
Ampharete gagarae Uschakov, 1950			L			Bering Sea, NW Pacific; 1,928–2,133 m	Levenstein 1961, 1966
Ampharete sp.1		X		X	X		
Ampharete sp.2	X						
Amphicteis cf. *wesenbergae* Parapar, Helgason, Jirkov & Moreira, 2011		X				Greenland and Norwegian Sea, Bay of Biscay, Atlantic; 624–2,544 m	Parapar et. al. 2011; Aguirrezabalaga and Parapar 2014
Amphicteis japonica McIntosh, 1885	L		L			Japan Sea, Okhotsk Sea, Bering Sea, Aleutian Trench, Japan Trench, NW Pacific; up to 7,587 m	Annenkova, 1937; Levenstein, 1961, 1966, 1969, 1973
Amphicteis mederi Annenkova, 1929	L					Japan Sea, Okhotsk Sea, Japan Trench, NW Pacific; up to 8,100 m	Annenkova, 1937; Levenstein, 1969, 1973
Amphicteis sp.1		X		X	**X**		
Amphicteis sp.2				X	**X**		
Amphicteis sp.3					X		
Anobothrus apaleatus Reuscher, Fiege & Wehe, 2009		X				Kuril Basin of the Okhotsk Sea, NW Pacific; NE and SE Pacific; 2,206–3,352 m	Reuscher et. al. 2009; Alalykina 2018
Anobothrus auriculatus Alalykina & Polyakova, 2019				X	**X**	Kuril-Kamchatka Trench and adjacent abyssal plain, Pacific; 5,120–9,584 m	Alalykina and Polyakova 2019

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Anobothrus fimbriatus Imajima, Reuscher & Fiege, 2013		X		L	**X**	Kuril Basin of the Okhotsk Sea, western slope of the Kuril-Kamchatka Trench, Pacific coast of Hokkaido; 1,997–3,377 m	Imajima et. al. 2013; Alalykina 2018
Anobothrus gracilis (Malmgren, 1866)	L					Widely distributed in Arctic, North Atlantic, and North Pacific; up to 2,900 m	Annenkova 1937; Levenstein 1969
Anobothrus jirkovi Alalykina & Polyakova, 2019					**X**	Kuril-Kamchatka Trench and adjacent abyssal plain, NW Pacific; 3,360–5,780 m	Alalykina and Polyakova 2019
Anobothrus mironovi Jirkov, 2009		X			**X**	Pacific, widely distributed; 880–3,890 m	Jirkov 2009
Anobothrus patersoni Jirkov, 2009				X	**X**	North Pacific and North Atlantic; 3,260–8,292 m	Jirkov 2009
Anobothrus sonne Alalykina & Polyakova, 2019		X		X	**X**	Kuril Basin of the Sea of Okhotsk, Kuril-Kamchatka Trench and adjacent abyssal plain, NW Pacific; 3,300–7,123 m	Alalykina & Polyakova 2019
Anobothrus sp.nov.1		X		X	**X**		
Glyphanostomum pallescens (Théel, 1879)			L			Arctic, Pacific; 2,622–3,788 m	Levenstein 1961, 1966
Glyphanostomum sp.nov.1		X			X		
Glyphanostomum sp.nov.2		X			X		
Grubianella antarctica McIntosh, 1885				X	**X**	Weddell Sea, Antarctic; Japan Trench, Aleutian Trench, Pacific; 3,300–5,020 m	Hartman 1966; Kucheruk 1976, 1981; Hilbig et al. 2006
Jugamphicteis sp.				X	**X**		
Lysippe labiata Malmgren, 1866			L			Arctic, North Pacific, North Atlantic; 29–4,400 m	Levenstein 1961, 1966
Lysippe nikiti Jirkov, 2016		X		X	**X**	North Pacific and Indian Oceans; 4,180–6,210 m	Jirkov 2016
Lysippe sexcirrata (Sars, 1856)			L			Arctic, North Pacific, North Atlantic; up to 4,820 m	Levenstein 1961; Jirkov 2001

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Lysippe sp.1				X	**X**		
Lysippe sp.2				X	**X**		
Melinantipoda quaterdentata Kucheruk, 1976				L	**X**	Japan (off east of Honshu and Hokkaido), Hjort Trench, Pacific; 2,970–4,000 m	Kucheruk 1976; Levenstein 1978
Melinna cf. *cristata* (M. Sars, 1851)			**L**	X	**X**	Cosmopolitan, eurybathic	Levenstein 1961, 1966; Jirkov 2001
Melinna elisabethae McIntosh, 1914	L					Arctic, North Pacific and North Atlantic; up to 2,900 m	Annenkova 1937; Levenstein 1969
Melinna ochotica Uschakov, 1950			L			Bering Sea, Okhotsk Sea, NW Pacific; 1,366–2,420 m	Levenstein 1961, 1966
Melinnampharete eoa Annenkova, 1937	L	**X**	**L**	X	**X**	Japan Sea, Bering Sea, Kuril-Kamchatka Trench, Pacific; Icelandic waters, NE Atlantic; 78–6,150 m	Annenkova 1937; Levenstein 1969; Buzhinskaja 2013; Parapar et al. 2014
Melinnopsis annenkovae (Ushakov, 1952)		**X**	**L**	L	**X**	Bering Sea, Kuril Basin of the Okhotsk Sea, off South-East Kamchatka, Pacific; 3,940–4,200 m	Uschakov 1952; Levenstein 1961, 1969;Buzhinskaja 2013; Alalykina 2018
Noanelia cf. *hartmanae* Desbruyères & Laubier, 1977		X			**X**	Bay of Biscay, Reykjanes Ridge, Charlie-Gibbs Fracture Zone, Atlantic; 1,550–4,251 m	Parapar et al. 2014
Noanelia sp.nov.				X	**X**		
Paiwa abyssi Chamberlin, 1919				L	**L**	Kuril-Kamchatka Trench, Japan Trench, North Pacific; 3,620–5,200 m	Kucheruk 1976, 1981
Samythella elongata Verrill, 1873			L	X	**X**	Atlantic, Arctic and NW Pacific Ocean; 125–5,461 m	Levenstein 1961, 1969; Jirkov 2001; Buzhinskaja 2013
Samythopsis sp.nov.		X			X		
Sosane sp.nov.					X		
Sosane sp.1		X		X	X		
Sosane sp.2		X		X	**X**		
Sosane sp.3					X		
Tanseimaruana vestis (Hartman, 1965)		X			**X**	West Atlantic, Antarctic, NE Pacific (Alaska Bay); 37–3,350 m	Hartman 1965, Parapar et.al. 2011

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Ymerana sp.nov.		X					
Ampharetidae Gen. sp.1				X	**X**		
Terebellidae							
Artacama proboscidea Malmgren, 1866			L			Arctic, North Atlantic and North Pacific; 1,928–3,260 m	Levenstein 1961, 1966
Lanassa sp.		X					
Laphania sp.		X			X		
Leaena sp.				X	**X**		
Lysilla pacifica Hessle, 1917			**L**	L		Bering Sea, off Japan (east of Honshu), Pacific; 3,789 m	Levenstein 1961, 1966
Pista agassizi Hilbig, 2000			L			Bering Sea, Okhotsk Sea, Japan Sea, Pacific; up to 2,995 m	Levenstein 1961; Hilbig 2000; Leontovich and Jirkov 2011
Pista incarrientis Annenkova, 1925	L						Annenkova 1937; Levenstein 1969
Pista mirabilis McIntosh, 1885				L	**X, L**	Antarctic, Pacific; 100–5,000 m	Saphronova 1884
Pista paracristata Saphronova, 1988		X	L		**L**	Kuril Basin of the Okhotsk Sea, Bering Sea, Aleutian, Kuril-Kamchatka Trench, Japan and Peru-Chile trenches, Pacific; 1,680–3,875 m	Levenstein 1961; Saphronova 1988; Alalykina 2018
Pista pencillibranchiata Saphronova, 1984				L	**L**	From Aleutian to Japan Trench, Pacific; 3,990–4,180 m	Saphronova 1884
Pista sp.1					X		
Pista sp.2					X		
Polycirrus sp.	X			X	**X**		
Proclea sp.		X					
Streblosoma bairdi (Malmgren, 1866)	L		L			Japan, Okhotsk and Bering Seas, Pacific; NE Atlantic; up to 2,200 m	Annenkova 1937; Levenstein 1961, 1969
Streblosoma sp.		X					
Stschapovella tatjanae Levenstein, 1957			L			Bering Sea, NW Pacific; 2,622–3,034 m	Levenstein 1957, 1961, 1969
Thelepus cincinnatus (Fabricius, 1780)	L		L			Cosmopolitan; up to 3,940 m	Annenkova 1937; Levenstein 1961, 1969

Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Terebellidae Gen. sp.1		X		X	**X**		
Terebellidae Gen. sp.2		**X**					
Trichobranchidae							
Terebellides cf. *stroemi* Sars, 1835	X, L		L			Cosmopolitan; up to 3,980 m	Annenkova 1937; Levenstein 1961, 1969; Alalykina 2013
Terebellides sp.		X		X	**X**		
Trichobranchus sp.1		X			X		
Trichobranchus sp.2		**X**					
Sabellidae							
Chone sp.		X		X	**X**		
Euchone cf. *incolor* Hartman, 1965		X				Off New England, Atlantic; Bering Sea, Pacific; 97–2,500 m	Hartman 1965; Reish 1965
Euchone papillosa (Sars, 1851)	L					Japan Sea, Arctic, Atlantic; up to 2,900 m	Uschakov 1955; Levenstein 1969
Euchone sp.		X		X	**X**		
Fabriciola sp.		X					
Jasmineira filatovae Levenstein, 1961			**L**	L		North Pacific; 3,747–6,757 m	Levenstein 1961, 1966, 1973
Jasmineira pacifica Annenkova, 1937	L					Japan Sea, North Pacific; up to 2,900 m	Annenkova 1937; Levenstein 1969
Jasmineira sp.		X		X	**X**		
Potamethus sp.1		X		X	**X**		
Potamethus sp.2		X					
Potamilla abyssicola Uschakov, 1952		**X**	**L**	L	**X**	Bering Sea, off east Kamchatka, Pacific; 2,440–4,200 m	Uschakov 1952; Levenstein 1961, 1969
Serpulidae							
Bathyditrupa hovei Kupriyanova,1993				L	**L**	Kuril-Kamchatka Trench, North and Central Pacific Ocean; 4,104–6,330 m	Kupriyanova 1993; Kupriyanova et. al. 2011
Bathyvermilia zibrowiusi Kupriyanova, 1993					**L**	Kuril-Kamchatka Trench, Aleutian Trench; 3,610–4,550 m	Kupriyanova 1993; Kupriyanova et. al. 2011

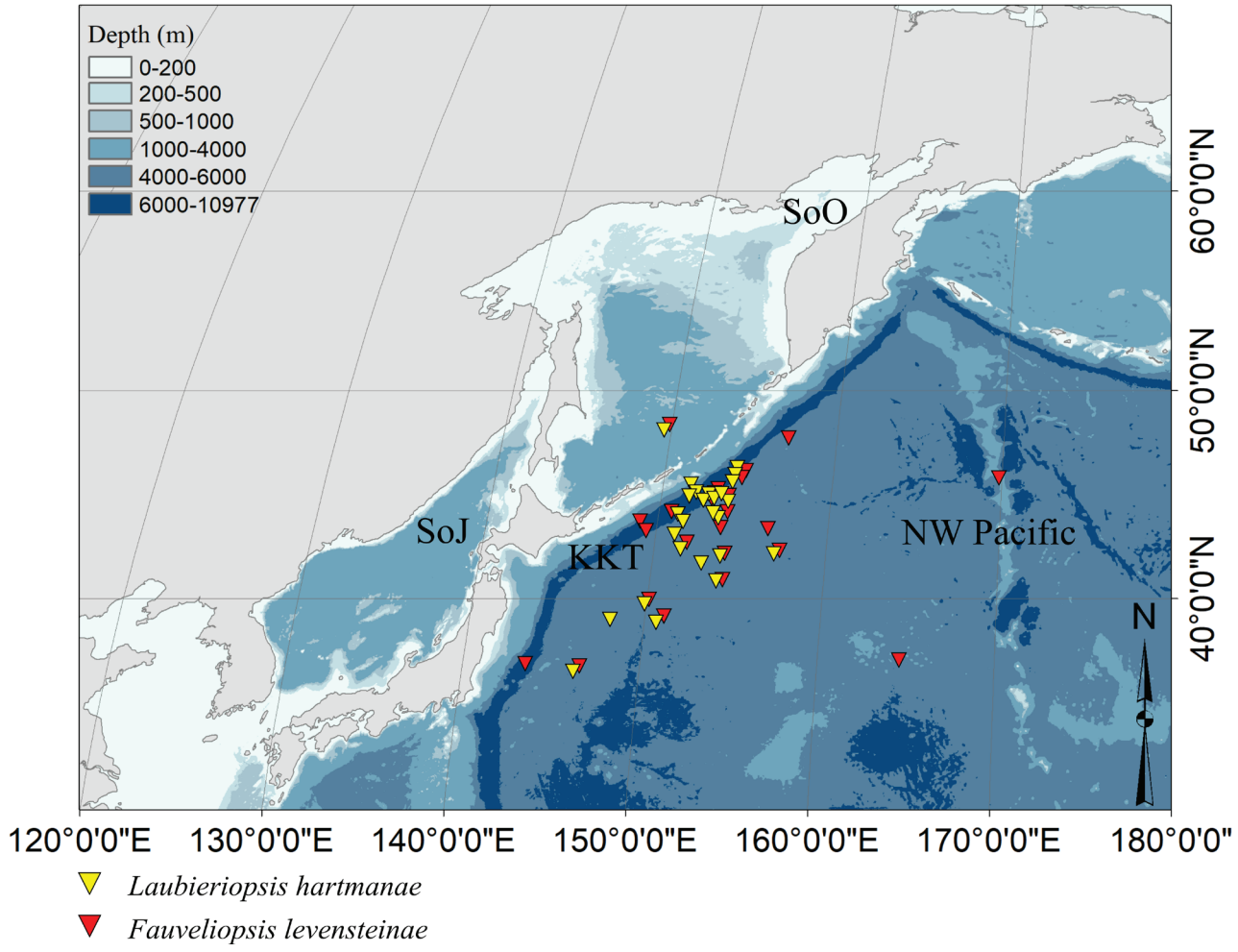
Species	Japan Sea	Okhotsk Sea	Bering Sea	NW Pacific abyssal plain	KKT	Distribution	Reference
Bathyvermilia challengeri Zibrowius, 1973				L		Mid-Pacific Ocean; 4,246–5,719 m	Kupriyanova 1993; Kupriyanova et. al. 2011
Hyalopomatus mironovi Kupriyanova, 1993					**L**	Kuril-Kamchatka Trench, off California, Pacific; 5,110–5,120 m	Kupriyanova 1993
Hyalopomatus sikorskii Kupriyanova, 1993					**L**	Kuril-Kamchatka Trench, North Pacific Ocean south of Japan; 4,000–4,550 m	Kupriyanova 1993; Kupriyanova et. al. 2011
Hyalopomatus sp.				X	**X**		
Protis polyoperculata Kupriyanova, 1993					L	Kuril-Kamchatka Trench, Pacific; 5,020–5,110 m	Kupriyanova 1993
Serpulidae Gen.sp.							
Spirorbidae							
Spirorbidae Gen.sp.		**X**			**X**		
Siboglinidae							
Siboglinidae Gen.sp.		**X**			**X**		
Trochochaetidae							
Trochochaeta sp.		X		X	X		
Tomopteridae							
Tomopteris (Johnstonella) pacifica (Izuka, 1914)				L		Bering Sea, Okhotsk Sea, Pacific; up to 4,000 m	Uschakov 1952, 1972
Tomopteris sp.					X		
Typhloscolecidae							
Sagitella kowalewskii Wagner, 1872				L	X	Cosmopolitan; up to 4,800 m	Uschakov 1952, 1972
Travisiopsis levinseni Southern, 1910				L	L	Kuril-Kamchatka Trench, Pacific; up to 4,000 m	Uschakov 1952, 1972
Travisiopsis sp.					X		
Polychaeta fam.1 indet.		X			X		
Polychaeta fam.2 indet.				X			
Polychaeta fam.3 indet.				X	X		
Number of species	50	163	56	178	235		

(Belyaev 1966, 1989; Jamieson et al. 2011) and is also confirmed by the presented results.

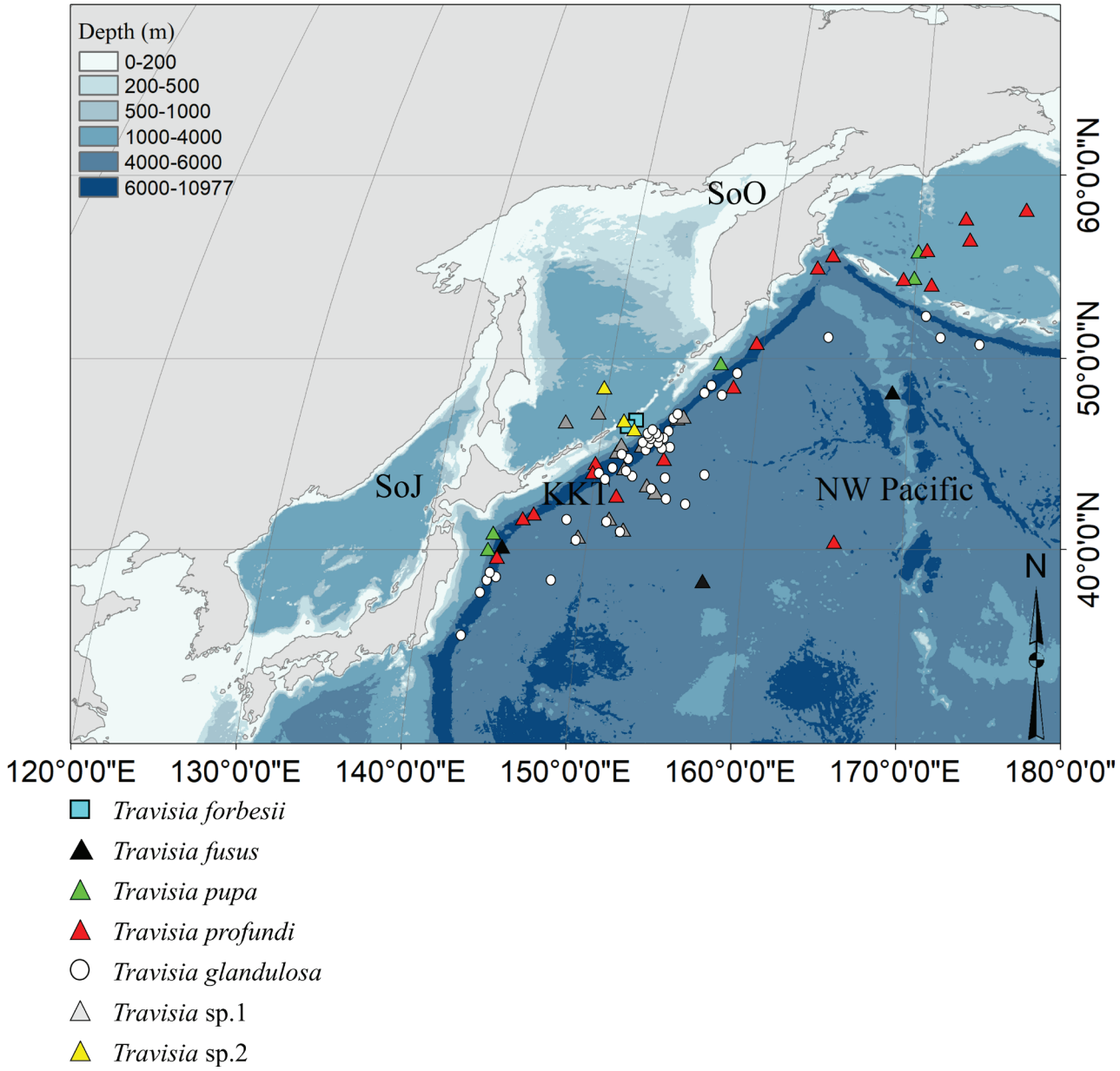
5. Discussion

In general, analyses of geographical distribution patterns indicate that many deep-sea polychaetes have wide distribution ranges at depths below 2,000 m (Hilbig 2004; Hilbig et al. 2006; Méndez 2007; Kupriyanova et. al. 2011; Wilmsen and Schüller 2011). The wide geographical distribution of deep-water polychaetes, resulting from population connectivity among the Antarctic, Atlantic, and Pacific faunas, has been already shown in previous studies (Hilbig 2004; Hilbig et al. 2006; Méndez 2007; Wilmsen and Schüller 2011). Recently, the wide distribution of the deep-sea sternaspid *Sternaspis* cf. *williamsae* in the NW Pacific Ocean has been also confirmed by mitochondrial DNA sequence data (Kobayashi et al. 2018).

Despite the species composition change between the studied areas (see Table 1), the polychaete composition of the studied NW Pacific region does not seem to differ at higher taxonomic level



Map 2. Distribution of NW Pacific fauveliopsid species *Laubieriopsis hartmanae* and *Fauveliopsis levensteinae*.



Map 3. Distribution of NW Pacific species of genus *Travisia*.

from that of other deep-sea regions worldwide. Our results based on the collected samples are comparable to that reported from the abyssal regions of the Pacific (Fauchald and Hanckock 1981; Méndez 2006), Atlantic (Böggemann 2009), and Antarctic regions (Wilmsen and Schüller 2011). Similar to our findings, the authors above listed Ampharetidae as the most species-rich in the abyss.

To date, considering literature data on polychaete species occurring below 2,000 m in the NW Pacific region, limited between 40 and 60 degrees North latitude and 120–180 degrees East longitude, the deep-sea polychaete fauna accounts 365 species from 54 families. From abyssal depths of the semi-enclosed Sea of Japan and the Bering Sea, a similar number of species (50 and 56, respectively) have been recorded

so far (Table 1). A similar number of the abyssal species was also recorded in the Sea of Okhotsk (163 species) and in the abyssal Pacific plain (178 species). From abyssal and hadal depths of the KKT a total of 235 polychaete species were reported (Table 1).

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CHAPTER 11

ECHIURA

A REVIEW ON BIOGEOGRAPHY OF THE DEEP-SEA ECHIURA ALONG THE NW PACIFIC

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1. Introduction

Echiurans are unsegmented coelomate marine worms, considered a separate annelid group with completely reduced segmentation (see Nielsen 1995; Staton 2003; Stephen and Edmonds 1972; Struck et al. 2011; Zenkevitch 1958). They have a sausage-shaped body with a highly extensible anterior proboscis. We have limited knowledge about the life processes of these worms; however, they are typical deposit feeders. Their highly mobile proboscis is used to collect detritus and also as a sensory and respiratory organ (Stephen and Edmonds 1972).

Echiurans inhabit all regions of the World Ocean from littoral to hadal depths, supporting high abundance in a wide bathymetric range from 0 to 10,210 m (Biseswar 2009, 2010, 2012; Stephen and Edmonds 1972; Zenkevitch 1958, 1966, 1969), with a maximal number of species found at bathyal and abyssal depths (Murina 1978). Approximately 190 species of echiurans have been described to date (see Biseswar 2009, 2010, 2012, 2015; WoRMS, 2019).

The most recent classification of the echiurans was published by Goto (2016). Echiura comprises two superfamilies, Echiuroidea (with the families Echiuridae Quatrefages, 1847, Urechidae Monro, 1927, and Thalassematidae Forbes & Goodsir, 1841) and Bonellioidea (with the families Bonelliidae Lacaze-Duthiers, 1858 and Ikedidae Bock, 1942) (Goto 2016).

Further systematic divisions of echiurans are based on the absence or presence of marked sexual dimorphism (presence of dwarf males), the proboscis shape, the number of gonoducts, the absence or presence of anterior ventral or posterior chaetae rings and the shape of the anal sacs (Stephen and Edmonds 1972).

The sexual dimorphism of dwarf males in Bonelliidae was hypothesized to be an adaptation to the deep-sea environment (Goto et al. 2013; Zenkevitch 1966). It has also been suggested that dwarf males may have evolved in shallow waters, and the sexual dimorphism of the dwarf males may have been a preadaptation for the deep-sea environment (Goto 2016).

Current knowledge of the deep-sea echiuran fauna in the northwestern Pacific (NWP) is based on the results of several cruises of the RV *Albatross* in 1906, RV *Gagara* in 1932, the RV *Vityaz* in 1949–1954 to the Kuril-Kamchatka and Japanese Trenches and RV *Lavrentyev* in 2015 to the Sea of Okhotsk (Goto 2016; Fisher 1946, 1949; Maiorova and Adrianov 2018; Makarov 1950; Murina 1976, 1978; Zenkevitch 1957, 1958, 1964; 1969; Zenkevitch and Murina 1976). Until now, over 30 species in 20 genera were known to occur in this region at depths ranging from 0 to 9,700 m (Makarov 1950; Murina 1976, 1978; Zenkevitch 1957, 1958, 1964). Most of these species were originally described in the NWP, except for *Echiurus echiurus* (Pallas, 1766) and *Sluiterina sibogae* (Sluiter, 1902).

Six echiuran species, *Alomasoma nordpacificum* Zenkevitch, 1958, *Alomasoma belyaevi* (Zenkevitch, 1964) (1 specimen in Zenkevitch and Murina, 1978), *Bonelliopsis* sp. (in Maiorova and Adrianov, 2018), *Pseudoikedella achaeta* (Zenkevitch, 1958), *Jakobia birsteini* (Zenkevitch, 1957), *Vitjazema ultraabyssalis* (Zenkevitch, 1958), have been reported from the Kuril-

Kamchatka Trench (KKT) area (Maiorova and Adrianov 2018; Zenkevitch 1957; 1958; 1969; Zenkevitch and Murina 1976). Three species of echiurans have been reported from the nearby Japan Trench and six from the semi-enclosed Sea of Okhotsk (Zenkevitch and Murina 1976): *Alomasoma nordpacificum* Zenkevitch, 1958, *Pseudoikedella achaeta* (Zenkevitch, 1958), *Prometor grandis* (Zenkevitch, 1957), *Jakobia birsteini*, *Protobonellia* sp., *Bengalus* sp. have been reported in this area (Zenkevitch 1957; 1958; 1969; Zenkevitch and Murina 1976). In the Sea of Japan, echiurans have been reported only at depths less than 900 m (Ikeda 1904, 1924; Sato 1937; Makarov 1950; Murina and Chernishev 2009). The high-density population of unknown echiurans has been observed by ROV at depth 400–700 m at the slope of Gamov Canyon (collection of NSCMB FEBRAS). Recent re-descriptions of some species from Japan have provided new data on the morphology of echiurans from the NWP (Nishikawa 2002; Tanaka and Nishikawa 2013; Tanaka et al. 2014). Perhaps the future number of species in the declared region will change since some descriptions of new species are based on only the proboscis or on damaged specimens whose important diagnostic characters cannot be seen (e.g., Murina 1976; Zenkevitch 1964).

2. Objectives

In this chapter we are providing a review of the biogeography of the deep-sea Echiura of the NW Pacific Ocean (NWP).

3. Material and Methods

The data used herein represents a compilation of the works published previously Makarov (1950), Zenkevitch (1957, 1958, 1969) and Maiorova and Adrianov (2018, 2019) for the NWP region on Echiura group. Distribution of all echiuran species recorded in NWP at a depth below 2,000 m from 40 to 60 N and between 120 and 180 E are displayed in Map 1.

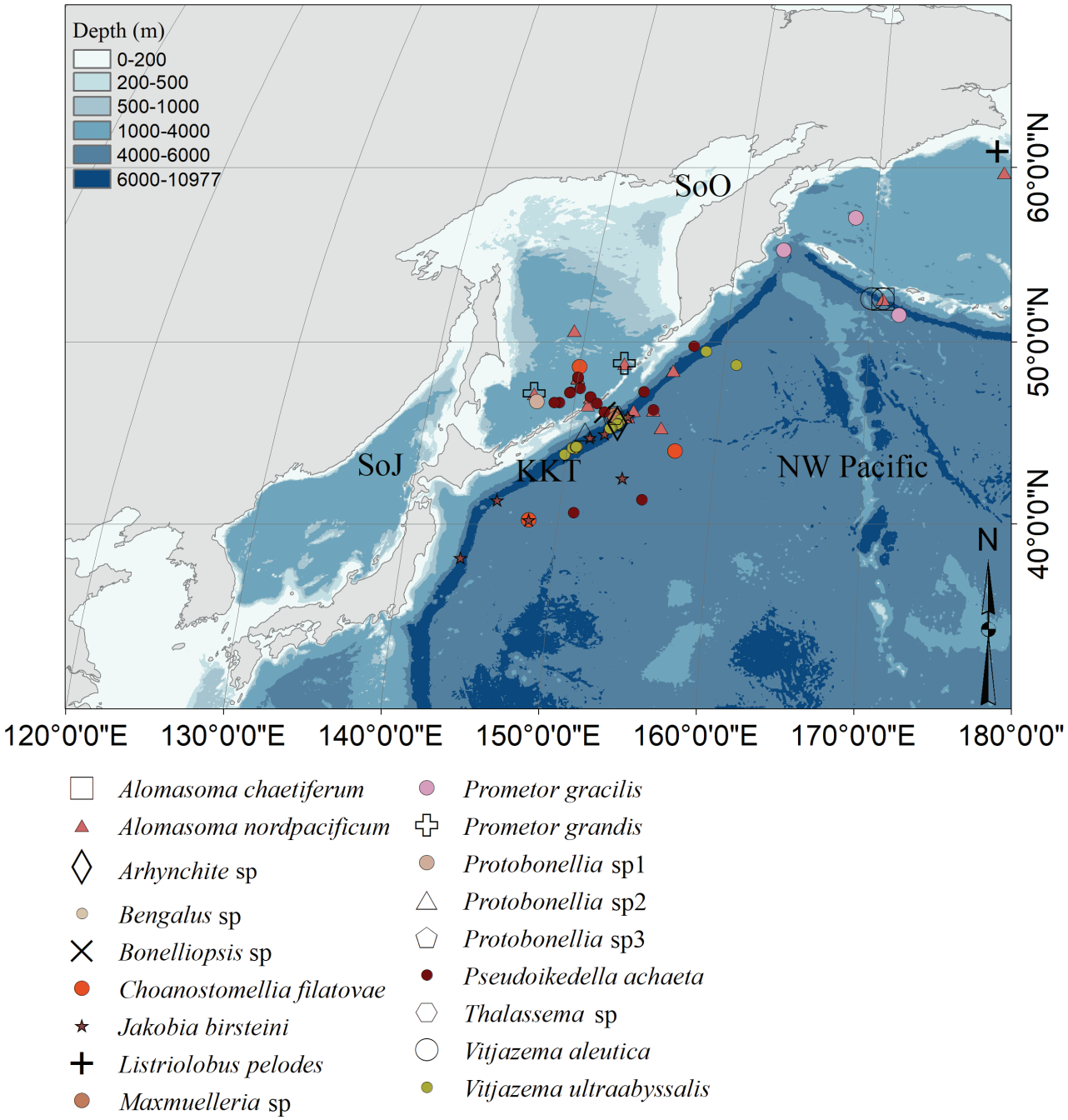
4. Results

4.1. Family Bonelliidae Lacaze-Duthiers, 1858

Genus *Alomasoma* Zenkevitch, 1958

Alomasoma chaetiferum Zenkevitch, 1958

Diagnosis. Proboscis and trunk unknown in life, greyish in preserved state. Trunk from sausage-shaped 40–44 mm in length and up to 20 mm wide across the broadest part. Trunk covered with small rounded papillae. Truncate proboscis equal to trunk length. Lateral edges of proboscis free at base. Distal part of proboscis without distinct lateral lobes. Ventral chaetae present. Single pair of small, sac-like gonoducts which join under the ventral nerve cord and open into a common duct with a single central gonopore. Two anal sacs consist of a main tube with numerous branches terminating in ciliated funnels. Intestine filled with fine, sandy mud moulded into oval faecal pellets.



Map 1. Distribution of deep-sea echiurans in NWP.

Biogeographical remarks. All four species of genus *Alomasoma* inhabit cold water at depths of 418–7,820 m. *A. chaetiferum* is known only from the type locality of the Aleutian Trench at a depth of 7,286 m. *A. rhynchollulus* DattaGupta, 1981 was recorded only from the type locality of the Labrador Sea (North Atlantic). The remaining two *Alomasoma* species are known from widely separated locations. *A. belaevi* Zenkevitch, 1964 was described from the NE Pacific, and later recorded from the Gulf of Panama (single record) and in the Antarctic (numerous records) (Zenkevitch 1964, 1966; Zenkevitch and Murina, 1976; Saiz-Salinas 1996).

***Alomasoma nordpacificum* Zenkevitch, 1958**
(Figure 1)

Diagnosis. Proboscis and trunk bright green in life, greyish in preserved state. Trunk from sausage-shaped to sub-ovoidal, up to 100 mm in length and up to 20 mm wide across the broadest part. Trunk covered with small rounded papillae. Truncate proboscis 2/3 of trunk length. Lateral edges of proboscis smooth and free at base. Distal part of proboscis T-shaped, with short lateral lobes. Ventral chaetae absent. Internally, there is a single pair of small, sac-like gonoducts. Gonoducts join under ventral nerve cord and open into a common duct with a single central gonopore that is clearly visible on ventral side of the trunk. Each gonoduct opens to the gonostome in a middle position, where its stalk still remains in the gonoduct body; thus, the gonostome opens to a coelom by plicated lips in a basal position. Stalk length approximately 1/3 of gonoduct length. Two anal sacs consist of a main tube with numerous branches terminating in ciliated funnels. Intestine filled with fine, sandy mud moulded into oval faecal pellets.

Biogeographical remarks. This species commonly occurs in the NWP, including the Sea of Okhotsk, Bering Sea, Kuril-Kamchatka Trench and adjacent abyssal plain, where it found at 418 to 7,820 m depth (Zenkevitch 1958; Zenkevitch and Murina 1976; Biseswar 2010; Maiorova and Adrianov 2018, 2020).

Genus *Bengalus* Biseswar, 2006

***Bengalus* sp.1.**
(Figure 2)

Diagnosis. Colour of proboscis and trunk whitish in life, greyish to nude in preserved specimens. Trunk ovoid in shape, 20–30 mm in length and 10-15 mm in width at its broadest part. Proboscis spatula-like with rounded distal part originating at the dorsal side of the mouth, forming a funnel around mouth. Ventral chaetae absent. Trunk papillae microscopic and more clearly discernible in contracted trunk. Spherical single gonoduct located on left side of nerve cord. Gonostome basal, gonostomal lips plicated and bilobed. Two spherical anal sacs, thin-walled and have sparsely distributed ciliated minute funnels. Sacs located on lateral sides of a thick and bulbous cloacal chamber. Intestine filled with fine sandy mud not moulded into faecal pellets. Egg size 150 μm. These worms may host colonial hydrozoans (*Halitholus* (?) sp.) on the surface of anterior end of trunk (Stepanjants and Chernyshev 2015).

Biogeographical remarks. This species, identified as a representative of the genus *Bengalus*, is characterized by the presence of a single gonoduct with a basal gonostome, unbranched anal sacs, and the absence of ventral chaetae. The main taxonomic characters of this species coincide well with those given by Biseswar (2006) for the representatives of this genus, except for the shape of the anal sacs (long and tubular). *Bengalus* sp. is similar to *Sluiterina vitjazi* (Murina, 1976) based on the shape of the proboscis and trunk, but both species differ by the position and morphology of the gonoduct. Four specimens were found at 4,988–4,998 m depth at the landward slope of KKT.

***Bengalus* sp.2.**
(Figure 3)

Diagnosis. Colour of proboscis and trunk is opal-yellow in life, greyish in preserved specimens. Trunk ovoid in shape, 20–40 mm in length and 10–20 mm in width at its broadest part.

Proboscis spatula-like with a rounded distal part originating at the dorsal side of the mouth, not forming a funnel around mouth. Ventral chaetae absent. Trunk papillae microscopic and more clearly discernible in contracted trunk. Short single gonoduct located on the right side of a nerve cord. Gonoduct tubular, distended in middle part. Gonostome terminal, gonostomal lips plicated and bilobed. Two spherical anal sacs, thin-walled and have sparsely distributed ciliated funnels. Sacs located on lateral sides of a thick and bulbous cloacal chamber.

Biogeographical remarks. The genus *Bengalus*, with the single species *B. longiductus* Biseswar, 2006, described from the Porcupine Abyssal Plain in the NE Atlantic from the depth 4,838–4,844 m (Biseswar 2006). Eight specimens were found at 3,300–3,350 m depth in the Kuril Basin of the Sea of Okhotsk. This is the first record of *Bengalus* representatives in the Pacific Ocean.

Genus *Bonelliopsis* Fisher, 1946

***Bonelliopsis* sp.**
(Figure 4)
Diagnosis. Colour of the trunk ranges from reddish to violet in a preserved state. Ovoid-shaped trunk 20 mm long and 12 mm wide across broadest part. Rounded papillae densely distributed over the entire surface of trunk. Integument thick, opaque and covered with mucous. Proboscis longer than trunk, forms funnel-like structure around mouth; distal part of proboscis missing. Pair of pen-shaped, gold-coloured ventral chaetae located on papillae-like structure. Distal tip of chaetae tridentate. Interbasal muscle present between chaetae. Single tubular gonoduct (half trunk length) located on the left side of the nerve cord. Distal gonostome stalked (stalk length 1/3 of gonostome) with petaloid gonostomal lips. Two anal sacs dendritic and apricot in colour, with long tubules aggregated in bushes with funnel at each tip.

Biogeographical remarks. There are only two previously described species of *Bonelliopsis*, an intertidal species, *B. alaskana* Fisher, 1946 (Alaska), and a deep-water (2,240 m) species, *B. minutus* DattaGupta, 1981 (47°36'N 8°33'W, NW Atlantic). Two specimens were found at 4,700 m depth at the landward slope of KKT. It is the only record of *Bonelliopsis* representative from the NW Pacific Ocean.

Genus *Choanostomellia* Zenkevitch, 1964

***Choanostomellia filatovae* (Zenkevitch, 1964)**
(Figure 5)
Diagnosis. Colour of the trunk is yellow-brownish in life, greyish in preserved state. Trunk spindle-shaped and up to 70 mm in length and 10–15 mm wide across broadest part. Skin moderately opaque. Elongated trunk papillae minute and densely arranged in transverse rows on the contracted body; relaxed trunk looks smooth and devoid of papillae. Distal end of the proboscis is rounded, lateral edges close together, giving proboscis a tubular appearance, and joining near the mouth to form a funnel. Single gonoduct, thin-walled voluminous with basal gonostome and petaloid gonostomal lips located on the right side of the nerve cord. Pair of long (up 1/6 of trunk length) anal sacs covered by long tubular funnels, opening into rectum on lateral sides of cloacal chamber. Each anal sac consists of a primary tube with many lateral branching tubules terminating in ciliated funnels. Egg size 500 μm.

Biogeographical remarks. DattaGupta (1981) recorded *C. bruuni* and *C. filatovae* in the Bay of Biscay in the Atlantic Ocean. *Choanostomellia bruuni* (Zenkevitch, 1964) which was firstly recorded by Zenkevich from the northern part of the Arabian Sea and off east coast of South Africa (Zenkevitch 1964a, 1966). Previously, *Choanostomellia filatovae* known to be distributed near northern Japan, in the Sea of Okhotsk and the Philippine Sea (Zenkevitch 1964b).

Genus *Jakobia* Zenkevitch, 1958

Jakobia birsteini Zenkevitch, 1958

(Figure 6)

Diagnosis. Colour of trunk is light brown to greenish brown in life, beige pink to light grey in preserved state (formalin); the proboscis distal tip of small and medium sized worms is porcelain white. Trunk 30–70 mm long and up to 8 mm wide across broadest section. Trunk papillae rounded and flattened. Papillae at most posterior trunk nearly triangular, bent and pointing forward to anterior end of trunk. Proboscis thickened and as long as trunk with distal end flattened to form capitulum that is about two times wider than main stem of proboscis. Proboscis cross-section oval. Mouth surrounded on sides by two well-developed lips forming V-shaped mouth opening. Ventral chaetae absent. Single gonoduct located on the right side of the nerve cord, and consists of a sac and long V-shape muscular gonostome tube. Gonostome tube stalked, funnel-shaped with petaloid gonostomal lips. Expanded pharynx anchored to body wall by strong muscles. Intestine attached by minute mesenteries to body wall. Single anal sac tubular, 1/10 – ½ of trunk length and opening to cloaca on right side (close to nerve cord). Cloacal chamber thick and bulbous. Tubular surface of anal sac covered by small ciliated funnels. Egg size 300 μm.

Biogeographical remarks. *Jakobia birsteini* differs from other representatives of the genus (*J. similaris* DattaGupta, 1981; *J. densopapillata* Biseswar, 2006; *J. edmondsi* Murina, 2008) by the shape of the dermal papillae (triangular at the posterior end) and by the unbranched anal sac (Biseswar 2006; DattaGupta 1981). *J. birsteini* burrows deep in the sediment and trawling gear cannot pull them out intact. Distributed in the Sea of Okhotsk (Maiorova and Adrianov 2018), Kuril-Kamchatka and Japan Trenches, as well as from the Gulf of Alaska and off the coast of Peru (Zenkevitch 1958; Zenkevitch and Murina 1976) at depths ranging from 3,300 to 8,737 m (Maiorova and Adrianov 2020). The shallowest recorded specimen of *J. birsteini* found at depth 769 m near Coco Guyot (Pacific Ocean) by RV *Lavrentyev* (cruise 86, July-August 2019) (own data).

Genus *Maxmuelleria* Bock, 1942

Maxmuelleria sp.

(Figure 7)

Diagnosis. Colour of the proboscis and trunk is yellow cream in life, greyish in preserved specimens. Trunk ovoid in shape, 23 mm in length and 10 mm across broadest part. Proboscis long (30 mm in length) ribbon-like, truncate, and distal tip unknown. Lateral margins of proboscis unite at base, forming a narrow funnel around mouth. Pair of pen-shaped, golden-yellow ventral chaetae located on papillae-like structure, strong interbasal muscle present between chaetae. Trunk papillae uniformly distributed over the entire surface of trunk. One pair of gonoducts, each

open outside by its own gonopore. Gonoducts small, oval, located posterior to ventral chaetae. Gonostome long, tubular, located basally. Opening of gonostome with simple gonostomal lip. Two elongated anal sacs branching three times and covered by slender tubules with apical funnels. Each sac located on lateral side of bulbous cloacal chamber and anchored to body wall by mesenteries. Egg diameters 300 μm.

Biogeographical remarks. *Maxmuelleria* is one of the most difficult genera to determine species reliably based on the position of gonostome, construction of anal sacs and shape of chaetae. The existing descriptions of five *Maxmuelleria* species have little difference between them. Only two specimens of *M.* sp were found at 6,183–7,154 m depth at the landward slope of KKT.

Genus Prometor Fisher

***Prometor grandis* Zenkevitch, 1957**

(Figure 8)

Diagnosis. Proboscis long ribbon-like and truncate, the borders fusing at the base to form a funnel that leads to the mouth. At the junction of the proboscis and the trunk, the tissues are greatly thickened. Thin-walled trunk 82 mm in length. Pair of articulated ventral chaetae. Zenkevitch (1957) also noted pair of large long gonoducts with adjacent excretory ducts and a common gonopore. Anal sacs with a great number of excretory tubules which have apical ciliated funnels.

Biogeographical remarks. All four valid species of *Prometor* are known from great depths (1,670–4,293 m), mostly found in the northern Pacific Ocean, but with a single record in the Bay of Biscay (Atlantic) (Fisher 1948; Zenkevitch 1957; Hartman and Barnard 1960; DattaGupta 1981). *P. grandis* was collected twice by RV *Vityaz* in the Sea of Okhotsk at depths of 2,970–3,400 m.

***Prometor gracilis* Zenkevitch, 1957**

Diagnosis. Proboscis distal edge twice as long as its width. According to Zenkevitch (1957), the proboscis is more than five times as long as the trunk (three times in *P. grandis*). Milk-white trunk is 40 mm in length. Chaetae set in two pads (six in total) and they are solid, unlike to *P. grandis*, in which they are articulated. Anal vesicles long and thin. This species is closely related to *P. grandis* (see Zenkevitch 1957), but there are conspicuous differences in size and in the proportions between different parts of the body.

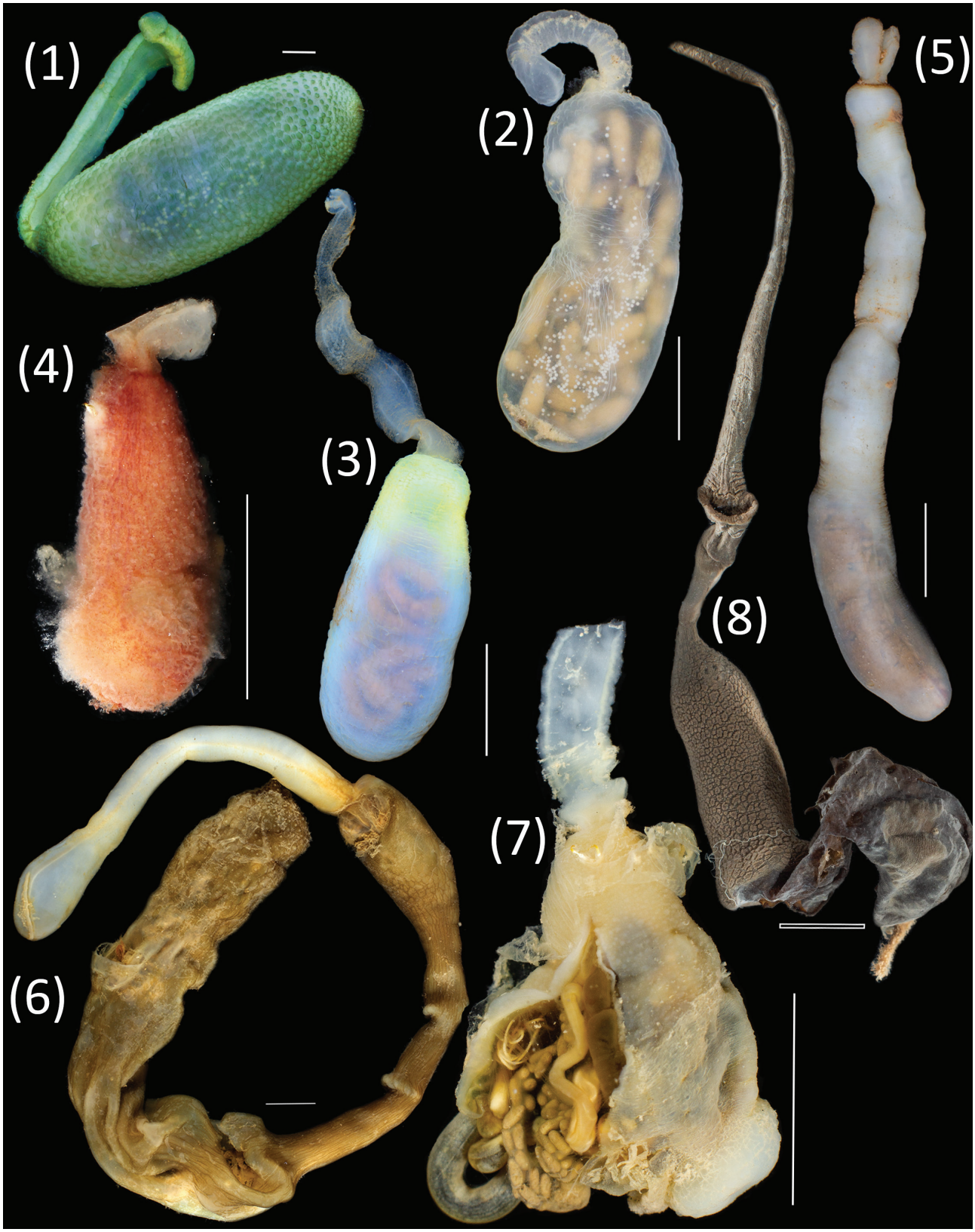
Biogeographical remarks. This species was collected in the Bering Sea and nearby, sometimes in great number, at depths of 3,940–5,020 m.

Genus *Protobonellia* Ikeda, 1908

***Protobonellia* sp.1.**

(Figure 9)

Diagnosis. Colour of proboscis and trunk is light green in life, greyish in preserved specimens. Trunk ovoid in shape, 10 mm in length and 6 mm across broadest part. Proboscis 9 mm in length, and spatula-like with a rounded distal part originating at the dorsal side of the mouth, lateral margins of proboscis unite at the base forming a narrow lower lip, ventral to the mouth. Pair of pen-shaped, golden-yellow ventral chaetae located on a papillae-like structure, with a straight cylindrical shaft (4 mm) and a flattened, curved terminal blade (1 mm), terminating in a pointed tip. Internally, bases of chaetae are supported by radiating



Figures 1–8. *Alomasoma nordpacificum* Bar, 10 mm., *Bengalus* sp.1, *Bengalus* sp.2, *Bonelliopsis* sp., *Choanostomellia filatovae*, *Jakobia birsteini*, *Maxmuelleria* sp., *Prometor grandis*.

muscle strands. Strong interbasal muscle present between chaetae. Trunk papillae are transversely aligned over the entire surface of the trunk, and are more prominent and densely aggregated at the anterior end. Single gonoduct located on the right side of the nerve cord. Gonoduct sac expended by large eggs. Gonostome basal in position, on a long stalk, and with the gonostomal lip with small lobes around margin. The two elongated anal sacs (1.5 mm length) thin-walled and both have sparsely distributed ciliated funnels. Each sac located on the lateral side of a bulbous cloacal chamber. Alimentary canal and vascular system damaged. Specimen are female with eggs in coelom and gonoducts (diameter 500 μm). Males are not observed.

Biogeographical remarks. *Protobonellia* includes six valid species. Most of species have been collected from the northern Pacific Ocean (Ikeda 1908; Murina 1976; Biseswar 2010). *Protobonellia mitsukurii* Ikeda, 1908 was collected at 554 m depth in Sagami Bay (Ikeda 1908). Two species *P. nikitini* Murina, 1976 (5,595–5,660 m, single specimen) and *P. zenkevitchi* Murina, 1976 (5,681–5,740 m, 27 specimens) were collected in Aleutian Trench. A detailed morphological description of *P. zenkevitchi* is provided by Temereva et al. (2017). A single specimen of *Protobonellia* sp.1 found at 5,229–5,266 m depth at the landward slope of KKT.

***Protobonellia* sp.2.**

(Figure 10)

Diagnosis. Colour of the trunk ranges from reddish to violet in life, whitish in a preserved state. Trunk is 20 mm long and 8 mm wide across broadest part. Proboscis of unclear shape, with a low lip it forms a funnel-like structure with furrows around the mouth. Coarse rounded papillae densely distributed over entire surface of trunk. Pair of golden-yellow ventral chaetae located on a papillae-like structure, each chaeta with a straight cylindrical shaft and a wide, flattened, pointed terminal blade. Internally, bases of chaetae supported by strong radiating muscle strands. Interbasal muscle present between chaetae, and foregut fixed between chaetae by a muscle sheath. Longitudinal musculature of the body wall thickened into narrow longitudinal bands. Single sac-like gonoduct located on the right side of the nerve cord. Basal gonostome with gonostomal lips. Egg size 200 μm.

Biogeographical remarks. Single incomplete specimen of *Protobonellia* sp. 2 found at 7,256–7,245 m depth at the landward slope of KKT.

***Protobonellia* sp. 3**

(Figure 11)

Diagnosis. Trunk ovoid in shape and colourless in the preserved specimen. Trunk is 14 mm in length and 7 mm wide at broadest part. Proboscis funnel-shaped around the mouth, distal part is unknown. Ventral edge of proboscis festoon-like. Pair of minute ventral chaetae pen-like, and golden in colour. Interbasal muscle between chaetae present. Single, sac-like gonoduct located on the right side of the nerve cord. Basal gonostome stalked, with fine, petaloid gonostomal lips. Two anal sacs on lateral sides of cloaca dendritic, branching once or twice before terminating in funnels.

Biogeographical remarks. Only one specimen of *Protobonellia* sp. 3 was found at 3,300 m depth in the Kuril Basin of the Sea of Okhotsk.

Genus *Pseudoikedella* Murina, 1978

***Pseudoikedella achaeta* (Zenkevitch, 1958)**
(Figure 12)

Diagnosis. Colour of the proboscis and trunk nude to whitish. Cylindrical trunk up to 55 mm in length and up to 10 mm across broadest part. Minute papillae over the trunk, integument easy to destroy on preserved specimens. Distal tip of proboscis is unknown. Ventral chaetae absent. In some highly contracted specimens, the integument is thick and opaque at trunk extremities where longitudinal muscles can be seen arranged in bands. Body wall thin and transparent in the middle region of trunk. Single sac-shaped gonoduct located on right side of nerve cord and bears a proximal funnel-like gonostome with lips on a stalk that opens at midsac and runs posterior. Two slender anal sacs with thin-walled tubules open to small cloaca on the ventral side, via a single common pore. Surface of anal sacs covered by minute ciliated funnels. Intestine filled with fine, sandy mud not moulded into faecal pellets. Egg size 200 μm.

Biogeographical remarks. Only one species in the *Pseudoikedella* genus. Distributed in the Kuril-Kamchatka Trench and adjacent abyssal plain at depths ranging from 3,800 to 5,404 m (Zenkevitch 1958; Zenkevich and Murina 1976; Maiorova and Adrianov 2018, 2020).

Genus *Vitjazema* Zenkevitch, 1958

***Vitjazema aleutica* Zenkevitch, 1958**

Diagnosis. Colour of the trunk and proboscis is green in life. Trunk sausage-shaped, up to 55 mm in length and up to 23 mm wide across the broadest part. Proboscis is truncate, up to one-half times that of the trunk length. Integument thin and transparent, internal organs visible. Small papillae uniformely cover trunk. Pair of pointed ventral chaetae. Pair of gonoducts, each open outside by its own gonopore. Gonostome located distally. Pair of tubular end anal sacs branch off from cloacal chamber.

Biogeographical remarks. V. *aleutica* described originally by Zenkevitch (1958), is based on two incomplete specimens collected from the Aleutian Trench at a depth of 7,286 m.

***Vitjazema ultraabyssalis* Zenkevitch, 1958**
(Figure 13)

Diagnosis. Colour of the trunk and proboscis is dark green in life, beige in a preserved state. Trunk is sausage-shaped, up to 35 mm in length and up to 10 mm wide across the broadest part. Proboscis is truncate, up one-third of the trunk length. Lateral margins of the proboscis curl ventrally with narrow lower lip. Integument thin and transparent, internal organs visible. Small papillae uniformly cover the trunk. Pair of pointed ventral chaetae, with the bases of the chaetae supported by radiating muscle strands. Pair of gonoducts, each open outside by its own gonopore. Gonoducts small, spherical, located posterior to the ventral chaetae, filled with eggs in some specimens. Gonostome long, tubular, and located distally. Contents of the gut not moulded into faecal pellets. Pair of anal sacs branch off from cloacal chamber. Each anal sac consists of a tubular end sac, one-eights the length of the trunk. Egg size 250 μm.

Biogeographical remarks. All *Vitjazema* species have been found at great depths. V. *aleutica* described originally by Zenkevitch (1958), is

based on two incomplete specimens collected from the Aleutian Trench at a depth of 7,286 m. Specimens of V. *planirostris* were collected from the Philippine Trench at depths ranging from 9,400–9,750 m. V. *micropapillosa* were collected from the North Atlantic, at depths ranging from 2,604–4,632 m. V. *ultraabyssalis* was recorded from the Kuril-Kamchatka, Japan, Izu-Ogasawara, and Marian Trenches at depths ranging from 5,560–9,700 m in the NW Pacific in high abundance. Up 32 specimens per m^2. Also, it was recorded by Murina (1978) from the Great Australian Bight at a depth of 3,880 m.

4.2. Family Thalassematidae Forbes & Goodsir, 1841

Genus Arhynchite Satô, 1937

***Arhynchite* sp.1**

(Figure 14)

Diagnosis. Colour of the trunk and proboscis is camel in life, and flesh colour in a preserved state. Proboscis ribbon-like, truncate, borders fusing at the base to form a funnel, and the distal end is damaged. Trunk is cylindrical, 35 mm in length and 8 mm in width at its broadest part. Body is covered with flattened medium size papillae at the midtrunk and minute papillae at both extremities. Pair of golden chaetae with a straight cylindrical shaft and curved, pointed terminal blades. Internally, the bases of the chaetae are supported by radiating muscle strands. Interbasal muscle well-developed; it ties together ends of ventral chaetae. Alimentary canal damaged, except the anterior part, prominent pharynx and esophagus. Vascular system damaged. Longitudinal and inner oblique layers of muscles continuous and not grouped into bands or fascicles. One pair of short tubular gonoducts, each open outside by its own postchaetal gonopore. Gonostome basal, gonostomal lips damaged. Anal sacs two short slender, thin-walled tubules (one-tenth of the trunk length) opening to small cloaca on ventral side. Minute funnels cover sparsely anal sacs.

Biogeographical remarks. It is eight species of genus *Arhynchite* described for today, and seven of them inhabit the Pacific (except the littoral species A. *paulensis* Amor, 1971 from São Sebastião, Brasil). Also A. *hayaoi* and A. *hiscoki* inhabiting littoral area (Tanaka and Nishikawa, 2013; Fisher, 1949). Low bathyal species are A. *californicus* (55–452 m), A. *pugettensis* (0–70 m), and A. *rugosus* (Fisher, 1946; Chen and Yeh, 1958). Two species, A. *arhynchite* (4,912 m, OBIS) and A. *inamoenus* (4,000 m, DattaGupta, 1991) known from abyssal depth. In KKT this species occur at depth ranging from 8,704–8,738 m and it is the deepest for genus *Arhynchite*.

Genus Thalassema Pallas, 1774

***Thalassema* sp.1**

(Figure 15)

Diagnosis. Proboscis unknown. Trunk ovoid in shape, 35 mm in length and 12–15 mm in width at its broadest part. Body covered with dome-shaped papillae, regularly arranged in few rings over the entire body. Between these rings several smaller papillae scattered. Alternation of regular and scattered papillae more noticeable on the anterior and posterior parts of the trunk. Pair of dark golden chaetae with straight cylindrical shaft and flattened, slightly curved, pointed terminal blade. Internally, bases of chaetae supported by radiating muscle strands. Alimentary canal very long and convoluted,

several times longer than body; oesophagus and foregut relatively short; midgut attached to body wall by numerous fine mesenteries. Longitudinal and inner oblique layers of muscles continuous and not grouped into bands or fascicles, except the most anterior end where oblique muscles plicated. One pair of tubular gonoducts. Gonostome basal on short stalk, with plicated fan-shape upper and minute lower gonostomal lips. Anal sacs two short slender, thin-walled tubules (up quarter of the trunk length) opening to cloaca on lateral sides of thick and bulbous cloacal chamber. Egg size 300 μm in diameter. These worms may host kamptozoa (Borisanova and Chernyshev 2019).

Biogeographical remarks. The deepest record of genus *Thalassema* in general. Only two specimens were found at 6,183–6,185 m depth at the landward slope of KKT.

Genus *Listriolobus* Fischer, 1926

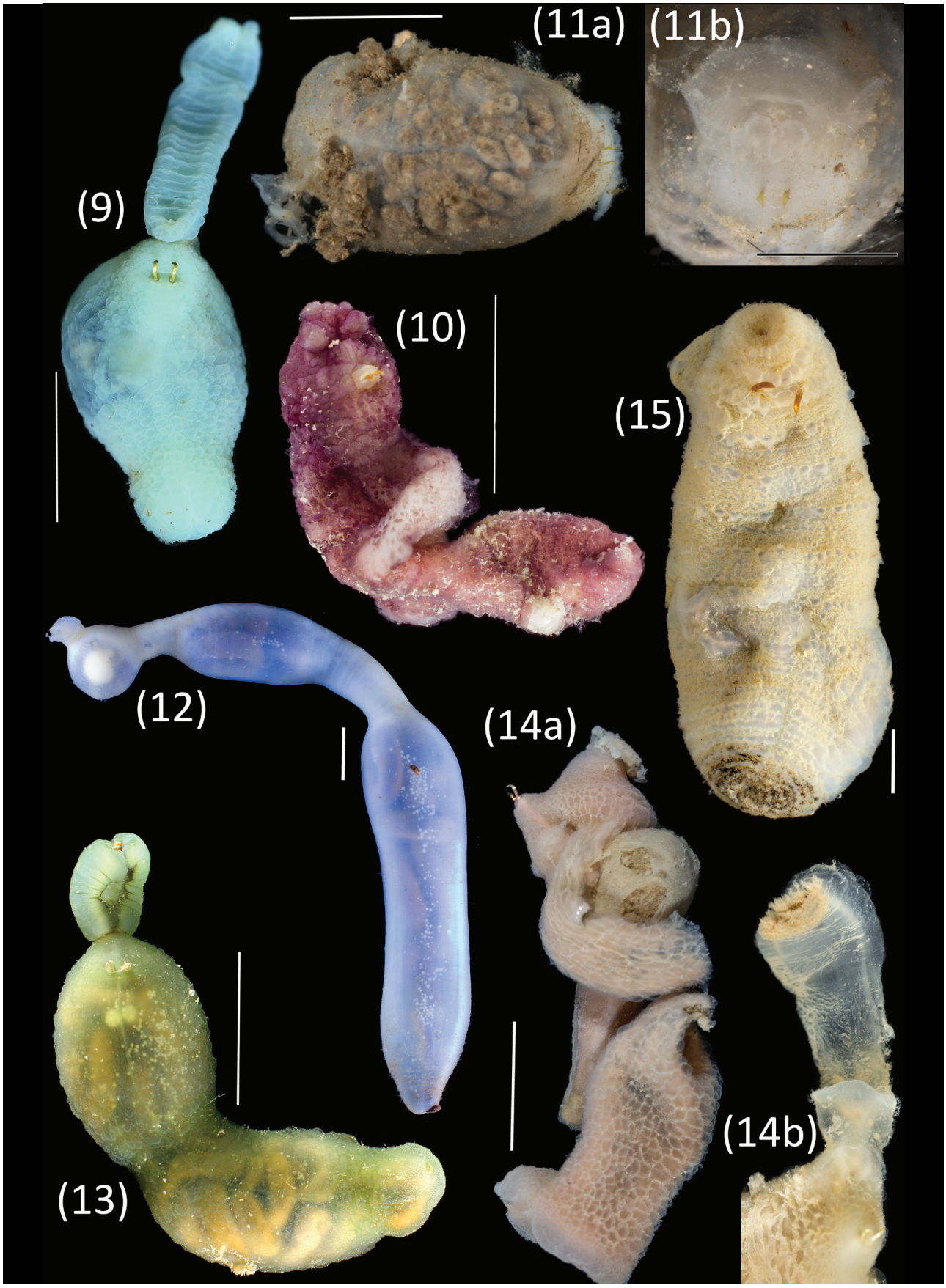
Listriolobus pelodes Fisher, 1946

Diagnosis. Proboscis like that of *Thalassema*. Trunk 40–60 mm in length, 12–25 mm in broadest part. Ventral setae with interbasal muscle. Longitudinal muscles of body wall grouped into eight longitudinal muscle-bands bands. Two pairs of nephridia; the ciliated funnel of the nephrostomes is set on a short stalk and the lips of the nephrostomes are long and coiled. Anal vesicles two in number, capable of great extension and with very small and scattered ciliated funnels.

Biogeographical remarks. *Listriolobus* is one of the most confusing genera within Echiura as far as some of *L.* species were changing their taxonomic position several times (see Nishikawa 2004; Biseswar 2010). Most of the *Listriolobus* species are inhabit tropical intertidal zones except *L. pelodes* from the Baja California (Fisher 1946). According to Barnard and Hartman (1959), a remarkable concentration of *L. pelodes* is found between Santa Barbara and Ventura on the Californian coast at depths of 27–45 m. The total weight of the species in the area is several hundred thousand tons. The record of LA Zenkevitch (1958) of the presence of *L. pelodes* is based on the incomplete specimen with poor preservation. The author also suggested that specimen might be a new species, but the condition of it does not allow for us to describe it as a new species.

5. Discussion

The most ubiquitous NWP echiura species is *Alomasoma nordpacificum*. This species inhabits the Sea of Okhotsk and KKT. Other widespread echiurans are *Vitjazema ultraabyssalis*, *Pseudoikedella achaeta and Jakobia birsteini*. The remaining species (*A. chaetiferum*, *Bengalus* sp1, *B.* sp.2, *Bonelliopsis* sp., *Prometor grandis*, *P. gracilis*, *Protobonellia* sp.1, *P.* sp. 2, *P.* sp. 3, *Maxmuelleria* sp., *Arhynchite* sp.1 *Thalassema* sp.1) are represented by a few specimens mostly, from single locations. Concerning the vertical distribution, *A. nordpacificum and J. birsteini* have one of the broadest depth ranges, many of the other species are more restricted, found either on in the abyss, abyss-hadal, or bathyal-abyssal/hadal. The deepest record of echiurans in the selected area belongs to *V. ultraabyssalis* from 9,700 m in the KKT.



Figures 9-15. *Protobonellia* sp.1, *Protobonellia* sp.2, *Protobonellia* sp.3, *Pseudoikedella achaeta, Vitjazema ultraabyssalis, Arhynchite* sp.1, *Thalassema* sp.1.

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CHAPTER 12

NEMATODA

A REVIEW ON THE DEEP-SEA NEMATOFAUNA ALONG THE NW PACIFIC

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1. Introduction

Nematodes are the most successful metazoan of higher taxa in deep-sea sediments, representing often >90% of the total multicellular animals' abundance (Giere 2009; Ramirez-Llodra et al. 2010). Several thousand individuals and several tens of nematode (morphological) species per 10 cm^2 of bottom sediments have been previously found (Danovaro et al. 2013; Mokievsky 2009). According to some authors, the high abundance and fast life cycle of nematodes, determines their significant contribution to energy and material flows in benthic communities (Coull 1999; Kuipers et al. 1981; McLusky 1981; Warwick and Price 1979). The role of nematodes in the conditioning of bottom sediments is particularly important, as they participate in the formation of sediment texture, changes in the drainage regime, the amount of interstitial water, and dissolved gases (Coull 1999; Findlay Tenore 1982; Nehring et al. 1990).

Nematodes are characterized by a wide variety of morphologies, life histories, and feeding strategies (Decraemer et al. 2014; Moens et al. 2014; Tchesunov 2006). Usually they are small thread-like whitish organisms. However, some representatives are characterized by very deviating body shapes, sizes and colours; and living nematodes can be bright and colourful (Figure 1A). Many species of Desmoscolecidae Shipley, 1896 have a strongly annulated appearance, specimens of Draconematidae Filipjev, 1918 usually have S-shaped bodies and Epsilonematidae Steiner, 1927 have ε-shaped (Figure 1B, C). The adult body size of free-living marine nematodes can be less than 100 microns (for example, *Hapalomus minutus* (Steiner, 1916) Lorenzen, 1969) and more than 40,000 microns (some Leptosomatidae Filipjev, 1916, for example, *Cylicolaimus magnus* (Villot, 1875) de Man, 1889, *Deontostoma magnificum* (Timm, 1951) Platonova, 1962, and *D. timmerchioi* Hope, 1974). The adults of Benthimermithidae Petter, 1980 and Marimermithidae Rubtzov & Platonova, 1974 can reach 17 and 15 cm, respectively. However, typically, free-living deep-sea nematodes are smaller than 1 mm and are considered in studies of the meiobenthos fauna retained on 32-μm sieves (Mokievsky 2009). At the same time, deep-sea nematodes are often found in the macrobenthic size fraction (retained on ≥300-μm mesh sieves), and there they often dominate in numbers and are characterized by high species richness (Gunton et al. 2017; Sharma et al. 2011).

Most marine nematodes have endobenthic life styles; however, some are associated with macroalgae, wood, and dead and decaying animals (Heip et al. 1985; Lorenzen et al. 1987; Rasmussen 1973; Schwabe et al. 2015). Moreover, numerous non-parasitic associations between nematodes and aquatic multicellular animals are known. Nematodes from different taxonomic groups are found in sponges (Schuurmans Stekhoven 1942a; Tsalolikhin 1974; Bongers 1983), bryozoans (Schuurmans Stekhoven 1933) and bivalve molluscs (Schuurmans Stekhoven 1942b), as well as in actively moving animals like annelids (Hopper 1966; Platonova and Potin 1972), crustaceans (Sudhaus 1974; Lorenzen 1986a), gastropods (Holovachov et al. 2011), and whales (Roussel de Vauzème 1834; Baylis 1923). Some genera (*Odontobius* Roussel del Vauzème, 1834, *Gammarinema* Kinne & Gerlach, 1953, and *Tripylium* Cobb, 1920) are exclusively epibiotic (Lorenzen 1986b; Tchesunov 2006). Representatives of Benthimermithidae and

Marimermithidae parasitise the body cavity and internal organs of marine invertebrate hosts as juveniles and emerge in sediments as adults.

It has been suggested that nematodes have a wide range of potential food sources (e.g., dissolved organic carbon (DOC), detritus, bacteria, fungi, microalgae, ciliates, flagellates, foraminiferans, metazoan heterotrophs, and decaying organisms) and may consume a highly mixed diet (Ingels et al. 2011; Moens and Vincx 1997; Moens et al. 1999, 2005, 2014; Pape et al. 2013; Vafeiadou et al. 2014). For some nematode species, close association with chemosynthetic prokaryotes has been shown. Representatives of the subfamily Stilbonematinae Chitwood, 1936 are generally associated with specific ectosymbionts which are attached to the outer cuticle and utilized as the primary food source (Bayer et al. 2009). Species of Astomonematinae Kito & Aryuthaka, 2006 lack a buccal cavity; sulphur-oxidizing bacterial endosymbionts fill almost the entirety of the gut lumen and provide the nematode with nutrition (Musat et al. 2007).

Generally, the entire life cycle of a free-living marine nematode takes place in the bottom sediments (without planktonic or pelagic larvae) and involves an egg, four juvenile stages, and the adult (appearance of juveniles and adults are usually similar). Due to this life style, as well as relatively small body sizes (the inability to overcome long distances), marine nematodes are assumed to have low dispersal capacities. However, many genera of deep-sea nematodes have cosmopolitan or nearly cosmopolitan distributions and quite a number of species show widespread geographic distribution, at least based on morphological criteria for species identification (Miljutin et al. 2010). This implies the possibility of long-distance dispersal of deep-sea nematodes. Various ways of dispersal, both active and passive, have been shown. Nematodes are able to actively move in the sediment (Schratzberger et al. 2004); moreover, some species can actively emerge into and swim in the water column (Jensen 1981). As a result of such mobility, large-bodied nematodes of the family Oncholaimidae Filipjev, 1916 rapidly colonize carcasses of fish and macrofauna (Lorenzen et al. 1987). Some nematode species are often found attached to other invertebrates and thus can spread over considerable distances (Deryck et al. 2013; Sudhaus 1974). Passive dispersal of marine nematodes can occur through movement of sediments, currents, and ballast water of ships (Boeckner et al. 2009; Palmer 1988; Radziejewska et al. 2006).

The composition and structure of deep-sea nematode communities at genus level are significantly determined by macrohabitat heterogeneity and regional differences, and so different deep-sea habitats (for example, abyssal, cold seeps, slope etc.) are characterized by specific nematode assemblages (Vanreusel et al. 2010). At the same time, identifying patterns in the distribution of deep-sea nematodes at the species level, as well as conducting biogeographic analysis, is rather difficult. The determination of the species composition of deep-sea nematode communities is significantly complicated by high species richness and evenness, usually small body sizes of specimens, their high phenotypic plasticity and the presence of cryptic species. For these reasons, species identification requires the time-consuming and laborious process of compound microscopy, highly specialized

personnel and involves the use of molecular approaches. According to "moderate" estimates, only about 12% of the total number of free-living marine nematode species are described to date (Appeltans et al. 2012) and the fauna of deep-sea floor is the least studied. The deep-sea benthic communities occupy tremendous areas of the ocean floor (more than 90%), while only about 16% of all known valid species of nematodes are described from here (Miljutin et al. 2010). Obviously, the currently known deep-sea species (less than 700) are "a drop in the sea".

Population genetic studies confirmed restricted nematode dispersal in shallow-water environments at large geographical scales (>100 km) and revealed cryptic diversity in a wide range of marine nematodes (Armenteros et al. 2014; Bhadury et al. 2008; Derycke et al. 2007, 2008, 2010). Although some of these cryptic species showed restricted geographical distributions, others were widespread and even cosmopolitan, several of them were distributed sympatrically (De Oliveira et al. 2017; Derycke et al. 2007, 2008, 2010; Sahraean et al. 2017). For deep-sea nematodes, the presence of cosmopolitan species has also been shown (Bik et al. 2010a), as well as the presence of cryptic species (De Groote et al. 2017; Hauquier et al. 2017) and barriers to gene flow (Hauquier et al. 2017). Apparently, the dispersal features are determined by the complex interactions between habitat, hydrodynamics, and species-specific traits (Deryck et al. 2013). A quantification of the role of such potential long-distance dispersal on the biogeography of deep-sea nematodes is unavailable, and the relative role of different vectors and barriers on dispersal is still debated. Despite the more than 90-year history of studying deep-sea nematodes, our knowledge about their dispersal, distribution, biogeography, ecology, their role in benthic communities remains limited and the NW Pacific is one of the least studied regions.

2. Objectives

The aim of this study was to review previously published and newly obtained information about the NW Pacific deep-sea nematofauna.

3. Material and Methods

The review includes data from a variety of sources on NW Pacific nematode species occurring below 2,000 m depth from 40 to 60°N degrees latitude and 120 to 180°E degrees longitude.

4. Results

Nematodes were found at all investigated stations at depth ranges from about 2,500 to 9,500 m (Map 1) and were the most abundant meiobenthic organism at all stations except several deepest in the Sea of Japan (below 3,000 m) where polychaetes dominated (Itho et al. 2011; Mordukhovich unpublished; Schmidt et al. 2015, 2019; Trebukhova et al. 2013). The meiobenthic nematode density varied from 1.01 ind./10 cm^2 (the Sea of Japan, 3,666 m) to 1,164.08 ind./10 cm^2 (the Kuril-Kamchatka Trench slope, 4,972 m). Moreover, nematodes were usually encountered in macrofauna communities (retained on ≥300-μm mesh sieves) and sometimes dominated in numbers (Brandt et al. 2013, 2015, 2018, 2019; Fisher, Brandt, 2015).

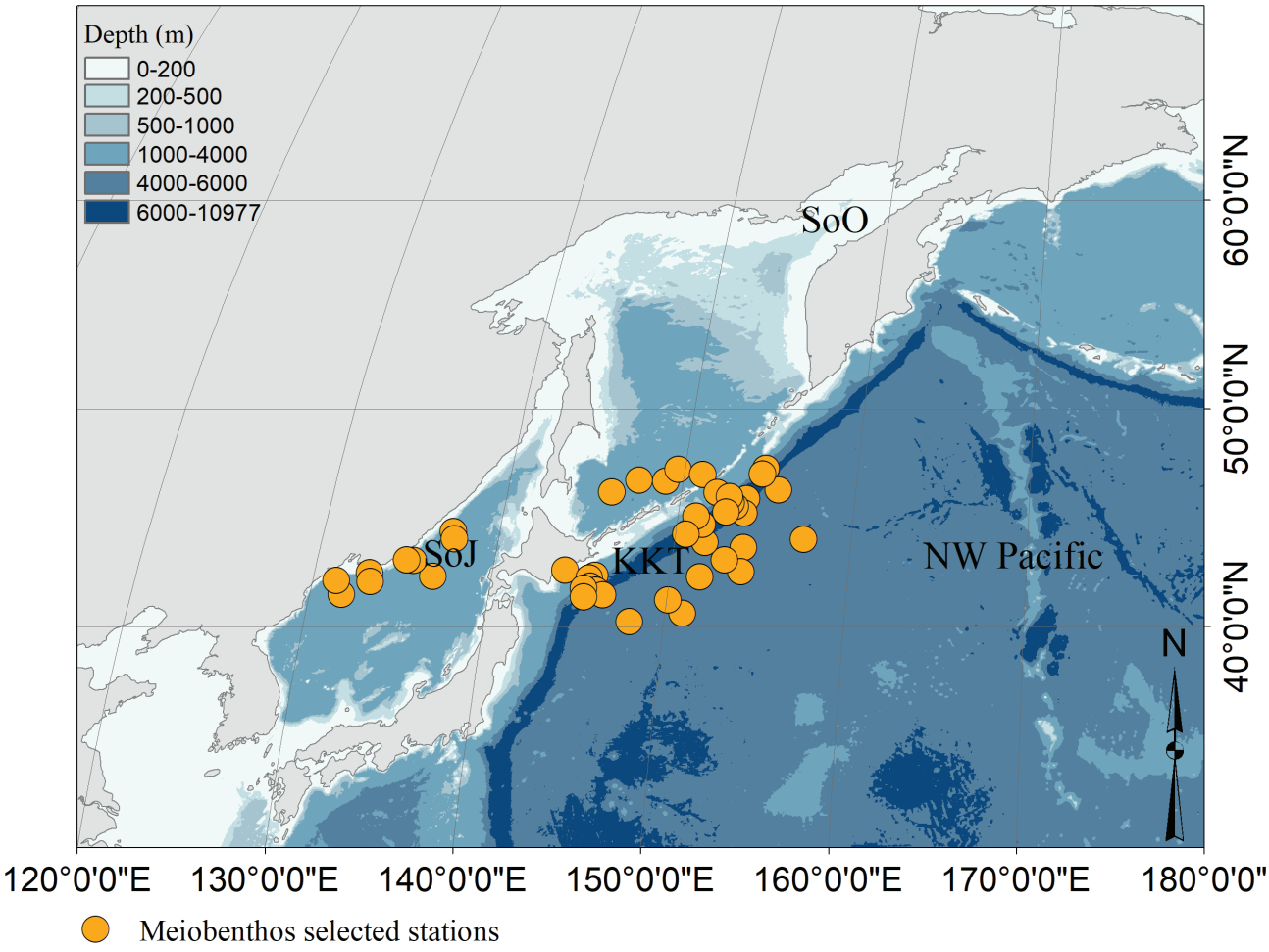
So far, there are only seven taxonomic studies of free-living nematodes from the deep sea (below 2,000 m) of the NW Pacific (Fadeeva et al. 2015, 2016a, 2016b; Miljutina & Miljutin 2015; Mordukhovich et al. 2019; Zograf et al. 2015, 2016). There by, only 13 valid nematode species are known from the studied area (Table 1). In addition to that, in four ecological studies (Miljutin and Miljutina 2015; Mordukhovich et al. 2018; Schwabe et al. 2015; Trebukhova et al. 2013), the nematodes were identified to family and genus level, or as "working species". Moreover, there is one investigation of genetic and morphology variability in genus *Acantholaimus* (Miljutin and Miljutina 2016).

5. Discussion

It is known that deep-sea sediments can contain up to one hundred morphotypes of nematodes per sample with an area of 10 cm^2 and five hundred or more morphotypes in one study area with a limited number of stations (Miljutin et al. 2010). Thus, the number of all recorded NW Pacific deep-sea nematode species is less than can be found in one sample. Obviously, current knowledge about deep-sea nematodes from the NW Pacific does not allow us yet to correctly describe the composition of the nematode fauna. However, despite

Table 1. List of valid nematode species from deep-sea NW Pacific.

Species	Depth (m)	Area
Campylaimus minutus Fadeeva, Mordukhovich & Zograf, 2016	3,367	the Sea of Japan, abyssal
Desmodorella tenuispiculum (Allgén, 1928)	5,379	NW Pacific, abyssal
Halichoanolaimus brandtae Zograf, Trebukhova & Pavlyuk, 2015	2,697	the Sea of Japan, slope
Metaphanoderma improvisa Fadeeva, Mordukhovich & Zograf, 2015	4,981–5,774	KKT, slope
Micoletzkyia kamchatika Fadeeva, Mordukhovich & Zograf, 2015	4,981–5,006	KKT, slope
Paracanthonchus mamubiae Miljutina & Miljutin, 2015	5,350	NW Pacific, abyssal
Phanodermopsis nana Zograf, Trebukhova & Pavlyuk, 2015	2,697	the Sea of Japan, slope
Phylloncholaimus palmaris Fadeeva, Mordukhovich & Zograf, 2015	4,760–5,221	NW Pacific, abyssal
Platonova magna Mordukhovich et al., 2019	3,374–5,152	NW Pacific, abyssal; KKT, slope
Platonova verecunda Mordukhovich et al., 2019	4,991–9,436	NW Pacific, abyssal; KKT, slope, hadal
Siphonolaimus japonicus Zograf, Trebukhova & Pavlyuk, 2015	2,697	the Sea of Japan, slope
Zalonema granda Fadeeva, Mordukhovich & Zograf, 2016	4,977–5,389	NW Pacific, abyssal; KKT, slope
Zalonema kamchatkaensis Fadeeva, Mordukhovich & Zograf, 2016	4,861–5,687	NW Pacific, abyssal; KKT, slope



Map 1. Study area showing stations where deep-sea nematodes were found.

limited information, several interesting facts are highlighted. For example, very interesting results were obtained for deep-sea nematodes assemblages from the Sea of Japan (Trebukhova et al. 2013). Very low abundance of nematodes was observed at depths below 2,000 m (at least 10 times less than had been recorded for the adjacent Pacific Ocean), along with absence or low density of common deep-sea genera. The authors explain such unusual features of nematode assemblages by the origin of the Sea of Japan, which has not been connected at great depth with the deep Pacific, and the possibly high concentration of H_2S (Hydrogen sulphide) in sediments at this depth.

Another interesting result were revealed in the study of nematodes from wood fragments obtained from Agassiz trawl samples in the abyssal plain area off the Kuril-Kamchatka Trench (Schwabe et al. 2015). In total, 44 individual nematode specimens were found, and nine nematode morphotypes were distinguished from three stations. Seven of nine species were represented by typical taxa of deep-sea sediments. However, the most abundant species was representative of family Anguinidae Nicholl, 1935 (Tylenchida Thorne, 1949), comprising 52% of all nematodes found. The order Tylenchida includes freshwater species, fungal feeders, and parasites of plant, insects or mites (Subbotin,

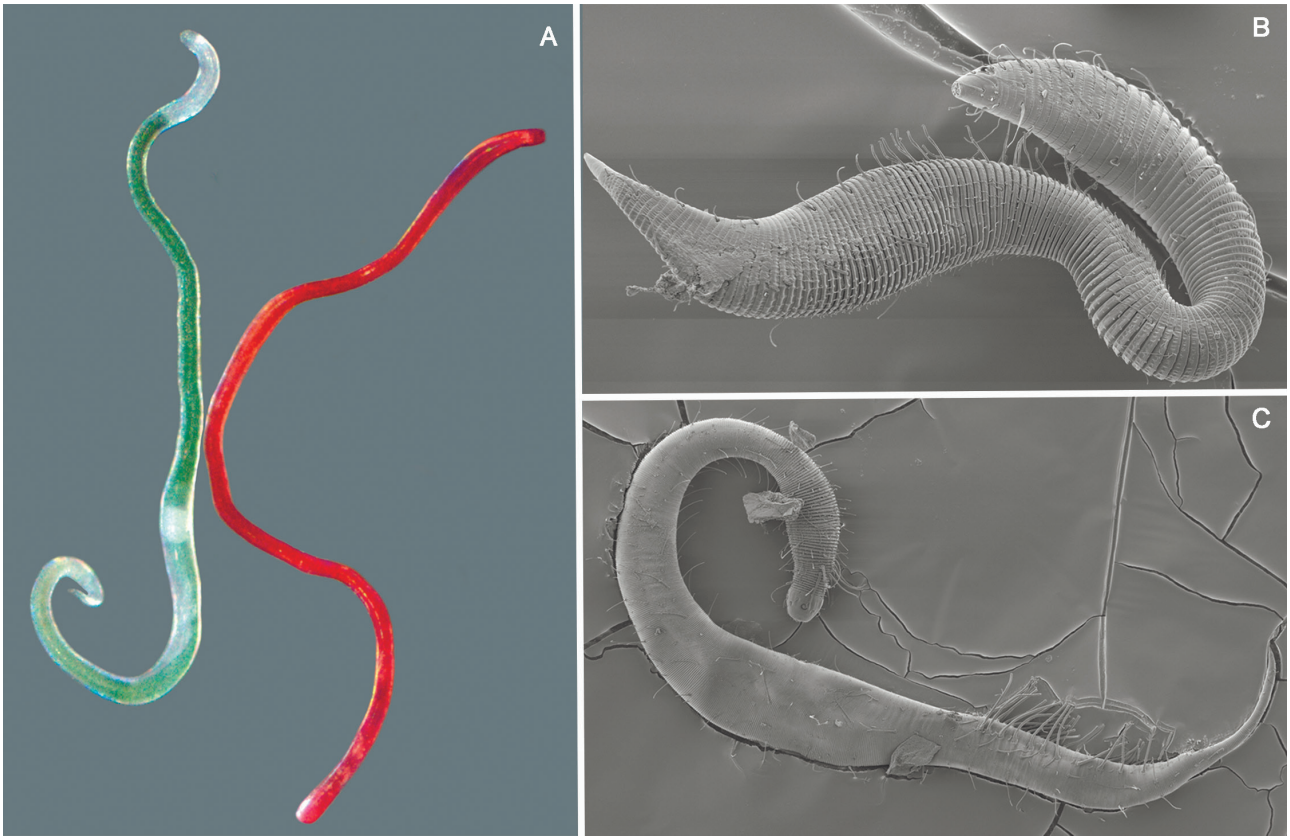
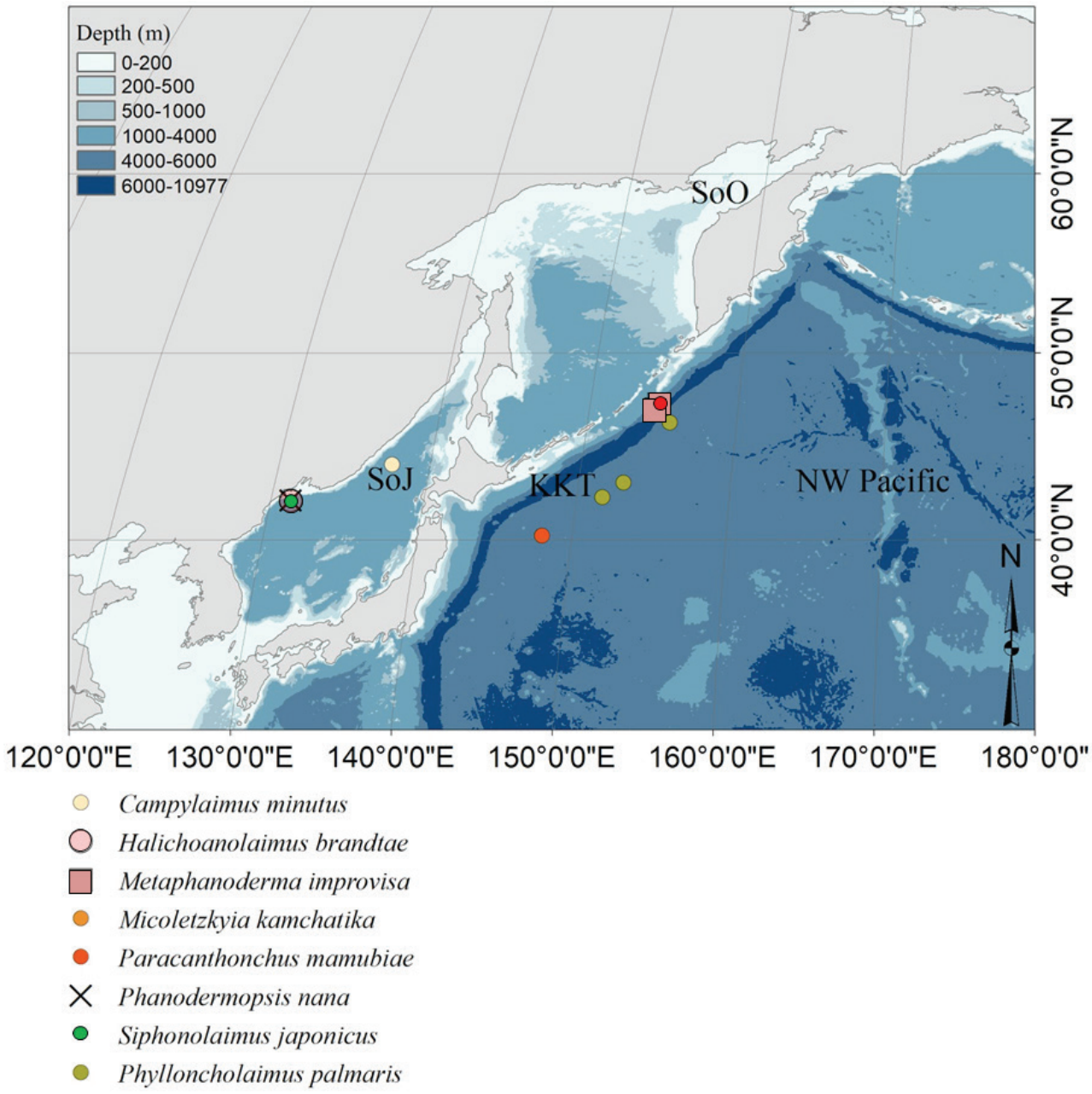


Figure 1. Examples of nematode colors and body shapes. (A) Colourful deep-sea Desmodorinae; (B) Epsilonematidae; (C) Draconematidae.

2014). The discovery of tylenchid nematodes is striking as it is the first finding of a tylenchid at abyssal depths of the deep sea. The authors emphasize that specimens of Anguinidae were found at two stations at a distance of ca. 200 km from each other. Therefore, this species appears to be widely distributed in the studied area and, possibly, preferentially inhabits sunken wood pieces. The mechanism of their dispersal from one piece of wood to another is; however, unclear.

As already noted above, data on the species composition of deep-sea nematode assemblages of the NW Pacific are practically absent. In many of the taxonomic studies, only type localities (Map 2) of new to science species were described without data on the presence/absence of these species elsewhere. Based on the available data, only for representatives of three genera – *Desmodorella* Cobb, 1933, *Platonova* Mordukhovich et al., 2019, and *Zalonema* Cobb, 1920 – it is possible to analyze some features of their spatial distribution.

Most species of *Zalonema* have been described from shallow waters or intertidal zones, and different species are typically reported from different sites, suggesting a potentially restricted distribution. However, representatives of the genus – *Z. granda* (Figure 2) and *Z. kamchatkaensis* (Figure 3) – were found almost everywhere in the abyssal plain area off the Kuril-Kamchatka Trench (Map 3). These species had different levels of abundance and frequency in their



Map 2. Study area showing stations where *Campylaimus minutus*, *Halichoanolaimus brandtae*, *Metaphanoderma improvisa*, *Micoletzkyia kamchatika*, *Paracanthonchus mamubiae*, *Phanodermopsis nana*, *Phylloncholaimus palmaris*, and *Siphonolaimus japonicus* were found.

occurrence, which may be due to their ecology. At the same time, both species were recorded at stations hundreds of kilometers apart, which may be evidence of their widespread distribution, including outside the studied area.

Species of *Platonova* (Figure 4, 5) were found only in the Kuril-Kamchatka Trench and adjacent water areas, and were totally absent in the Sea of Okhotsk and the Sea of Japan (Map 4). In addition, these species exhibited different spatial distribution patterns. *P. magna* was only found at abyssal depths on both sides of the trench. In contrast, *P. verecunda* was found within the trench, up to the greatest depths recorded. Moreover, a sample of almost identical *P. verecunda* was obtained off the coast

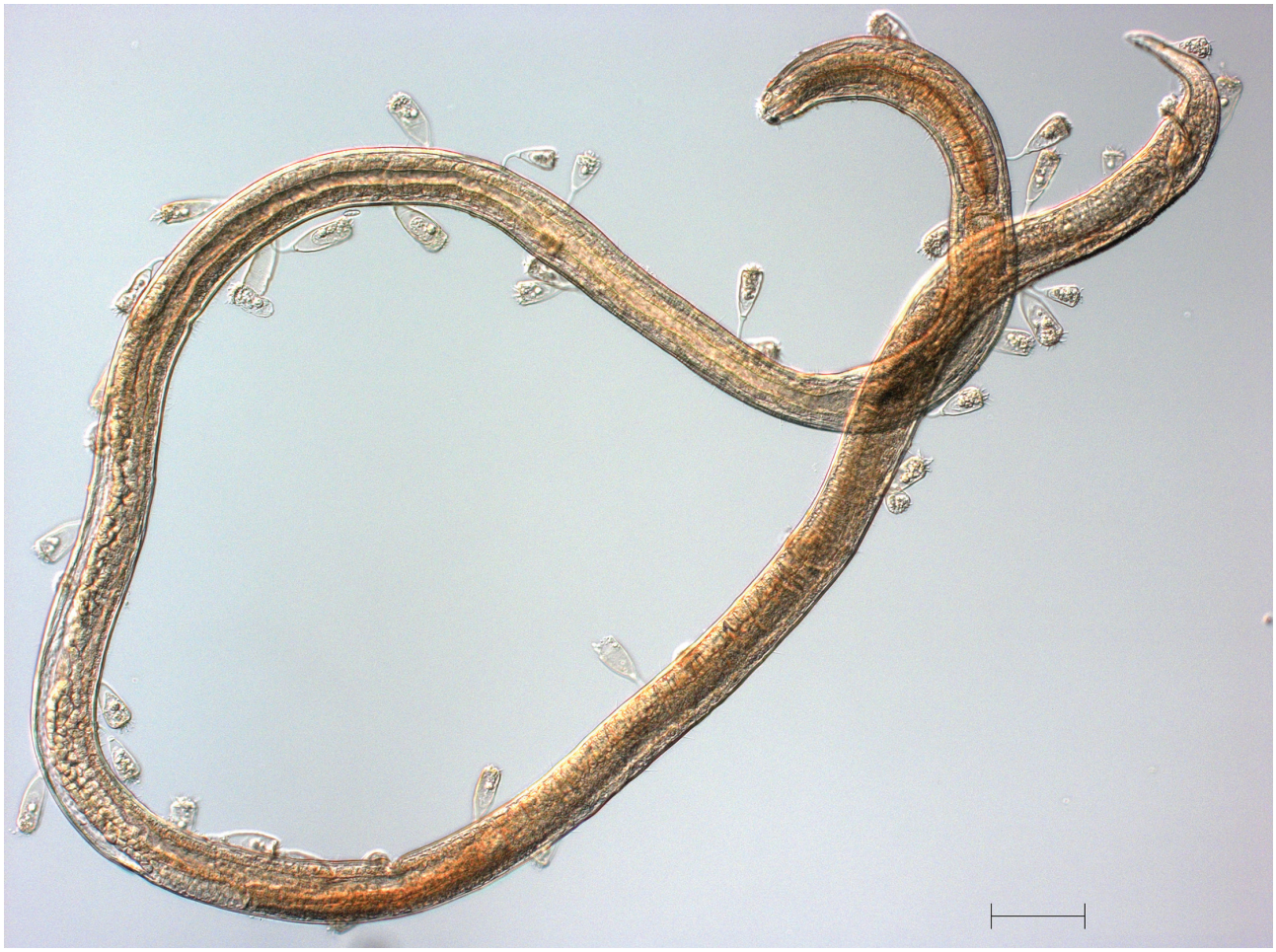


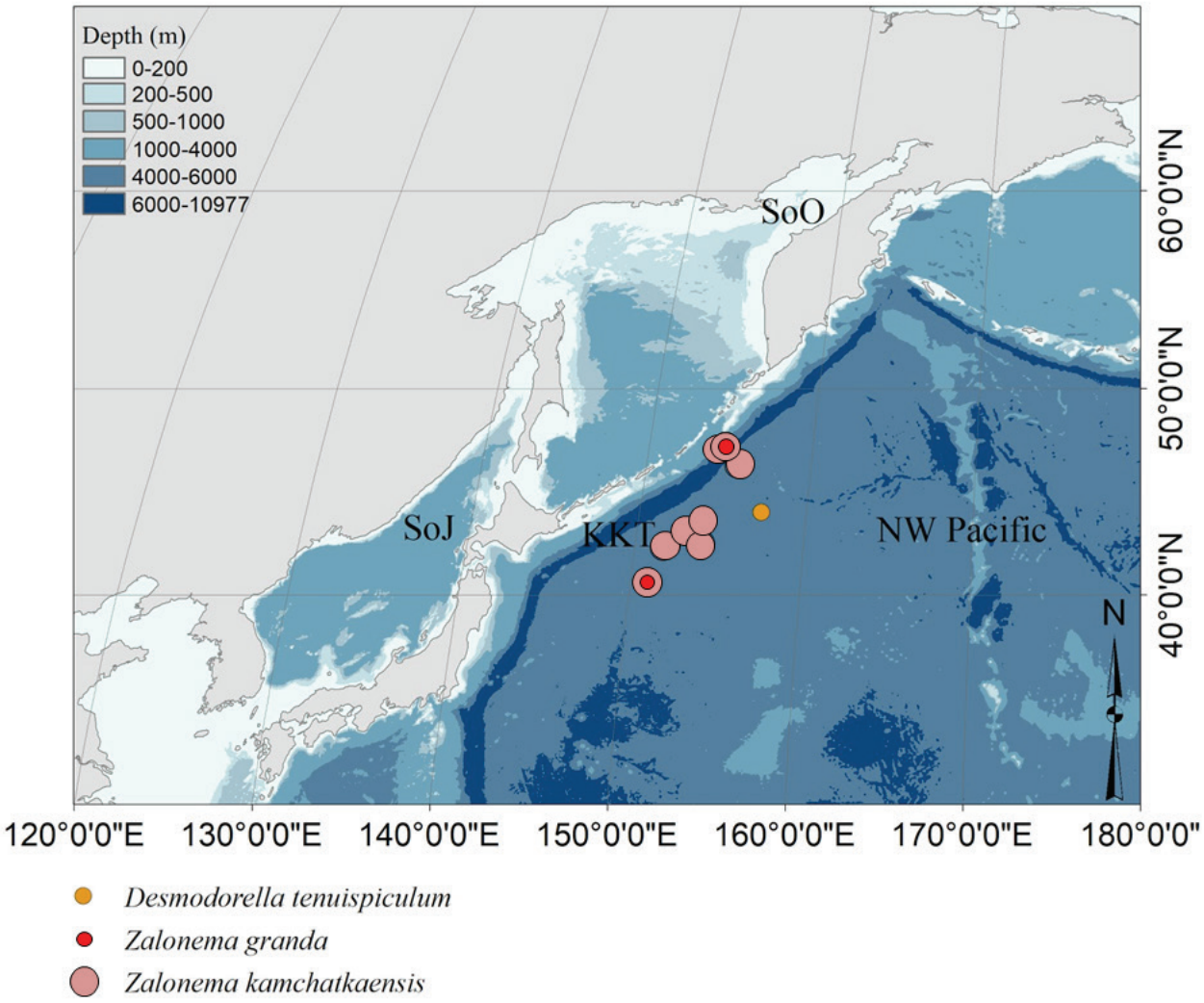
Figure 2. *Zalonema granda*, entire male, lateral view.

of California at a depth of 2,695 m (Bik et al. 2010a, 2010b). High similarity between the sequences on both sides of the Pacific Ocean may indicate the absence of barriers and high connectivity. Thus, 1) in spite of the absence of a pelagic stage of development in their life cycle, deep-sea nematodes can potentially be characterized by an extremely wide spatial distribution (in our case, an amphi-Pacific distribution); 2) for the *Platonova* species, the deep-sea trench is not considered a barrier to dispersal; and 3) the vertical range of distribution for some species may be more than 6,500 m. However, the lack of species in the Sea of Okhotsk and the Sea of Japan may indicate the impossibility of overcoming straits with relatively shallow depths.

Species of the genera *Desmodorella* are widespread over large geographical areas from shallow-water sediments to deep-sea. Specimens of *Desmodorella* from the abyssal NW Pacific (Map 4) agree well with the original description of the specimen of *Desmodorella tenuispiculum* from Campbell Island in general morphology. Unfortunately, the original description of this species is insufficiently illustrated to allow any further comparisons and does not show sufficient deviation to be assigned to a different species (Allgén 1928). The new findings of *Desmodorella* specimens together with literature data confirm the cosmopolitan character of *D. tenuispiculum*, which can be found in all oceans (Atlantic, Indian, Pacific, Arctic, and Southern) and colonizes both

shallow and deep sea-sediments (Raes et al. 2007; Leduc and Wharton 2010; Riera et al. 2012; Annapurna et al. 2012).

The relatively wide range of variation in morphology of *D. tenuispiculum* possibly masks a complex of cryptic species. Preliminary studies show the presence of high genetic diversity in representatives of various genera of deep-sea nematodes of the NW Pacific. For example, 27 Molecular Operational Taxonomic Units (MOTU) were identified based on nuclear sequence data (the D2-D3 region of 28S rRNA and the V1-V2 region of 18S rRNA gene) for 59 *Acantholaimus* specimens from two deep-sea locations in NW Pacific abyssal (Miljutin and Miljutina 2016). While only 12 *Acantholaimus* MOTU were represented by more than one individual. A similar picture of high diversity was found for the genus *Curvolaimus* Wieser, 1953. Only five valid species are currently known for this genus; however, eleven MOTU were identified for 36 *Curvolaimus* specimens from the Sea of Okhotsk and Kuril-Kamchatka Trench (Mordukhovich and Semenchenko unpublished). Thus, further studies of cosmopolitan species (identified only by morphological data) may reveal complexes of species,



Map 3. Study area showing stations where *Desmodorella tenuspiculum*, *Zalonema granda*, and *Z. kamchatkaensis* were found.

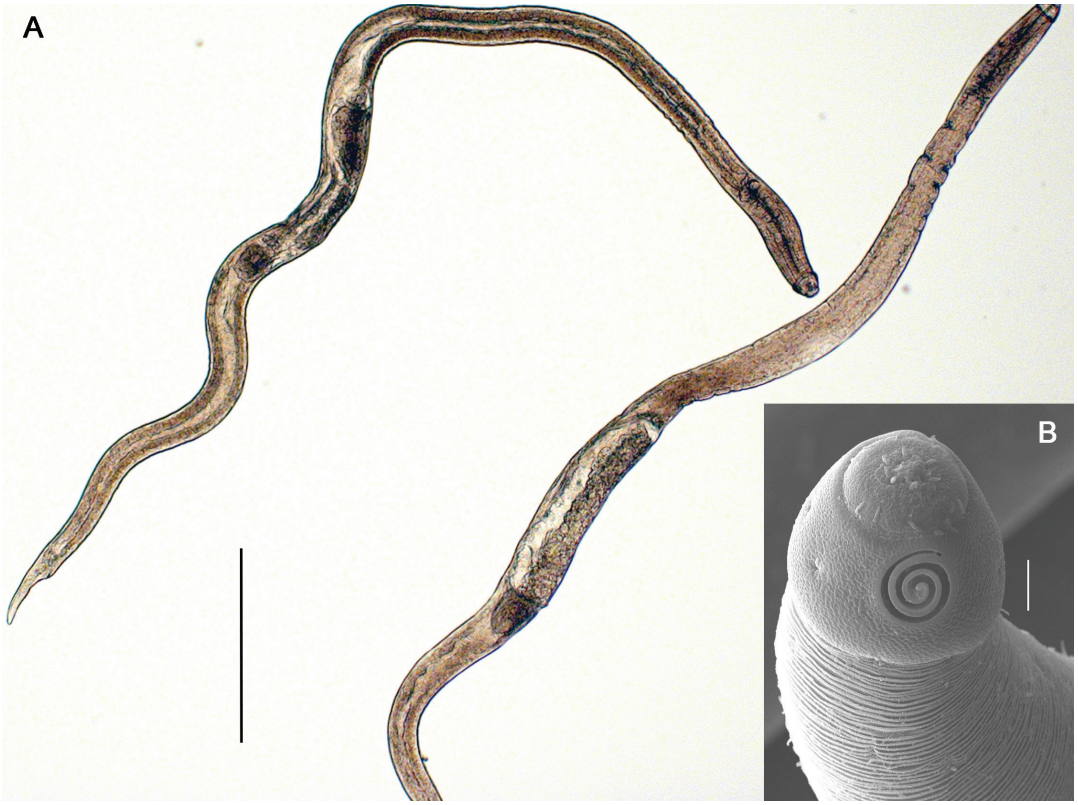
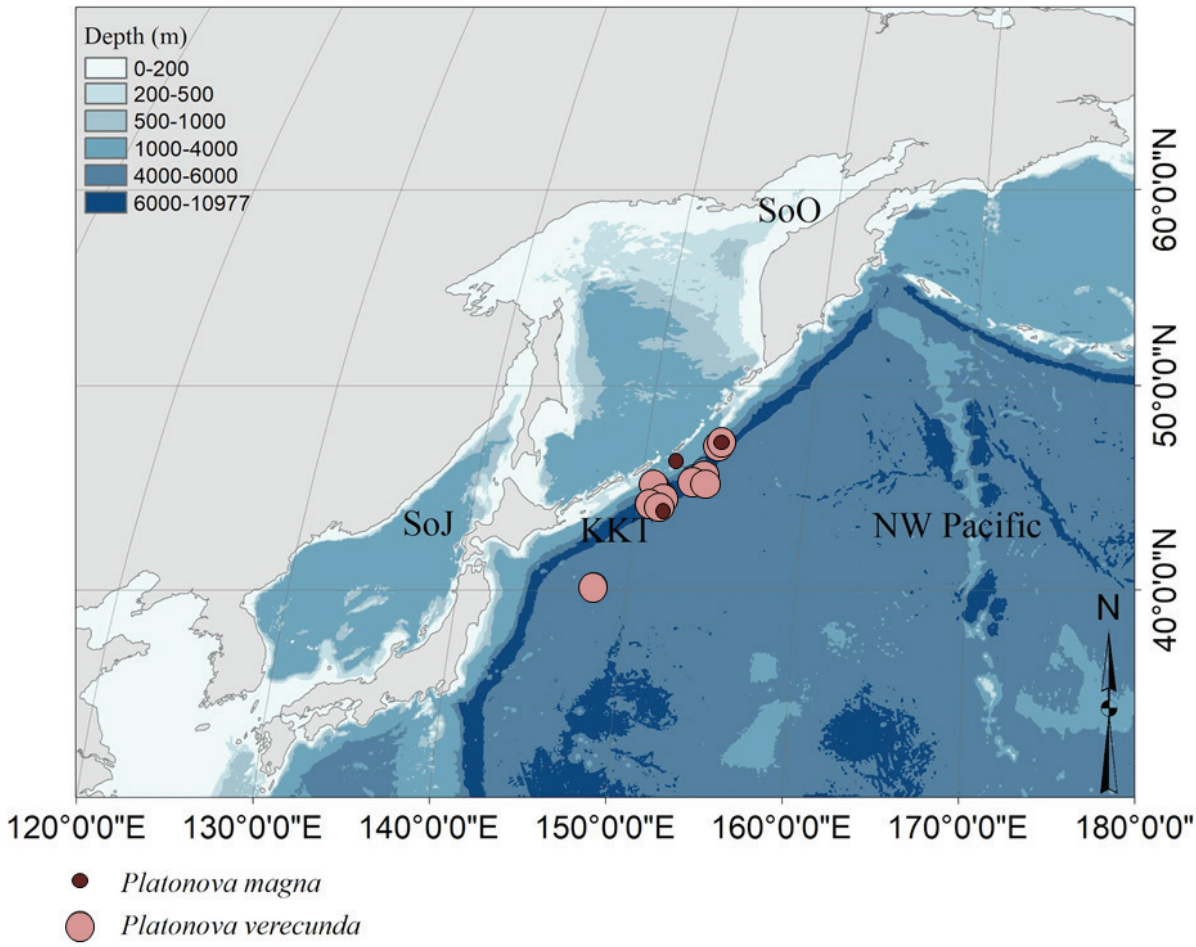


Figure 3. *Zalonema kamchatkaensis.* (A) Entire females, lateral view. (B) Head of female, lateral view.



Map 4. Study area showing stations where *Platonova magna* and *P. verecunda* were found.

each of which can be characterized by its distribution features. In addition, these examples of high genetic diversity of various genera, once again, clearly demonstrates that for deep-sea nematodes of the NW Pacific, the primary data collection phase is currently ongoing.

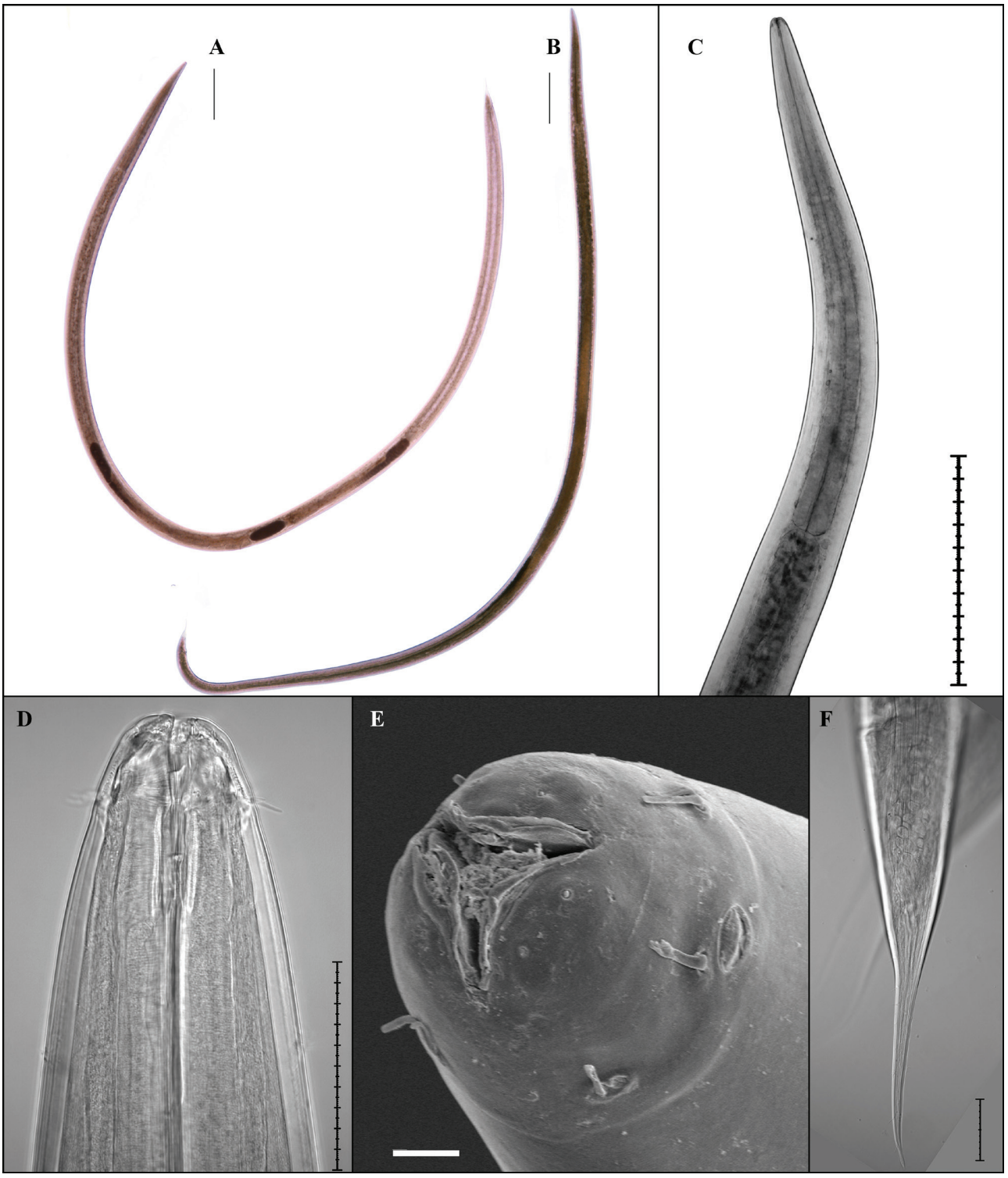


Figure 4. *Platonova magna*. (A) Entire female. (B) Entire male. (C) Anterior end of female. (D) Anterior end of male. (E) Male head. (F) Female tail. Scale bars: A, B, C 1,000 μm; D, F 100 μm; E 10 μm.

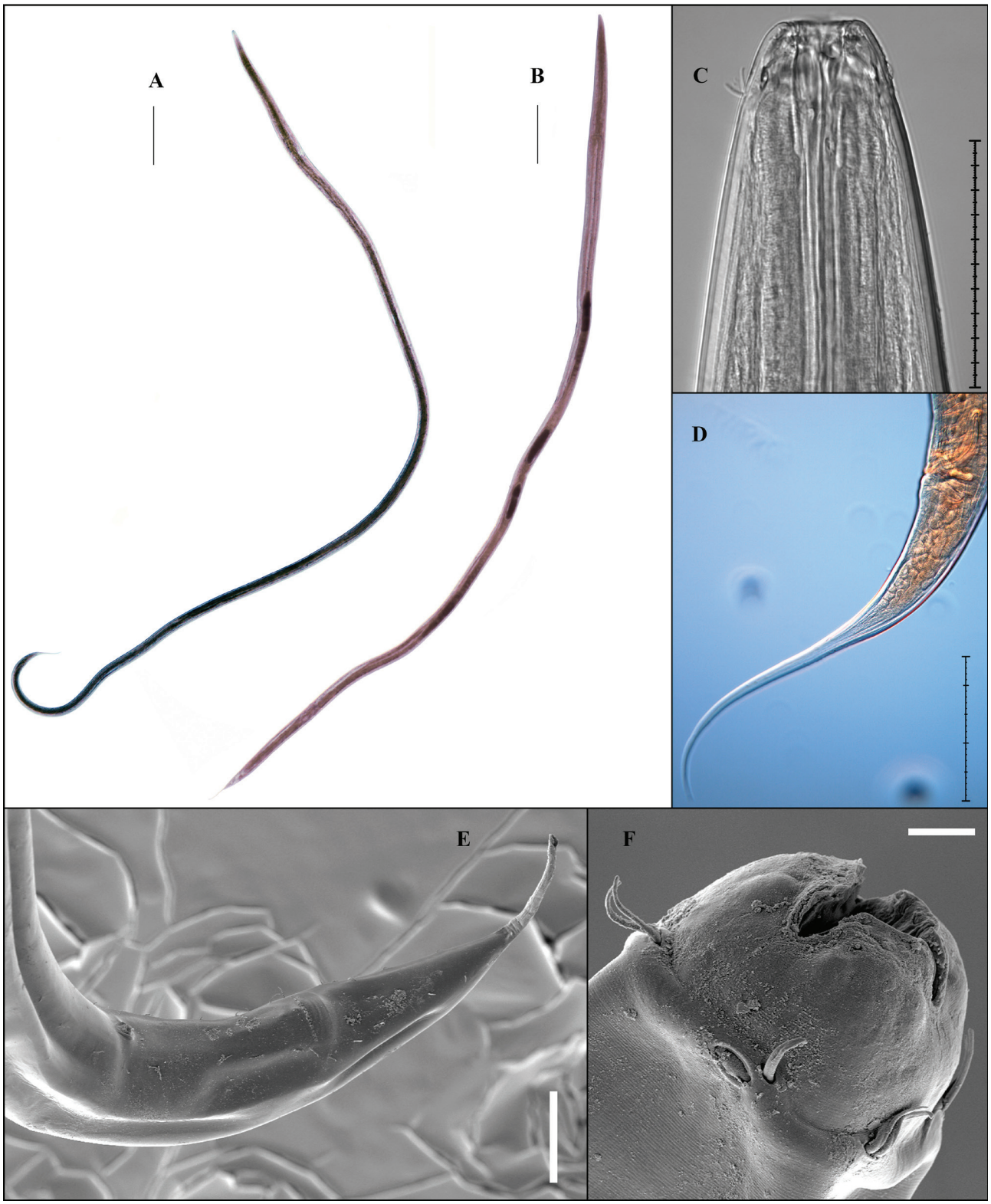


Figure 5. *Platonova verecunda*. (A) Entire male. (B) Entire female. (C) Anterior end of female. (D, E) Male tail. (F) Male head. Scale bars: A, B 1,000 µm; C, D, E 100 µm; F 10 µm.

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CHAPTER 13

KINORHYNCHA

A REVIEW ON BIOGEOGRAPHY OF THE DEEP-SEA KINORHYNCHA (PHYLUM: CEPHALORHYNCHA MALAKHOV, 1980) ALONG THE NW PACIFIC

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1. Introduction

Kinorhyncha are superficially segmented, exclusively marine, free-living worms. All are meiobenthic, from 0.12 to 1.2 mm in body length. They are worldwide in distribution, usually inhabiting the upper few centimeters of various marine sediments from the littoral zone to ultra-abyssal depth up to 9,500 m. Kinorhynchs generally inhabit the upper 1–3 cm of muddy sediments, calcareous or siliceous sand, but are also found in the associated fauna of different algae, kelp holdfasts, sponges and aggregations of molluscs.

Currently, the taxon is considered as an independent phylum, as a class of the phylum Cephalorhyncha, or as a class in the phylum Scalidophora (see Adrianov and Malakhov 1999; Neuhaus 2012). Since the first description, about 280 species, grouped into 31 genera, have been described from the world oceans.

Kinorhynchs appear very common and numerous in the abyss and even ultra-abyss (see Neuhaus 2012; Adrianov and Maiorova 2015, 2016, 2018 a, b, 2019; Sørensen et al. 2018). Nevertheless, information on their species composition in the deep-sea is still very limited, because most of our knowledge about kinorhynchs is restricted to shallow water species living in coastal environments and on the continental shelf.

There are a number of records of unidentified kinorhynchs from various deep sea localities. One of the hadal kinorhynch sampling locations is at 7,800 m in the Acatama Trench off Chile, East Pacific (see Danovaro et al. 2002), but unfortunately, this material was identified at group level only. Unidentified species of *Echinoderes* Claparède, 1863 were reported from a depth of 5,649 m at the Angola Basin in the SE Atlantic and at about 9,000 m depth in the Kermadec Trench (see Sørensen 2008a; Sørensen et al. 2018).

The first kinorhynchs described from below 1,000 m at bathyal depth were species of *Fissuroderes* Neuhaus & Blasche, 2006 collected in the South-West Pacific, near New Zealand – *F. novaezealandia* Neuhaus, 2006 (at 1,254–1,468 m depth); *F. papai* Neuhaus, 2006 (at 1,849–1,957 m depth), and *F. rangi* Neuhaus, 2006 (at 2,378–3,202 m depth) (see Neuhaus and Blasche 2006). More recently, bathyal species *Polacanthoderes martinezi* Sørensen, 2008 was described at 2,274–2,290 m depth off South Shetland Islands, near the Antarctic Peninsula in the Southern Ocean (see Sørensen, 2008a). *Pycnophyes schornikovi* Adrianov, 1999 in Adrianov && Malakhov, 1999, is a very abundant kinorhynch in the Sea of Japan, and was also recently found at depths below 1,000 m (see Adrianov and Maiorova 2015).

Recently, two new bathyal species of *Echinoderes*, *E. bathyalis* Yamasaki et al., 2018 and *E. unispinosus* Yamasaki et al., 2018, were reported from depths 2,721–2,875 m near the Azores Islands in the NE Atlantic (see Yamasaki et al., 2018 b,c). *E. drogoni* Grzelak et Sørensen, 2017, described from the NE Atlantic, is also known down to 2,128 m on the deep water plain between Norway and the North Pole (see Sørensen et al. 2018). About the same time, the first deep-water representative of *Meristoderes* Herranz, Thormar, Benito, Sánchez & Pardos, 2012, *M. okhotensis* Adrianov & Maiorova, 2018, has been described at 3,351 m depth from the deepest depression of the Sea of Okhotsk, in the NW Pacific (see Adrianov and Maiorova 2018a).

Very recently, seven new bathyal species, *Echinoderes anniae* Sørensen et al., 2018; *E. dubiosus* Sørensen et al., 2018; *E. hamiltonorum* Sørensen et al., 2008; *E. hviidarum* Sørensen et al., 2018; *E. juliae* Sørensen et al., 2018; *E. lupherorum* Sørensen et al., 2018; *E. yamasaki* Sørensen et al., 2018 and three known species, *E. hakaiensis*, *E. unispinosus* Yamasaki et al., 2018; *Fissuroderes higginsi* were reported from bathyal depths (2,702–3,854 m) in the NE Pacific, near the North American West coast (see Sørensen et al. 2018).

The first identified kinorhynch species from the abyss was *Campyloderes vanhoeffeni* Zelinka, 1913, which is believed to have the global distribution (see Neuhaus and Sørensen 2013). This species was found at 2,893 m depth off South Shetland Islands in the Southern Ocean; at 5,064 m depth in East Guinea Basin in the East Atlantic; at 5,055–5,118 m depth off Canary Islands in the NE Atlantic; at 5,050 m depth in Clarion-Clipperton area in the Central Pacific (see Neuhaus, Sørensen, 2013). Specimens of *Campyloderes* cf. *vanhoeffeni* were also found at 5,200 m depth on the abyssal plain adjacent to the Kuril-Kamchatka Trench (own data).

Three abyssal species, *Cristaphyes nubilis* (Sanchez et al., 2014), *Krakenella farinelli* (Sanchez et al., 2014) and *Mixtophyes abyssalis* Sanchez et al., 2014 were described from the Angola Basin (see Sanchez et al. 2014 a, b). Recently, three abyssal species, *Cristaphyes abyssorum* (Adrianov & Maiorova, 2015) (at 5,766 m depth), *Condyloderes kurilensis* Adrianov & Maiorova, 2016 (at 5,222 m depth) and *Parasemnoderes intermedius* Adrianov & Maiorova, 2018 (at 5,348 m depth) were described from the abyssal plain at the south border of the Kuril-Kamchatka Trench, in the NW Pacific (see Adrianov and Maiorova 2015, 2016, 2018 a, b). Presence in the abyss is also noted for *Echinoderes pterus* Yamasaki et al., 2018 with wide distribution in the Arctic Ocean and North Atlantic (see Yamasaki et al. 2018 a). A few deep-water echinoderids were described from the seamounts and adjacent deep-sea floor in the NE Atlantic and Mediterranean (see Yamasaki et al. 2018 b, c).

Very recently, the first hadal species of kinorhynchs, *Echinoderes ultraabyssalis* Adrianov & Maiorova, 2019, was described from oxidized brown clay at the deepest depression of the Kuril-Kamchatka Trench, NW Pacific, at the depth 9,411-9,541 m (see Adrianov, Maiorova, 2019). Now, it constitutes the deepest kinorhynch species described so far and the first hadal representative of the Kinorhyncha in the World Ocean.

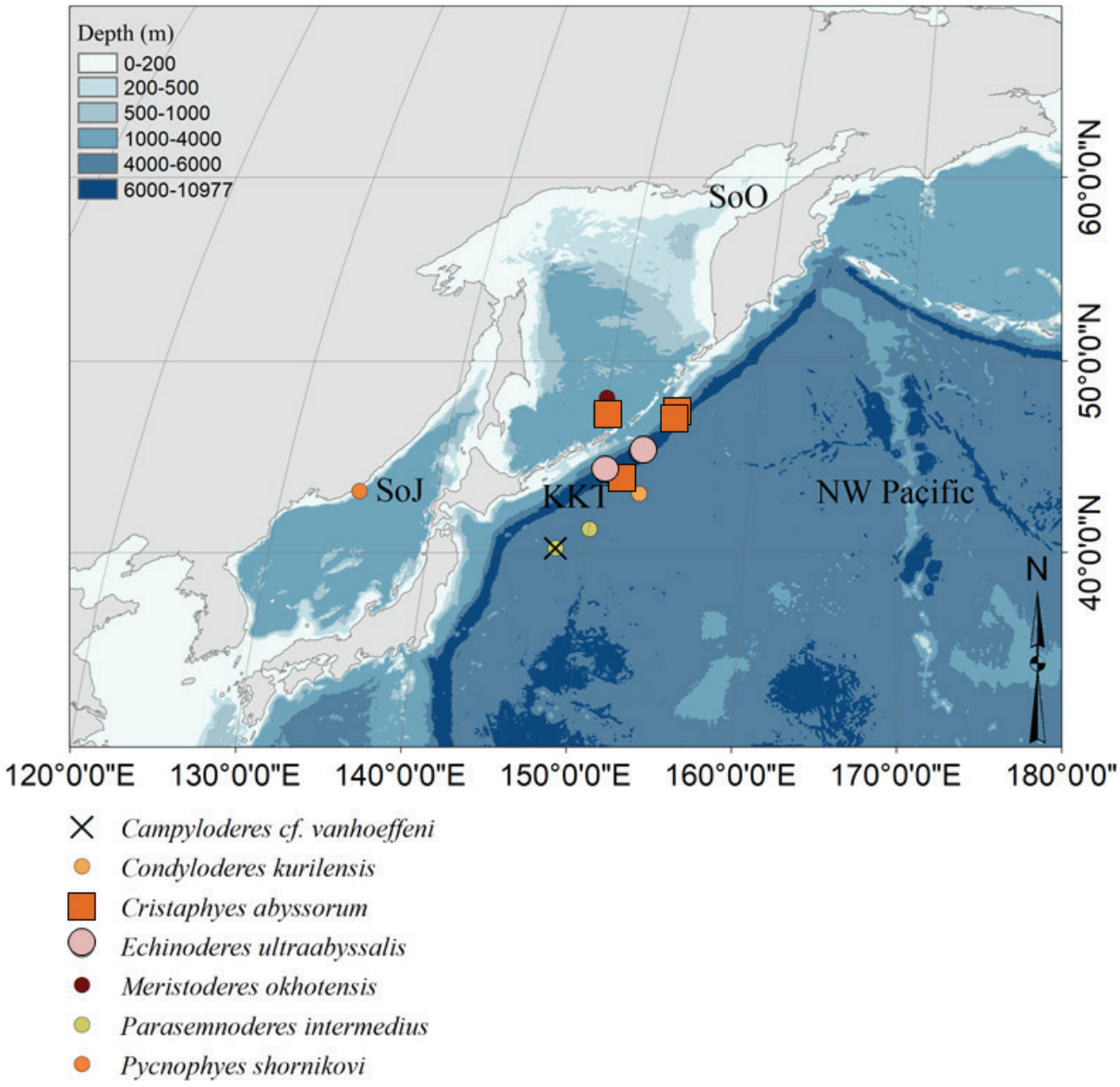
During recent years, several deep-sea expeditions in the NW Pacific revealed many undescribed species of kinorhynchs. Among the genera found in deep water localities in NW Pacific are *Pycnophyes* Zelinka, 1907, *Cristaphyes*, *Campyloderes* Zelinka, 1907, *Condyloderes* Higgins, 1969, *Semnoderes* Zelinka, 1907, *Parasemnoderes*, *Meristoderes*, *Echinoderes*. Several new species of these genera have already been described as being the deepest representatives of these taxa. Many new species from these localities are still waiting to be described in the near future.

2. Objectives

In this chapter we are providing a review of the biogeography of the deep-sea Kinorhyncha of the NW Pacific Ocean (NWP).

3. Material and Methods

The data used herein represents a final compilation of all the works published previously by Adrianov & Maiorova (2015, 2016, 2018a, b, 2019) on Kinorhyncha. Distribution of all Kinorhyncha species recorded in the NW Pacific Ocean (NWP) at a depth below 2,000 m from 40 to 60°N and between 120 and 180°E are displayed in Map 1.



Map 1. Distribution of kinorhyncha in the deep-sea of NWP.

4. Results

Class Kinorhyncha Reinhard, 1881

Order Cyclorhagida Zelinka, 1896

Family Echinoderidae Zelinka, 1894

Genus *Echinoderes* Claparede, 1863

***Echinoderes ultraabyssalis* Adrianov & Maiorova, 2019**

(Figure 1)

Diagnosis. Trunk segment 1 consisting of closed cuticular ring; trunk segment 2 consisting of closed cuticular ring with intracuticular fissures of anterior pachycyclus in lateroventral position, corresponding to the tergosternal articulations of following trunk segments; trunk segments 3-11 consisting of one tergal and two sternal plates; trunk segment 2 with one pair of tubules in ventrolateral positions; trunk segment 5 with one pair of tubules in lateroventral position; trunk segment 8 with one pair of lateral accessory tubules; trunk segment 9 with one pair of tubules in laterodorsal position; middorsal spines on trunk segments 6 and 8; lateroventral spines on trunk segments 6–9; tergal extensions pointed, about 1/3 longer than sternal plates, with an extra tooth at the inferior margin; prominent middorsal protuberance between trunk segments 10 and 11.

Biogeographical remarks. *Echinoderes* is the most species-rich genus of the Kinorhyncha, which is already composed of more than one hundred valid species. Nevertheless, only 16 species of this genus have been described from the NW Pacific. *E. tchefouensis* Lou, 1934, *E. aspinosus* Sørensen et al., 2012, *E. microaperturus* Sørensen et al., 2012, and *E. cernunnos* Sørensen et al., 2012 are described from the Yellow Sea (see Sørensen et al. 2012). *E. tchefouensis* and *E. microaperturus* are also found in the East China Sea (see Sørensen et al. 2012). Five species are known from the Sea of Japan: *E. filispinosus* Adrianov, 1989; *E. multisetosus* Adrianov, 1989; *E. ulsanensis* Adrianov, 1999; *E. koreanus* Adrianov, 1999; *E. obtuspinosus* Sørensen et al., 2012 (see Adrianov and Malakhov 1999; Sørensen et al. 2012). *E. lanceolatus* Chang et Song, 2002 and *E. rex* Lundbye et al., 2011 were also found in the Korean waters (see Lundbye et al. 2011). Five valid species of *Echinoderes* are described from Japan: *E. sensibilis* Adrianov et al., 2002, *E.*



Figure 1. *Echinoderes ultraabyssalis* scale bar, 100 μm.

aureus Adrianov et al, 2002 from the east coast of Honshu (see Adrianov et al. 2002 a, b); *E. ohtsukai* Yamasaki et Kajihara, 2012 from the Seto Inland Sea (see Yamasaki and Kajihara 2012); *E. komatsui* Yamasaki et Fujimoto, 2014, *E. hwiizaa* Yamasaki et Fujimoto, 2014 from Ryukyu Island (see Yamasaki and Fujimoto 2014). All these echinoderids are shallow-water species, found in intertidal and subtidal environments (from 0 to 140 m depth) and differ significantly from the new species by the spine arrangements. Some still undescribed species of *Echinoderes* were collected at the east coast of Kamchatka Peninsula and from the Bering Sea (own data).

Until now, deep-water representatives of the genus *Echinoderes* have never been described from the NW Pacific. Quite recently, Sørensen et al. (2018) have published an excellent monograph on deep-sea echinoderids from the NE Pacific with descriptions of seven new species of *Echinoderes*: *E. anniae*, *E. dubiosus*, *E. hamiltonorum*, *E. juliae*, *E. lupherorum*, *E. yamasakii* and *E. hviidarum*, the last one being most similar to the new species by a combination of the main characters (see above). Two other deep-sea species of *Echinoderes* were also found near the US coast of the NE Pacific: *E. hakaiensis* Herranz et al., 2017 and *E.* cf. *unispinosus* Yamasaki et al., 2018 (see Sørensen et al. 2018). But all these species were collected only at bathyal depths and representatives of the genus *Echinoderes* have never been found in the abyss in the North Pacific. The only species of *Echinoderes* noted at the abyssal depth (4,403 m) is *E. pterus* Yamasaki et al., 2018, widespread in the Arctic Ocean and the North Atlantic (see Yamasaki et al. 2018 a).

E. ultraabyssalis constitutes the deepest kinorhynch species described so far (9,538 m), the first deep-sea *Echinoderes* in the NW Pacific and the first hadal representative of the Kinorhyncha in the world oceans (see Adrianov and Maiorova 2019).

Genus *Meristoderes* Herranz, Thormar, Benito, Sanches et Pardos, 2012

Meristoderes okhotensis Adrianov & Maiorova, 2018

(Figure 2)

Diagnosis. Trunk segments 1–2 consisting of closed cuticular rings, and trunk segments 3–11 of one tergal and two sternal plates; trunk segment



Figure 2. *Meristoderes okhotensis* scale bar, 100 μm.

2 having indistinct intracuticular fissures in lateroventral position, corresponding to the tergosternal articulations of following trunk segments, thus forming indistinct differentiation into one tergal and one sternal plate; intracuticular lateroventral fissures strongly curved into midial direction; trunk segment 2 with three pairs of well-developed tubules in subdorsal, laterodorsal, and ventrolateral positions; trunk segment 5 with tubules in lateroventral position; trunk segment 8 with tubules in lateral position; middorsal spines on trunk segments 6 and 8; lateroventral spines on trunk segments 6–9; spines hirsute at distal half of their length; tergal extensions of trunk segment 11 with remarkably long terminal dagger-like spines.

Biogeographical remarks. The first two species, *M. macracanthus* and *M. galatheae*, were described by Herranz et al. (2012) from the Mediterranean, NE Atlantic, and Solomon Island archipelago, South-West Pacific, correspondently. Four species, *M. herranzae*, *M. imugi*, *M. elleae*, and *M. glaber*, were described by Sørensen et al. (2013) from Korean waters (southern sector of the Sea of Japan and the East-China Sea), and the NW Pacific. In addition, Sørensen et al. (2013) provided a description of *Meristoderes* sp., a yet formally undescribed species from the Sea of Japan. *M. boylei*, was collected off the east coast of Florida, West Atlantic, and described by Herranz and Pardos (2013). All these representatives of *Meristoderes* are shallow-water species collected from 4 to 200 m depth only. The only deep-sea representative of the genus is *M. okhotensis*, collected at the north slope of the deepest depression in the Sea of Okhotsk, NW Pacific at 3,351 m depth.

Family Centroderidae Zelinka, 1896

Genus *Condyloderes* Higgins, 1969

Condyloderes kurilensis Adrianov & Maiorova, 2016

(Figure 3)

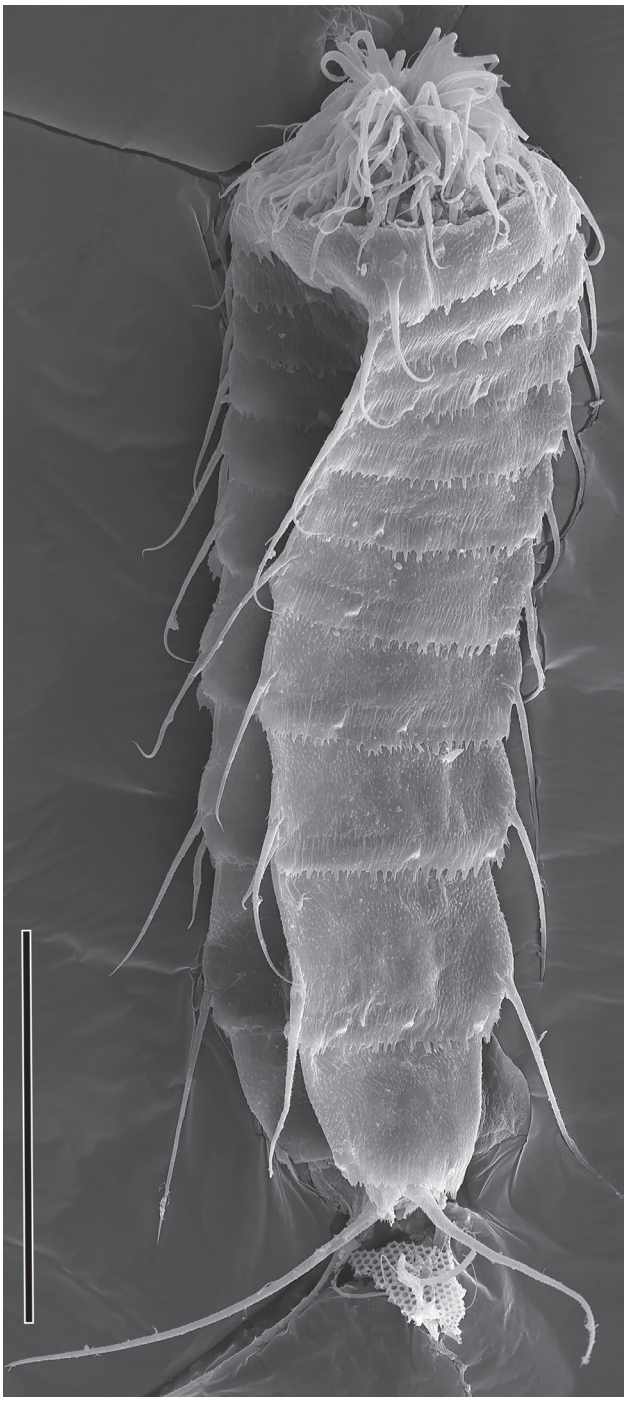


Figure 3. *Condyloderes kurilensis* scale bar, 100 μm.

Diagnosis. Trunk segment 1 consisting of one closed cuticular ring, trunk segments 2–10 of one tergal and two sternal plates, and trunk segment 11 of one tergal and one sternal plates. Tergal and sternal plates with prominent pectinate fringe at posterior margin. Middorsal spines aciculate, on trunk segments 1–9 in female and 1–10 in male. Lateroventral spines aciculate, on trunk segment 1-9. Lateroventral accessory spines are cuspidate, only on trunk segment 8 in both sexes. Laterodorsal spines on trunk segment 10 in males only. Ventromedial appendages (tubules) on trunk segments 7 and 8 in females only.

Biogeographical remarks. Only six species of the genus *Condyloderes* have been described to date: *C. paradoxus* Higgins, 1969; *C. multispinosus* (McIntyre, 1962) Higgins, 1969; *C. setoensis* Adrianov, Murakami et Shirayama, 2002; *C. storchi* Martorelli et Higgins, 2004; *C. megastigma* Sørensen, Rho et Kim, 2010; and *C. kurilensis* Adrianov & Maiorova, 2016.

The first species, *C. multispinosus* (McIntyre, 1962) Higgins, 1969 was found in the North Sea at the depth up to 100 m, in Scotland (Fladen, Lock Nevis, Lock Torridon) (see McIntyre 1962) and at the coast of Netherlands (Westerscheld Mouth) (see Huys and, Coomans 1989). The second species, *C. paradoxus* Higgins, 1969 was described from the Indian Ocean at the depth of about 40 m (Kakinaba Bay, Indian coast of the Bay of Bengal) (see Higgins 1969). Specimens of *C. setoensis* Adrianov, Murakami & Shirayama, 2002 were collected at the depth of 15–27 m in Tanabe Bay (Kii Peninsula of Honshu Island, Japan), NW Pacific (see Adrianov & al. 2002 c). A single specimen of *C. storchi* Martorelli & Higgins, 2004 was found in the stomach contents of a shallow-water shrimp from the coast of Argentina (San Jorge Gulf), SW Atlantic (see Martorelli and Higgins 2004). Specimens of *C. megastigma* Sørensen, Rho & Kim, 2010 were collected in the Korea Strait between Korea and Japan (the Sea of Japan), NW Pacific, at depths from 90 to 109 m (see Sørensen et al. 2010).

C. kurilensis Adrianov & Maiorova, 2016 is the only deep-water representative of this genus, described from the abyssal plain at the south border of the Kuril-Kamchatka Trench, NW Pacific, at 5,222 m depth (see Adrianov & Maiorova 2016).

Genus *Campyloderes* Zelinka, 1913

Campyloderes cf. *vanhoeffeni* Zelinka, 1913

(Figure 4)

Diagnosis. Outer oral styles fused nearly over their entire length; primary scalids of the first ring with numerous internal septa giving the chambered appearance; spinoscalids of the second ring very short and acicular, at least twice shorter than neighboring scalids; neck closing apparatus consisting of 14 placids; midventral placid very broad, at least twice or three times wider than neighboring triangular paraventral placids; narrow triangular placids alternating with broader, nearly rounded placids; first trunk segment with remarkably long acicular spines in lateroventral position, usually longer than trunk segments 2–4 together; females with ventrolateral and ventromedial papillae on trunk segments 6–7 or 5–7; midterminal spine and lateral terminal accessory spines with thin areas in the cuticle.

Biogeographical remarks. Four species of the genus *Campyloderes* have been described in

literature so far, *C. vanhoeffeni* Zelinka, 1913; *C. vanhoeffeni* var. *kerguelensis* Zelinka, 1913 (= *C. kerguelensis* Johnston, 1938); *C. macquariae* Johnston, 1938, and *C. adherens* Nyholm, 1947 (see Adrianov and Malakhov 1999). *C. adherens* is now designated as a member of the genus *Centroderes* (see Neuhaus 2004). These species differ from each other only by minute details and are also considered now as a one species, *C.* cf. *vanhoeffeni*, with very broad distribution in the world oceans (see Neuhaus and Sørensen 2013). *C.* cf. *vanhoeffeni* is a first species of kinorhynchs described from the abyss, but also reported from a broad depth range from intertidal to 5,200 m (see Neuhaus and Sørensen 2013; this paper).



Figure 4. *Campyloderes* cf. *vanhoeffeni* scale bar, 100 μm.

In the Pacific Ocean, abyssal representatives of this species were collected in the Central Pacific, Manihiku Plateau, at 4,925 m depth, in the Clarion-Clipperton Fracture Zone, at 5,050 m depth (see Neuhaus and Sørensen 2013), and in the NW Pacific, on the abyssal plain adjacent to the Kuril-Kamchatka Trench, at 5,200 m depth (this paper). Bathyal specimens of *C.* cf. *vanhoeffeni* were collected in the Central American East Pacific Ocean, near the Galapagos Islands, at 2,119–2,995 m depth and near the Cocos Ridge, at 1,048 m depth; in the South-West Pacific, Hikurangi Plateau, at 1,605–1,940 m depth (see Neuhaus and Sørensen 2013). Many shallow-water representatives of this species were found in the South-West Pacific, near the Solomon Islands, at 14 m depth, and near New Zealand, Chatham Rise, at 885 m depth; and in the NW Pacific, South Korea waters, at 30–50 m depth (see Neuhaus and Sørensen 2013).

Family Semnoderidae Remane, 1936

Genus *Parasemnoderes* Adrianov & Maiorova, 2018

Parasemnoderes intermedius Adrianov & Maiorova, 2018

(Figure 5)

Diagnosis. Neck with 16 placids, middorsal and midventral ones most narrow; middorsal placid nearly rod-shaped. Trunk segment 1 consisting of one closed cuticular ring or with intracuticular tergosternal junctions thus forming additional



Figure 5. *Parasemnoderes intermedius* scale bar, 100 µm.

weakly developed trapesoid midventral plate; trunk segments 2–11 with one tergal and two sterna plates. Cuticular ring of trunk segment 1 with deep narrow middorsal incision and significantly broader midventral incision filled by midventral placid. Middorsal spines aciculate, on trunk segments 1–11. Lateroventral spines aciculate, on trunk segments 3–9. Lateroventral accessory spines, if present, minute, only on trunk segment 5. Laterodorsal spines on trunk segment 10.

Biogeographical remarks. Three species of the genus *Semnoderes* have been described to date: *S. armiger* Selinka, 1928; *S. ponticus* Bacescu et Bacescu, 1956; and *S. pacificus* Higgins, 1967. *S. armiger* is widespread in European waters (Mediterranean, Black Sea, North Europe) (see Zelinka 1928; Sørensen et al. 2009). *S. pacificus* was firstly described from the South-West Pacific (New Caledonia) and later also recorded from the Californian coast, while *S. ponticus* is known from the Black Sea only (see Higgins 1967).

The genus *Sphenoderes* is now composed of only two species: *S. indicus* Higgins, 1969 from the Bay of Bengal and the Gulf of Kutch, Indian Ocean, and *S. poseidon* Sørensen et al., 2010 from the Korean Strait and the East China Sea, NW Pacific (see Sørensen et al. 2010).

Parasemnoderes intermedius Adrianov & Maiorova, 2018 is the only representative of this genus and the only deep-sea semnoderid known to date. This species was described from the abyssal plain at the southern sector of the Kuril-Kamchatka Trench, in the NW Pacific at 5,348 m depth. All another semnoderid representatives

above are all shallow water species collected at depths of less than 200 m.

Order Homalorhagida Zelinka, 1896

Family Pycnophyidae Zelinka, 1896

Genus *Pycnophyes* Zelinka, 1896

Pycnophyes schornikovi Adrianov, 1999 in Adrianov & Malakhov, 1999

(Figure 6)

Diagnosis. Lateral terminal spines (LTS) about 18–20% of trunk length (TL) in males and about 10–11% in females; middorsal processes (MP) small, obtuse, slightly protruding beyond posterior tergal margin, on trunk segments 1–6; midsternal plate (MSP) trapezoidal, anterior margin less than ½ of posterior margin; anterior margin of MSP only slightly projecting beyond anterior margins of episternal plate (ESP); anteromesial thickening of ventral pachycyclus (MT) on trunk segments 7–10; ped-and-socket tergal/sternal articulations on trunk segments 1–9; tergal plate of trunk segment 11 with two papilla-like protuberances; posterior margin of terminal tergal plate even, with minute fringe and two lateral papillae.

Biogeographical remarks. Only ten species of picnophiids have been described from the NW Pacific. Two species, *Pycnophyes tubuliferus* Adrianov, 1989 and *Kinorhynchus yushini* Adrianov, 1989 (= *Cristaphyes yushini* (Adrianov, 1989)) were described from the Peter the Great Bay in the north-west part of the Sea of Japan and were also found at the Korean and Japanese coasts (see Adrianov 1989; Adrianov and Malakhov 1999; Murakami et al. 2001; Yamasaki et al. 2012). Two species, *Pycnophyes furugelmi* Adrianov, 1999 (= *Cristaphyes furugelmi* (Adrianov, 1999)), and *P. schornikovi* Adrianov, 1999, also were described from the Peter the Great Bay, the latter species later being found in the deep-

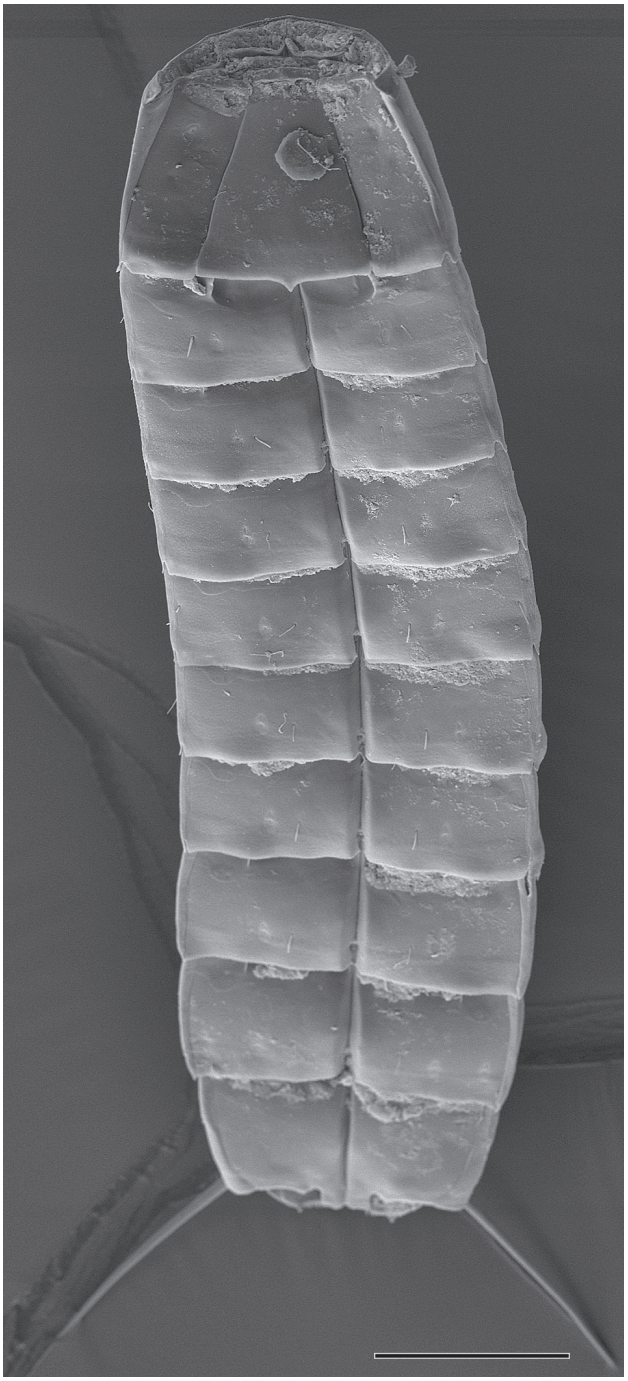


Figure 6. *Pycnophyes schornikovi* scale bar, 100 μm.

sea basin of the Sea of Japan at the depth about 1,000 m (see Adrianov and Malakhov, 1999; own data). *Pycnophyes oshoroensis* Yamasaki et al., 2012 was reported from Hokkaido Island, North Japan (see Yamasaki et al. 2012). Recently, four new species, *Pycnophyes pardosi* Sanchez et al., 2013 (= *Leiocanthus pardosi* (Sanchez et al., 2013)), *P. chalgap* Sanchez et al., 2013 (= *Leiocanthus chalgap* (Sanchez et al., 2013)), *P. cristatus* Sanchez et al., 2013 (= *Cristaphyes cristatus* (Sanchez et al., 2013)), and *P. smaug* Sanchez et al., 2013 (= *Krakenella smaug* (Sanchez et al., 2013)), were described from the Korean waters and the East China Sea (see Sanchez et al. 2013, 2016). Quite recently, the first abyssal pycnophiid, *Pycnophyes abyssorum* Adrianov & Maiorova, 2015 (= *Cristaphyes abyssorum* (Adrianov & Maiorova, 2015)) was described from the abyssal plain at the south border of the Kuril-Kamchatka Trench (see Adrianov & Maiorova 2015).

Genus *Cristaphyes* Sanchez, Yamasaki, Pardos, Sørensen et Martinez, 2016

Cristaphyes abyssorum (Adrianov & Maiorova, 2015)

(Figure 7)

Diagnosis. Lateral terminal spines (LTS) about 27-30% of trunk length in both sexes; four dorsal and two ventral neck placids with even anterior margin; long and spine-like middorsal processes on all trunk segments; middorsal processes hirsute (hairy) on trunk segments 1–9 and bare on trunk segment 10; anterior margin of first tergal plate strongly denticulated, with wide submarginal area of reticulate cuticle; midsternal plate of first trunk segment with oval-shaped area of thin reticulate cuticle; anterior margin of midsternal plate about 43–53% of posterior margin; episternal plates with wide area of thin reticulate cuticle; posterior margins of all tergal and sternal plates with minute pectinate fringe; only one paradorsal setae on trunk segments

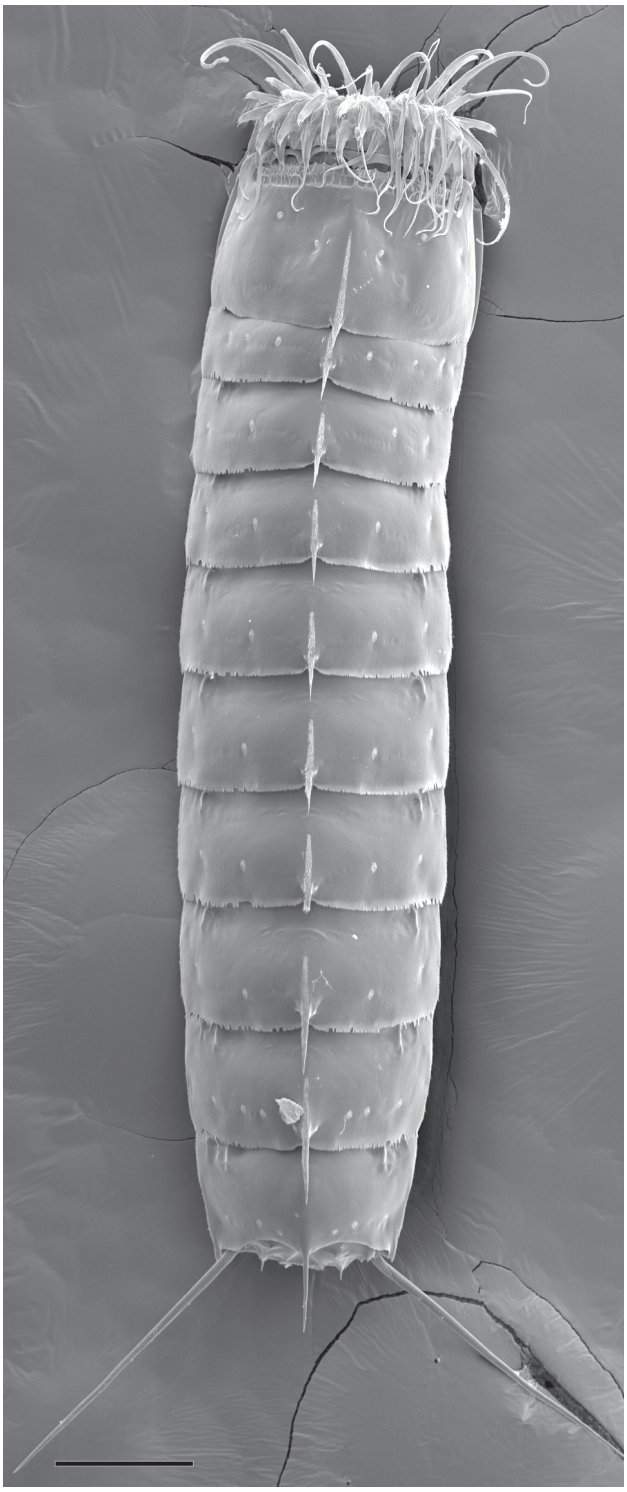


Figure 7. *Cristaphyes abyssorum* scale bar, 100 μm.

2–4 and 7–9; tergal-sternal articulations hirsute; posteriormost tergite with two pairs of sensory papillae and two terminal tubular papillae; anteromesial thickenings (Mittelwuelste) of ventral pachycycli absent in both sexes; trunk segment 10 with two pairs of lateroventral setae closely adjacent to tergal-sternal articulation; males with adhesive tubes on sternal plates of trunk segment 2 and two pairs of penile spines between trunk segments 10 and 11.

Biogeographical remarks. Four representatives of the recently introduced genus, *Cristaphyes*, *C. yushini* (Adrianov, 1989), *Cristaphyes furugelmi* (Adrianov, 1999 in Adrianov & Malakhov, 1999), *Cristaphyes cristatus* (Sanchez et al., 2013), and *Cristaphyes abyssorum* (Adrianov & Maiorova, 2015), have been described from the NW Pacific (see Adrianov, 1989; Adrianov, Malakhov, 1999; Sanchez, et al., 2013, 2016; Adrianov, Maiorova, 2015). As already noted, ten species of pycnophiids are known now from this region (see above).

In addition to these ten species from the NW Pacific, another twelve species of pycnophiids have been found in the Pacific Ocean. Six species, *Pycnophyes faveolus* Brown, 1985 (= *Leiocanthus faveolus* (Brown, 1985)); *P. newzealandiensis* Adrianov, 1999; *P. newguiniensis* Adrianov, 1999; *P. australensis* Lemburg, 2002 (= *Setaphyes australensis* (Lemburg, 2002)), *Kinorhynchus phyllotropis* Brown et Higgins, 1983 (= *Cristaphyes phyllotropis* (Brown et Higgins, 1983)), and *K. rabaulensis* Adrianov, 1999 in Adrianov & Malakhov, 1999 (= *Cristaphyes rabaulensis* (Adrianov 1999 in Adrianov & Malakhov, 1999) were described from the South-West Pacific. Four species, *P. sanjuanensis* Higgins, 1961; *P. parasanjuanensis* Adrianov & Higgins, 1996; *Kinorhynchus ilyocryptus* Higgins, 1961 (= *Pycnophyes ilyocryptus* (Higgins, 1961)), and *K. cataphractus* Higgins, 1961 (= *Higginsium cataphractus* (Higgins, 1961)) were found in the NE Pacific. Two species, *Pycnophyes chiliensis* Lang, 1953 (= *Cristaphyes chiliensis* (Lang, 1953)) and *Kinorhynchus anomalus* Lang, 1953 (= *Cristaphyes anomalus* (Lang, 1953)) were described from the South-East Pacific.

Within these 22 pycnophiids from the Pacific, only two species were known from the deep-sea, bathyal *Pycnophyes schornikovi* and abyssal *Cristaphyes abyssorum.*

5. Discussion

Most of our knowledge about kinorhynchs is restricted to shallow-water species living in coastal environments and on the continental shelf. The information on their occurrence in the deep-water environments is still very limited for detailed biogeographical conclusions. Within the family Echinoderidae, only 21 species have been described from bathyal to ultra-abyssal depths. The only species of *Echinoderes* noted at the abyssal depth (4,403 m) is *E. pterus* Yamasaki et al., 2018, which is widespread in the Arctic Ocean and the North Atlantic (see Yamasaki et al., 2018). *E. ultraabyssalis* constitutes the deepest kinorhynch species described so far (9,538 m), the only hadal *Echinoderes* representative of the Kinorhyncha in the world oceans.

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CHAPTER 14

PYCNOGONIDA

DEEP-WATER PYCNOGONIDA COLLECTED BY THE SOKHOBIO AND KURAMBIO CAMPAIGNS ALONG THE NW PACIFIC

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1. Introduction

The pycnogonids of the NW Pacific have been relatively well-studied in the past. Following upon the classical works by Schimkewitsch (1929-1930) on the Russian marine fauna, is a broad body of literature, mainly by Losina-Losinsky (1933, 1961), Losina-Losinsky & Turpaeva (1958), and Turpaeva (1971a, b, 1973, 2007) which describe the pycnogonids of the eastern marine waters of Russia from the Sea of Japan to the Sea of Okhotsk and the Kuril-Kamtchatka trench. In addition, the classical studies by Ortmann (1891), Hilton (1942a, b), Hedgpeth (1949), Ohshima (1933), Utinomi (1955) have to be considered, and also newer studies by Nakamura (1987), Nakamura and Child (1991), and Child (1995). Many of these studies include data about deep-water creatures found below 1,000 meters. With the addition of Turpaeva (1971), a publication which is solely dedicated to deep-water pycnogonids of the Kuril-Kamtchatka trench becomes available which includes data covering to a depth down to 6,710 m. In addition, some distributional data can be accessed on Pycnobase (Bamber et al. 2019).

In the framework of the SokhoBio and KuramBio cruises in 2015 and 2012, respectively, a total number of 30 samples (63 individuals) of pycnogonids were transferred to our collections and subsequently identified by the authors of this paper. Among the species found in the samples are some characteristic deep-sea species which are typical for the region.

2. Objectives

The aim of the present study is to identify the species collected during the SokhoBio and KuramBio campaigns and compare their distribution and bathymetric range with collected data from the literature.

3. Material and Methods

The sample localities and depths of each specimen are given in the paragraphs about the species and on maps (Map 1 to Map 4). The sea spiders were identified via conventional imaging using stereomicroscopes and microscopes. For identification, the relevant literature was used (see introduction and literature cited). In addition, for some of the species, the original descriptions and old samples housed in the ZSM collections were consulted and examined. Photos were taken with a Wild Macroscope, extended depth of field photos were calculated with Helicon Focus v. 5.

4. Results

The collection analysed in this study includes 28 lots of SokhoBio pycnogonids covering a depth range from 2,346 m (event ID: 8–6) to 4,760 m (event ID 10-8), and two lots of KuramBio, So223/06-09 (5,293–5,307 m) and So223/03-10 (4,977–4,986 m). Altogether, 63 pycnogonids

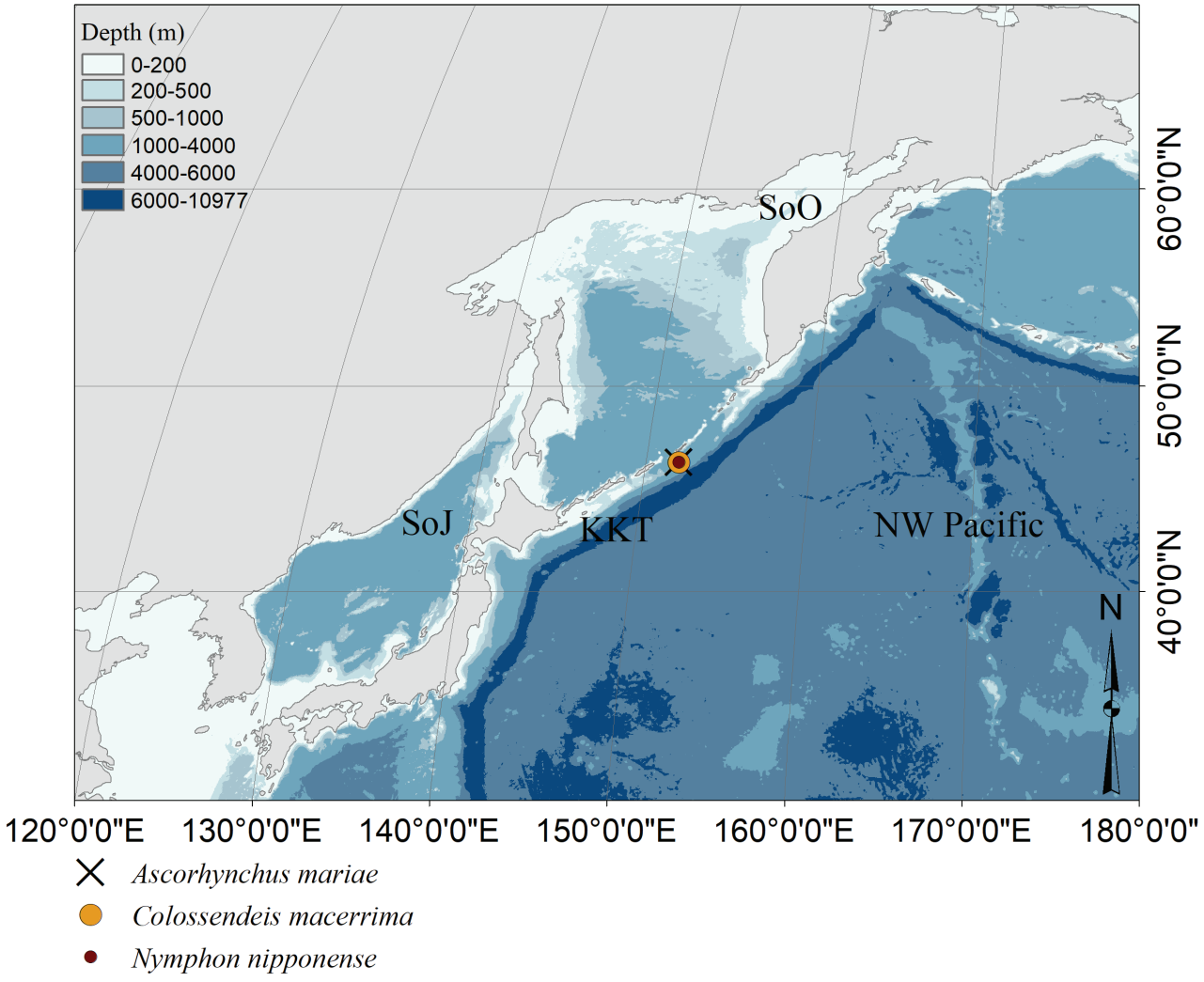
were studied. Samples SokhoBio 9–10 and 9–9 contained 22 and 11 pycnogonids of the genus *Nymphon*, respectively. Sample 9–9 included two individuals of *Colossendeis* and sample 4–10 had two individuals of *Pantopipetta*. All other lots comprised a single pycnogonid individual. Altogether, nine species of Pycnogonida were identified. They are listed here in an alphabetical order.

Ascorhynchus mariae Turpaeva, 1971

(Map 1, Figure 1a)

Collection number: ZSMA20171098, SokhoBio 9–9, RV Lavrentjev, 152.0503 - 151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melzer/L. Dietz.

In her 1971 paper about the Kuril-Kamtchatka trench, Turpaeva found three species of *Ascorhynchus*, *A. mariae*, *A. losinalosinskii* Turpaeva, 1971 and *A. inflatum* Stock, 1963, and indicated that they are found at specific depth ranges (*A. mariae*: 3,145–3,250 m; *A. losinalosinskii* 3145–3250 m; *A. inflatum* 4,915–4,985 m). The depth at which the SokhoBio specimen of *A. mariae* was found (c. 3.5 km) corresponds well with the depth distribution presented in Turpaeva's paper.



Map 1. Sample localities of *Ascorhynchus mariae, Colossendeis macerrima* and *Nymphon nipponense*.

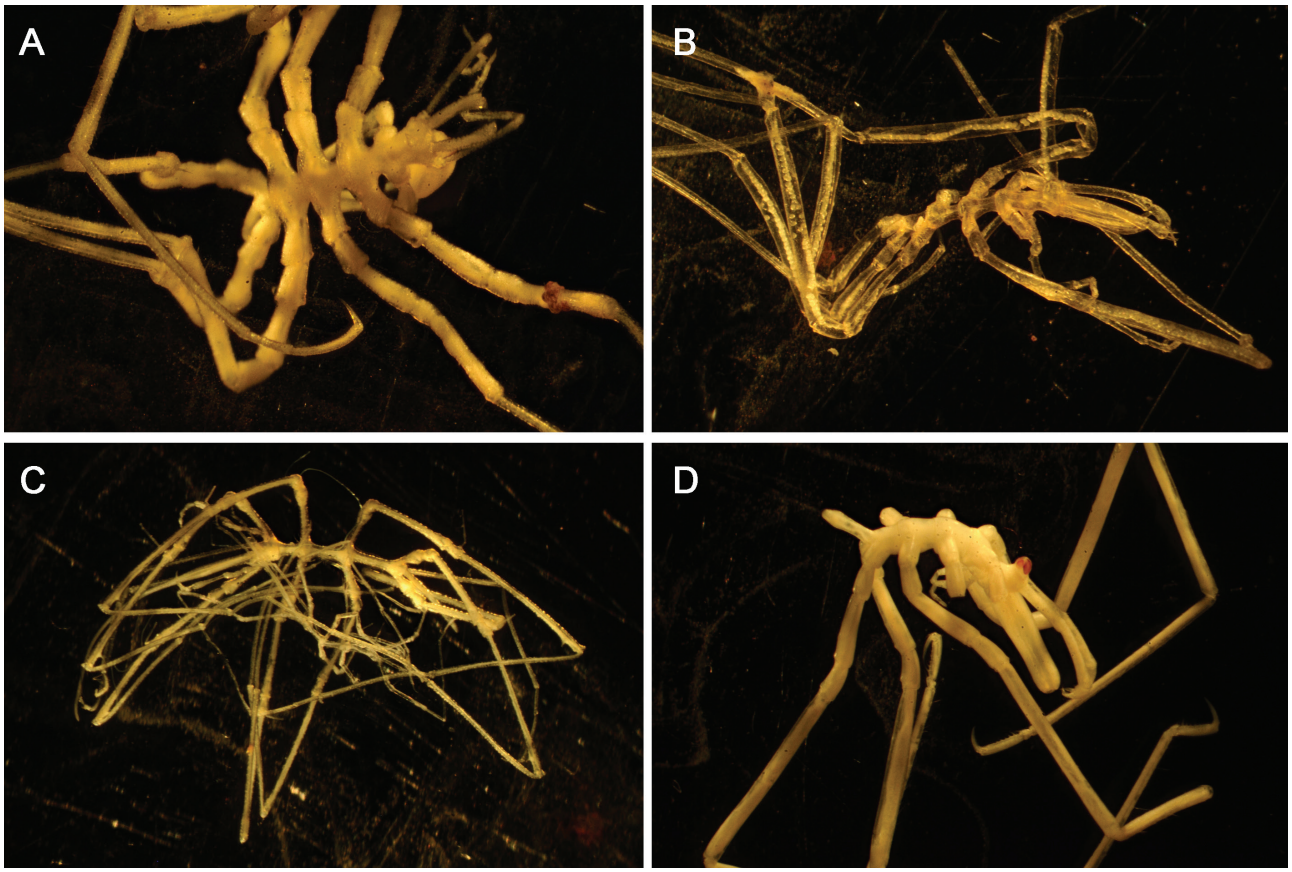


Figure 1. Surveys of some of the sampled pycnogonids. A. *Ascorhynchus mariae,* SokhoBio 9-9, ZSMA20171098. B. *Heteronymphon bioculatum,* SokhoBio 9-10, ZSMA20171091. C. *Pantopipetta longituberculata,* SokhoBio 4-10, ZSMA20171108. D. *Phoxichilidium ungellatum,* SokhoBio 8-5, ZSMA20171104.

***Colossendeis angusta* Sars G. O., 1877**

(Map 2)

Collection number: ZSMA20171080, SokhoBio 6–8, RV Lavrentjev, 150.0183–150.00028, 48.084–48.0847, depth: 3,351 m. det.: J. Hübner.

Collection number: ZSMA20171085, SokhoBio 10–7, RV Lavrentjev, 152.1675–152.18472, 46.1189–46.1175, depth: 4,469 m. ID: J. Hübner.

Collection number: ZSMA20171086, SokhoBio 8–6, RV Lavrentjev, 151.369–151.568, 46.363–46.6013, depth: 2,346 m. det.: J. Hübner.

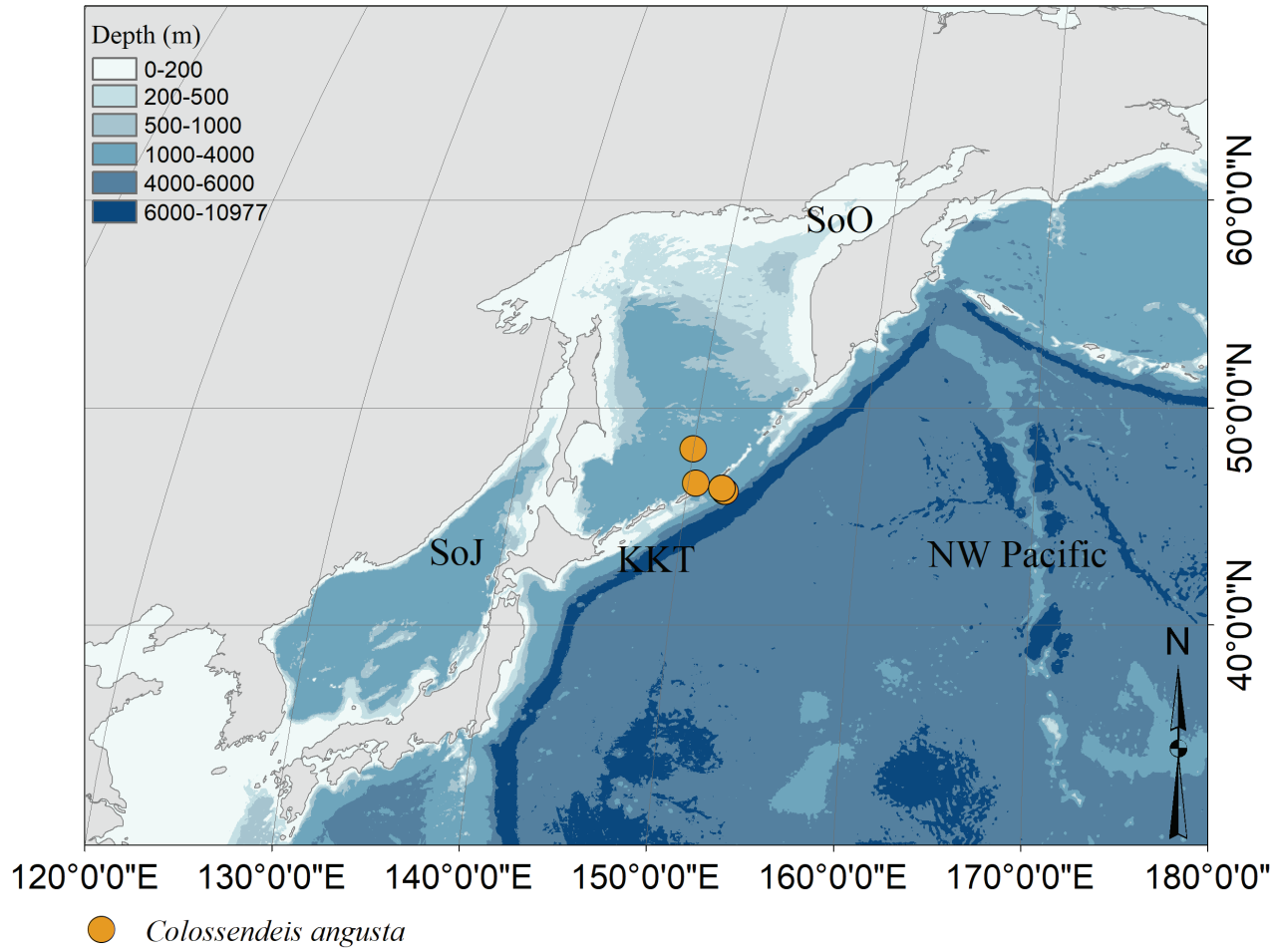
Collection number: ZSMA20171087, SokhoBio 10–8, RV Lavrentjev, 152.1833–152.2506, 46.1353–46.0856, depth: 4,760 m. det.: J. Hübner.

Collection number: ZSMA20171090, SokhoBio 10–8, RV Lavrentjev, 152.1833–152.2506, 46.1353–46.0856, depth: 4,760 m. det.: J. Hübner.

Collection number: ZSMA20171097, SokhoBio 9–9, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melzer/L. Dietz.

Collection number: ZSMA20171113, SokhoBio 9–10, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melzer/L. Dietz.

Collection number: ZSMA20171120, SokhoBio 9–9, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: L. Dietz.



Map 2. Sample localities of *Colossendeis angusta*.

This cosmopolitan species has been recorded before from the NW Pacific deep waters, e.g., in the Sea of Japan and the Bering Sea. Records from the Kuril-Kamchatka area are presented in Turpaeva (1971), where *C. angusta* has been found as far down as 5,200 m. Hedgpeth (1949) presents records from the east coast of Japan and the Sea of Okhotsk at depths from 500 to 1,200 m, and Nakamura & Child (1991) from off Honshu at between c. 400 and 500 m depth.

Colossendeis macerrima Wilson, E.B., 1881
(Map 1)
Collection number: ZSMA20171096, SokhoBio 9–10, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: L. Dietz.

As *C. angusta*, *C macerrima* is a common, cosmopolitain deep-water species. Turpaeva (1971) recorded this species at depths between 2,500 and 4,000 m, Nakamura & Child (1991) off Honshu at between c. 500 and 2,000 m depths.

Colossendeis sp., juvenile
Collection number: ZSMA20171101, SokhoBio 8–4, RV Lavrentjev, 151.5669, 46.6013, depth: 2,348 m. det.: L. Dietz.

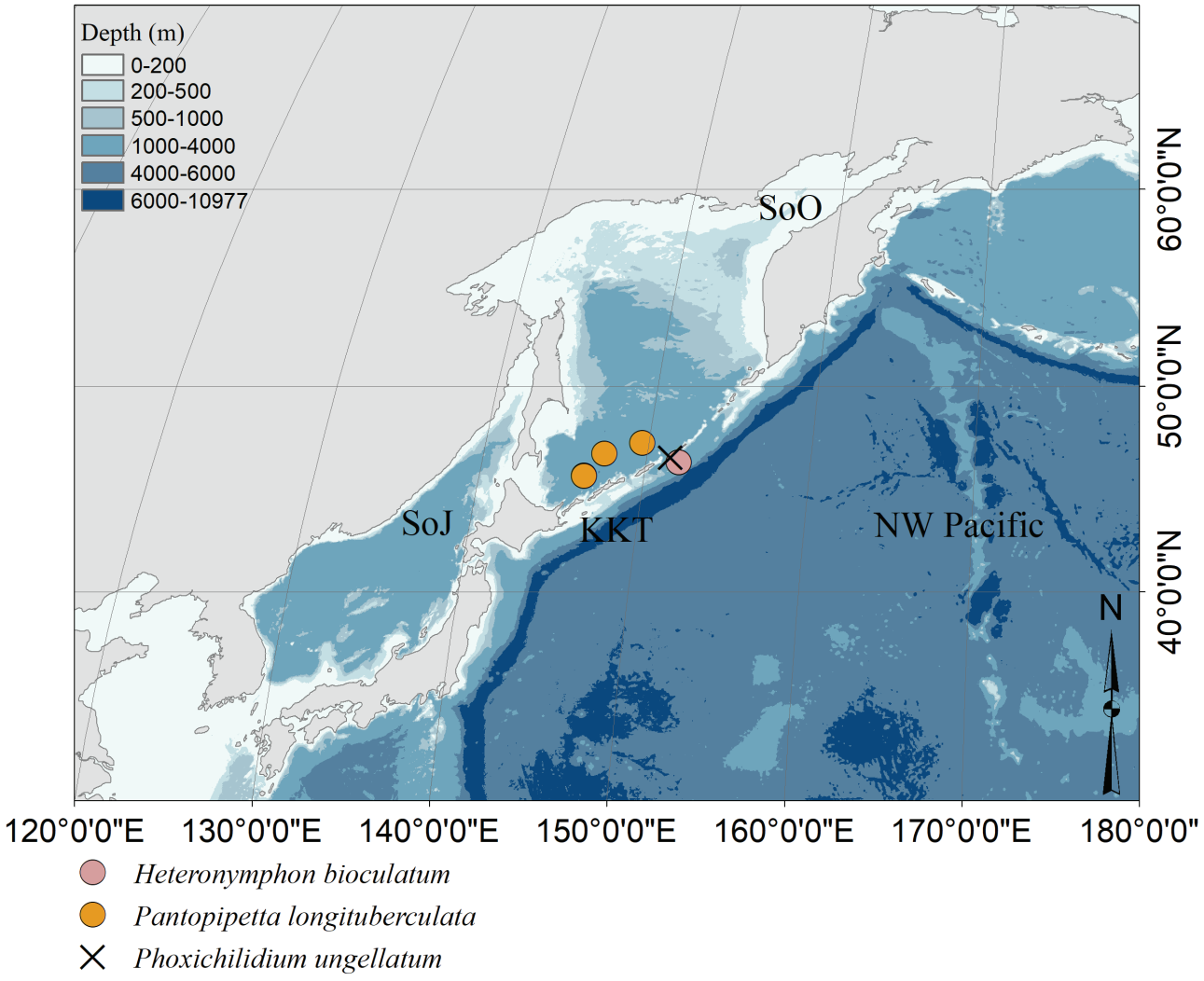
A juvenile specimen which couldn't be attributed using morphology alone to one of the species of *Colossendeis* present in the area.

***Heteronymphon bioculatum* Turpaeva, 1956**
(Map 3, Figure 1b)
Collection number: ZSMA20171091, SokhoBio 9–10, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melzer/L. Dietz.

Collection number: ZSMA20171094, SokhoBio 9–9, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melzer/L. Dietz.

Turpaeva (1971) surveys records of *H. bioculatum* in the Sea of Okhotsk and the Kuril-Kamchatka trench at depths between c. 2,500 and 4,000 m, which corresponds well with the record presented here. At depths between 5,000 and 6,800 m, a second species of *Heteronymphon* is found, *H. profundum* Turpaeva, 1956. The third species known from this area, *H. birsteini*, is found at a lower depth c. 1,000 m (Turpaeva 1971).

***Nymphon longitarse* Krøyer, H., 1844**
(Map 4)
Collection number: ZSMA20171081, SokhoBio 8–6, RV Lavrentjev, 151.369–151.568, 46.363–46.6013, depth: 2,346 m. det.: J. Hübner.



Map 3. Sample localities of *Heteronymphon bioculatum, Pantopipetta longituberculata* and *Phoxichilidium ungellatum*.

Collection number: ZSMA20171088, SokhoBio 8–6, RV Lavrentjev, 151.369–151.568, 46.363–46.6013, depth: 2,346 m. det.: R. Melzer/J. Hübner.

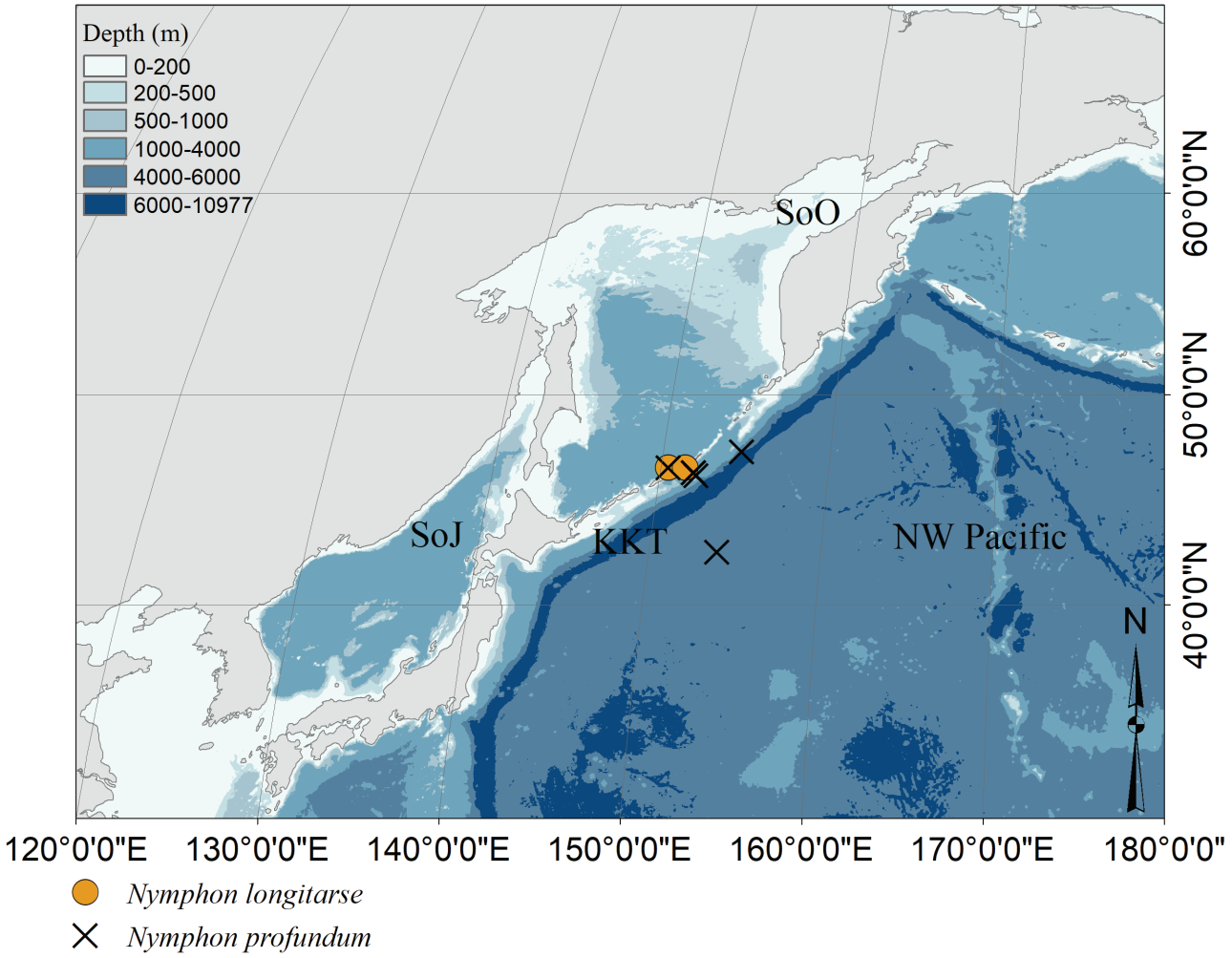
N. *longitarse* is a circumarctic and boreal species of the northern hemisphere recorded by Hedgpeth (1949) for the Sea of Japan, the Sea of Okhotsk, and the Bering Sea. Child (1995) recorded the species from the Aleutians. Losina-Losinsky (1961) and Turpaea (2007) reported a maximum depth of 1,600 m which is surpassed to some extent by our samples.

***Nymphon nipponense* Hedgpeth, 1949**

(Map 1)

Collection number: ZSMA20171093, SokhoBio 9–10, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melzer/L. Dietz.

This species of *Nymphon* has been described by Hedgpeth from the Albatross collection from the Sea of Okhotsk and east of Japan, where it was found at depths between c. 500 and 1,500 m. Compared to this, our record of 3.5 km of depth surpasses that of Hedgpeth.



Map 4. Sample localities of *Nymphon longitarse* and *Nymphon profundum*.

***Nymphon profundum* Hilton, 1942**
(Map 4)
Collection number: ZSMA20171083, SokhoBio 9–9, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melzer/L. Dietz.

Collection number: ZSMA20171089, SokhoBio 10–7, RV Lavrentjev, 152.1675–152.18472, 46.1189–46.1175, depth: 4,469 m. det.: R. Melzer/L. Dietz.

Collection number: ZSMA20171095, SokhoBio 9–10, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melzer.

Collection number: ZSMA20171099, SokhoBio 9–9, RV Lavrentjev, 152.0503–151.9858, 46.2519–46.2672, depth: 3,432 m. det.: R. Melz er.

Collection number: ZSMA20171102, SokhoBio 9–7, RV Lavrentjev, 152.0502–152.0508, 46.2672–46.2672, depth: 3,374 m. det.: R. Melzer.

Collection number: ZSMA20171117, SokhoBio 8–6, RV Lavrentjev, 151.369–151.568, 46.363–46.6013, depth: 2,346 m. det.: R. Melzer.

KuramBio So223/06-09, RV Sonne, 154°0.05‘–153°59.73, 42°29.25‘–42°28.32›, depth 5,293–5,307 m. det.: R. Melzer

KuramBio So223/03-10, RV Sonne, 154°42.17–154°43.18, 47°14.27‘–47°14.94‘, depth 4,977–4,986 m. det.: R. Melzer

This species of *Nymphon* is the most common in the SokhoBio and KuramBio samples, and occurs at depths between c. 2,000 and 5,000 m. This corresponds well with Hilton's (1942) and Hedgpeth's (1949) observations. Remarkably, deep-sea studies from the same area (Turpaeva, 1971) included no blind species without accessory claws such as *N. profundum*.

***Pantopipetta longituberculata* (Turpaeva, 1955)**
(Map 3, Figure 1c)
Collection number: ZSMA20171108, SokhoBio 4–10, RV Lavrentjev, 149.6166, 47.2, depth: 3,366 m. det.: R. Melzer/L. Dietz.

Collection number: ZSMA20171109, SokhoBio 2–8, RV Lavrentjev, 147.4005, 46.6836, depth: 3,350 m. det.: R. Melzer/L. Dietz.

Collection number: ZSMA20171110, SokhoBio 11–7, RV Lavrentjev, 146.3678–146.367, 45.618–45.619, depth: 3,216 m. det.: R. Melzer/L. Dietz.

Collection number: ZSMA20171111, SokhoBio 11–2, RV Lavrentjev, 146.3838, 45.6008, depth: 3,206 m. det.: R. Melzer/L. Dietz.

P. longituberculata had been described by Turpaeva (1955) from the Kuril-Kamchatka trench, and later on, more records from this region were published with the depth record being at 6,700 m (Turpaeva 1971). All of the five specimens from the SokhoBio campaign were caught at depths between c. 3,200 and 3,500 m confirming previous data on the depth range of the species.

***Phoxichilidium ungellatum* Hedgpeth, 1949**
(Map 3, Figure 1D)
Collection number: ZSMA20171104, SokhoBio 8–5, RV Lavrentjev, 151.6172–151.568, 46.5852–46.6014, depth: 2,267 m. det.: R. Melzer/L. Dietz (fig. 4).

This species of *Phoxichilidium* is common in the NW Pacific. Hedgpeth (1949) found this species in the Sea of Japan, the east coast of Japan, and the Sea of Okhotsk. Earlier records of this species were collected in depths between 150 and 1,200 m (Hedgpeth 1949, Turpaeva 2007). This depth range is thus enlarged by the present study.

5. Discussion

The pycnogonid species harvested by SokhoBio and KuramBio represent a section of the deep-water communities known from the NW Pacific (summarized in Hedgpeth 1948, Turpaeva 1971). Two species of *Colossendeis* are cosmopolitan deep-water species, while endemic species of *Colossendeis* as described in Losina-Losinsky & Turpaeva (1958) were absent in the samples. Similarly, with *Nymphon longitarse*, a circumarctic and boreal species is present (Turpaeva 2007). The other two species of *Nymphon* are northern or NW Pacific species, respectively. A more restricted area, i.e., the Sea of Japan, the east coast of Japan and the Sea of Okhotsk, is characteristic of *Phoxichilidium ungellatum* (Turpaeva 2007). According to our current knowledge, *Ascorhynchus mariae*, *Heteronymphon bioculatum*, and *Pantopipetta longituberculata* are endemic to the Kuril-Kamchatka trench and surrounding waters (Turpaeva 1971). Bathymetric data of most species are in accordance with earlier records. However, the depth ranges of *Nymphon longitarse*, *Nymphon nipponense*, and *Phoxichilidium ungellatum* were enlarged considerably from about 1 km depth to 2 or even 3 km.

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CHAPTER 15

ASCOTHORACIDA

A REVIEW ON BIOGEOGRAPHY OF THE DEEP-SEA ASCOTHORACIDA LACAZE-DUTHIERS, 1880 (CRUSTACEA: THECOSTRACA) ALONG THE NW PACIFIC

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1. Introduction

The Ascothoracida is an infraclass of the Thecostraca Gruvel, 1905, which comprises 105 species exclusively parasitic on both Echinodermata and Cnidaria. There are two orders of the ascothoracidans, the Laurida Grygier, 1987, which mostly parasitize Anthozoa, and Dendrogastrida Grygier, 1987, which are only found on echinoderms (Grygier, 1996). The laurids are parasites of various corals such as Scleractinia, Zoantharia, Antipatharia and Alcyonacea. However, the genus *Waginella* Grygier, 1983, is found on crinoid echinoderms. The dendrogastrids are parasites of other echinoderms such as Asteroidea, Ophiuroidea, and Echinoidea.

By their mode of life, the Ascothoracida range from primitive ectoparasites, to mesoparasitic forms and highly specialized endoparasites. Most of the ascothoracidans are dioecious, with larger females accompanied by smaller, sometimes dwarf, cypridiform males (Kolbasov 2007), but members of the Petrarcidae Gruvel, 1905 and possibly Ctenosculidae Thiele, 1925 are simultaneous hermaphrodites (Grygier 1983a, b). The life cycle includes up to six free-swimming naupliar instars, one or two cypridiform ascothoracid larvae, a juvenile, and an adult. The larval stages could be free living or brooded.

The morphology of the Ascothoracida is characterized by several specific features that are outlined below. In more primitive or basal forms, the inner body of the parasite is covered by a bivalved carapace, with valves often fused in females of advanced parasites. The carapace contains gut diverticlum and gonads. The head bears 4–6-segmented, Z-shaped prehensile antennules, equipped with a movable claw distally. Developed compound eyes are absent in adults. Piercing mouthparts including paired mandibles, maxillules and maxillae are sheathed by a labrum to form a conical oral cone, considered as a special adaptation to feeding as parasites. Primitively ascothoracidans have 6 thoracic segments with biramous, setose thoracopods, abdomen with 5 segments including a telson terminating with unsegmented furcal rami. Number of trunk segments and thoracopods are often reduced in advanced forms.

The general geographical distribution of the Ascothoracida is cosmopolitan, with species found in tropical, boreal and Polar Regions (Map 1). Vertical distribution is remarkable, with organisms found from shallow waters to abyssal and even hadal depths.

2. Objectives

In this chapter we are providing a review of the biogeography of the deep-sea Ascothoracida of the NW Pacific Ocean (NWP) based on published literature and our own unpublished data obtained within the framework of the research cruise KuramBioII (Kuril-Kamchatka Biodiversity Studies II).

3. Material and Methods

Three species of the Ascothoracida were obtained in the Kuril-Kamchatka trench (KKT) during the Russian-German expedition KuramBioII (16.08.2016–26.09.2016) at depths

ranging from 5,200 to 6,200 m. Agassiz trawls (AGT) collected hosts specimens of ophiuroids *Ophiacantha pacifica* (Lütken & Mortensen, 1899) and *Amphiophiura pacifica* (Litvinova, 1971), and sea stars *Eremicaster crassus* (Sladen, 1883) and *Eremicaster vicinus* Ludwig, 1907, which were infested with ascothoracidan parasites. Echinoderm specimens were firstly examined alive and live parasites were dissected out of hosts to be photographed and fixed with 96% ETOH (for molecular analyses) and 2,5% Glutaraldehyde in sea water (for morphological studies). Further examination of the ethanol fixed brittle stars (ophiuroids) revealed additional specimens of parasites. Material was studied using both light and scanning electron microscopy (SEM). For the SEM analysis, the samples were post-fixed in 2% OsO4 (Osmium tetroxide) for 2 hrs, dehydrated in acetone and critically-point dried with CO_2. Dried specimens were sputter-coated with platinum–palladium and examined on a JEOL JSM-6380LA SEM operating at voltages of 15–20 kV at Moscow State University.

4. Results

The region of NW Pacific contains 3 genera of the deep-sea ascothoracid parasites belonging to the Dendrogastrida (families Ascothoracidae Grygier, 1987 and Dendrogastridae Gruvel, 1905).

4.1. Family Ascothoracidae

Species belonging to this family are exclusively parasitic on ophiuroid echinoderms (Figure 1). These are considered to be mesoparasitic as they are found in the genital bursae of the ophiuroid hosts. Large, bivalved female forms a cyst and is often accompanied by one or several dwarf, cypridiform males (Figure 1D). The female body is fully enclosed by the bivalved caparace or mantle (Figure 1C, D). However, the head and all 11 trunk somites with appendages are retained in these parasites. The prehensile antennules are 5-segmented and armed with a claw used to fix onto the host tissues. An oral cone formed by the transformed labrum which encloses piercing mouthparts is used for feeding on host tissues. The trunk of parasite consists of a well-developed thorax bearing 5-6 pairs of thoracopods and a 5-segmented abdomen terminated with a pair of furcal rami.

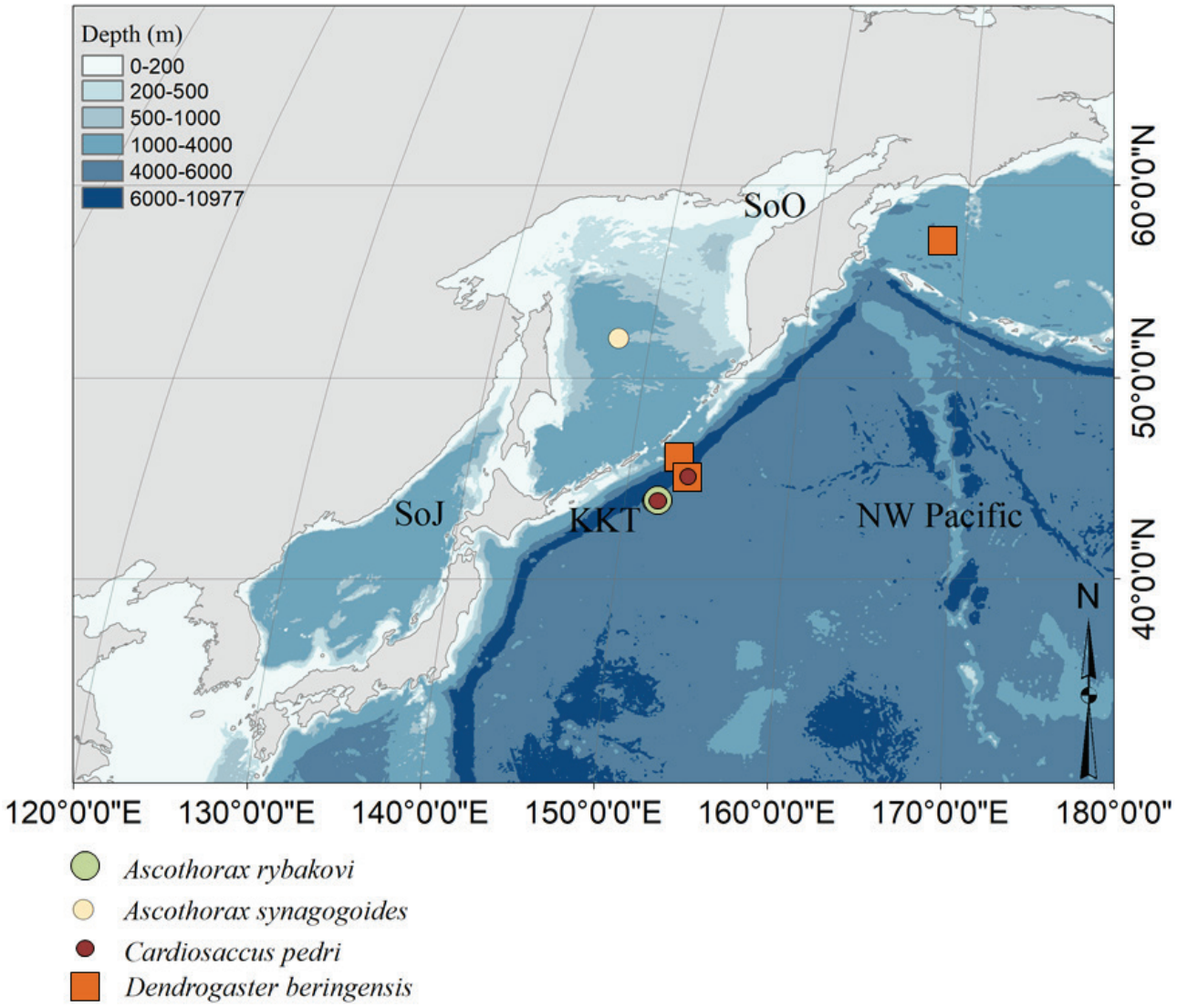
The type genus *Ascothorax* Djakonov, 1914 contains 10 species with a type species *Ascothorax ophioctenis* Djakonov, 1914 described from *Ophiocten sericeum* (Forbes, 1852) (Djakonov 1914).

Two new ascothoracid species belonging to two genera were recently described from the abyssal depths of KKT (Kolbasov and Petrunina 2018). *Ascothorax rybakovi* Kolbasov & Petrunina, 2018 was found in *Ophiacantha pacifica* (Figure 1A) at depths ranging from 5,150 to 5,700 m. Each of the four infested host brittle stars contained only one cyst with a larger female and one dwarf male. The live female parasite is pink in colour, with a peach shaped carapace (Figure 1C). One of the specimens was hosting a hyperparasitic isopod cryptoniscus larva (Figure 1C).

A new monotypic genus *Cardiosaccus* was established with a type species *Cardiosaccus pedri* Kolbasov & Petrunina, 2018 found in *Amphiophiura pacifica* (Figure 1B) at depths from 5,200 to 5,700 m. (Kolbasov and Petrunina

2018). Remarkably the females of the new genus *Cardiosaccus* possess a very characteristic cordate carapace forming brood chamber (Figure 1D) lack the first thoracopod, and have a very prominent ventral extension of the fourth abdominal segment. Both newly described species, *C. pedri* (Figure 1D) and *A. rybakovi* (Figure 1C), coexisted at the same locations at depths ranging from to 5,150 to 5,700 m. which makes them the deepest records for the family Ascothoracidae.

Ascothorax synagogoides (Wagin, 1964) is another species of the deep-sea Ascothoracida from NWP. Firstly it was described by Wagin as *Parascothorax synagogoides* parasitizing *Ophiophthalmus normani* (Lyman 1879) from the Sea of Okhotsk at 1197m depth (Wagin 1964). However, later studies showed that no strict morphological traits could be found to distinguish *Parascothorax* from *Ascothorax* (Grygier 1983c, 1991; Kolbasov and Petrunina 2018). One of the key defining characters established by Wagin actually corr-



Map 1. Distribution of the deep-sea Ascothoracida.

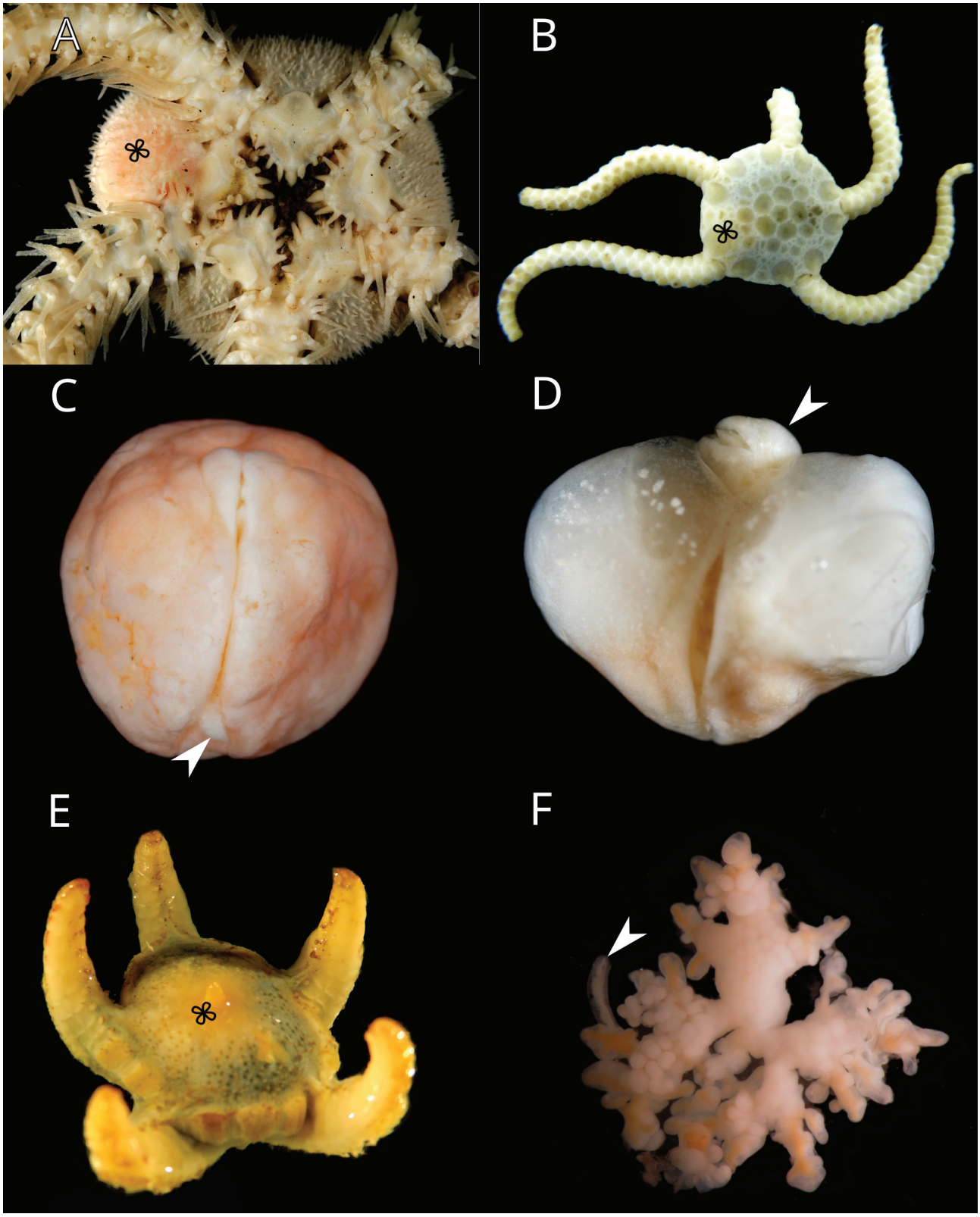


Figure 1. Diversity of the deep-sea Ascothoracida and their hosts. (A) *Ophiacantha pacifica* with *Ascothorax rybakovi* in genital bursa (indicated by asterisk); (B) *Amphiophiura pacifica* with *Cardiosaccus pedri* in genital bursa (indicated by asterisk); (C) Female of *A. rybakovi* with hyperparasitic cryptoniscus larva (indicated by arrowhead); (D) Female of *C. pedri* with cypridiform dwarf male (indicated by arrowhead); (E) *Eremicaster vicinus* with *Dendrogaster beringensis* (indicated by asterisk); (F) Female of *D. beringensis*, male posterior projection indicated by arrowhead. A, C, D used with kind permission of Dr. Anastassya Maiorova.

esponds to the host, not to the parasite (Wagin 1964). Such characters could not be used as diagnostic for the genus. Thus, *Parascothorax* was eventually synonymized with the genus *Ascothorax* (Kolbasov and Petrunina 2018). Remarkable geographic and vertical distribution was revealed for *A. synagogoides* when additional specimens were found at wide range of depths from 900 to 1,900 m in the Eastern Pacific, coast of California (Grygier 1991).

Species of the Ascothoracidae are typically restricted to a particular host species.

4.2. Family Dendrogastridae

The family Dendrogastridae (genera *Dendrogaster* Knipovich, 1890, *Bifurgaster* Stone & Moyse, 1985, and *Ulophysema* Brattström, 1936) is the most species rich within Ascothoracida, comprising the most advanced and specialised parasites. Over 30 species of the genus *Dendrogaster* are found in the coelomic cavity of different asteroid echinoderms and thus are endoparasitic. The female has a transformed mantle with bizarre branching outgrowths and a small inner body with a reduced thorax and abdomen (Figure 1F). The head bears 4-segmented antennules and the oral cone with maxillae. The parasite is enclosed with host epithelium and feeds on its coelomic cells. The dwarf, cypridiform males retain more crustacean traits including segmented thorax and abdomen as well as developed thoracopods. However, the most prominent part of their body is the posterior projections or testes containing spermatozoa (Figure 1F, arrowhead). These males are found within the mantle of the female and are believed to be parasitizing there.

Deep-sea fauna of Dendrogastridae family in the NW Pacific is represented by two species of the genus *Dendrogaster*. *D. beringensis* Wagin, 1957 was described from a sea star *Eremicaster tenebrarius* Fischer from 3,940 m depth of the Bering sea (Wagin, 1957). The second finding was made in the KKT (2,590 m depth) in 1968 during one of RV *Vityaz* expeditions (Wagin, 1976). *D. beringensis* (Figure 1F) was rediscovered again from the KKT during the KuramBioII cruise from the sea stars *Eremicaster crassus* (Figure 1 E) and *Eremicaster vicinus* obtained from depths 5,700 m and 6,200 m respectively. The parasite occupies the coelomic cavity of the host above the stomach. Infested sea stars could be distinguished from non-infested ones by the yellowish colour of the aboral side, because the dendrogaster could be seen through the skin and it contrasts against the grey coloured stomach full of sediment. Out of 72 examined host specimens only two contained a single parasite. *D. beringensis* was obtained from the hadal depth of 6,200 m and is the deepest record not only for the Dendrogastridae but for the Ascothoracida in general.

Dendrogaster astropectinis (Yosii, 1931) was originally described from *Astropecten scoparius* Müller & Troschel, 1842 from shallow waters in Misaki Bay (Japan) (Yosii 1931). However, deep-sea specimens were firstly obtained by Wagin in the Bering Sea in 1932 and 1950 from the sea star *Psilaster pectinatus* (Fisher, 1905). Material dredged from 2,000 m and 2,300 m depth yielded more than 30% of infested hosts from these expeditions (Wagin 1976).

5. Discussion

Investigation of the deep-sea fauna of the Ascothoracida in the NW Pacific enabled us to describe a new genus and a new species as well as revise the taxonomy of the major family of these parasites - the Ascothoracidae (Kolbasov and Petrunina, 2018). Our data show that the biodiversity of the deep-sea ascothoracidans in the NWP comprise only about 5% of the known species. The region of the NWP is a home to the most deep dwelling Ascothoracida.

Most of the Ascothoracida are characterized with high host specificity. For example, within the family Ascothoracidae all the species are restricted to a particular species of host. However, *Dendrogaster* despite being a highly specialized endoparasitic genus was shown to have much lower host specificity. Thus, for *D. beringensis* three species of hosts belonging to the genus *Eremicaster* were recorded. Moreover, the host species of *D. astropectinis* belong to two genera of sea stars, *Astropecten* and *Psilaster*. Taking into account the endoparasitic nature of all dendrogastrids such low host specificity is very unlikely. Most probably species of *Dendrogaster* represent complexes of cryptic species. Current taxonomy of Dendrogastridae is based solely on morphology of adult females and the structure of the mantle in particular. Being highly transformed endoparasitic forms these ascothoracidans lack many of the morphological characters that might be used for taxonomic identification. Thus, molecular-genetics analysis is needed for clarification of this phenomenon.

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CHAPTER 16

OSTRACODA

BIODIVERSITY AND BIOGEOGRAPHY OF OSTRACODA (CRUSTACEA) FROM THE DEEP NW PACIFIC

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1. Introduction

1.1. Biological Studies in the NW Pacific

The Northwest (NW) Pacific is now one of the better investigated deep-sea areas in the world. More than 20 expeditions have been performed in this region on board the RV *Vityaz* in the mid-twentieth century (Monin 1983). Subsequently, the diverse and abundant deep-sea benthic fauna found in the Kuril-Kamchatka Trench (KKT) and the adjacent abyssal plain, one of the most productive oceanic regions in the world, and has been described in numerous publications, e.g. in volumes of the transactions of the P. P. Shirshov Institute of Oceanology 1955, 1970, 1971 (Sokolova 1976, 1981). In these volumes, information on biotic and abiotic environmental parameters of this unique area, such as the composition of taxa, first data on hydrology, topography, chemical characteristics, and organic matter of the bottom water, and the characteristics of sediments of the KKT area, are presented. Based on these data, a checklist of free-living invertebrate species of the Russian Far Eastern Seas was published (Sirenko 2013). Recently (2010-2016), four international deep-sea expeditions to the NW Pacific were performed as German-Russian joint ventures for the study of the composition of meio-, macro and megafauna.

Numerous studies have investigated Recent and fossil assemblages of ostracods from shallow-marine environments in the NW Pacific (e.g.Ikeya and Cronin 1993, Ikeya 2003; Hou and Gou 2007; Yasuhara et al. 2017), but, as usual, deep-sea environments were much less investigated. There are relatively limited numbers of studies of deep-sea podocopes in the open NW Pacific (Benson 1971; Schornikov 1975; Karanovic & Brandão 2015; Yasuhara et al. 2019), marginal seas (Sea of Japan: Ishizaki and Irizuki 1990; Huang et al. 2018, 2019; East China Sea: Ruan and Hao 1988; Zhao and Whatley 1997; Zhao et al. 2004; South China Sea: Ruan 1989; Zhao and Zheng 1996; Zhao 2005), deep basins (Tanaka et al. 2012), hydrothermal vents (Tanaka and Yasuhara 2016), and geological outcrop sections showing deep-sea (mostly upper bathyal) environments (Yamada et al. 2005; Irizuki et al. 2007; Iwatani et al. 2014). These studies are mainly limited to bathyal environments, leaving the abyss and the oceanic trenches almost completely unknown until recently (see discussion on the German-Russian projects below).

Recently, Chavtur and Bashamov (2018) published a brief historic and taxonomic overview of the myodocopid ostracods from the NW Pacific. Although the study of this group in the region stretches back to the 1930s, only around 60 species have been reported so far. Unlike podocopids, almost all myodocopid records are of Recent taxa. Myodocopids of the NW Pacific belong to benthic (suborder Cladocopina Sars, 1865 and Myodocopina Sars, 1866) and pelagic groups (suborder Halocypridina Dana, 1853). Although, no genetic studies on myodocopids from the region have been conducted so far, most of the species seem to be endemic and with relatively narrow distributions (Chavtur and Bashamov, 2018).

The benthic, deep-sea fauna of the Sea of Japan, Sea of Okhotsk, KKT, as well as the adjacent abyssal plain was studied during the SoJaBio, SokhoBio and KuramBio I and II expeditions. The study area, sampling methods, as well as

the composition of taxa has been described in a number of publications from this region (e.g. Brandt 2016; Brandt et al. 2013; Malyutina and Brandt 2013; Brandt and Malyutina 2015, Brandt et al. 2015, 2018, Malyutina et al. 2018). In order to study the potential isolating barrier effect of the KKT, which might have reduced the exchange of the fauna of the Sea of Okhotsk and open NW Pacific and vice versa, we have tested whether macrofaunal composition and diversity at high taxonomic level differ across different geographic areas and depth zones (Brandt et al. 2019a, 2019b). The study of ostracods from these four expeditions are still ongoing, but the fauna, with at least 50 species in total, includes a diverse and abundant assemblage (herein, Brandão et al. 2019a; Yoo et al. 2019).

Based on this background, the Beneficial project (Biogeography of the northwest Pacific fauna: A benchmark study for estimations of alien invasions into the Arctic Ocean in times of rapid climate change), was designed to better document and visualize the wealth of data on the biogeography of the deep-sea fauna of the NW Pacific area and adjacent Arctic Ocean. Therefore, the main aim of the present chapter is to deliver a sound biogeographic baseline study of the NW Pacific ostracod distribution. This analysis is based on a compilation of all published data on Recent ostracods and a non-exhaustive search on data on fossil ostracods.

1.2. An Overview on the Biology and Ecology of Ostracoda

Ostracoda Latreille, 1802 is a class of small-sized (0. 2 to 2 mm) crustaceans, with soft body enclosed in a generally well-calcified, bivalved carapace. As a consequence, the group has left an impressive fossil record, starting in the Ordovician period (ca. 450 million years) (Siveter et al. 2014). Of the estimated 33,000 described species (Brandão et al. 2019a; Eugene Kempf, personal communication, June 2001 apud Horne et al. 2002) almost 80% are fossil. Concerning only the Recent species, the class is divided in three subclasses, Myodocopa Sars, 1866, Podocopa Sars, 1866 and Platycopa Sars, 1866. Two of these, i.e., Myodocopa and Platycopa, comprise only marine species, while the representatives of Podocopa live in both marine and freshwater ecosystems.

Most marine species reproduce sexually, while parthenogenesis has been recorded in several freshwater lineages. There are cases of ancient asexual lineages, (Schön et al. 2009), as well as spatial and temporal parthenogenesis (Horne and Martens 1998). In few parthenogenetic species, sexual and asexual lineages coexist in one population (Bode et al. 2010). Depending on the lineage, ostracods go through four to eight moulting stages, before reaching the adult stage. The first instar is already enclosed in a carapace and has three or four pairs of limbs (e.g. Karanovic 2012: 59). In many lineages, brood care has also been recorded (Ozawa 2013), and drought resistant eggs are common in several freshwater lineages.

Most marine and all freshwater ostracods are deposit feeders, and only a few lineages are filter feeders (e.g. Platycopa and myodocopin Cylindroleberididae Müller, 1906), or scavengers (e.g. *Cytheropteron* Sars, 1866) (e.g. Karanovic, 2012: 62). Although the majority of ostracods are free-living animals, there are a few lineages with commensal representatives living on sponges,

echinoids, or other crustaceans (Hobbs 1971; Tanaka and Arai 2017).

Ostracods can be found in all geographic regions, but their distribution is limited by low dispersal abilities (benthic juveniles, no larvae) and physical and biological factors. There is a high rate of endemism at the species level, but deep-sea genera and families are found to be mostly cosmopolitan.

1.3. Ostracod Habitat

The long evolutionary history of ostracods has resulted in adaptations to various environmental conditions, and today, the species can be found in all aquatic habitats, and even forest floors with wet litter (e.g. Karanovic 2012). With the exception of a few freshwater species and only one marine group (suborder Halocypridina) that are planktonic, all other ostracods are benthic. They are traditionally regarded as a meiofaunal group, but many taxa in the deep sea and a few in freshwater environments show macrofaunal body size (>500 μm in length). Most specimens analysed herein are macrofaunal sized. They are part of epibenthic or endobenthic communities.

Higher gamma diversities of ostracods have been recorded from shallow marine environments than from the deep-sea, but these differences have been shown to be correlated to the sampling effort, which is much larger in the continental shelves, diminishing gradually towards the abyss and even more extremely towards hadal areas (e.g. Brandão et al. 2019b: Figure 2). The relationship of the ostracod alpha diversity and bathymetry is variable. In the North Atlantic, for example, it is highest at intermediate depths, as is found from many other deep-sea animals (Jöst et al. 2019). However, in the Southern Ocean, no clear pattern was found, and varied randomly between the ostracod (and also bryozoan and isopod) species richness and depth at a range of 0 and 7,000 m deep, with the highest richness found at 6,000 m (Kaiser et al. 2011: Figure 6.C). Globally, the number of Recent ostracod species described from freshwater bodies of different sizes (from small pools to lakes) equals 10% of the total diversity of the class. The group is also a common inhabitant of more rarely investigated environments, such as subterranean (Karanovic 2007), interstitial waters (Tanaka 2014), and submarine caves (Chiu et al. 2016, 2017). In the deep sea, ostracods have been recorded from all habitats and depth zones, like continental margins, abyssal plains, trenches, wood falls, hydrothermal vents, and cold seeps (Karanovic and Brandão, 2015; Brandão et al. 2019b).

1.4. Geographical Distribution of ostracods in the deep-sea

Many deep-sea ostracod species have been traditionally regarded as cosmopolitan, since the very first comprehensive study published by Brady (1880), from samples collected during the HMS Challenger Expedition from all oceans (e.g. Benson 1988: 5). Several studies have; however, shown that many cosmopolitan species which were analysed in detail were narrowly distributed, and that, at least in these cases, the cosmopolitan distribution was the result of very broad species morphological concepts and also numerous subsequent misidentifications (e.g. Schornikov 2005; Brandão 2013; Brandão and Yasuhara 2013). In this way, many deep-sea ostracod species seem to be restricted to one

or few adjacent basins, but other species (or at least groups of similar species) may present wide geographical distributions (see discussion below on *Cytheropteron pherozigzag* Whatley, Ayress & Downing, 1986, *Cytheropteron higashikawai* Ishizaki, 1981 and *Croninocythereis cronini* Yasuhara, Hunt, Okahashi and Brandão, 2015).

However, at higher taxonomic levels, the ostracod fauna is cosmopolitan, with most genera and almost all families present in all oceans. Some examples of deep sea, cosmopolitan genera are *Krithe* Brady, Crosskey and Robertson, 1874, *Legitimocythere* Coles and Whatley, 1989, *Macropyxis* Maddocks, 1990 and *Poseidonamicus* Benson, 1972. Some typically deep-sea genera also contain some shallow water species inhabiting cold regions, possibly indicating emergence from the deep sea and colonisation of shallow areas.

Other genera common in the deep sea, include *Argilloecia* Sars, 1866 (104 valid species) and *Cytheropteron* Sars, 1866 (453 valid species), occur from shallow marine environments to the deep sea. However, these wide distributions are likely related to the very wide morphological concepts adopted for their taxonomy.

Bathymetrical distribution of NW Pacific, deep-sea ostracods have not been compiled comprehensively, unlike other oceans (Ayress et al. 1997), although it is very well-studied for shallow-marine ostracods (e.g.Wang et al. 1988; Yasuhara and Seto 2006; Cheung et al. 2019; Hong et al. 2019). There are a number of individual studies for important genera (e.g. Zhao and Whatley 1997; Zhou and Ikeya 1992; Zhao et al. 2000) or certain areas (e.g. Ozawa 2004; Tanaka et al. 2012). However, most of these studies cover only bathyal depths or depth zones <3,000 m. In the mid-high latitude NW Pacific, ostracod abundance tend to be very low in continental margins (Zhou 1995). There are only a few large carbonate mounds in the NW Pacific Ocean that yield abundant calcareous deep-sea benthic microfossils, like ostracods (Yasuhara et al. 2019).

Recent studies based on samples from the German-Russian joint expedition KuramBio I and KuramBio II investigated regions deeper than the Carbonate Compensation Depth (i.e. abyssal depths), substantially expanding our knowledge on the bathymetric distribution of NW Pacific deep-sea ostracods (Brandão et al. 2019b, Yoo et al. 2019;).

In this chapter, we summarise all data on (geologically) Recent Ostracoda from the deep NW Pacific, discuss fossil occurrences in the Pacific Ocean, and analyse biodiversity and biogeographical patterns in the NW Pacific.

2. Objectives

We aim to compile all existing data on Recent Ostracoda from the deep NW Pacific, analyze biodiversity trends, and discuss the deep-sea ostracod biogeography of the deep NW Pacific.

3. Material and Methods

3.1. Data compilation

All records of (geologically) Recent, deep-sea Ostracoda were compiled. Firstly, all data from published studies (40 to 60°N and 120 to 180°E),

excluding species recorded by Brady (1880), due to the very confusing taxonomy. Secondly, we compiled data from a few "Kuril Kamchatka Biodiversity Study" (KuramBio) samples studied so far (mostly unpublished data). However, it is important to state that there are still numerous KuramBio samples being studied, which are not included in the present analysis.

3.2. Ostracods from the KuramBio Project

For the present chapter, we studied 215 ostracods collected on board the R. V. *Sonne* during the and II expeditions from 39.17 N to 47.24 N, 147.17 E to 155.55 E, and 4,868 to 9,305 m depth (see further details in Tables 1 and 2).

3.2. Bathymetrical and latitudinal patterns

In order to estimate the influence of sampling effort on patterns observed, the sampling effort was plotted against latitude and longitude in the study area of the present book (40 to 60°N and 120 to 180°). We also plotted the number of records and species against latitude and depth. One record is herein defined as the occurrence of one species in one locality (= sample), so if one sample provided 10 species, there will be 10 records for this locality (= sample).

To characterize the latitudinal and bathymetrical species composition, and density of species geographical distribution range, we excluded duplicate latitudinal records for each species within a respective family, and created the violin plot built with the R package ggplot2 (Wickham 2016), to represent the density of data estimated by the kernel method (Saeedi et al. 2019a).

Finally, we applied hierarchical cluster analysis (latitude as samples and species (presence/absence) as variable) with the vegan package in R (Oksanen et al. 2010, 2015), using a Bray–Curtis similarity index (Bray and Curtis 1957), and group-average linkage, recommended for analysis of species composition. Bootstrap support was obtained via ordinary bootstrap resampling and multiscale bootstrap resampling (AU) (Shimodaira 2004), using the R package Pvclust (Suzuki et al. 2015; Saeedi et al. 2019 a; Saeedi et al., 2019b).

3.3. Abbreviations

AGT, Agassiz Trawl; BC, boxcorer (sampler) (GKG in the cruise report, from the German word Grosskastengreifer); EBS, epibenthic sledge; KKT, Kuril-Kamchatka Trench; KuramBio, Kuril Kamchatka Biodiversity Studies; KuramBio I*, first expedition of the KuramBio Project; KuramBio II, second expedition of the KuramBio Project; MUC, Multicorer sampler; NW, Northwest; SNB,

*Initially the first expedition of the KuramBio project was simply named KuramBio, without the number one (I). Only after the second expedition (KuramBio II), the number I was added to this expedition's name. Herein we prefer to use KuramBio I, instead of the historical KuramBio, in order to avoid ambiguity with the project's name and the name of the second expedition.

Table 1. Stations of KuramBio I and II expeditions of the German Research Vessel *Sonne* in the NW Pacific with ostracods studied herein. Abbreviations: AGT, Agassiz Trawl; BC, boxcorer; EBS, epibenthic sledge; KuramBio, Kuril-Kamchatka Biodiversity Studies; KuramBio I*, first expedition of the KuramBio Project; KuramBio II, second expedition of the KuramBio Project; MUC, Multicorer sampler.

Cruise name	Cruise abbreviation	Station	Date (begin)	Time UTC (begin)	Gear	Latitude (begin)	Longitude (begin)	Depth (begin) (m)	Latitude (end)	Longitude (end)	Depth (end) (m)
KuramBio I	SO223	5-5	10/August/2012	11:50	BC	43° 34,97' N	153° 58,03' E	5,379	-	-	-
KuramBio I	SO223	10-4	25/August/2012	23:55	BC	41° 12,02' N	150° 5,76' E	5,249	-	-	-
KuramBio I	SO223	11-4	29/August/2012	03:55	BC	40° 12,86' N	148° 5,92' E	5,348	-	-	-
KuramBio I	SO223	11-5	29/August/2012	07:59	BC	40° 12,86' N	148° 6,02' E	5,350	-	-	-
KuramBio I	SO223	12-2	31/August/2012	16:22	BC	39° 43,43' N	147° 9,98' E	5,243	-	-	-
KuramBio I	SO223	2-4	02/August/2012	02:47	BC	46° 13,95' N	155° 33,15' E	4,868	-	-	-
KuramBio I	SO223	2-5	02/August/2012	06:37	BC	46° 13,99' N	155° 33,10' E	4,869	-	-	-
KuramBio I	SO223	3-10	05/August/2012	23:01	AGT	47° 14,27' N	154° 42,17' E	4,977	47° 14,94' N	154° 43,18' E	4986
KuramBio I	SO223	3-4	04/August/2012	15:23	BC	47° 14,32' N	154° 42,26' E	4,982	-	-	-
KuramBio I	SO223	3-5	04/August/2012	19:18	BC	47° 14,30' N	154° 42,23' E	4,984	-	-	-
KuramBio I	SO223	4-5	07/August/2012	10:57	BC	46° 57,97' N	154° 32,49' E	5,766	-	-	-
KuramBio I	SO223	6-4	13/August/2012	00:23	BC	42° 28,98' N	153° 59,97' E	5,297	-	-	-
KuramBio I	SO223	7-4	16/August/2012	15:23	BC	43° 2,31' N	152° 59,16' E	5,222	-	-	-
KuramBio I	SO223	8-4	19/August/2012	19:16	BC	42° 14,57' N	151° 43,51' E	5,130	-	-	-
KuramBio I	SO223	9-4	23/August/2012	00:08	BC	40° 35,03' N	151° 0,06' E	5,404	-	-	-
KuramBio I	SO223	9-5	23/August/2012	04:23	BC	40° 34,96' N	151° 0,07' E	5,401	-	-	-
KuramBio II	SO250	10-1	20/August/2016	1:05	EBS	43° 48,602' N	151° 47,124' E	5,352	43° 48,455' N	151° 47,171' E	5104
KuramBio II	SO250	14-1	21/August/2016	09:18	BC	45° 50,879' N	153° 47,991' E	8,251	-	-	-
KuramBio II	SO250	20-1	24/August/2016	01:18	AGT	45° 52,105' N	153° 51,287' E	8,191	45° 52,203' N	153° 51,435' E	8199
KuramBio II	SO250	25-1	25/August/2017	07:33	BC	45° 55,235' N	152° 47,464' E	6,068	-	-	-
KuramBio II	SO250	26-1	25/August/2017	13:40	MUC	45° 55,226' N	152° 47,468' E	6,065	-	-	-
KuramBio II	SO250	36-1	28/August/2017	08:40	BC	45° 38,610' N	152° 55,921' E	7,135	-	-	-

Cruise name	Cruise abbreviation	Station	Date (begin)	Time UTC (begin)	Gear	Latitude (begin)	Longitude (begin)	Depth (begin) (m)	Latitude (end)	Longitude (end)	Depth (end) (m)
KuramBio II	SO250	37-1	28/August/2017	14:52	BC	45° 38,604' N	152° 55,911' E	7,136	-	-	-
KuramBio II	SO250	5-1	18/August/2016	09:08	MUC	43° 49,192' N	151° 45,599' E	5,147	-	-	-
KuramBio II	SO250	51-1	05/September/2017	11:38	MUC	45° 28,751' N	153° 11,644' E	8,735	-	-	-
KuramBio II	SO250	6-1	18/August/2016	1:39	BC	43° 49,197' N	151° 45,609' E	5,497	-	-	-
KuramBio II	SO250	61-1	08September/2017	16:08	BC	45° 9,997' N	153° 45,419' E	5,741	-	-	-
KuramBio II	SO250	63-1	09/September/2017	00:00	MUC	45° 10,007' N	153° 45,420' E	5,739	-	-	-
KuramBio II	SO250	74-1	12/September/2017	03:10	MUC	44° 39,883' N	151° 28,106' E	8,221	-	-	-
KuramBio II	SO250	75-1	12/September/2017	08:42	BC	44° 39,883' N	151° 28,136' E	8,221	-	-	-
KuramBio II	SO250	77-1	13/September/2017	05:43	EBS	45° 13,892' N	152° 50,774' E	9,577	45° 14,219' N	152° 49,956' E	9583
KuramBio II	SO250	83-1	15/September/2017	01:23	MUC	45° 1,356' N	151° 2,901' E	5,211	-	-	-
KuramBio II	SO250	86-1	15/September/2017	20:55	AGT	45° 1,202' N	151° 6,008' E	5,572	45° 1,371' N	151° 6,001' E	5530
KuramBio II	SO250	89-1	16/September/2017	22:36	EBS	44° 39,325' N	151° 27,340' E	8,215	44° 39,053' N	151° 27,343' E	8217
KuramBio II	SO250	90-1	17/September/2017	11:29	AGT	44° 41,759' N	151° 26,554' E	8,271	44° 41,992' N	151° 26,321' E	8273
KuramBio II	SO250	94-1	18/September/2017	03:54	BC	44° 6,852' N	151° 25,539' E	6,531	-	-	-
KuramBio II	SO250	98-1	19/September/2017	08:54	AGT	44° 6,152' N	151° 25,705' E	6,441	44° 6,253' N	151° 25,935' E	6442
KuramBio II	SO250	100-1	20/September/2017	03:58	BC	44° 12,378' N	150° 39,053' E	9,305	-	-	-

*Initially the first expedition of the KuramBio project was simply named KuramBio, without the number one (I). Only after the second expedition (KuramBio II) the number I was added to this expedition's name. Herein we prefer to use KuramBio I, instead of the historical KuramBio, in order to avoid ambiguity with the project's name and the name of the second expedition.

Table 2. Ostracod specimens collected during the KuramBio I and II expeditions of the German Research Vessel *Sonne* in the NW Pacific, and studied herein.

SNB number	Species	KuramBio Id	Cruise	Station	Sample details	Comments
SNB 0998	*Bythocypris* sp. 1	KuramBio 3078	KuramBio I	2-4		
SNB 0999	*Legitimocythere* sp.	KuramBio 990	KuramBio I	2-4		Both valves broken.
SNB 1000	*Legitimocythere* sp.	KuramBio 2574	KuramBio I	3-5		
SNB 1001	*Cytheropteron pherozigzag* Whatley et al. 1986	No Id	KuramBio I	2-4		Subrecent valve.
SNB 1002	Bythocytheridae	No Id	KuramBio I	2-4		Poorly preserved, subrecent valve.
SNB 1003	*Cytheropteron pherozigzag* Whatley et al., 1986	No Id	KuramBio I	2-4		
SNB 1004	*Krithe* sp.	No Id	KuramBio I	11-4		
SNB 1005	*Legitimocythere* sp.	No Id	KuramBio I	3-10		The station number was wrong (3-11 is a OFOS, so no sediment collected).
SNB 1006	*Legitimocythere* sp.	No Id	KuramBio I	3-4		
SNB 1007	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	No Id	KuramBio I	3-4		
SNB 1008	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	No Id	KuramBio I	2-4		
SNB 1009	*Krithe* sp.	No Id	KuramBio I	11-4		No copulatory limb.
SNB 1010	*Vitjasiella belyaevi* Schornikov, 1976	No Id	KuramBio I	11-4		No copulatory limb. Both valves broken.
SNB 1011	*Abyssocythere* sp.	No Id	KuramBio I	6-4		
SNB 1012	*Bythocypris* sp. 1	No Id	KuramBio I	11-5		
SNB 1013	*Bythocypris* sp. 1	No Id	KuramBio I	11-5		No copulatory limb.
SNB 1014	*Bythocypris* sp. 1	No Id	KuramBio I	11-5		No copulatory limb.
SNB 1015	*Krithe* sp.	No Id	KuramBio I	11-5		
SNB 1016	*Abyssocypris* sp.	No Id	KuramBio I	3-4		
SNB 1017	*Abyssocypris* sp.	No Id	KuramBio I	3-4		
SNB 1018	*Cytheropteron higashikawai* Whatley et al., 1986	No Id	KuramBio I	3-4		
SNB 1019	Trachyleberididae	No Id	KuramBio I	11-4	0-2 cm, 500 µm	Valves broken into pieces.
SNB 1020	*Legitimocythere* sp.	No Id	KuramBio I	11-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1021	*Ryugucivis* sp.	No Id	KuramBio I	11-4	0-2 cm, 500 µm	No copulatory limb.

SNB number	Species	KuramBio Id	Cruise	Station	Sample details	Comments
SNB 1022	*Krithe* sp.	No Id	KuramBio I	11-4	0-2 cm, 500 µm	Both valves completely broken, not photographed.
SNB 1023	*Krithe* sp.	No Id	KuramBio I	11-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1024	*Argilloecia* sp. 2	No Id	KuramBio I	11-4	0-2 cm, 500 µm	No copulatory limb. One valve missing.
SNB 1025	*Argilloecia* sp. 2	No Id	KuramBio I	10-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1026A	*Paradoxostoma?* sp.	No Id	KuramBio I	10-4	0-2 cm, 500 µm	No copulatory limb, LV missing.
SNB 1026B	*Krithe* sp.	No Id	KuramBio I	10-4	0-2 cm, 500 µm	
SNB 1027	*Krithe* sp.	No Id	KuramBio I	10-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1028	*Zabythocypris kurilensis* Schornikov, 1980	No Id	KuramBio I	9-4	0-2 cm, 300 µm	No copulatory limb.
SNB 1029	*Ryugucivis* sp.	No Id	KuramBio I	9-4	0-2 cm, 500 µm	
SNB 1030	*Krithe* sp.	No Id	KuramBio I	9-4	0-2 cm, 300 µm	
SNB 1031	*Krithe* sp.	No Id	KuramBio I	9-4	0-2 cm, 300 µm	
SNB 1032	*Legitimocythere* sp.	KuramBio 176	KuramBio I	2-4	0-2 cm, 500 µm	Subrecent specimen (only RV).
SNB 1033	*Legitimocythere* sp.	KuramBio 176	KuramBio I	2-4	0-2 cm, 500 µm	Subrecent specimen (only LV).
SNB 1034	*Legitimocythere* sp.	No Id	KuramBio I	7-4	0-2 cm, 500 µm	Broken into pieces. Subrecent RV.
SNB 1035	*Bythocypris* sp. 2	No Id	KuramBio I	7-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1036	*Bythocypris* sp. 1	No Id	KuramBio I	7-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1037	*Krithe* sp.	No Id	KuramBio I	7-4	0-2 cm, 500 µm	Subrecent.
SNB 1038	*Henryhowella sol* Jellinek & Swanson, 2003	No Id	KuramBio I	3-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1039	*Krithe* sp.	No Id	KuramBio I	3-4	0-2 cm, 500 µm	
SNB 1040	*Abyssocythere* sp.	No Id	KuramBio I	8-4	2-20 cm, 500 µm	
SNB 1041	*Legitimocythere* sp.	No Id	KuramBio I	7-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1042	*Bythocypris* sp. 1	No Id	KuramBio I	7-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1043	*Bythocypris* sp. 1	No Id	KuramBio I	7-4	0-2 cm, 500 µm	No copulatory limb.
SNB 1044	*Bythocypris* sp. 2	No Id	KuramBio I	5-5	2-20 cm, 500 µm	LV missing. RV broken dorsally.
SNB 1045	Ostracoda	KuramBio 3032	KuramBio I	9-5	2-20 cm	
SNB 1046	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KuramBio 3460	KuramBio I	4-5	0-2 cm, 500 µm	No copulatory limb, RV broken into pieces.

SNB number	Species	KuramBio Id	Cruise	Station	Sample details	Comments
SNB 1047	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KuramBio 3460	KuramBio I	4-5	0-2 cm, 500 µm	Narrow calcified inner lamella, possibly a juvenile.
SNB 1048	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KuramBio 2478	KuramBio I	2-5	2-20 cm, 500 µm	Fixed in ethanol.
SNB 1049	*Poseidonamicus* sp.	KuramBio 2478	KuramBio I	2-5	2-20 cm, 500 µm	Fragmented soft parts.
SNB 1050	*Bythocypris* sp. 1	KuramBio 3504	KuramBio I	5-5	0-2 cm, 500 µm	
SNB 1051	Trachyleberididae	KuramBio 3504	KuramBio I	5-5	0-2 cm, 500 µm	RV and LV completely broken.
SNB 1052	*Bythocypris* sp. 2	KuramBio 3504	KuramBio I	5-5	0-2 cm, 500 µm	LV subtrapezoidal. LV broken.
SNB 1053	*Abyssocypris* sp.	KuramBio 2521	KuramBio I	12-2	0-2 cm	
SNB 1054	*Abyssocythereis vitjasi* Schornikov, 1975	KB2 674	KuramBio II	10	supranet, 500 µm	Fixed in ethanol 96%.
SNB 1055	*Abyssocythereis vitjasi* Schornikov, 1975	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1056	*Abyssocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1057	*Abyssocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1058	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1059	*Henryhowella sol* Jellinek & Swanson, 2003	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1060	*Henryhowella sol* Jellinek & Swanson, 2003	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1061	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	LV broken, RV with a hollow.
SNB 1062	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	RV with ventral margin slightly broken.
SNB 1063	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1064	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1065	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1066	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1067	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1068	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1069	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	RV slightly broken ventrally.
SNB 1070	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1071	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1072	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	

SNB number	Species	KuramBio Id	Cruise	Station	Sample details	Comments
SNB 1073	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1074	*Legitimocythere* sp.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1075	*Macropyxis* sp. nov.	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1076	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1077	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1078	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1079	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KB2 674	KuramBio II	10	supranet, 500 µm	LV broken ventrally.
SNB 1080	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KB2 674	KuramBio II	10	supranet, 500 µm	
SNB 1081	*Croninocythereis* sp. cf. *C. cronini* Yasuhara et al., 2015	KB2 674	KuramBio II	10	supranet, 500 µm	Left valve broken.
SNB 1082	*Vitjasiella belyaevi* Schornikov, 1976	KB2 2079	KuramBio II	86	300 µm	Fixed in ethanol 96%. Both valves broken into pieces.
SNB 1083	*Henryhowella sol* Jellinek & Swanson, 2003	KB2 2079	KuramBio II	86	300 µm	Fixed in ethanol 96%.
SNB 1084	*Krithe* sp.	KB2 2079	KuramBio II	86	300 µm	Black mass on posterior part of body.
SNB 1085	*Krithe* sp.	KB2 2079	KuramBio II	86	300 µm	
SNB 1086	*Argilloecia* sp. 1	KB2 2079	KuramBio II	86	300 µm	
SNB 1087	*Abyssocypris* sp.	KB2 2079	KuramBio II	86	300 µm	Pinkish-brownish collour of freshly collected carapace.
SNB 1088	*Legitimocythere* sp.	KB2 2079	KuramBio II	86	300 µm	Subrecent RV.
SNB 1089	*Legitimocythere* sp.	KB2 2079	KuramBio II	86	300 µm	
SNB 1090	*Legitimocythere* sp.	KB2 2079	KuramBio II	86	300 µm	
SNB 1091	*Legitimocythere* sp.	KB2 2079	KuramBio II	86	300 µm	
SNB 1092	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 1717	KuramBio II	61		
SNB 1093	*Argilloecia* sp. 1	KB2 1717	KuramBio II	61		
SNB 1094	*Ryugucivis* sp.	KB2 1717	KuramBio II	61		
SNB 1095	*Ryugucivis* sp.	KB2 1717	KuramBio II	61		
SNB 1096	*Legitimocythere* sp.	KB2 1717	KuramBio II	61		Juvenile.
SNB 1097	*Legitimocythere* sp.	KB2 1717	KuramBio II	61		
SNB 1098	*Legitimocythere* sp.	KB2 1717	KuramBio II	61		

SNB number	Species	KuramBio Id	Cruise	Station	Sample details	Comments
SNB 1101	*Cytheropteron* sp.	KB2 1392	KuramBio II	51		
SNB 1102	*Cytheropteron* sp.	KB2 1392	KuramBio II	51		
SNB 1103	*Cytheropteron* sp.	KB2 1392	KuramBio II	51		
SNB 1104	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2485	KuramBio II	90		
SNB 1105	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1106	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1107	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1108	*Krithe tsukagoshii* Yoo et al., 2019	KB2 3009	KuramBio II	94		RV missing.
SNB 1109	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1110	*Krithe* sp.	KB2 2648	KuramBio II	98	300 µm	
SNB 1111	*Krithe* sp.	KB2 2648	KuramBio II	98	300 µm	
SNB 1112	*Krithe angelicae* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1113	*Krithe tsukagoshii* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1114	*Krithe angelicae* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1115	*Krithe angelicae* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1116	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1117	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1118	*Krithe tsukagoshii* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1119	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1120	*Krithe* sp.	KB2 2648	KuramBio II	98	300 µm	LV missing.
SNB 1121	*Krithe* sp.	KB2 2648	KuramBio II	98	300 µm	
SNB 1122	*Krithe* sp.	KB2 2648	KuramBio II	98	300 µm	LV broken.
SNB 1123	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1124	*Krithe tsukagoshii* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1125	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1126	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1127	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1128	*Krithe angelicae* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	

SNB number	Species	KuramBio Id	Cruise	Station	Sample details	Comments
SNB 1129	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1130	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1131	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1132	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1133	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1134	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1135	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1136	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1137	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1138	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1139	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	Soft parts looked degraded.
SNB 1140	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	
SNB 1141	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2648	KuramBio II	98	300 µm	Soft parts looked degraded.
SNB 1142	*Retibythere (Bathybythere)* sp.	KB2 2648	KuramBio II	98	300 µm	
SNB 1143	*Retibythere (Bathybythere)* sp.	KB2 2648	KuramBio II	98	300 µm	
SNB 1144	*Retibythere (Bathybythere)* sp.	KB2 2648	KuramBio II	98	300 µm	
SNB 1145	*Retibythere (Bathybythere)* sp.	KB2 2648	KuramBio II	98	300 µm	
SNB 1146	*Retibythere (Bathybythere)* sp.	KB2 2648	KuramBio II	98	300 µm	RV broken ventrally.
SNB 1147	*Retibythere (Bathybythere)* sp.	KB2 2648	KuramBio II	98	300 µm	
SNB 1148	*Vitjasiella belyaevi* Schornikov, 1976	KB2 2648	KuramBio II	98	300 µm	
SNB 1149	*Vitjasiella belyaevi* Schornikov, 1976	KB2 2648	KuramBio II	98	300 µm	
SNB 1150	*Vitjasiella belyaevi* Schornikov, 1976	KB2 2648	KuramBio II	98	300 µm	
SNB 1151	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 999	KuramBio II	36		Both valves broken into pieces.
SNB 1152	*Krithe maxima* Yoo et al., 2019	KB2 999	KuramBio II	36		
SNB 1153	*Krithe maxima* Yoo et al., 2019	KB2 999	KuramBio II	36		
SNB 1154	*Krithe maxima* Yoo et al., 2019	KB2 999	KuramBio II	36		
SNB 1155	*Krithe maxima* Yoo et al., 2019	KB2 1000	KuramBio II	37	?300 µm	
SNB 1156	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 1000	KuramBio II	37	?300 µm	

SNB number	Species	KuramBio Id	Cruise	Station	Sample details	Comments
SNB 1157	*Krithe maxima* Yoo et al., 2019	KB2 1000	KuramBio II	37	?300 µm	
SNB 1158	*Krithe cerritula* Yoo et al., 2019	KB2 173	KuramBio II	5		Subrecent.
SNB 1159	*Krithe cerritula* Yoo et al., 2019	KB2 174	KuramBio II	6		
SNB 1160	*Krithe cerritula* Yoo et al., 2019	KB2 174	KuramBio II	6		
SNB 1161	*Krithe cerritula* Yoo et al., 2019	KB2 174	KuramBio II	6		
SNB 1162	*Krithe* sp.	KB2 174	KuramBio II	6		RV missing.
SNB 1163	*Krithe rara* Yoo et al., 2019	KB2 174	KuramBio II	6		
SNB 1164	*Krithe rara* Yoo et al., 2019	KB2 174	KuramBio II	6		
SNB 1165	*Krithe* sp.	KB2 174	KuramBio II	6		
SNB 1166	*Krithe* sp.	KB2 292	KuramBio II	14		
SNB 1167	*Krithe* sp.	KB2 998	KuramBio II	20	300 µm	
SNB 1168	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 998	KuramBio II	20	300 µm	
SNB 1169	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 998	KuramBio II	20	300 µm	
SNB 1170	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 998	KuramBio II	20	300 µm	
SNB 1171	*Krithe* sp.	KB2 998	KuramBio II	20	300 µm	
SNB 1172	*Krithe* sp.	KB2 600	KuramBio II	25		RV broken.
SNB 1173	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 600	KuramBio II	25		Both valves missing.
SNB 1174	*Krithe* sp.	KB2 601	KuramBio II	26		Both valves broken into pieces.
SNB 1175	*Krithe kamchatkaensis* Yoo et al., 2019	KB2 2080	KuramBio II	83		
SNB 1224	*Krithe* sp.	KB2 3010	KuramBio II	100		
SNB 1225	*Krithe* sp.	KB2 3010	KuramBio II	100		
SNB 1226	*Krithe* sp.	KB2 3010	KuramBio II	100		
SNB 1227	*Krithe* sp.	KB2 2077	KuramBio II	75		
SNB 1228	*Krithe* sp.	KB2 2077	KuramBio II	75		
SNB 1229	*Krithe* sp.	KB2 1800	KuramBio II	74		
SNB 1230	*Krithe* sp.	KB2 1752	KuramBio II	63		
SNB 1231	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1232	*Krithe* sp.	KB2 2485	KuramBio II	90		

SNB number	Species	KuramBio Id	Cruise	Station	Sample details	Comments
SNB 1233	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1234	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1235	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1236	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1237	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1238	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1239	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1240	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1241	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1242	*Krithe* sp.	KB2 2485	KuramBio II	90		
SNB 1243	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1244	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1245	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1246	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1247	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1248	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1249	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1250	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1251	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1252	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1253	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1254	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1255	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1256	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1257	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1258	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1259	*Krithe* sp.	No Id	KuramBio II	98	300 µm	
SNB 1260	*Krithe* sp.	No Id	KuramBio II	98	300 µm	

4. Results

4.1. Ostracods from the deep NW Pacific (40°–60°N, 120°–180° E)

After the KuramBio project, a total of 41 species, 24 genera and 11 families were identified. Most families recorded from the KKT region are represented by a single genus and one or two species, the exceptions being Trachyleberididae Sylvester-Bradley, 1948 (six genera, at least six species), Polycopidae Sars, 1865 (five genera, 10 species), Bythocytheridae Sars, 1866 (three genera, three species), Bythocyprididae Maddocks, 1969 (two genera, three species), Pontocyprididae Müller, 1894 (two genera, three species). The richest genus *Krithe* Crosskey & Robertson, 1874 with at least seven species.

The compilation of published records (Chavtur 1981; Schornikov 1975, 1976, 1980, 1981) yielded 13 species and eight genera from the KKT region. In the KuramBio samples, 31 species were present, among these 28 are new records from the KKT region, and most of these new records are likely new to science.

4.2. Taxonomy

Class Ostracoda Latreille, 1806
Higher classification based on Brandão et al. (2019a)
Subclass Myodocopa Sars, 1866
Order Halocyprida Dana, 1853
Suborder Cladocopina Sars, 1865
Superfamily Polycopoidea Sars, 1865
Family Polycopidae Sars, 1865 (Map 1)

Remarks: The ten polycopid species listed below were described from the KKT region in the NW Pacific (Chavtur 1981). Several polycopid specimens were found in the KuramBio samples studied so far, but will be discussed elsewhere (Tanaka et al. in prep).

Genus Archypolycope Chavtur, 1981
Archypolycope bonaducei Chavtur, 1981
Archypolycope cornea Chavtur, 1981
Archypolycope rotunda Chavtur, 1981
Archypolycope squalida Chavtur, 1981
Genus *Metapolycope* Kornicker and Morkhoven, 1976
Metapolycope echinata Chavtur, 1981
Genus *Polycope* Sars, 1866
Polycope bathyalis Chavtur, 1981
Polycope gulbini Chavtur, 1981
Polycope major Chavtur, 1981
Genus *Polycopsis* Mueller, 1894
Polycopsis compacta Chavtur, 1981
Genus *Pseudopolycope* Chavtur, 1981
Pseudopolycope vitjazi Chavtur, 1981
Subclass Podocopa Sars, 1866
Order Podocopida Sars, 1866
Suborder Bairdiocopina Gründel, 1967
Superfamily Bairdiodea Sars, 1865
Family Bythocyprididae Maddocks, 1969
Genus *Bythocypris* Brady, 1880

Remarks: First record of the genus *Bythocypris* from the KKT region.

Bythocypris sp. 1 (Map 2, Figure 1 A-H)

Remarks: Possibly a new species, widespread in the KuramBio study area (4 stations).

Bythocypris sp. 2 (Map 2, Figure 1 I-K)

Remarks: Possibly a new species, widespread in the KuramBio study area (2 stations).

Genus *Zabythocypris* Maddocks, 1969
Zabythocypris kurilensis Schornikov, 1980 (Map 2, Figure 1 L)

Remarks: Recorded in the deep NW Pacific by Schornikov (1980) and also herein.

Suborder Cypridocopina Jones, 1901

Superfamily Macrocypridoidea Müller, 1912

Family Macrocyprididae Müller, 1912

Genus *Macropyxis* Maddocks, 1990

Macropyxis sp. (Map 3, Figure 2 A-B)

Remarks: This likely new species is the first record of the genus from the KKT region (one KuramBio station).

Superfamily Pontocypridoidea Müller, 1894

Family Pontocyprididae Müller, 1894

Genus *Abyssocypris* Bold, 1974

Abyssocypris sp. (Map 3, Figure 2 C-H)

Remarks: First record of the genus *Abyssocypris* from the KKT region. Possibly a new species recorded from three stations of the KuramBio Project.

Genus *Argilloecia* Sars, 1866

Argilloecia sp. 1 (Map 3, Figure 3 A-E)

Remarks: First record of the genus *Argilloecia* from the KKT region.

Argilloecia sp. 2 (Map 3, Figure 3 F-K)

Remarks: Possibly one or two new species, each one recorded from two stations of the KuramBio Project. This species is similar to *Argilloecia keigwini* Yasuhara, Okahashi and Cronin, 2009.

Suborder Cytherocopina Baird, 1850

Superfamily Cytheroidea Baird, 1850

Family Bythocytheridae Sars, 1866

Bythocytheridae genus indet. Bythocytheridae genus indet. (Map 4, Figure 4 A)

Remarks: One valve of species is poorly preserved, but differs from the genera listed below.

Subgenus *Retibythere* (*Bathybythere*) Schornikov, 1987

Retibythere (*Bathybythere*) sp. (Map 4, Figure 4 B-D)

Remarks: First record of the genus *Retibythere* from the KKT region (one station of the KuramBio Project). This likely new species differs from *Retibythere* (*Bathybythere*) *scaberrima* (Brady, 1886) as illustrated by Schornikov (1987) by the presence of several thick spines along the anterior margin of the valves.

Genus *Vitjasiella* Schornikov, 1976

Vitjasiella belyaevi Schornikov, 1976 (Map 4, Figure 4 E-F)

Remarks: Recorded in the deep NW Pacific by Schornikov (1976) and herein (three stations of the KuramBio Project).

Family Cytheruridae Müller, 1894

Genus *Cytheropteron* Sars, 1866

Remarks: Although *Cytheropteron* is a cosmopolitan (recorded from all oceans and all depth zones), common and abundant genus, it had not been recorded from the KKT region. Each of the three species cited below occurred at a single station.

Cytheropteron higashikawai Ishizaki, 1981 (Map 5, Figure 5 A-C)

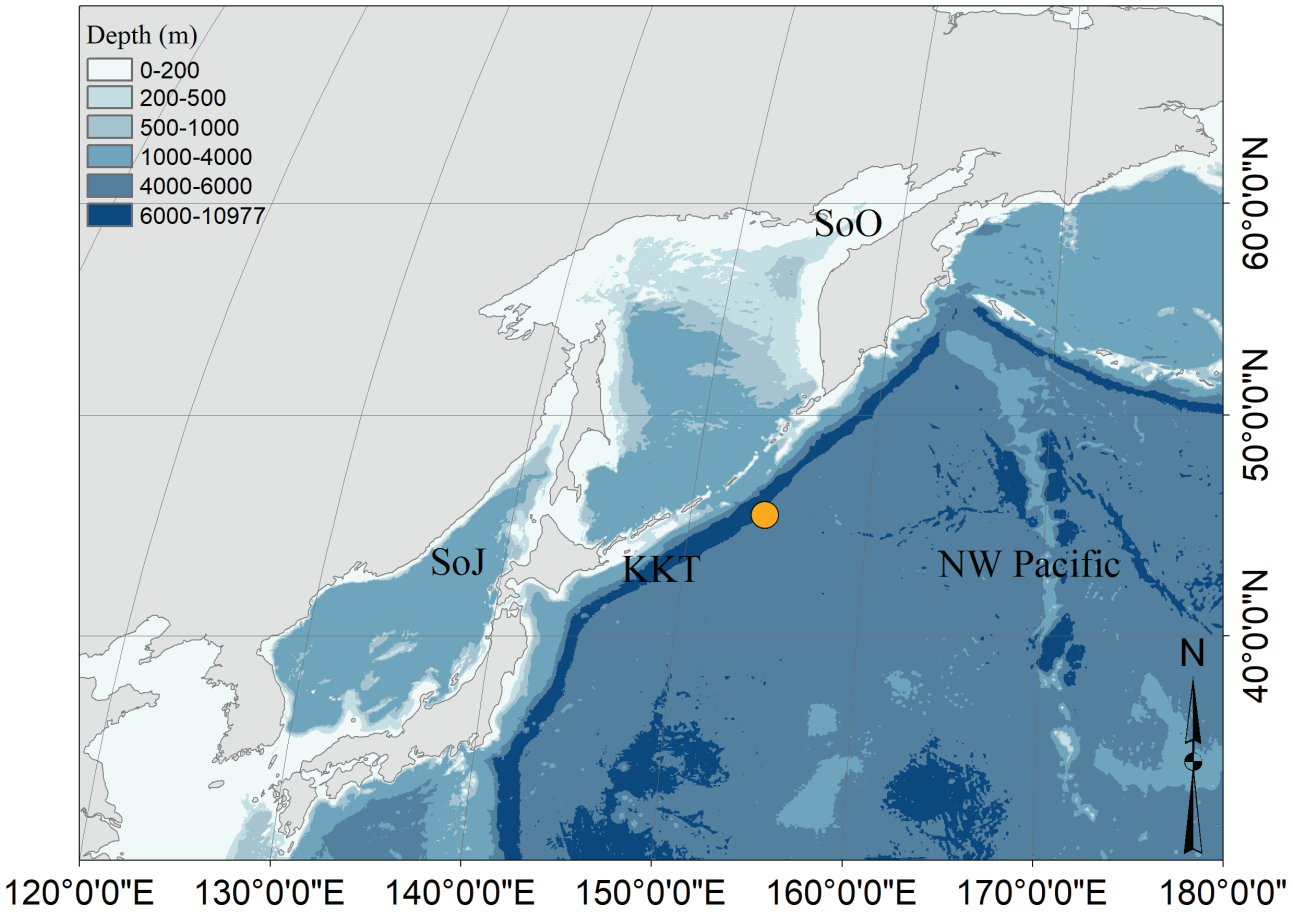
Remarks: First record of this species from the KKT regions, previously recorded from the Nordic seas, the Arctic, and the NW and SW Pacific (Yasuhara et al. 2014a, 2019; Jöst et al. 2018).

Cytheropteron pherozigzag Whatley, Ayress and Downing, 1986 (Map 5, Figure 5 D-G)

Remarks: First record of this species from the KKT regions, previously recorded from the eastern and western North Atlantic, and NW Pacific Oceans (Yasuhara and Okahashi, 2015; Jöst et al. 2018; Yasuhara et al. 2019).

Cytheropteron sp. (Map 5, Figure 5 H-I)

Remarks: This is likely a new species (collected from one KuramBio station), similar to *Cytheropteron carolinae* Whatley and Coles, 1987, *C. porterae* Whatley and Coles, 1987, *C. demenocali* Yasuhara, Okahashi and Cronin, 2009, *C. mason* Whatley and Coles, 1987.



- *Archypolycope bonaducei*
- *Archypolycope cornea*
- *Archypolycope rotunda*
- *Archypolycope squalida*
- *Metapolycope echinata*
- *Polycope bathyalis*
- *Polycope gulbini*
- *Polycope major*
- *Polycopsis compacta*
- *Pseudopolycope vitjazi*

Map 1. Distribution of Polycopidae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. All the species overlap on the map as they have same coordinates; the orange circle on the map is representative of all the 10 species shown on the legend.

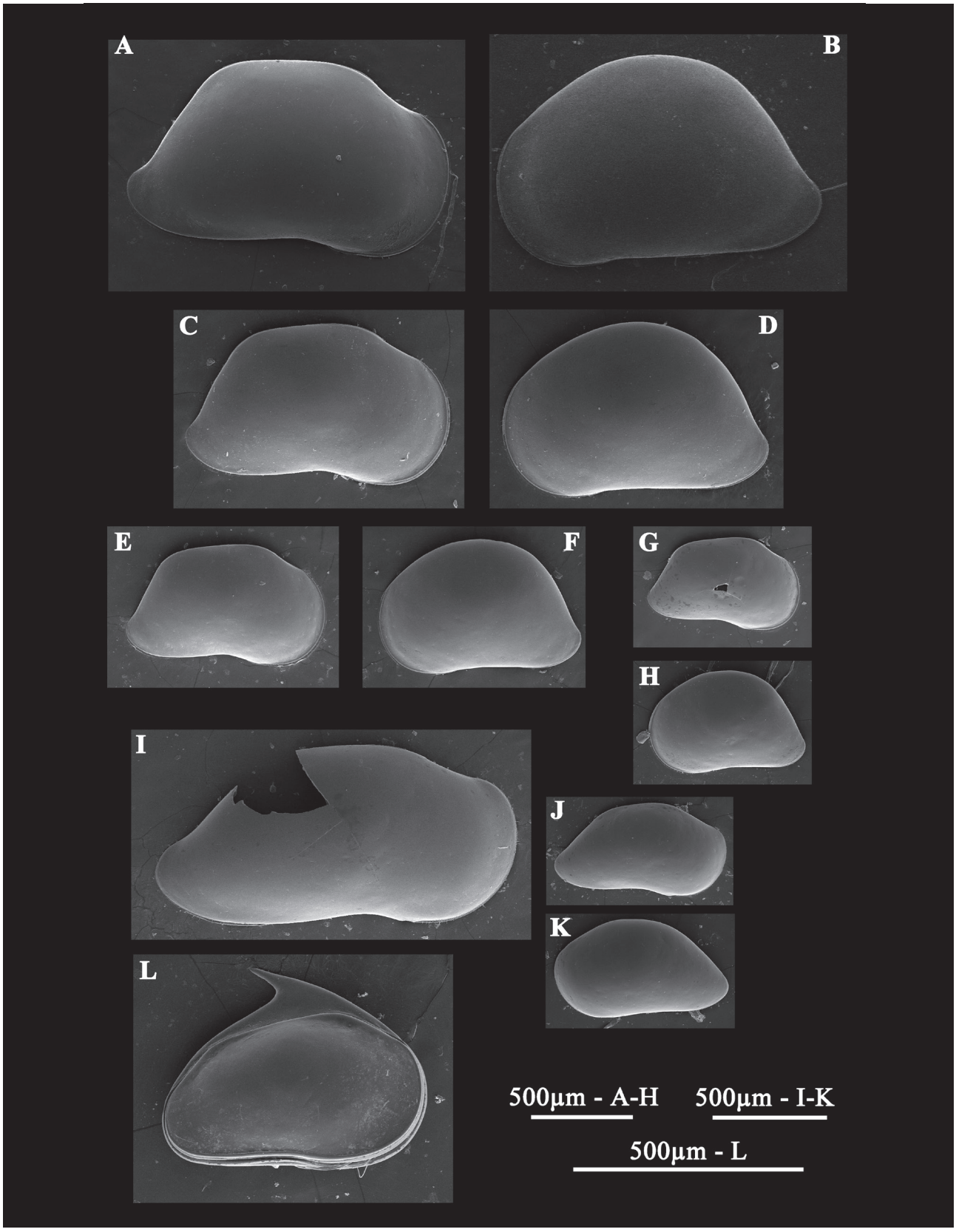
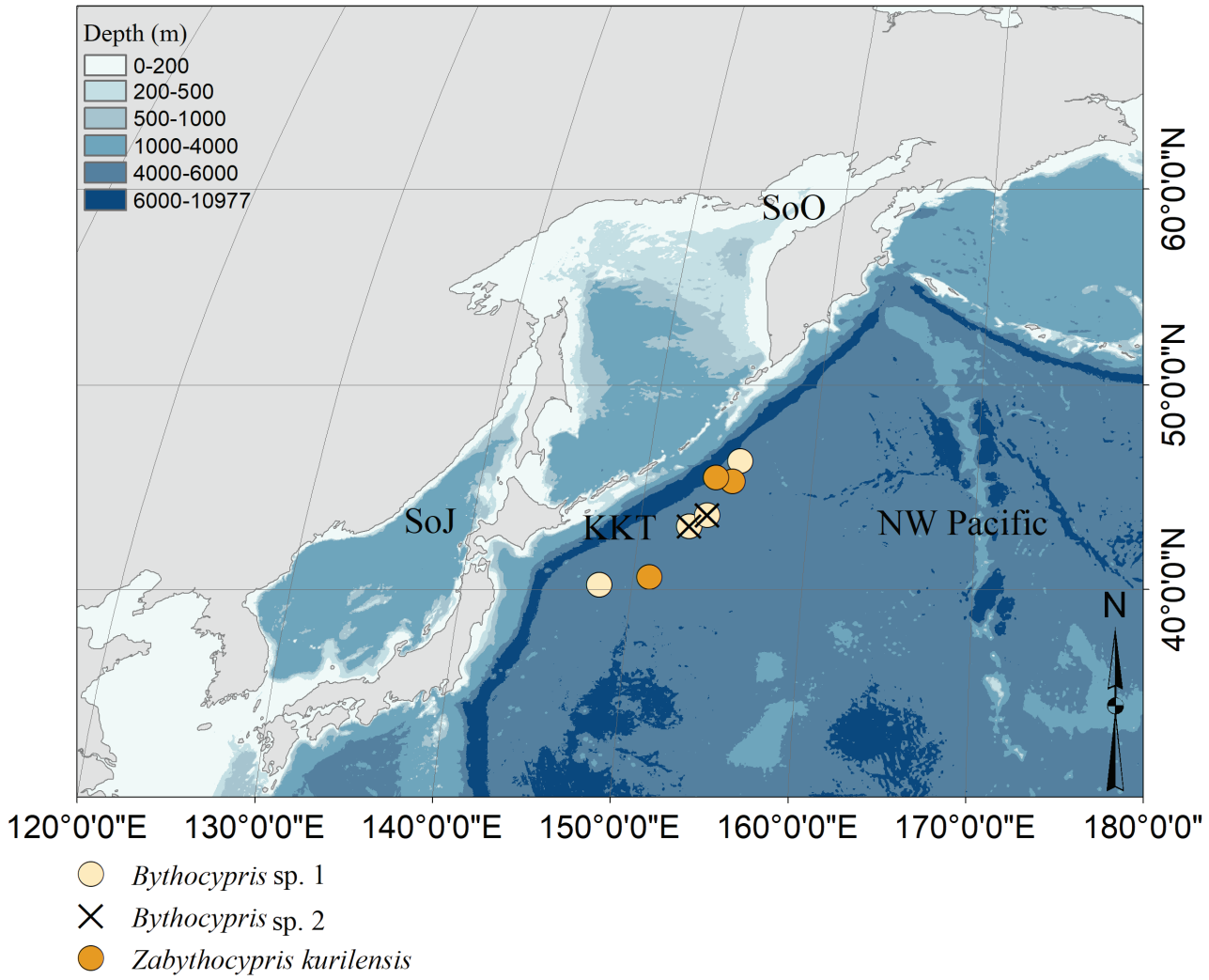


Figure 1. Bythocyprididae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Bythocypris* sp. 1: (A, B) SNB 0098; (C, D) SNB 1042; E, F, SNB 1050; (G, H) SNB 1028. *Bythocypris* sp. 2: I, SNB 1044; (J, K) SNB 1035. *Zabythocypris kurilensis* Schornikov, 1980: L, SNB 1028. A, C, E, G, I, J, L, RV; B, D, F, H, K, LV. For details on sampling localities see Tables 1 and 2.



Map 2. Distribution of Bythocyprididae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific.

Family Keysercytheridae Karanovic and Brandão, 2015

Genus *Keysercythere* Karanovic and Brandão, 2015

Keysercythere enricoi Karanovic and Brandão, 2015 (Map 5, Figure 5.J-K)

Remarks: This species, genus and family were described associated to a wood fall, which was collected from the KKT during the KuramBio I Expedition (Karanovic and Brandão, 2015).

Family Krithidae Mandelstam, 1958

Genus *Krithe* Brady, Crosskey and Robertson, 1874

Remarks: Although *Krithe* is a cosmopolitan genus (recorded from all oceans), which is common and abundant in the deep sea, it had not been recorded from 40° to 60°N and 120° to 180° E.

Krithe angelikae Yoo et al., 2019 (Map 6, Figure 6.A-D)

2019 *Krithe* sp. 1, Yasuhara, Hunt and Okahashi: Figure 3.I-K.

2019 *Krithe angelikae* Yoo et al.: 4, Figures 2.A-B, 3 A1, 3.A2, 3.B1

Remarks: The KuramBio II Expedition provided this new species and record (a single station) from the deep areas of the NW Pacific.

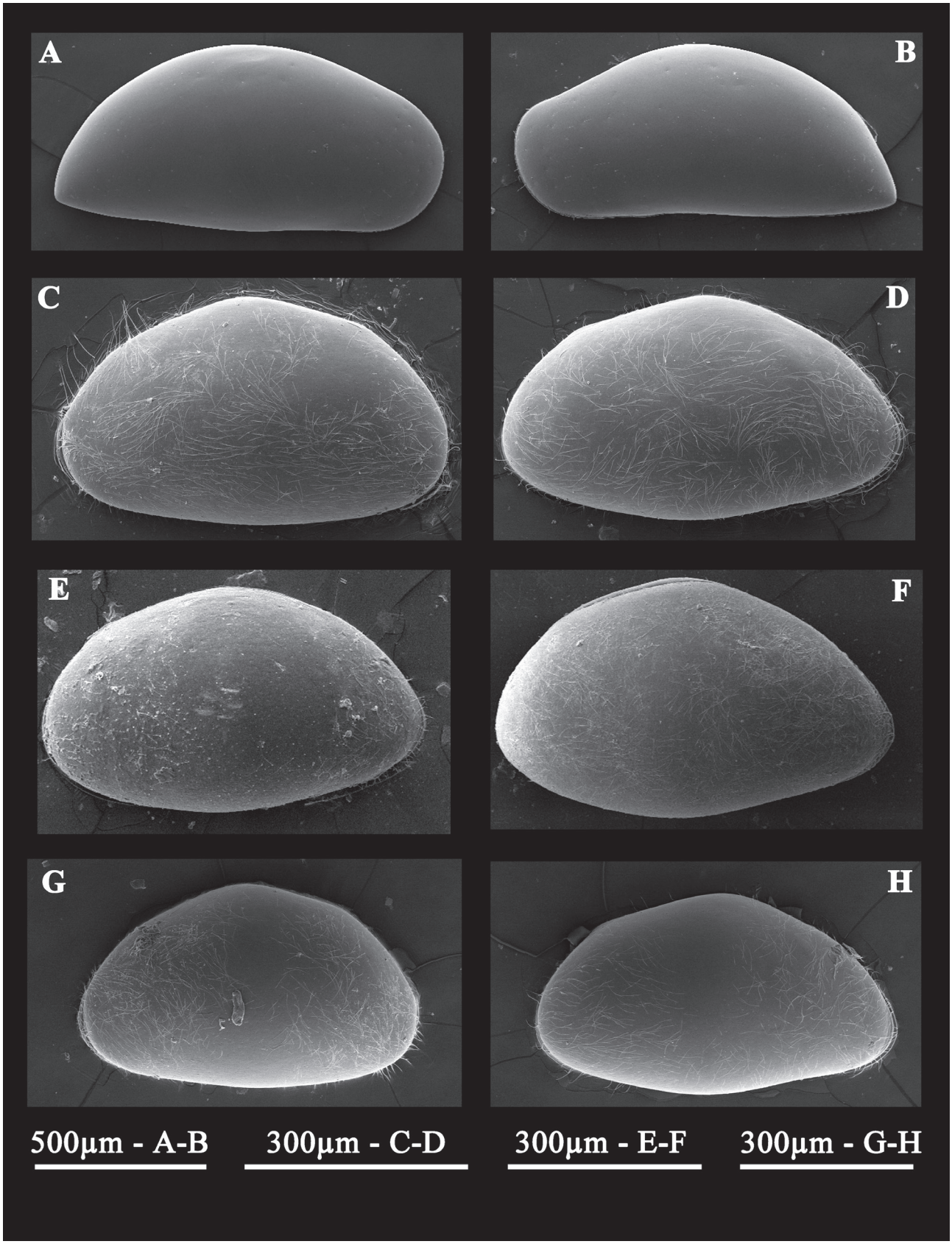
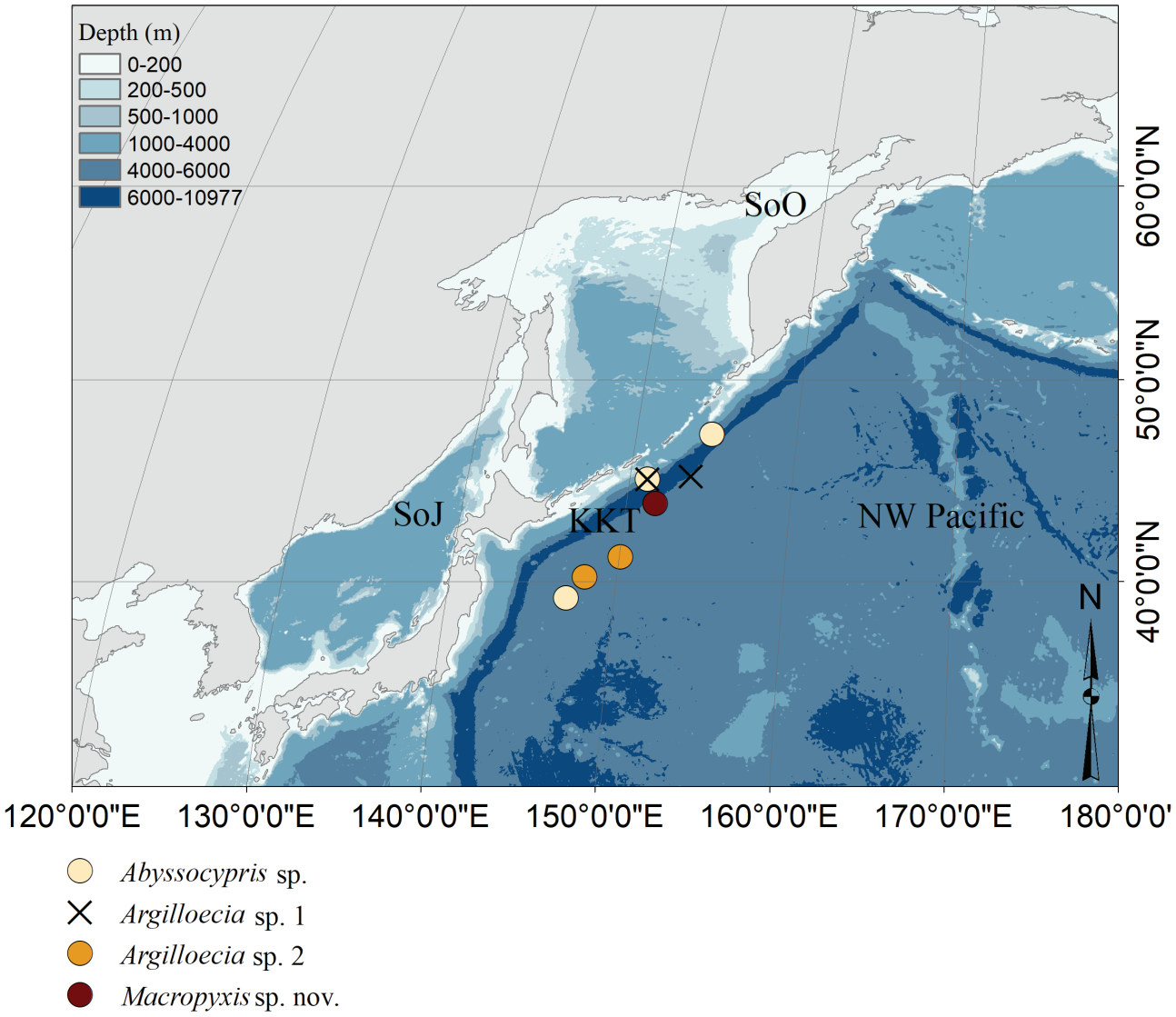


Figure 2. Macrocyprididae and Pontocyprididae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Macropyxis* sp.: (A, B) SNB 1075. *Abyssocypris* sp.: (C, D) SNB 1087; (E) SNB 1016; F, SNB 1017; (G, H) SNB 1053. A, C, G, RV; B, D, E-F, H, LV. For details on sampling localities see Tables 1 and 2.



Map 3. Distribution of Macrocyprididae and Pontocyprididae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific.

Krithe cerritula Yoo et al., 2019 (Map 6, Figure 6.E-F)

2019 *Krithe cerritula* Yoo et al.: 4, Figures 2.C, 3.A3

Remarks: The KuramBio II Expedition provided this new species and record (two stations) from the deep areas of the NW Pacific.

Krithe kamchatkaensis Yoo et al., 2019 (Map 6, Figure 6.G-J)

2019 *Krithe kamchatkaensis* Yoo et al.: 4, Figures 2.D-2.E; 3.A4, 3.A5, 3.B2

Remarks: The KuramBio II Expedition provided this new species and record (eight stations) from the deep areas of the NW Pacific.

Krithe maxima Yoo et al., 2019 (Map 7, Figure 7.A-F)

2019 *Krithe maxima* Yoo et al.: 5, Figures 2.F, 3. A6, 3.B3

Remarks: The KuramBio II Expedition provided this new species and record (two stations) from the deep areas of the NW Pacific.

Krithe rara Yoo et al., 2019 (Map 7, Figure 7.G-J)

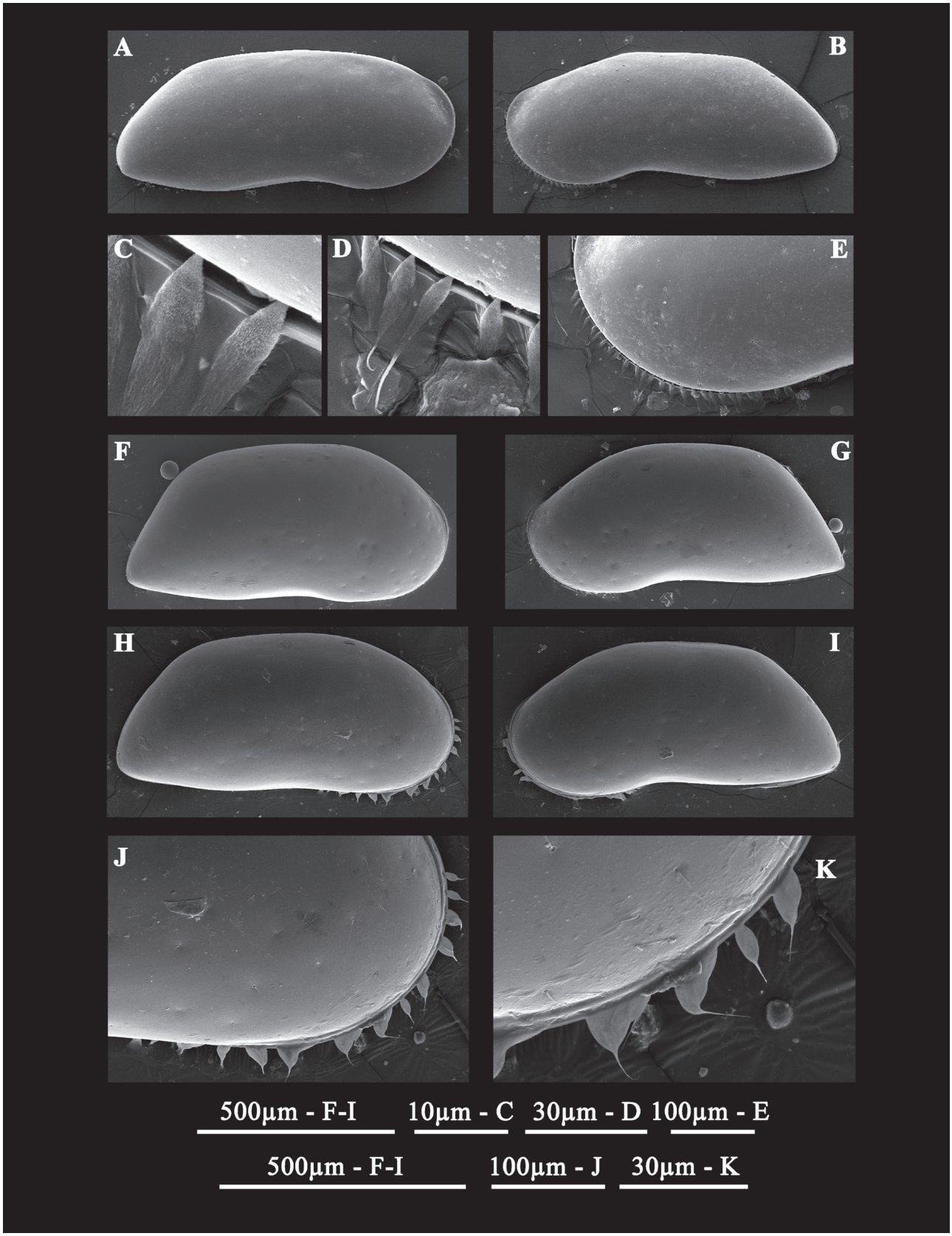
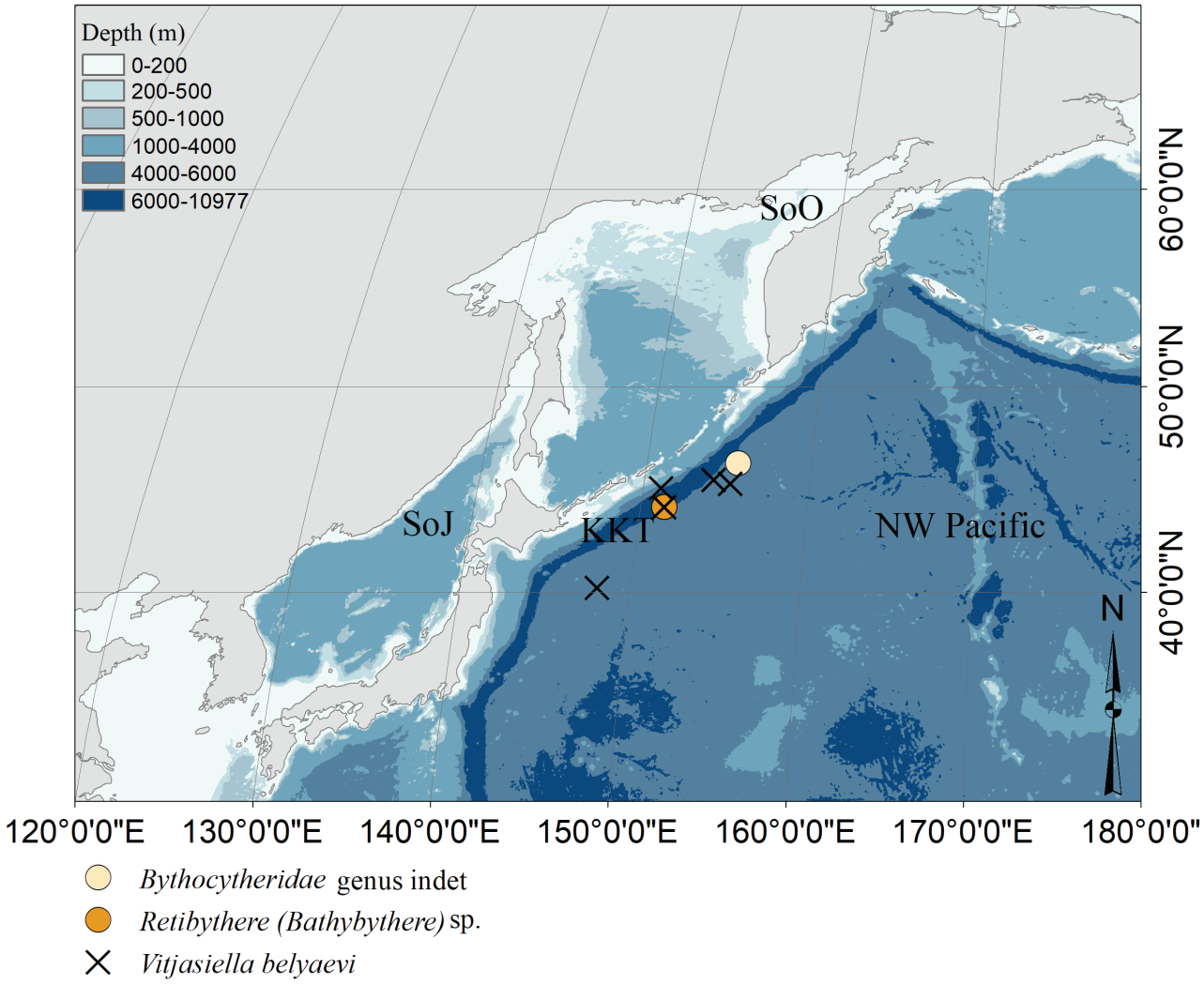


Figure 3. Pontocyprididae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Argilloecia* sp. 1: (A-E) SNB 1086; *Argilloecia* sp. 2: (F-G) SNB 1025; (H-K) SNB 1024. A, F, H, J-K, LV; B-E, G, I, RV. C-E, J-K, details of setae present on the anteroventral margin of LV (C-E) and RV (J-K). For details on sampling localities see Tables 1 and 2.



Map 4. Distribution of Bythocytheridae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific.

2019 *Krithe rara* Yoo et al.: Figures 2.G, 3.A7

Remarks: The KuramBio II Expedition provided this new species and record (a single station) from the deep areas of the NW Pacific.

Krithe tsukagoshii Yoo et al., 2019 (Map 7, Figure 8.A-D)

2019 *Krithe tsukagoshii* Yoo et al.: 6, Figures 2.H-2. I, 3.A8-3.A9, 3.B4

Remarks: The KuramBio II Expedition provided this new species and record (two stations) from the deep areas of the NW Pacific.

Krithe spp. (Map 8)

Remarks: At least three *Krithe* species, collected during the KuramBio II Expedition, could not be identified (taxonomic work is under way).

Family Paradoxostomatidae Brady and Norman, 1889

Genus *Paradoxostoma* Fischer, 1855

?*Paradoxostoma* sp. (Map 5, Figure 8.E)

Remarks: recorded from one KuramBio station.

Family Thaerocytheridae Hazel, 1967

Genus *Poseidonamicus* Benson, 1972

Poseidonamicus sp. (Map 9, Figure 9.A-B)

Remarks: KuramBio provided the first record of *Poseidonamicus* (a cosmopolitan, typically deep-

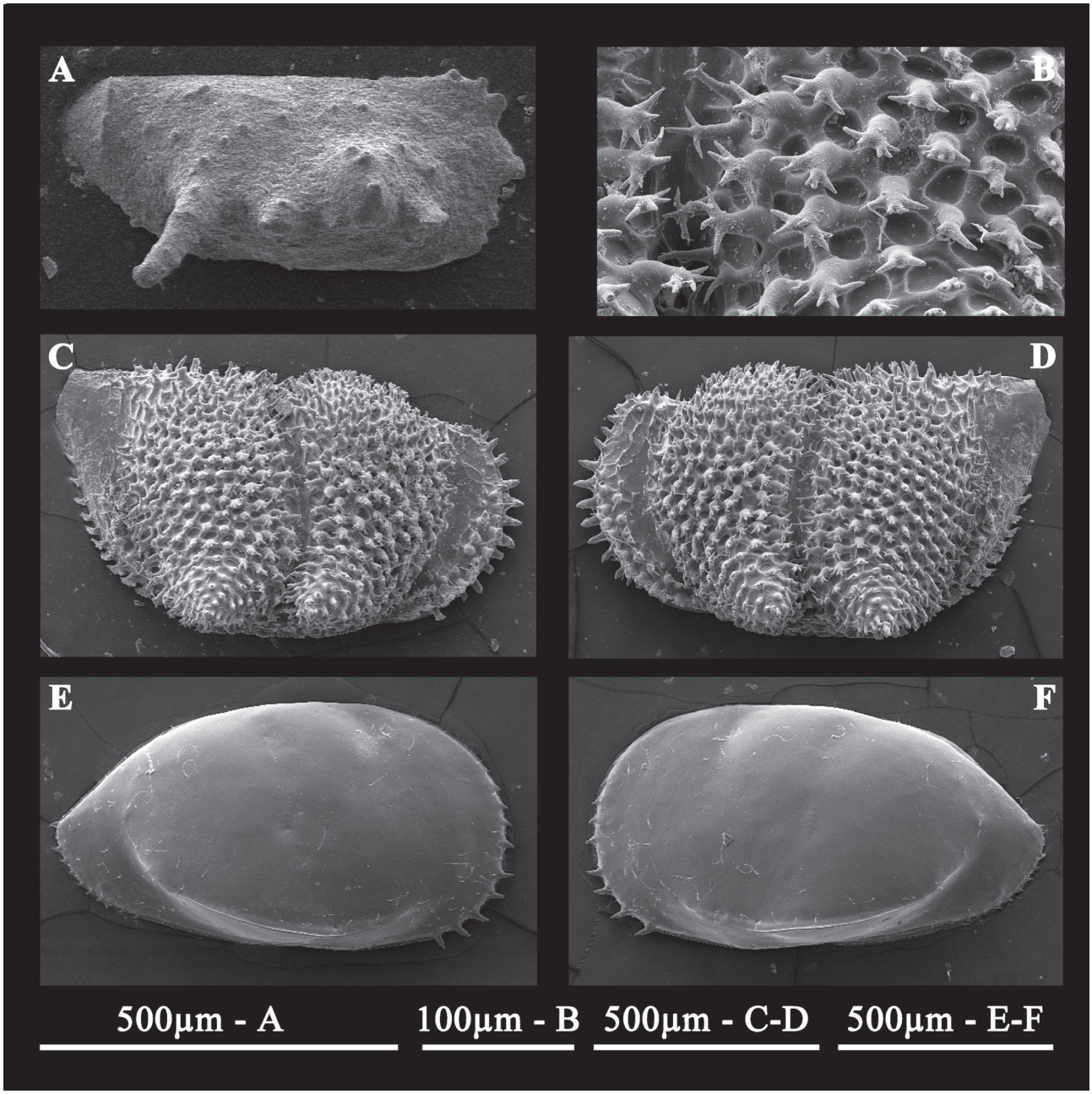
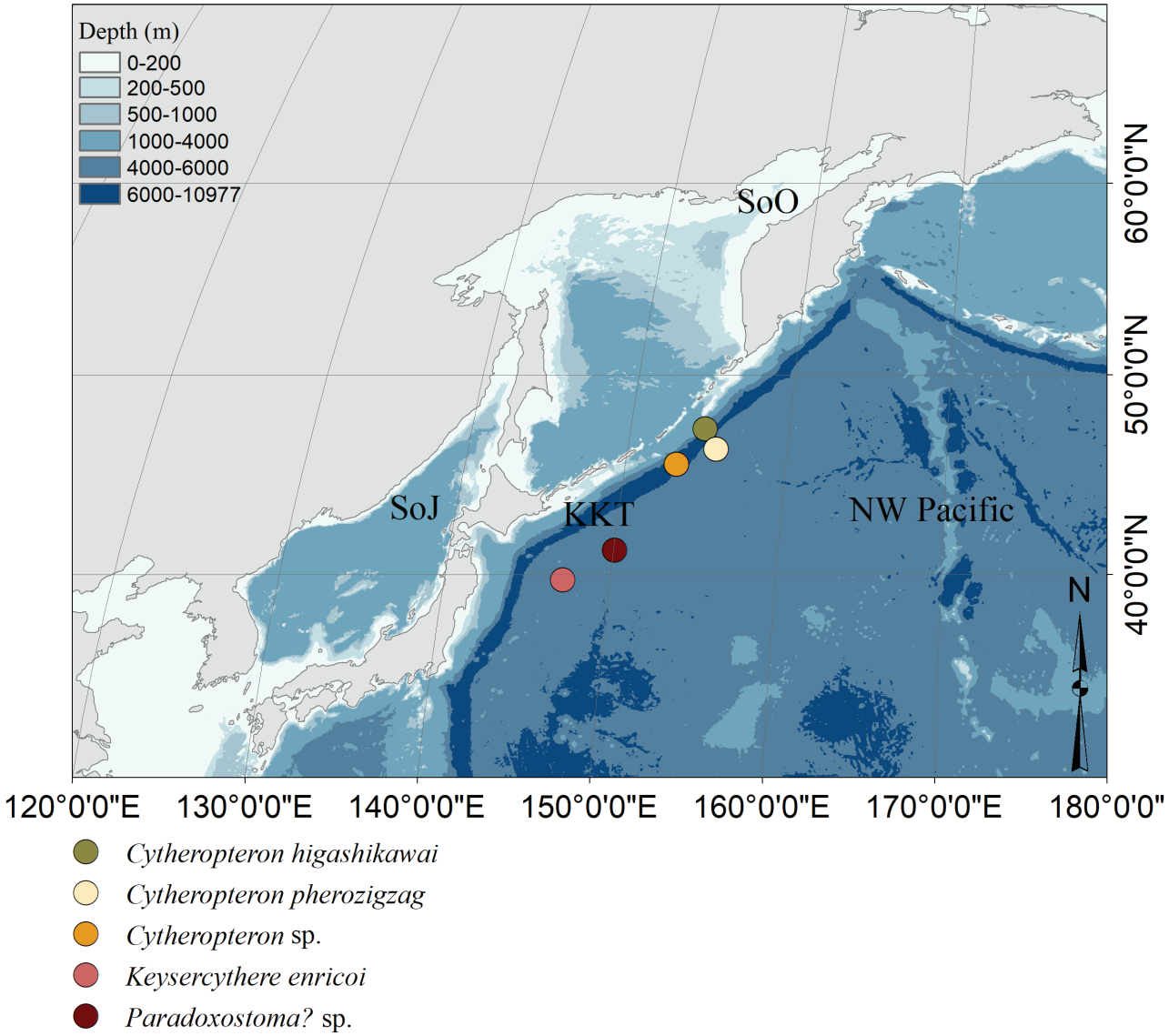


Figure 4. Bythocytheridae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. Bythocytheridae genus indet: (A) SNB 1002. *Retibythere (Bathybythere)* sp.: (B-D) SNB 1142. *Vitjasiella belyaevi* Schornikov, 1976: (E-F) SNB 1082. A-C, E, RV; D, F, LV; B, details of ornamentation of D. F or details on sampling localities see Tables 1 and 2.



Map 5. Distribution of Cytheruridae, Keysercytheridae and ?Paradoxostomatidae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific.

sea genus) from the KKT region (one KuramBio station).

Family Trachyleberididae Sylvester-Bradley, 1948

Genus *Abyssocythere* Benson, 1971

Abyssocythere sp. (Map 9, Figure 8.F-J)

Remarks: This species, collected from three KuramBio stations, is similar to *Abyssocythere japonica* Benson, 1971, but differs in some patterns of the primary ornamentation, and is therefore probably new to science.

Genus *Abyssocythereis* Schornikov, 1975

Abyssocythereis vitjasi Schornikov, 1975 (Map 9, Figure 9.C-H)

1975 *Abyssocythereis vitjasi* Schornikov: 522, Figures 2–3

?1982 *Protocythere* sp.; Cai: Pl. 4 [pl. 3 in caption erroneously], Figures 51–52

1989 *"Cythere" sulcatoperforata* Brady; Ruan:119, Pl. 21.2–21.4

?1996 *Abyssocythereis sulcatoperforata* (Brady); Zhao and Zheng: Pl. 1. 2

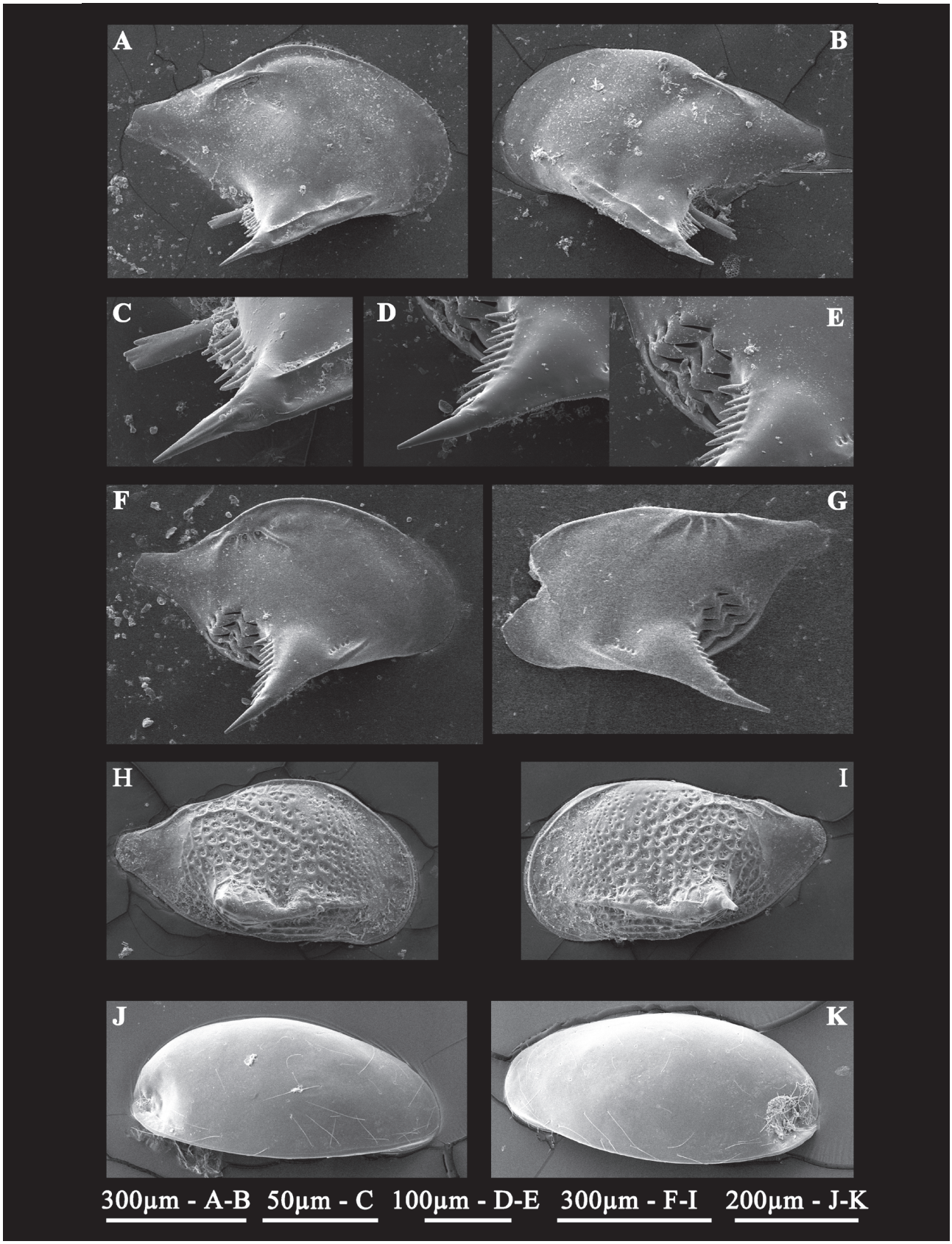
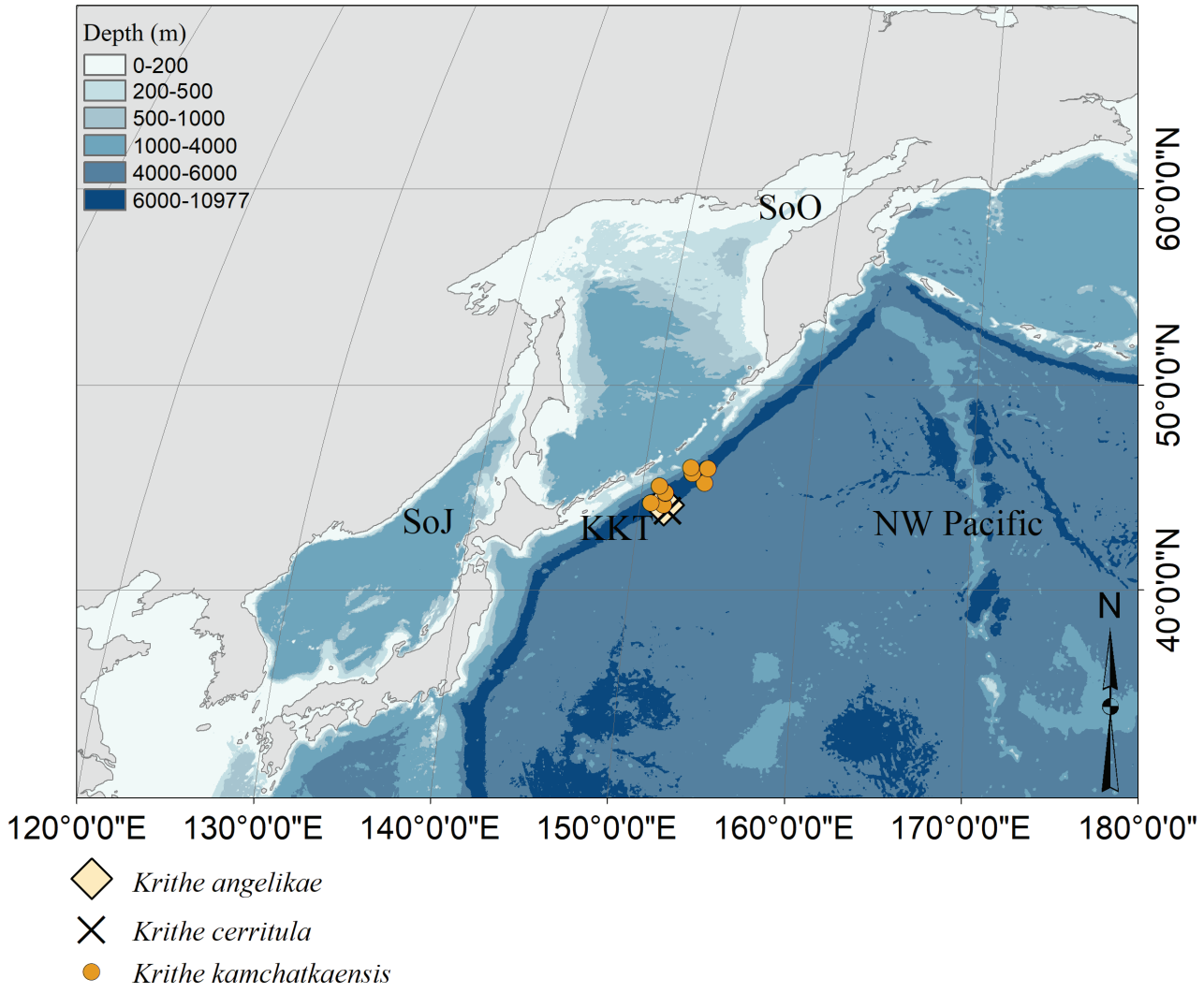


Figure 5. Cytheruridae and Keysercytheridae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Cytheropteron higashikawai* Ishizaki, 1981: (A-C) SNB 1018. *Cytheropteron pherozigzag* Whatley, Ayress and Downing, 1986: (D-G) SNB 1001. *Cytheropteron* sp.: (H-I) SNB 1101. *Keysercythere enricoi* Karanovic and Brandão, 2015: (J, K) no SNB number. A, C-F, H, J, RV; B, G, I, K, LV. For details on sampling localities see Tables 1 and 2.



Map 6. Distribution of *Krithe angelikae* Yoo et al., 2019, *Krithe cerritula* Yoo et al., 2019 and *Krithe kamtchakaensis* Yoo et al., 2019 (Ostracoda, Krithidae) from the Kuril-Kamchatka Trench region, NW Pacific.

?2005 *Abyssocythereis sulcatoperforata* (Brady); Zhao: Pl. 3.22

2007 *Abyssocythereis sulcatoperforata* (Brady); Hou and Gou: 502, Pl. 186.10–186.14

2015 *Protocythere vitjasi* (Schornikov, 1975); Yasuhara et al.: 32, Figures 9.G–9.J, 10. I–10. L

Remarks: This species was described from the KKT, NW Pacific (Schornikov 1975), and was also collected during the KuramBio Project (one station).

Genus *Croninocythereis* Yasuhara, Hunt, Okahashi and Brandão, 2015 (Map 10, Figure 10)

Croninocythereis sp. cf. C. *cronini* Yasuhara, Hunt, Okahashi and Brandão, 2015

?2015 *Croninocythereis cronini* Yasuhara et al.: 123, Figures 63.A–63.F, 63.I–63.J, 66. N–66. T, 68.

Remarks: KuramBio provided the first record of *Croninocythereis* from the KKT region (five KuramBio stations). Previously it has been recorded from the Atlantic, North Pacific and Indian oceans.

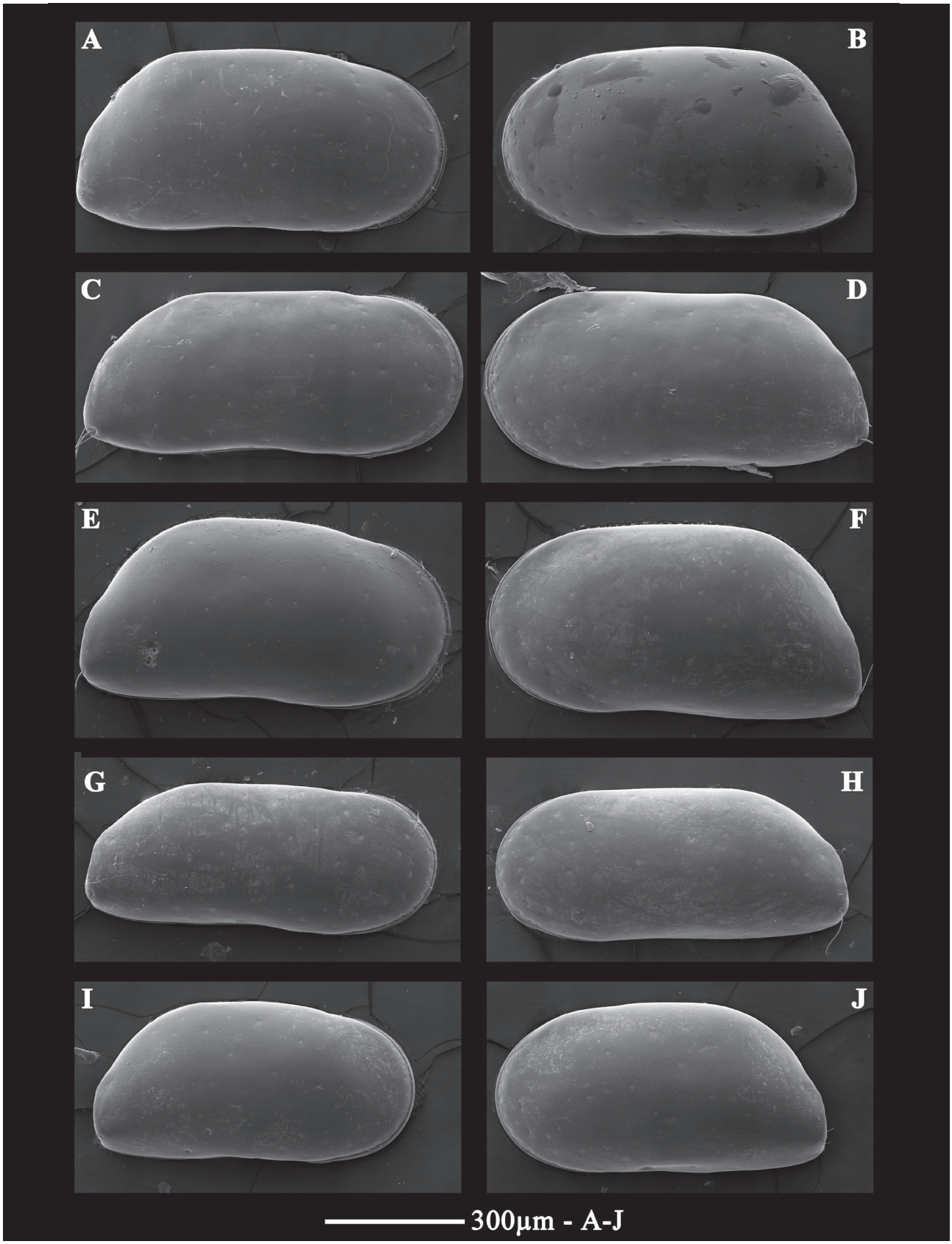
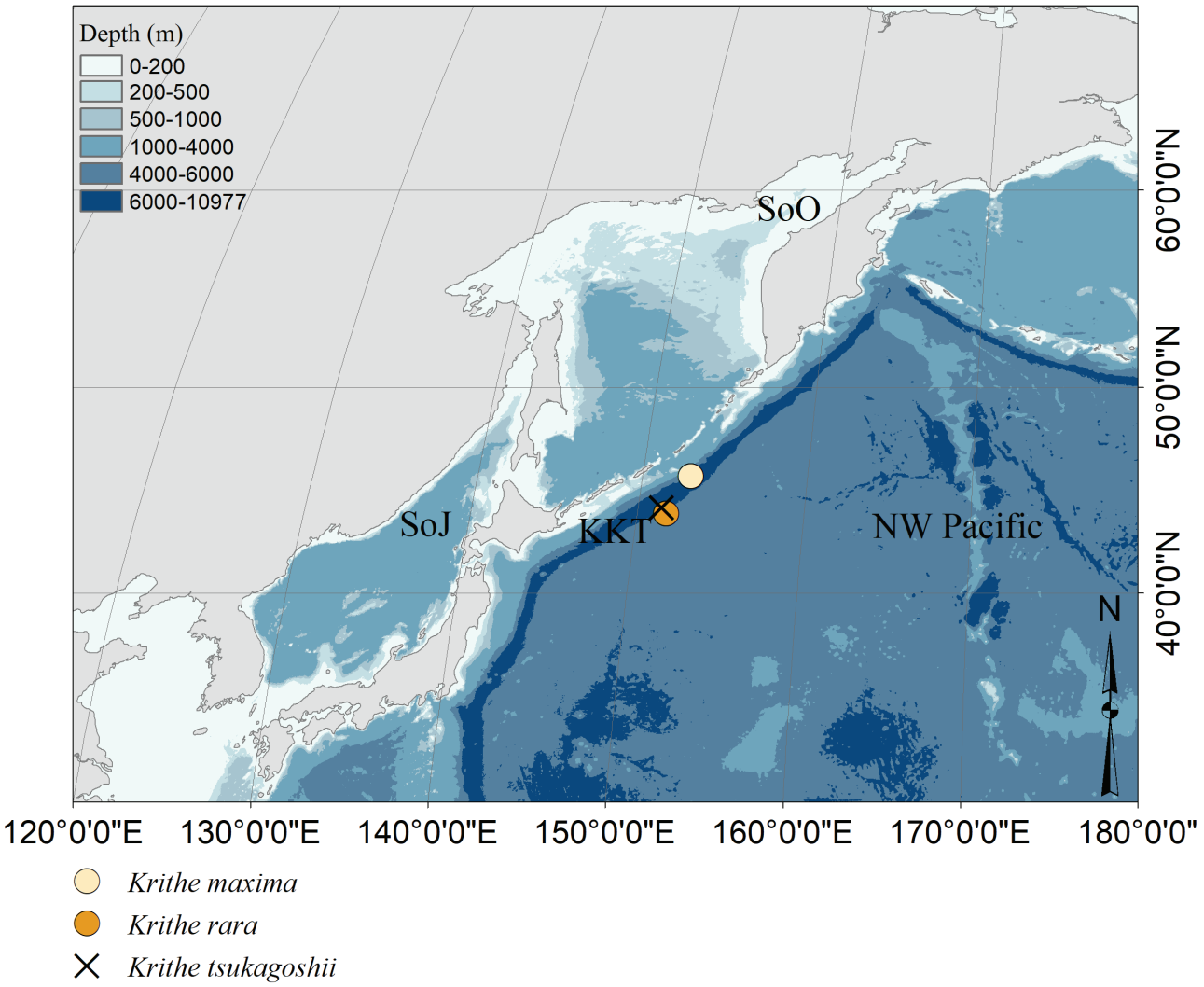


Figure 6. Krithidae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Krithe angelikae* Yoo et al., 2019: (A) SNB 1115; (B) SNB 114; (C, D) SNB 1128. *Krithe cerritula* Yoo et al., 2019: (E, F) SNB 1158. *Krithe kamtchakaensis* Yoo et al., 2019: (G, H) SNB 1104; (I, J) SNB 1116. A, C, E, G, I, RV; B, D, F, H, J, LV. For details on sampling localities see Tables 1 and 2.



Map 7. Distribution of *Krithe maxima* Yoo et al., 2019, *Krithe rara* Yoo et al., 2019 and *Krithe tsukgoshi* Yoo et al., 2019 (Ostracoda, Krithidae) from the Kuril-Kamchatka Trench region, NW Pacific.

Genus *Henryhowella* Puri, 1957

Henryhowella sol (Jellinek and Swanson, 2003) (Map 10, Figure 11)

2003 *Apatihowella (Fallacihowella) sol* Jellinek and Swanson: 44, Pl. 34.1–34.10, Pl. 35. 1–35. 6.

2003 *Apatihowella (Fallacihowella) caligo* Jellinek and Swanson: 45, Pl. 36.1–36. 6.

?2005 *Fallacihowella* sp. A Mazzini: 54, Figure 31.A–31. M.

?2005 *Fallacihowella* sp. B Mazzini: 57, Figure 32.A–32. Q.

2019 *Henryhowella sol* Jellinek and Swanson, 2003; Yasuhara et al.: 101, Figure 7.

Remarks: KuramBio provided the first record of *Henryhowella* (a cosmopolitan genus) from the KKT region (three KuramBio stations).

Genus *Legitimocythere* Coles and Whatley, 1989

Legitimocythere spp. (Map 10, Figure 12)

Remarks: KuramBio provided the first record of *Legitimocythere* (a cosmopolitan, mostly deep-sea genus) from the KKT region (nine KuramBio stations).

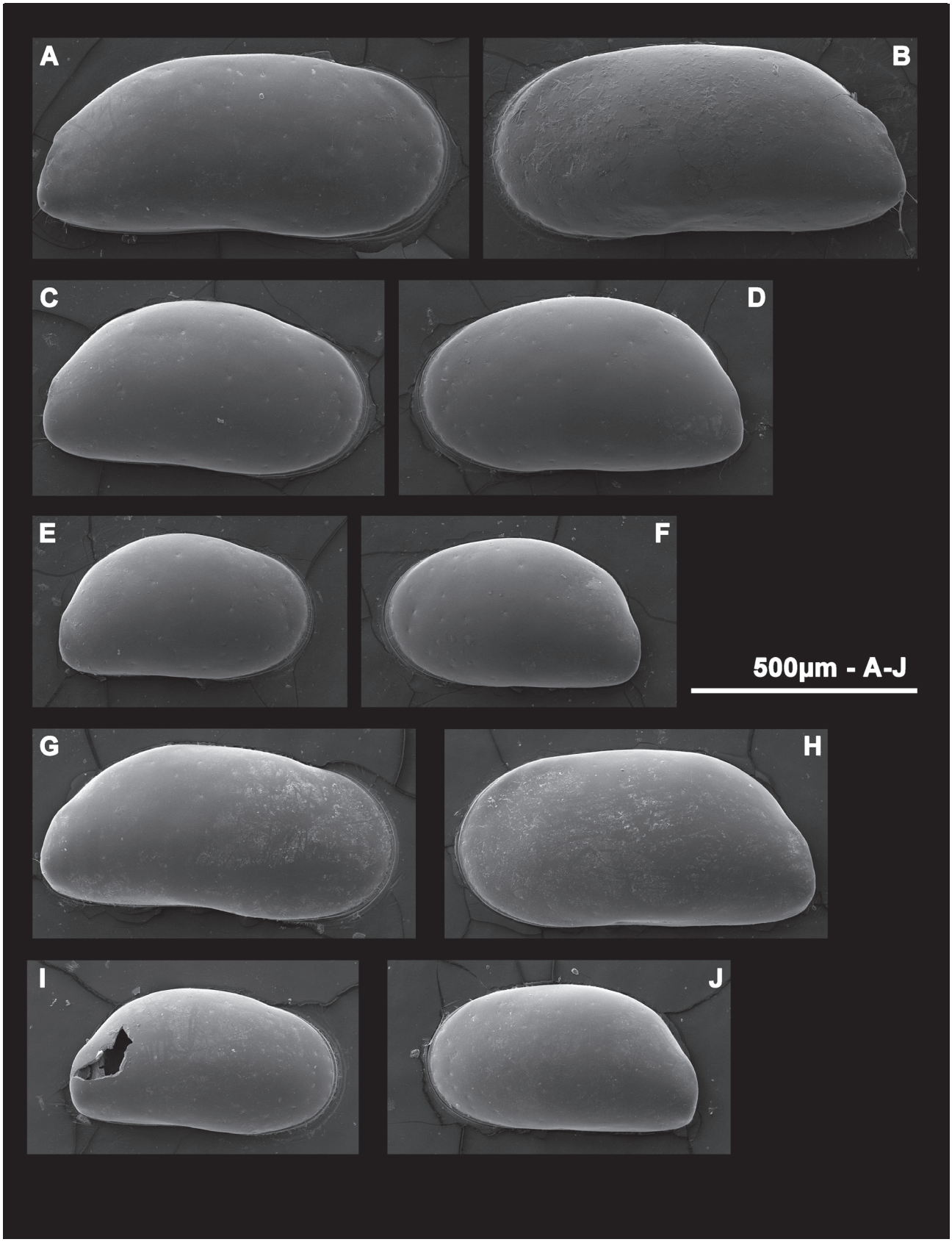
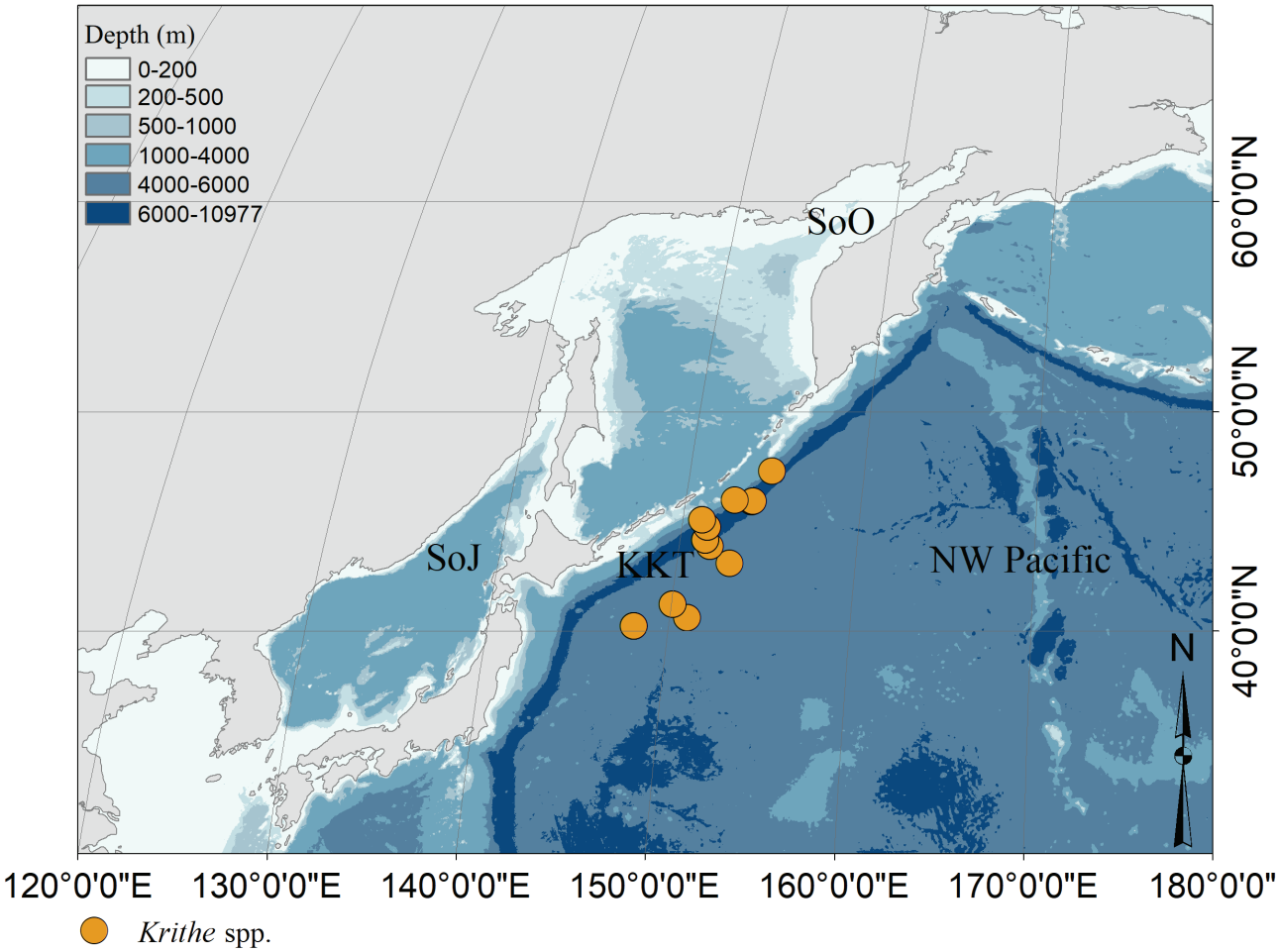


Figure 7. Krithidae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Krithe maxima* Yoo et al., 2019: (A, B) SNB 1152; (C, D) SNB 1153; (E, F) 1154. Krithe rara Yoo et al., 2019: (G, H) SNB 1163; (I, J) SNB 1164. A, C, E, G, I, RV; B, D, F, H, J, LV. For details on sampling localities see Tables 1 and 2.



Map 8. Distribution of *Krithe* spp. (Ostracoda, Krithidae) from the Kuril-Kamchatka Trench region, NW Pacific.

Genus *Ryugucivis* Yasuhara, Hunt, Okahashi and Brandão, 2015

Ryugucivis sp. (Map 10, Figure 13)

non 1987 *Cytheretta? iwasakii* Nohara: 47, Pl. 11.2a–11.2d.

Remarks: KuramBio provided the first record of *Ryugucivis* from the KKT region (nine KuramBio stations), previous recordings come from the Atlantic and NW Pacific.

4.3. Richness, bathymetrical and latitudinal patterns

The sampling effort is strongly concentrated at the latitudes 44 and 45°N and longitudes 151 to 154°E (Figure 14). The species richness of each family shows a variable, possibly random, pattern (families with only one species were excluded from this graph) (Figure 15). In relation to both latitude and depth, the ostracod species richness is strongly related to the sampling effort (i.e. number of records), indicating that the area is under-sampled for ostracods (Figures 16 and 17, respectively). The cluster analysis in 1° latitudinal bands splits the samples into two groups, the first with high richness (latitudes 44°N and 45°N), and the second with the remaining, less rich latitudes (39°, 40°, 43°, 46° and 47°N) (Figure 18). Finally, the cluster analysis of 100 m depth bands, shows three significant groups, plus one not sig-

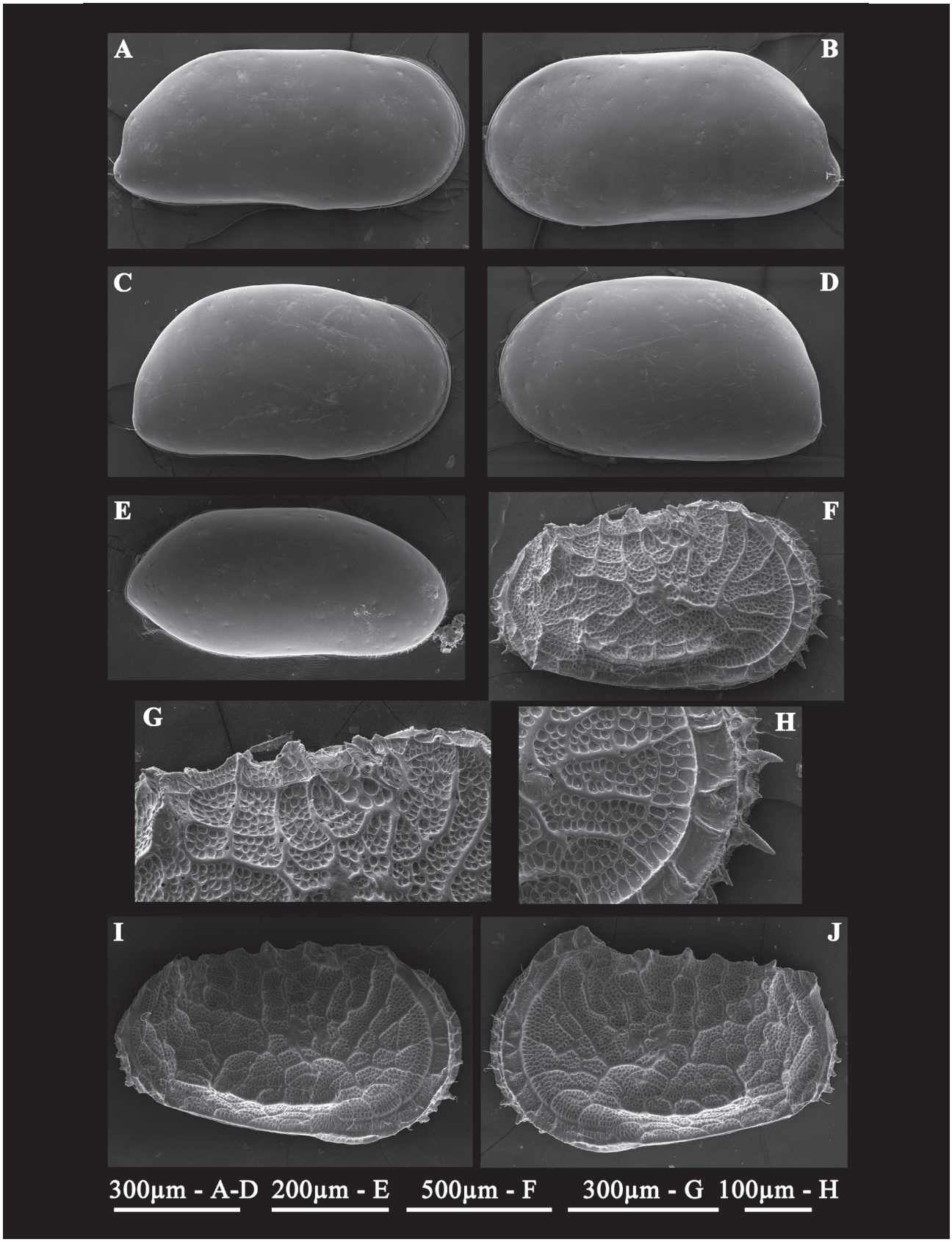
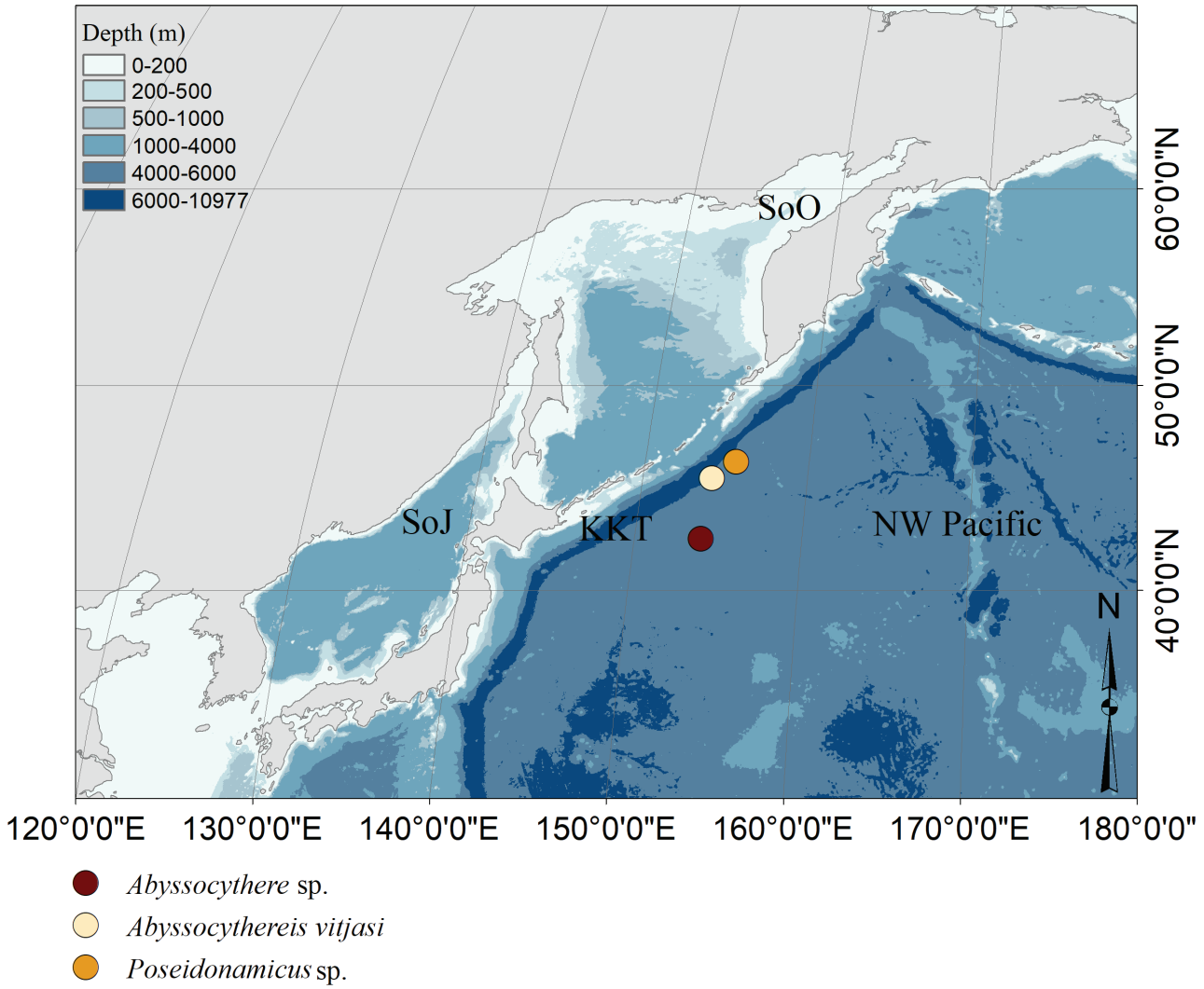


Figure 8. Krithidae, Paradoxostomatidae? and Trachyleberididae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Krithe tsukgoshi* Yoo et al., 2019: (A, B) SNB 1124; (C, D) SNB 1113. *Paradoxostoma*? sp.: (E) SNB 1126A. *Abyssocythere* sp.: (F-H) SNB 1011; (I, J) SNB 1056. A, C, E, F-I, RV; B, D. J, LV; G, H, details of ornamentation of F. For details on sampling localities see Tables 1 and 2.



Map 9. Distribution of *Poseidonamicus* sp. (Thaerocytheridae), and *Abyssocythereis* sp. (Trachyleberididae) (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific.

nificant cluster (depth bands 5,200 and 5,400 m) (Figure 19). Within the significant cluster, with very high bootstrap values (i.e. 99 and 100), one band (8,700 m) lies alone, and the remaining depth bands group in two distinct clusters with (1) deep abyssal (4,800, 4,900, 5,300, 5,700 m) and (2) trench (6,000–9,304 m) faunas.

5. Discussion

Diverse aspects of the dataset analysed herein show evidence for under-sampling in the NW Pacific (40°–60°N, 120°–180°E). Even if less than 1% of the ostracod specimens collected during the KuramBio I and II expeditions are already identified, the high number of new records at genus and species level in the KuramBio samples shows that the KKT regions is strongly under-sampled, at least for ostracods. We expect that the ostracod richness will further increase at genus, species and even at family levels in the KKT region, when all +11,000 KuramBio ostracods are studied. From the 24 genera now recorded from the KKT region, 11 are new records from the KuramBio Project: *Abyssocypris*, *Argilloecia*,

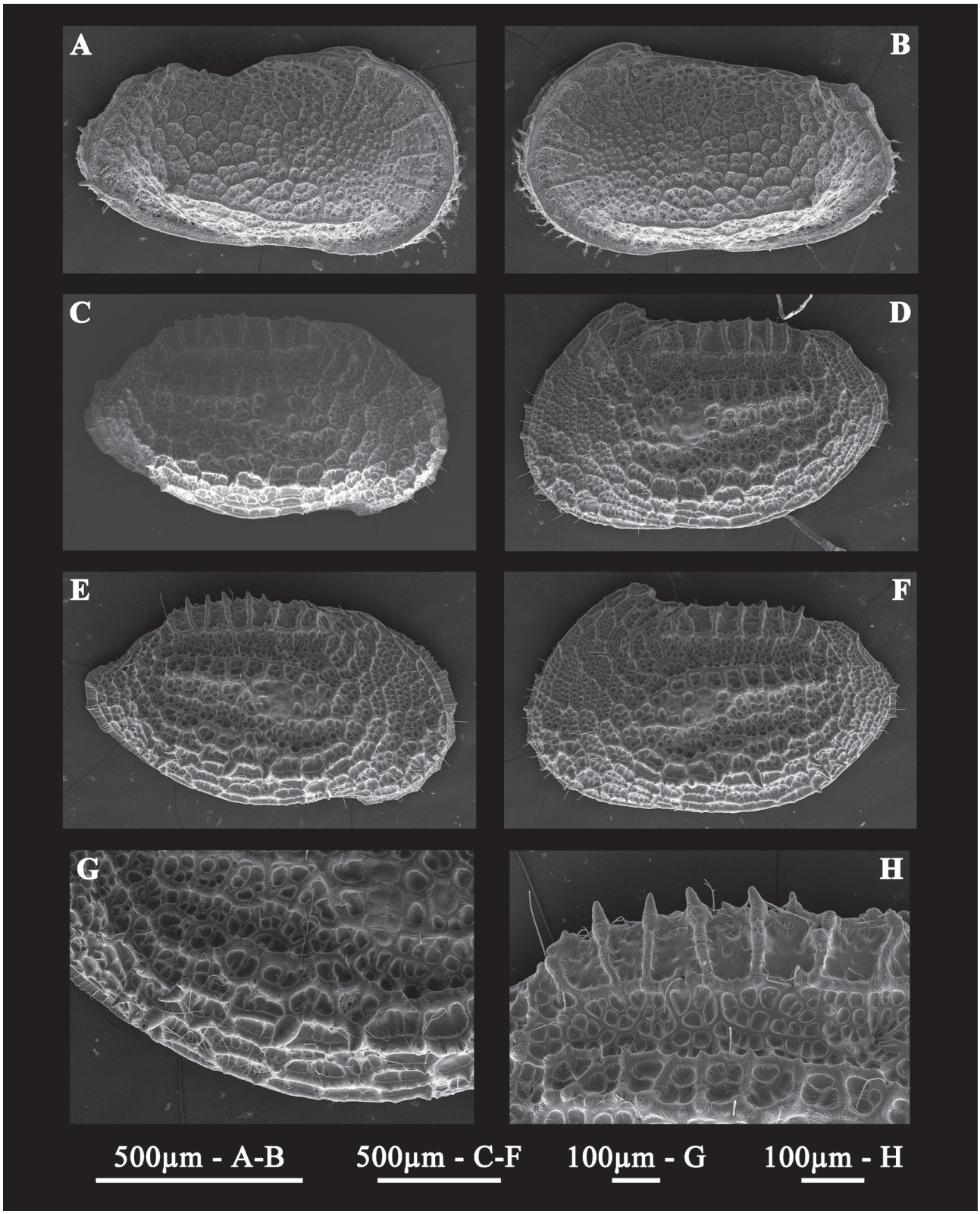
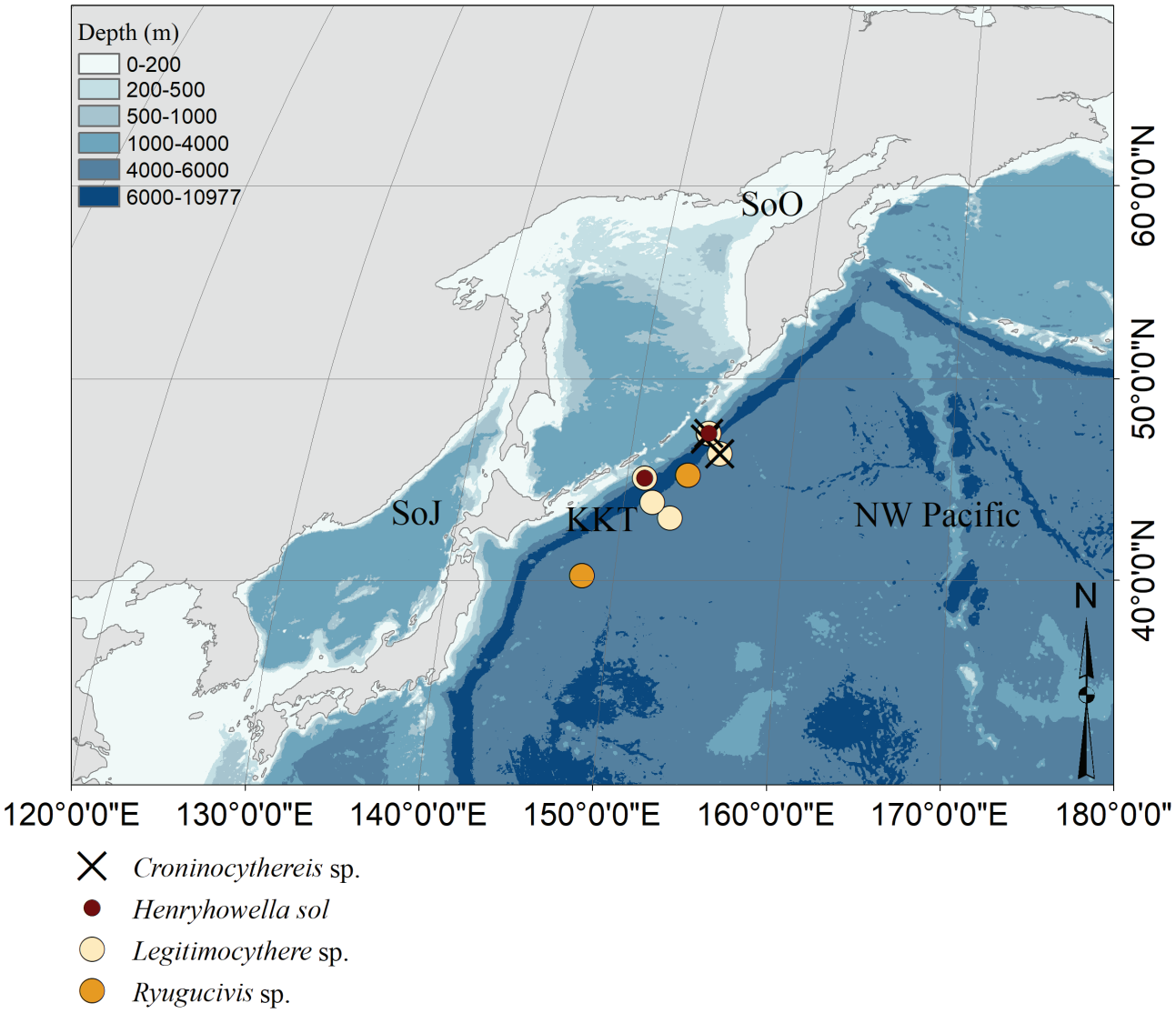


Figure 9. Thaerocytheridae and Trachyleberididae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Poseidonamicus* sp.: (A, B) SNB 1049. *Abyssocythereis* sp.: (C, D) SNB 1055; (E-H) SNB 1054. A, C, E, G, H, RV; B, D, F, LV; G, H, details of ornamentation of E. For details on sampling localities see Tables 1 and 2.



Map 10. Distribution of *Croninocythereis* sp., *Henryhowella sol* (Jellinek and Swanson, 2003), *Legitimocythere* spp., *Ryugucivis* sp. (Ostracoda, Trachyleberididae) from the Kuril-Kamchatka Trench region, NW Pacific.

Bythocypris, *Croninocythereis*, *Cytheropteron*, *Henryhowella*, *Krithe*, *Legitimocythere*, *Macropyxis*, *Poseidonamicus*, *Ryugucivis*. Most of these genera have a worldwide distribution, occurring in the Arctic as well as in other latitudes of the Pacific, and also in the Atlantic, Indian and Southern oceans (e.g. Yasuhara et al. 2015). At species level, ostracod diversity was also strongly increased by the KuramBio expedition: from the 41 species now known, only 13 had been previously recorded (Chavtur 1981; Schornikov 1975, 1976, 1980, 1981), while the remaining 28 species (plus three already previously recorded) were identified from the few KuramBio samples.

The highest ostracod species richness found in latitudes 43°N to 45°N (Figures 14-16) appears to be related to the gear utilised for the present study. As mentioned by Brandão et al. (2014, tab. 3), while one deployment of a AGT or a EBS sample thousands of m^2, the BC and MUC sample a few cm^2. However, the sediment collected with the

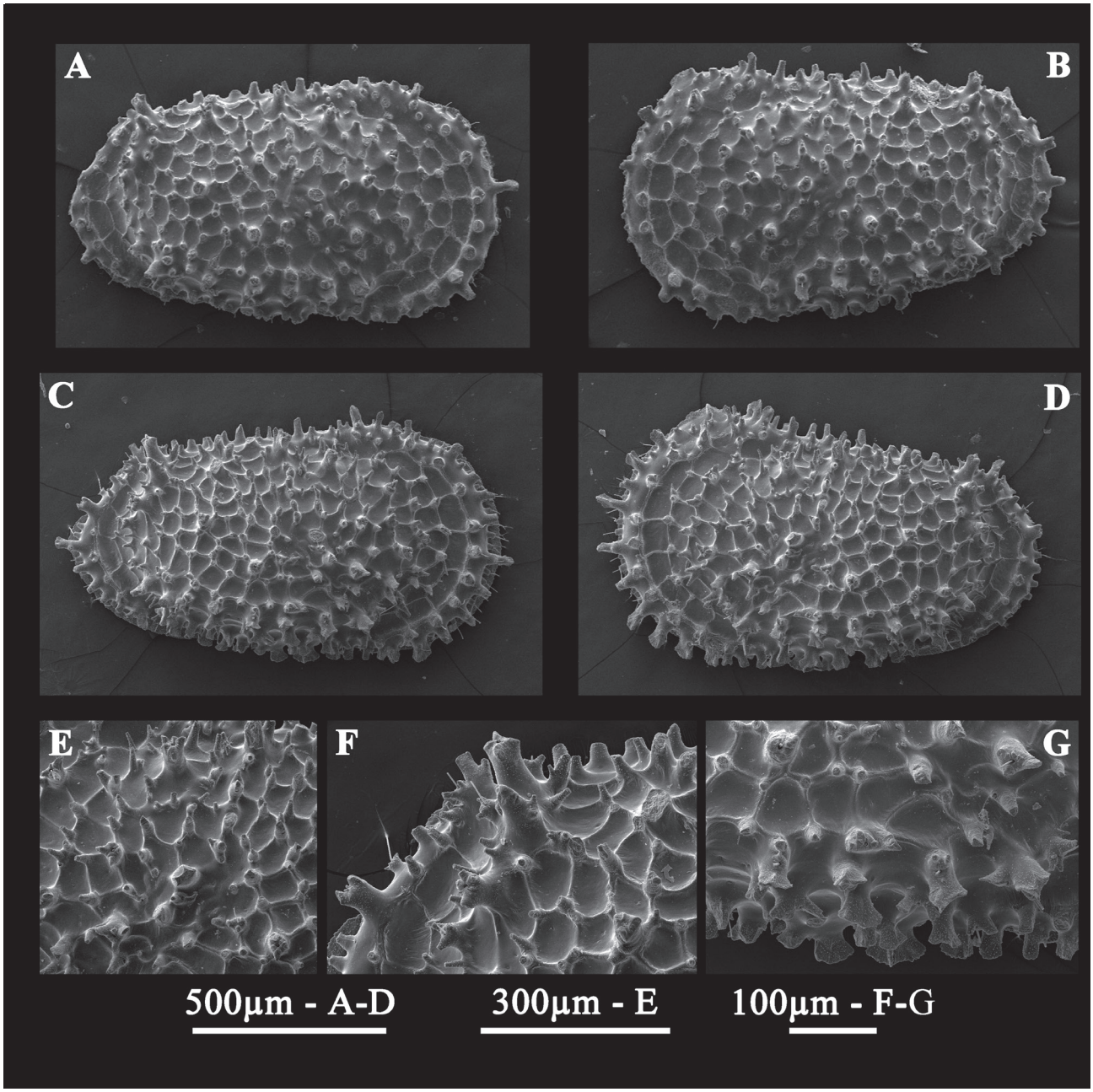


Figure 10. Trachyleberididae (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. *Croninocythereis* sp.: (A, B) SNB 1076; (C-G) SNB 1079. A, C, RV; B, D-G, LV; E-G, details of ornamentation of B. For details on sampling localities see Tables 1 and 2.

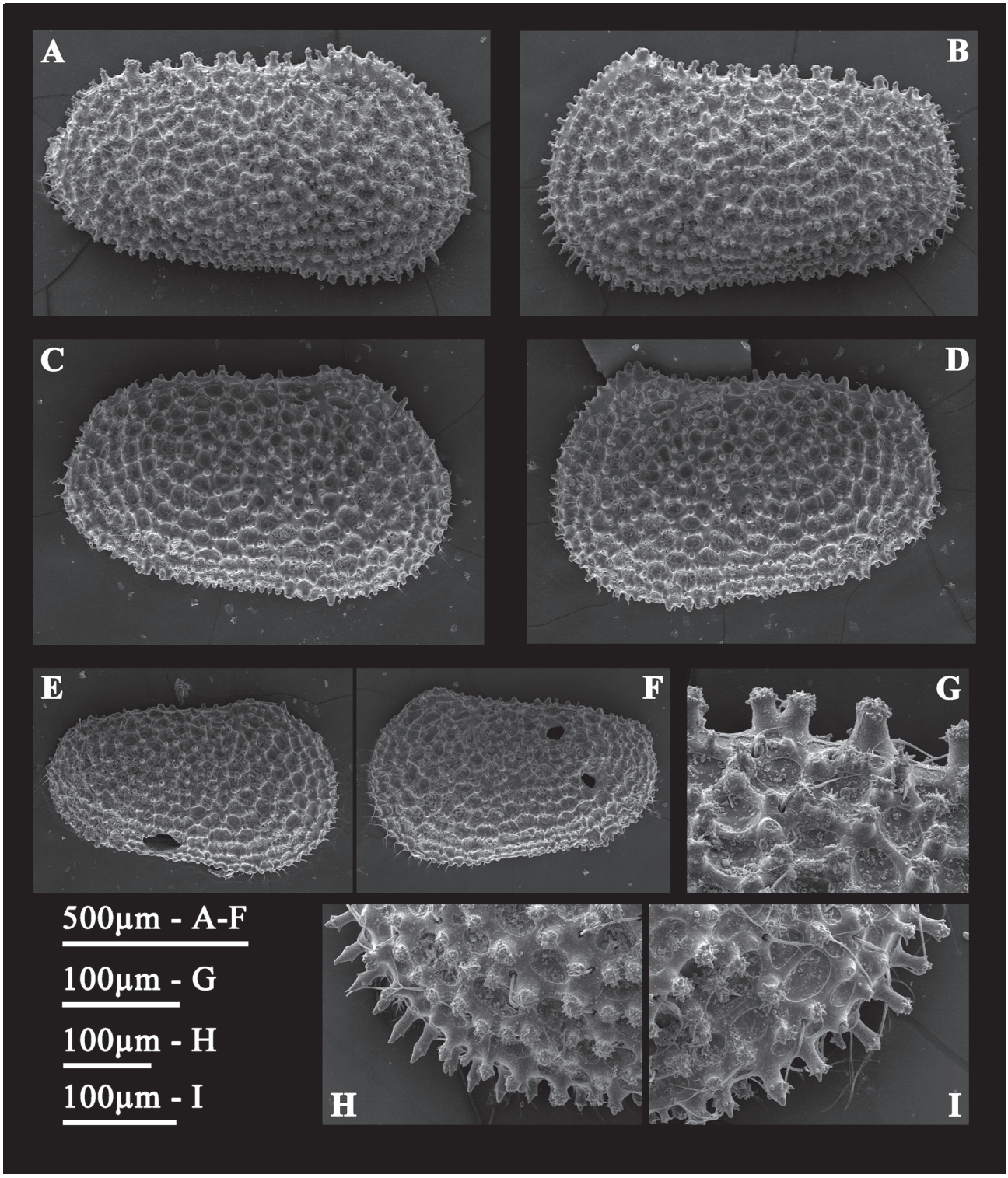


Figure 11. *Henryhowella sol* (Jellinek and Swanson, 2003) (Ostracoda) from the Kuril-Kamchatka Trench region, NW Pacific. (A, B), (G-I), SNB 1083; (C, D) SNB 1060; (E, F) 1038. A, C, E, RV; B, D, G-I, LV; (G-I) details of ornamentation of B. For details on sampling localities see Tables 1 and 2.

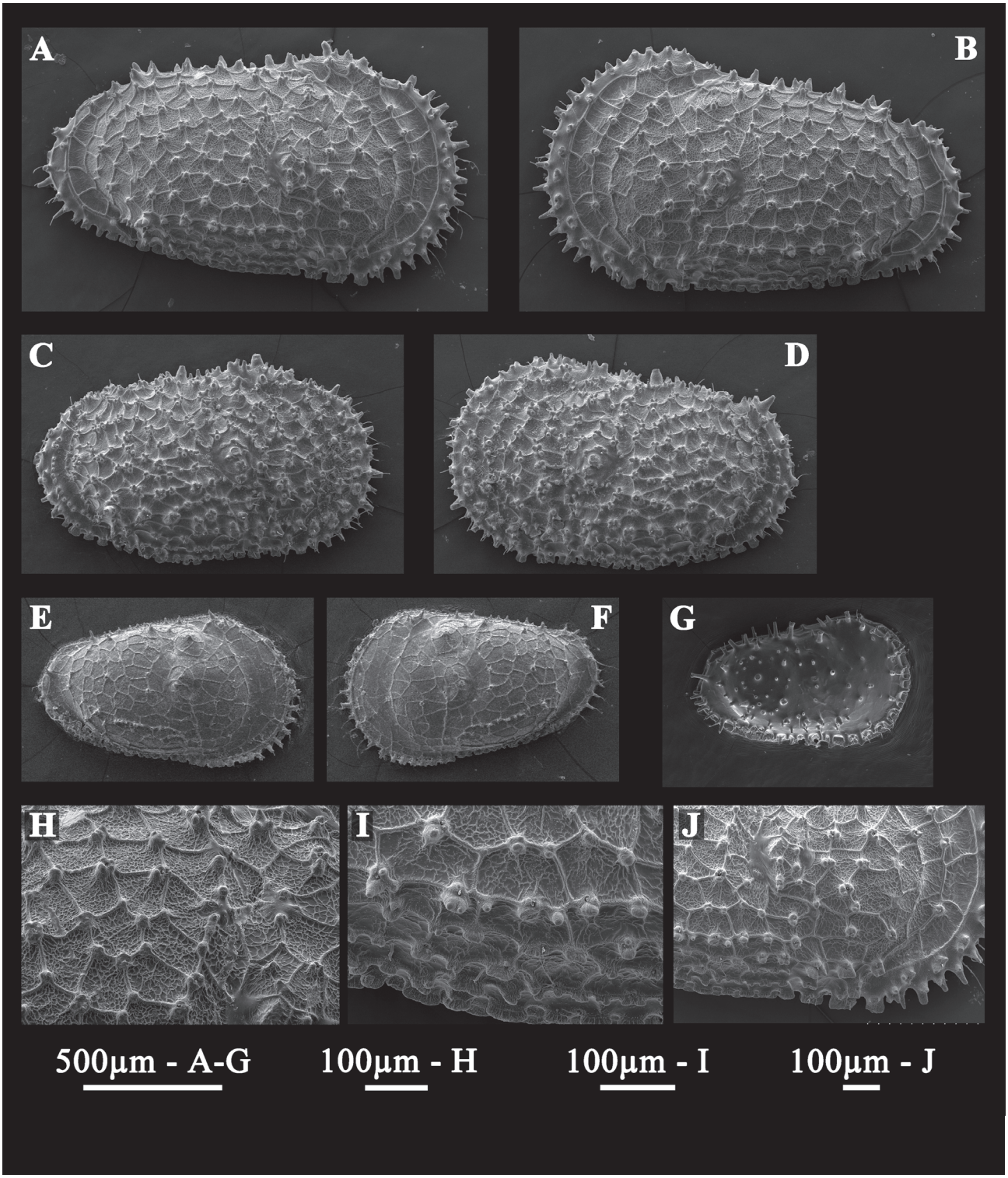


Figure 12. *Legitimocythere* spp. (Ostracoda) from Kuril-Kamchatka Trench region, NW Pacific. (A, B), (H-J) SNB 1074; (C, D) SNB 1070; (E, F) SNB 1097; (G) SNB 1034. A, C, E, G-J, RV; B, D, F, LV. (H-J) details of ornamentation of A. For details on sampling localities see Tables 1 and 2.

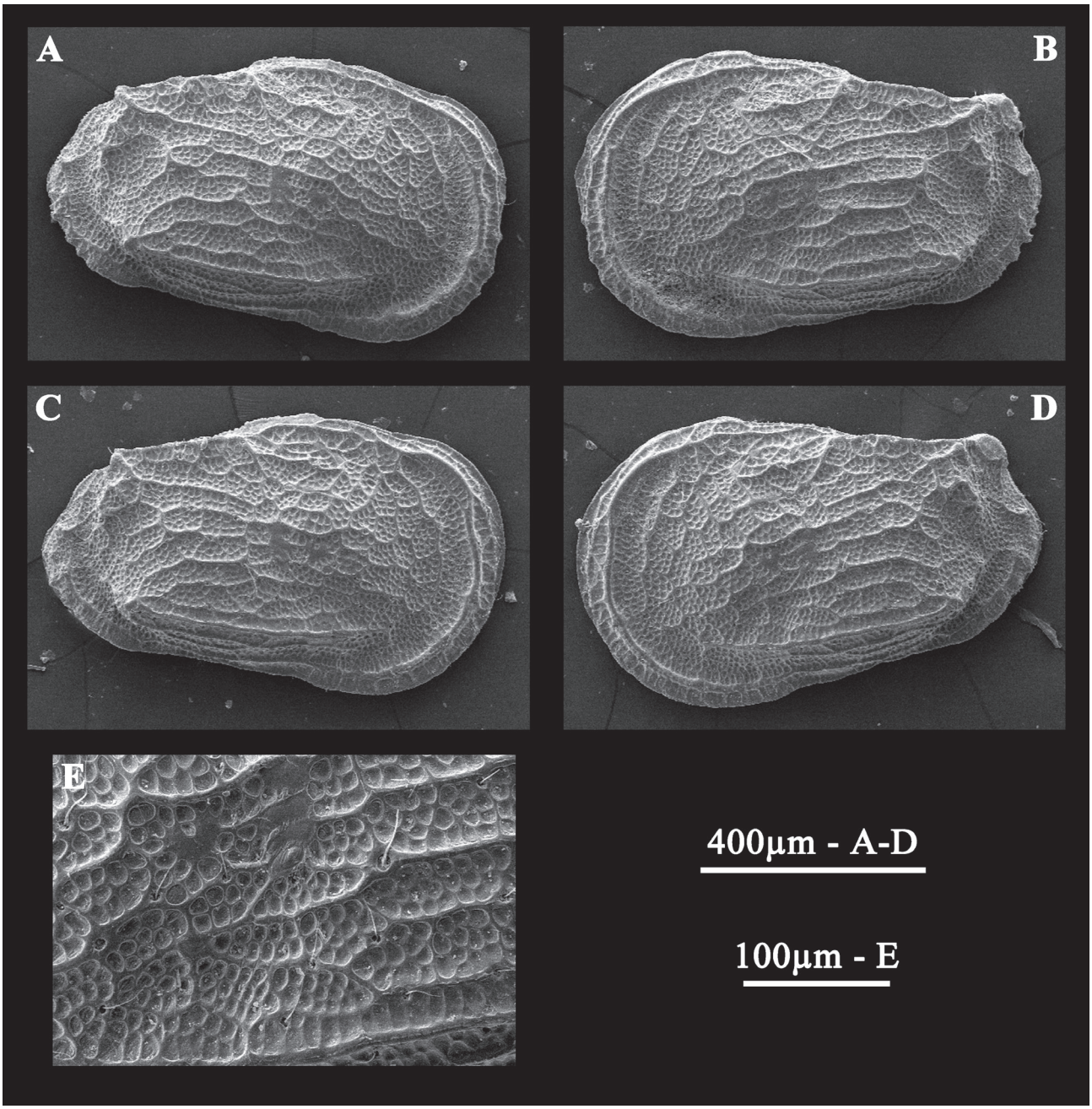


Figure 13. *Ryugucivis* sp. (Ostracoda). (A, B) SNB 1095; (C-E) SNB 1094. A, C, RV; B, D, E, LV; E, details of ornamentation of D. For details on sampling localities see Tables 1 and 2.

BC and MUC are sieved with a considerably fined mesh (usually 63, 100, 300, and 500 µm), being important for the study of the small-sized ostracods (e.g. Yasuhara et al. 2014b). In this way, only all four gears together have the potential to collect both abundant and diverse ostracod assemblages.

While in both KuramBio expeditions all gear (AGT, BC, EBS and MUC) were deployed in every station, for the present chapter, AGT and EBS samples only from latitudes 43°N to 45°N were studied (Tabs 1 and 2). For the other latitudes only ostracods from the BC and MUC were identified. Consequently, further work on KuramBio ostracods has a great potential of revealing the diversity and macroecological patterns in the KKT region.

Concerning the bathymetry, the highest species richness was found between 5,200 and 5,400 m depth, where a very abundant EBS sample (KuramBio II, Station 10-1) was collected (Figure 17). Not surprisingly these are exactly the depth bands that do not group with the remaining depths in Figure 19. Other high diversities are also related to AGT and EBS samples, i.e., 4,800 to 5,000 m (KuramBio I, AGT Station 3-10); 6,200 to 6,400 m (KuramBio II, AGT Station 89-1); 6,400 to 6,600 m (KuramBio II, AGT Station 98-1); 8,000 to 8,200 m (KuramBio II, AGT Station 20-1); 8,200 to 8,400 m (KuramBio II, EBS Station 89-1 and AGT Station 90-1). Two other richness peaks are related to previous studies, which only studied samples from 5100 and 5,200 m depth and recorded 13 species from this depth range (Schornikov 1975, 1976, 1980, 1981; Chavtur 1981). This confirms previous statements that the EBS is an important gear to study the ostracod biodiversity in the deep sea, where the abundances are usually very low, e.g. from 0. 0003 to 0. 54 specimens/m^2 in the Southern Ocean (Brandão 2010: 577).

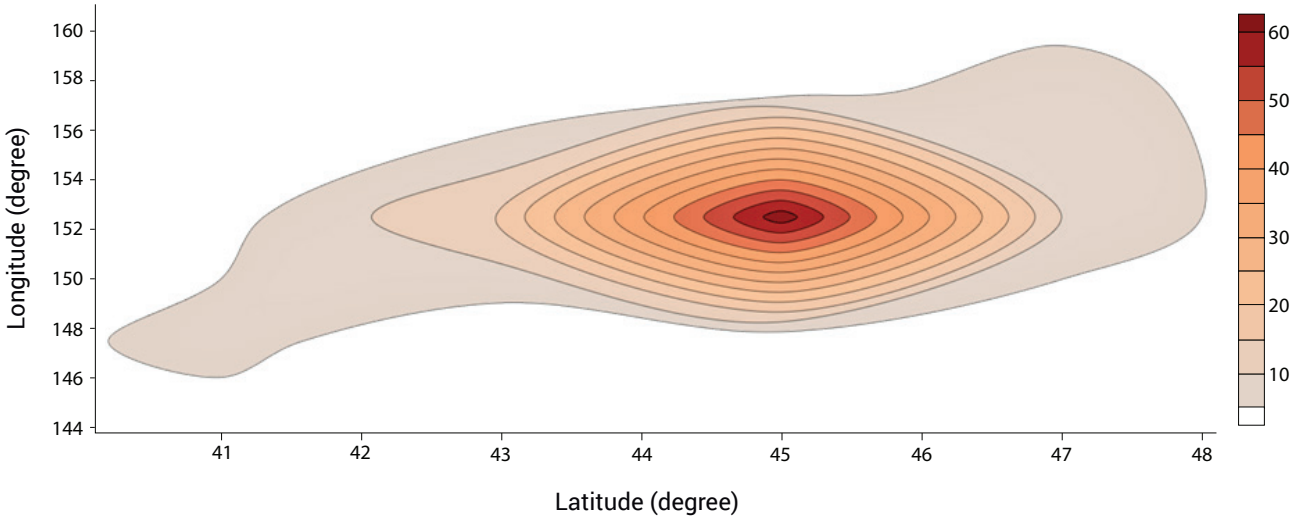


Figure 14. Records of ostracods from the Northwest Pacific. Each record is a report of one species in one sample (i.e.unique combination of latitude, longitude and depth). For example, ten species in one sample yield 10 records in the same location. The highest numbers of ostracods studied so far were collected from latitude 44° to 45°N and longitude 152° to 154°E.

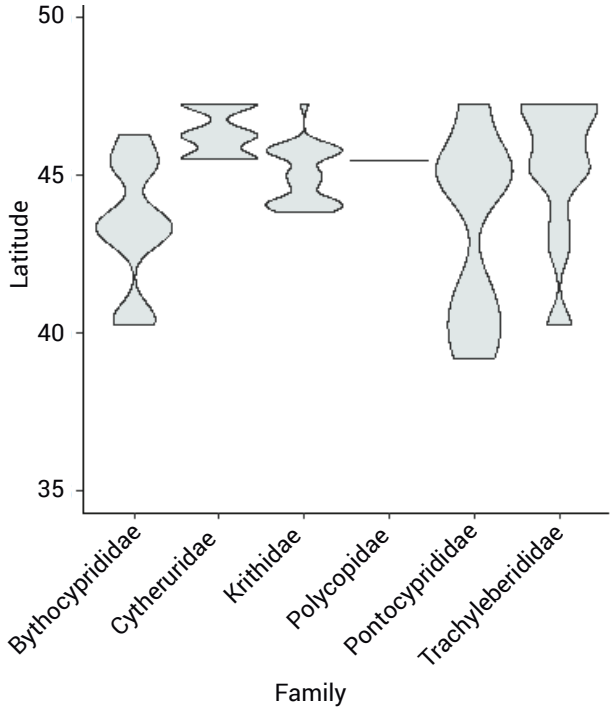


Figure 15. Violin plot representing the latitudinal distribution density-range of ostracod species for each family. Only families with more than one record were plotted here. Species of Cytheruridae, Krithidae, and Polycopidae had the narrowest distribution ranges.

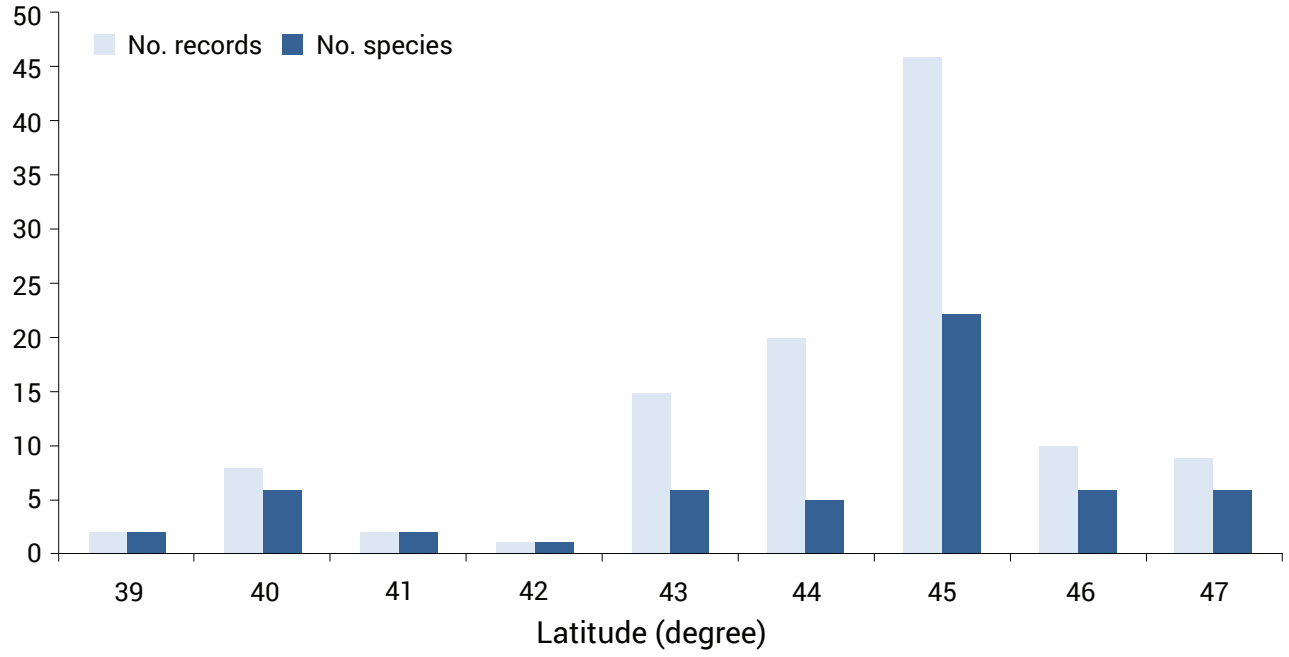


Figure 16. Sampling effort (number of records) and gamma species richness (total number of species richness) against 1° latitudinal bands. The highest sampling effort and species richness was in latitude 45°N.

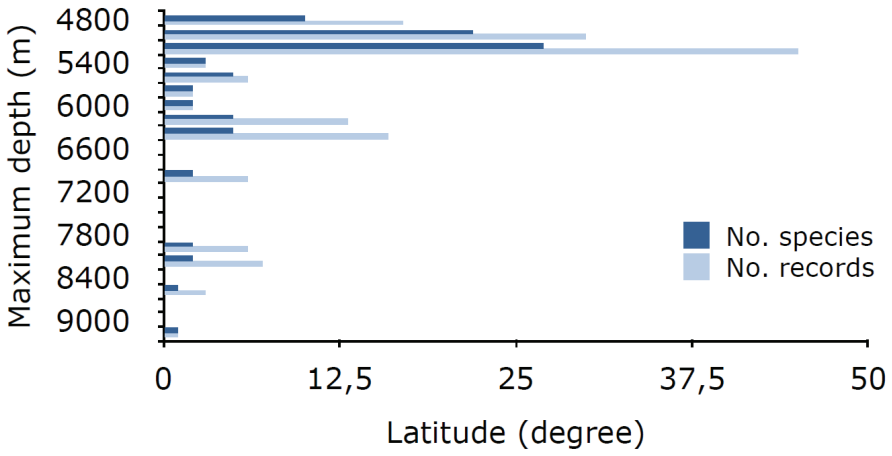


Figure 17. Sampling effort (number of records) and gamma species richness (total number of species) against 200 m depth intervals. The highest sampling effort and species richness was in depth from 5,200 to 5,400 m.

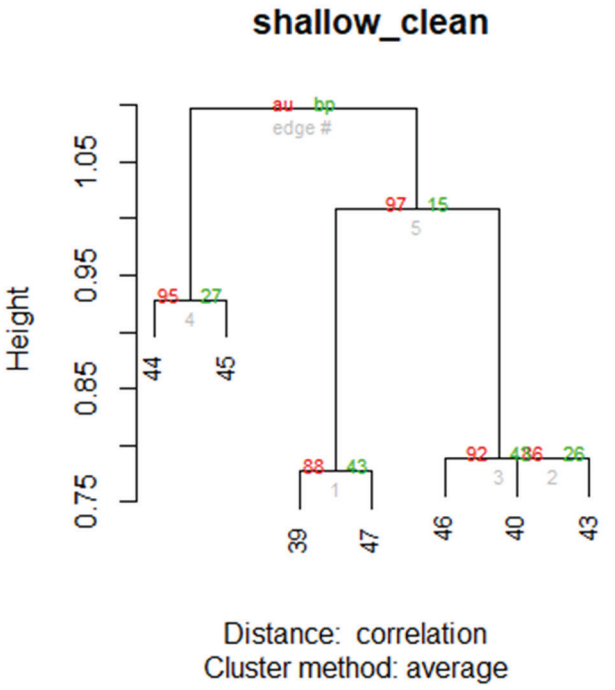


Figure 18. Cluster dendrogram of ostracod species in 1° latitudinal bands of the study area in the NW Pacific (i.e., 40°–60°N, 120°– 80°E). The numbers above each edge show the probability of nodes below that edge occurring as a cluster in resampled trees, via ordinary bootstrap resampling (BP, blue) or multiscale bootstrap resampling (AU, red). This shows that there is three significantly distinct geographic regions of ostracod distribution in our sampling area.

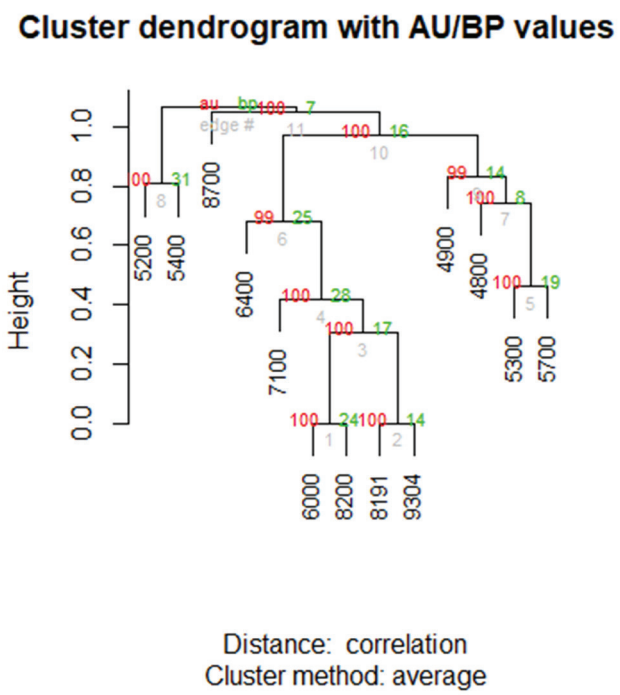


Figure 19. Cluster dendrogram of ostracod species in 100 m depth bands of the study area in the NW Pacific (i.e., 40° – 60°N, 120° – 180°E, 4,800–9,300 m depth). The numbers above each edge show the probability of nodes below that edge occurring as a cluster in resampled trees, via ordinary bootstrap resampling (BP, blue) or multiscale bootstrap resampling (AU, red).

Statistically distinct bathyal, abyssal and hadal faunas, similar to ostracods in the KKT region (see two significant clusters in Figure 19), have been widely recorded for several taxa in diverse oceanic regions, e.g. bacteria in the Mariana Trench (Liu et al. 2018: Figure 1), bait-attending fauna (mostly Chordata, Crustacea and Ophiurida) of the Kermadec Trench, SW Pacific (Jamieson et al. 2011), several macrofaunal groups in the KKT region (Brandt et al. 2019a) and in the Southern Ocean (Kaiser et al. 2011).

Some species recorded in the present study are known to have broad geographical distribution and offer insights on the biogeography of the deep NW Pacific. *Cytheropteron pherozigzag* is known from the North Atlantic, South Pacific, North Pacific Oceans (see Yasuhara et al. 2019). *Cytheropteron higashikawai* is known from the Pacific and Arctic oceans and from the Nordic seas (Atlantic-Arctic boundary) (Yasuhara et al. 2014a, 2019; Jöst et al. 2018). *Henryhowella sol* is known from the Southern Ocean, South and North Pacific (see Yasuhara et al. 2019). *Croninocythereis cronini*, which is possibly related to *Croninocythereis* sp. recorded herein, is known from the North Atlantic, Southern Ocean, and North Pacific (see Yasuhara et al. 2019). *Cytheropteron pherozigzag*, *Cytheropteron higashikawai* and *Croninocythereis cronini* are known from the Atlantic (including Nordic seas) and Pacific Oceans. There are four possible deep-water pathways connecting the Atlantic and Pacific Oceans (see Yasuhara et al. 2019). Firstly, the Drake Passage (Southern Ocean), established by 30 Ma (Lawver and Gahagan 2003; Livermore et al. 2005; Scher and Martin 2006). Secondly the Tethys Seaway, which had closed by 19–14 Ma (Harzhauser et al. 2002, 2007; Renema et al. 2008). Thirdly, the Central American Seaway, which had closed by 10 Ma regarding deep-water connection, and completely closed by 3 Ma (Schmidt 2007; O'Dea et al. 2016; Schmidt et al. 2016; Jaramillo 2018). And finally the Arctic Ocean Seaway via the Bering Strait, which opened about 4.8–7.4 Ma (Marincovich and Gladenkov 2001; Hu et al. 2015), and via the Fram Strait, which opened between 10 and 20 Ma (Engen et al. 2008; Ehlers and Jokat 2013). The Drake Passage is likely the major pathway (e.g. Yasuhara et al. 2019), and *Croninocythereis cronini* might have migrated from the Pacific Ocean to the Atlantic Ocean through the Southern Ocean (see Yasuhara et al. 2019). Yasuhara et al. (2019) argued that the Arctic was also an important pathway for some deep-sea species (e.g. *Cytheropteron pherozigzag*, *Cytheropteron higashikawai*) before the mid-Pleistocene. Although the Bering Strait is shallow, its cold temperatures might have allowed migration of deep-sea organisms (see Yasuhara et al. 2019 for detailed discussion). High polycopid diversity recoded in this study may also reflect an affinity to Arctic fauna that is known for high polycopid diversity (Yasuhara et al. 2014a; Gemery et al. 2017). Even if some of the nominal species we identify here are actually broader than biological species (e.g. species with cf.), in the case that the species studied herein and the previously described ones (e.g. *Croninocythereis* sp. and *C. cronini*) form a monophyletic group, they would still be useful for tracking biogeographical connections and dispersal events between oceanic basins.

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CHAPTER 17

DECAPODA

A REVIEW ON DEEP-WATER DECAPOD CRUSTACEANS (DEEPER THAN 2,000 m) IN THE NW PACIFIC

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1. Introduction

The lower bathyal and abyssal fauna decapods (Crustacea: Decapoda) of the NW Pacific (NW Pacific) is currently known from only a few studies. Several scientific cruises, using deep-water trawling, were accomplished in the area, which have allowed several researchers to fully describe the decapod fauna (e.g. Brazhnikov 1907; Derjugin & Kobjakova 1935; Makarov 1938, 1962, 1966; Kobjakova 1936, 1937, 1955, 1958, 1962; Vinogradov 1947, 1950; Ushakov 1953; Zarenkov 1960; Kurata 1964a, b; Birštein & Vinogradov 1951, 1953; Savilov 1961; Komai & Amaoka 1989; Komai 1991, 1994, 1997, 2015; Komai & Yakovlev 2000; Kim et al. 2000; Sedova 2004; Komai & Komatsu 2009; Sedova & Andronov 2013; Sedova & Grigoriev 2013; Matsuzaki et al. 2015; Komai & Matsuzaki 2016; Komai et al. 2016; Marin 2013, 2018). Nevertheless, many new deep-water records and species have been described more recently (e.g., Marin 2018), and it seems that the real biological diversity of the area is far from being completely studied. The present paper provides an overview of all available records of decapod crustaceans, living deeper than 2,000 m in the area between 40–60°N and 120–180°E in the NW Pacific. Presently, numerous species are recorded from the bathyal depth from collected specimens, but they need to be carefully and completely studied, as deep-sea decapod crustaceans represent an important macrofaunal component of all deep-water bottom communities, occupying rather unique niches in deep-sea ecosystems.

2. Objectives

The main objective of the review is to provide new data and insights on the geographical and bathymetric distribution and diversity of deep-sea decapod crustaceans in the NW Pacific Ocean, found in this publication and in previously published data.

3. Material and Methods

This review is based upon published data, with several new records obtained during the megafaunal sampling of the joint Russian–German deep-sea KuramBio 2015 (Kuril-Kamchatka Biodiversity Study) Expedition to the Kuril-Kamchatka Trench and abyssal plain on board of the RV *Sonne* and the German-Russian SokhoBio 2015 (Sea of Okhotsk Biodiversity Study) Expedition on the RV "*Akademik M.A. Lavrentyev*" in the Sea of Okhotsk.

4. Results

4.1. The list of decapod species found deeper than 2,000 meters in the NW Pacific.

Suborder Dendrobranchiata Spence Bate, 1888

Family Aristeidae Wood-Mason in Wood-Mason & Alcock, 1891

***Cerataspis monstrosus* Gray, 1828**

(Figure 1)

Cosmopolitan species, probably, distributed globally. Several specimens were collected off the central Kuril Islands, at the depths of 4,859–5,146 m (KuramBio 2013, stn. 3-10 (1♂) and stn. 12-5 (1♀)).

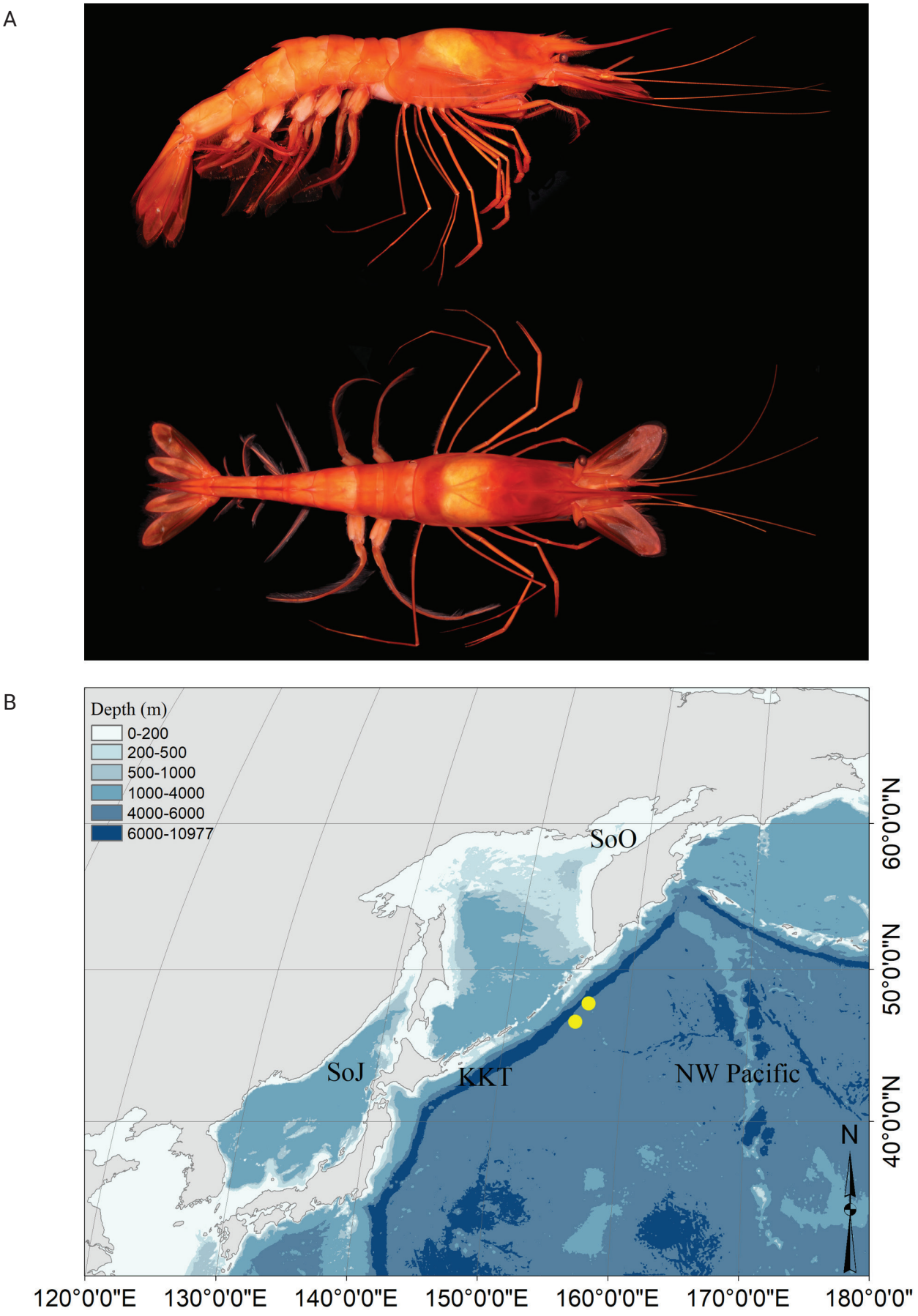


Figure 1. (A) Alive coloration of *Cerataspis monstrosus* Gray, 1828 and (B) its distribution in the NW Pacific.

***Hemipenaeus spinidorsalis* Spence Bate, 1881**
(Figure 2)
This species is known from off the Kuril Islands, based on several collected specimens collected during SochoBio 2015 (see Marin 2018) and KuramBio 2013 expeditions (stn. 5–12 (1 spec, 2♀, 1 male); stn. 7–11 (1♂, 1♀)), at the depths of 4,553–5,146 m. Cosmopolitan species, probably, distributed globally.

***Hepomadus gracialis* Spence Bate, 1881**
(Figure 3)
This species was originally described from the samples collected as *Challenger* stn. 237, near Yokohama, 34°37'N 140°32'E, at a depth of 3,429 m (1875 fms) (Bate 1888). Known along the Pacific coast of Japan, at the depths of 1,500–3,500 m (see Komai & Komatsu 2016).

Family Benthesicymidae Wood-Mason in Wood-Mason & Alcock, 1891

***Benthesicymus crenatus* Spence Bate, 1881**
(Figure 4)
This species has been recorded from off Kuril Islands (KuramBio 2013 expedition, stn. 10-11 – 1♀, 1 damaged spcm.), and off southwestern Honshu to central Pacific, at the depths of 3,530–6,350 m (Pérez-Farfante & Kensley 1997; Kikuchi & Nemoto 1991; Kim et al. 2000).

***Bentheogennema borealis* (Rathbun, 1902)**
(Figure 5)
Common meso- and bathypelagic species, widely distributed in the NW Pacific, at the depths of 200–2,500 m (Butler 1980; Aizawa 1974; Hayashi 1984, 1992; Komai et al. 1999; Kobjakova 1937; Komai 1991; Komai & Komatsu 2009; Marin 2018).

Family Sergestidae Dana, 1852

***Sergia japonica* (Bate, 1881)**
(Figure 6)
This species is recorded from Miyagi Prefecture of Honshu, Japan, at the depths of 2,043–2,183 m (Komai & Komatsu 2009) as well as off south-western coast, Suruga Bay and Ryukyu Islands (Bate 1888; Hayashi 1986a, 1992; Komai et al. 1999). It is suggested that this meso- and bathypelagic species is widely distributed in the tropics (after Komai & Komatsu 2009).

***Sergia prehensilis* (Bate, 1881)**
(Figure 7)
This species is recorded from Miyagi Prefecture of Honsu, Japan, at the depths of 2,968–4,128 m (Komai & Komatsu, 2009). Meso- and bathypelagic species, widely distributed in Indo–West Pacific, from South Africa to Japan; (Vereshchaka 2000).

Infraorder Axiidea

Family Axiidae Huxley, 1879

***Calocarides okhotskensis* Sakai, 2011**
(Figure 8)
This species is presently known from the deepest south-eastern part (the Derjugina Basin and bathyal slopes of the Kuril Basin) of the Sea of Okhotsk, at depths of 1,150–2,200 m (Kobjakova 1937 (as *Calastacus quinqueseriatus*); Marin 2018). The specimens, possibly of the same species, are reported from the Bering Sea by Birštein & Vinogradov (1953).

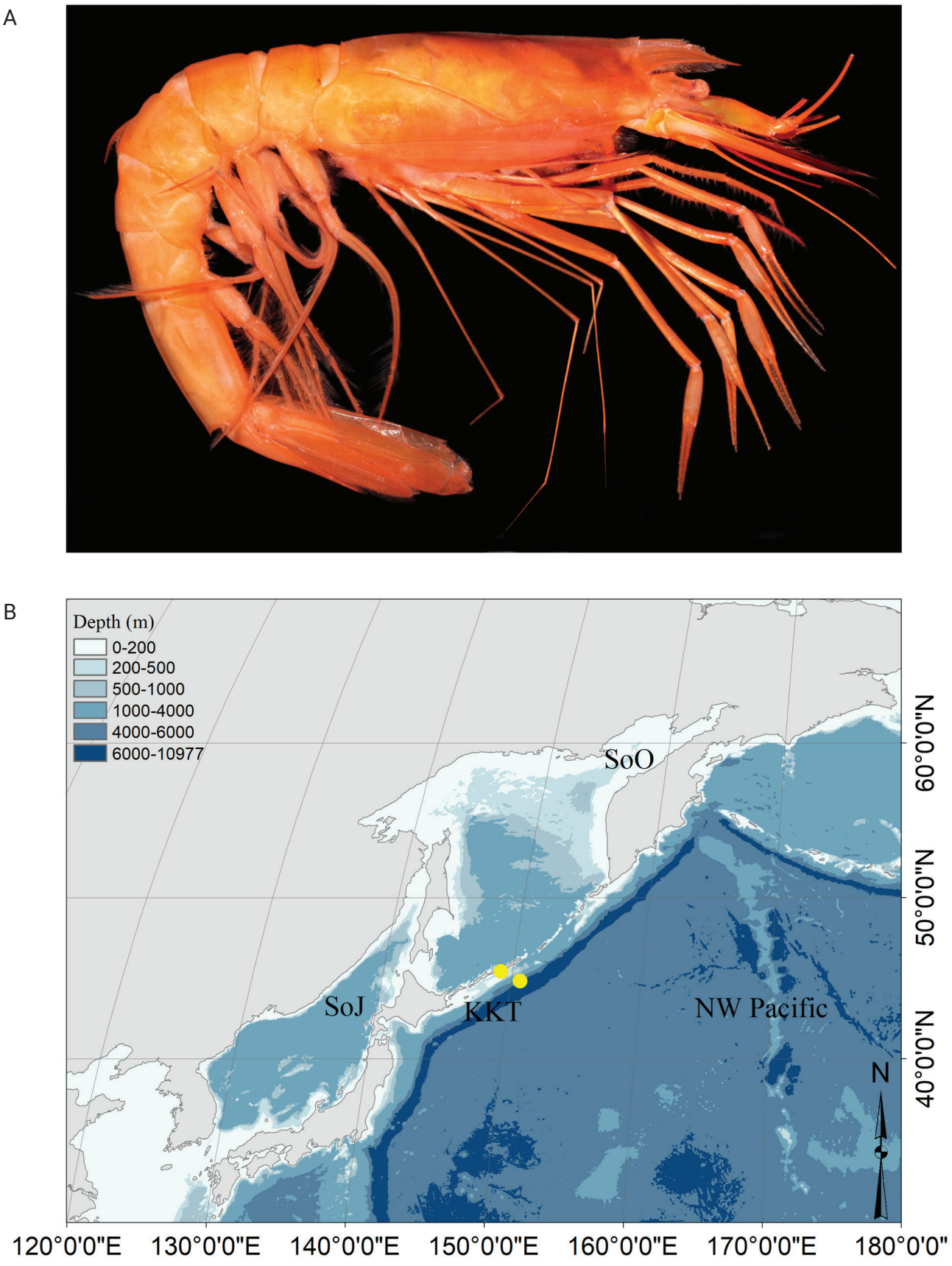


Figure 2. (A) Alive coloration of *Hemipenaeus spinidorsalis* Spence Bate, 1881 and (B) its distribution in the NW Pacific.

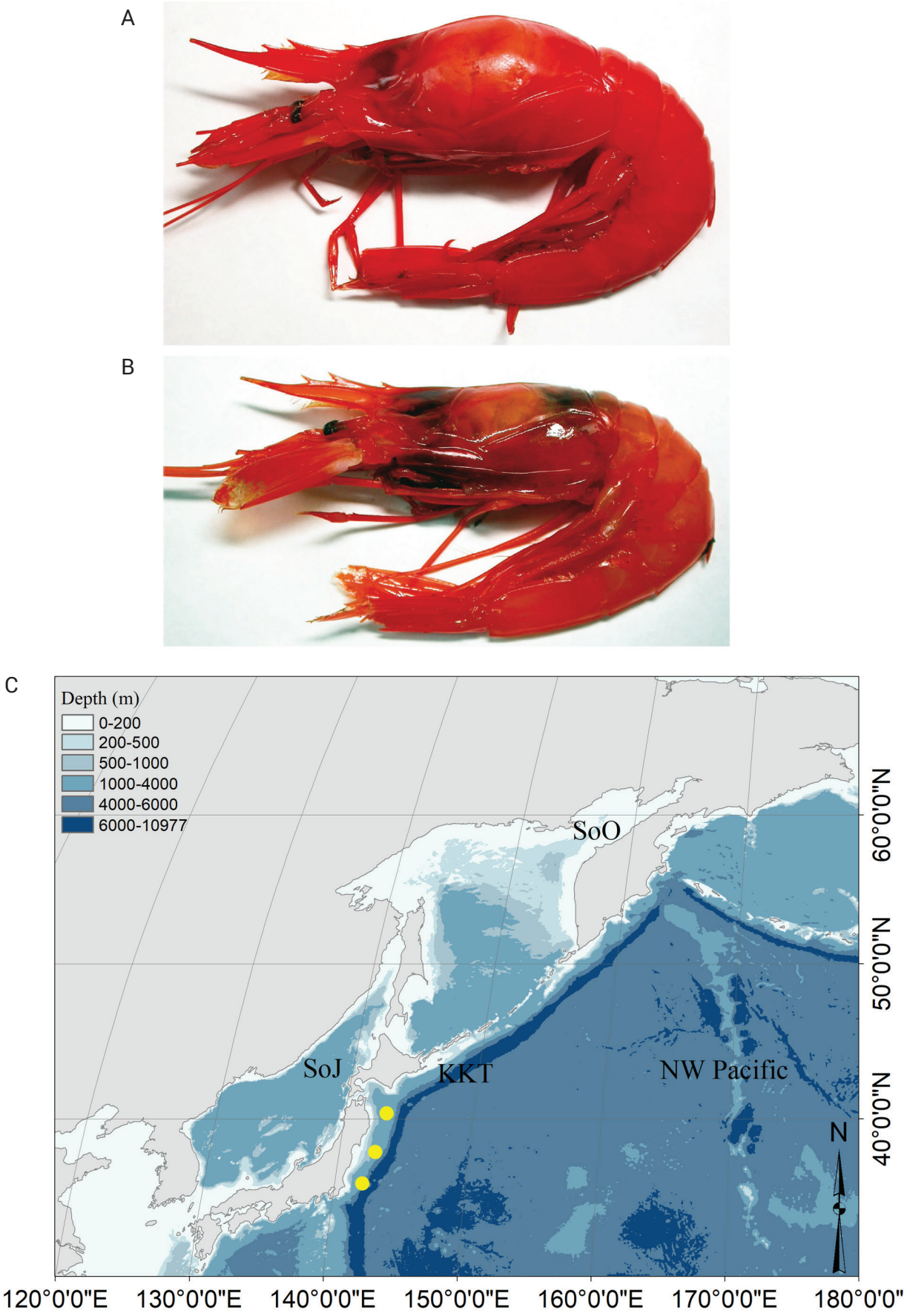


Figure 3. (A, B) Alive coloration of *Hepomadus gracialis* Spence Bate, 188 (photo credit – Komai & Komatsu, 2016) and (C) its distribution in the NW Pacific.

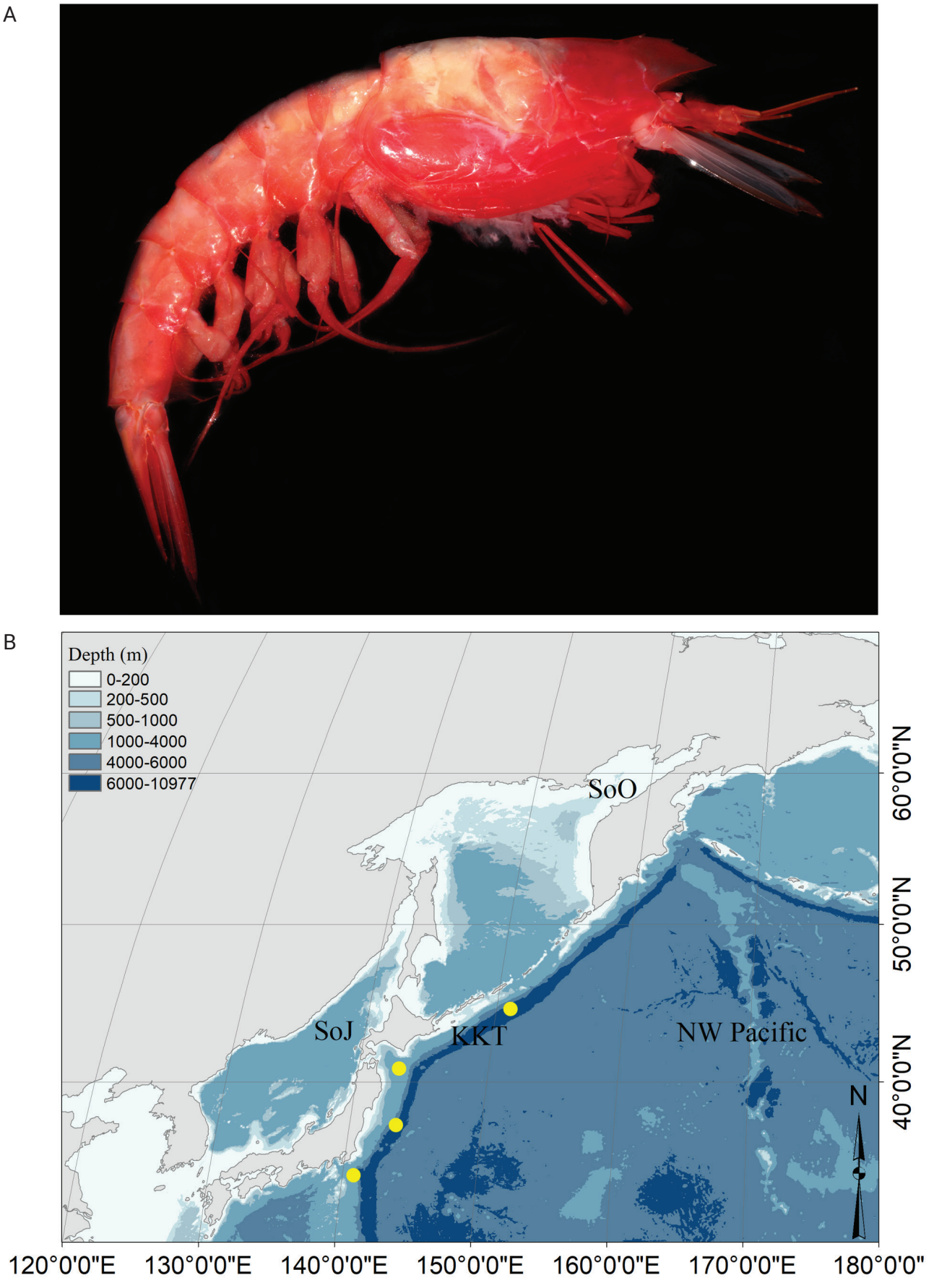


Figure 4. (A) Alive coloration of *Benthesicymus crenatus* Spence Bate, 1881 and its (B)distribution in the NW Pacific.

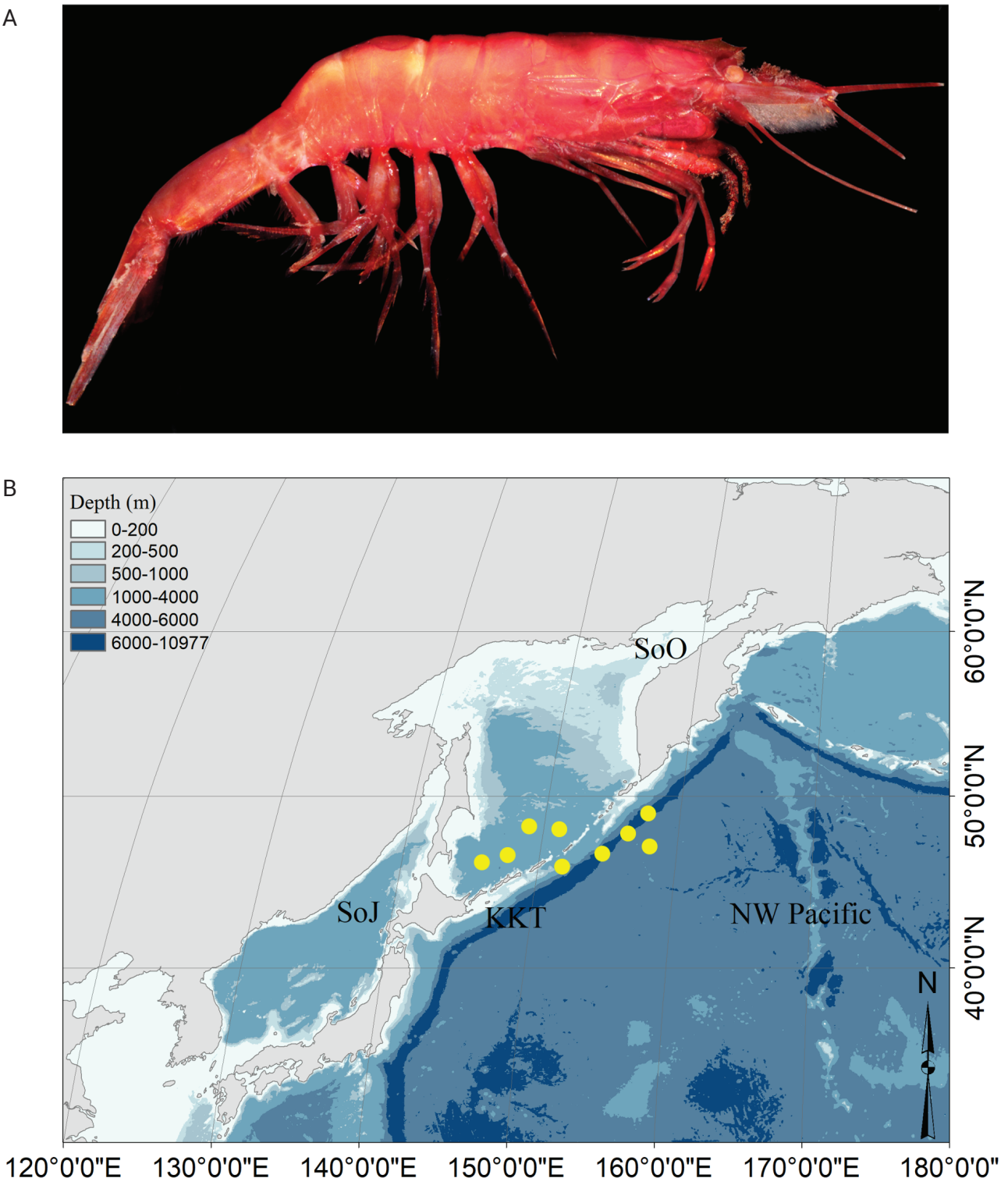


Figure 5. (A) Alive coloration of *Bentheogennema borealis* (Rathbun, 1902) and (B) its distribution in the NW Pacific. Actually, the species is widely distributed bathypelagic species and present map indicate the records from the joint Russian–German KuramBio 2012 and SochoBio 2015 expeditions.

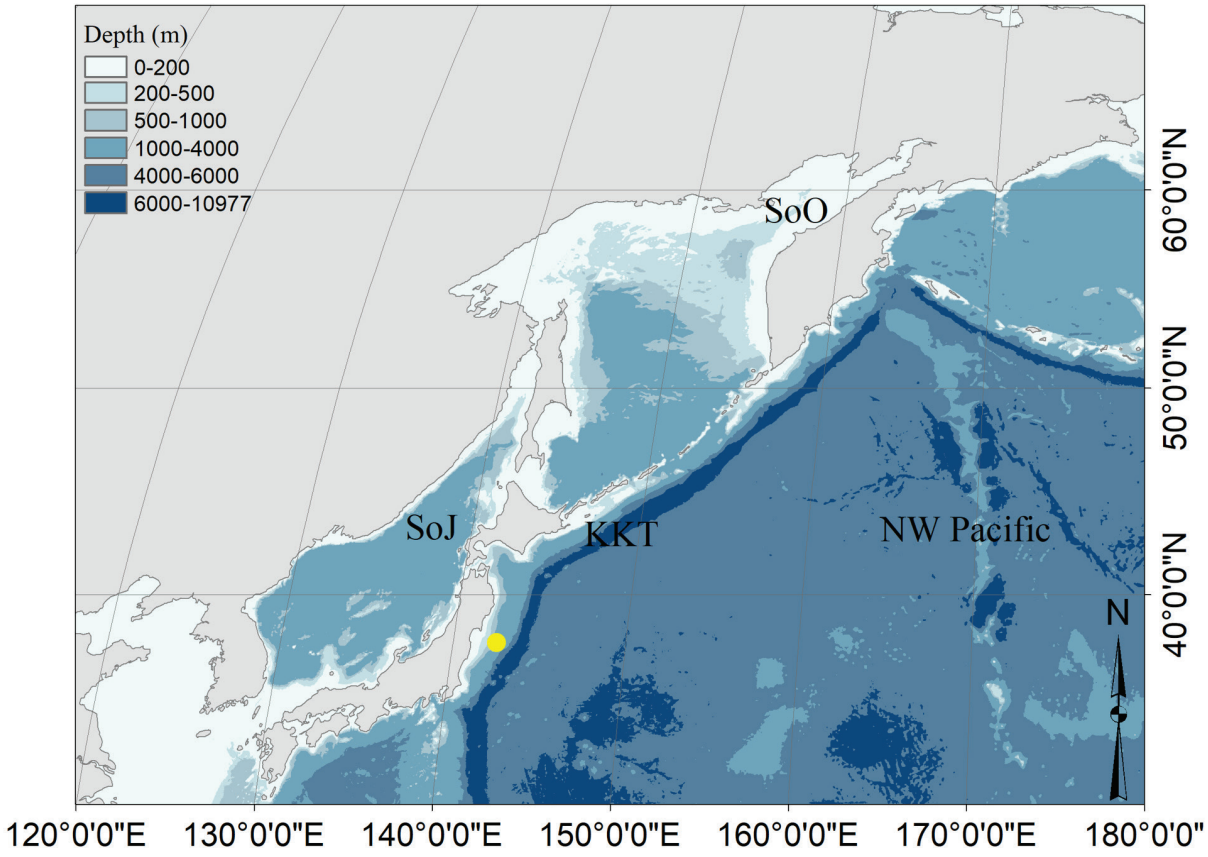


Figure 6. Distribution of *Sergia japonica* (Bate, 1881) in the NW Pacific.

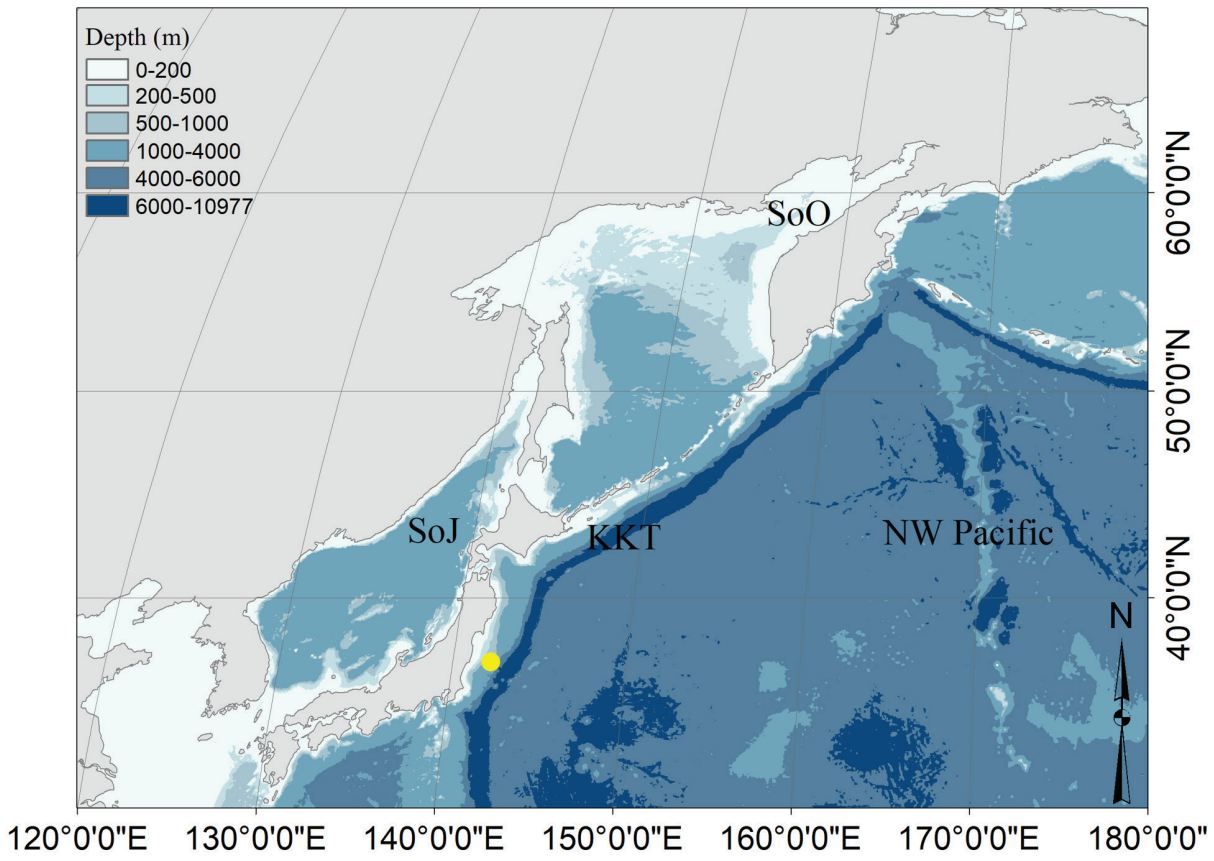


Figure 7. Distribution of *Sergia prehensilis* (Bate, 1881) in the NW Pacific.

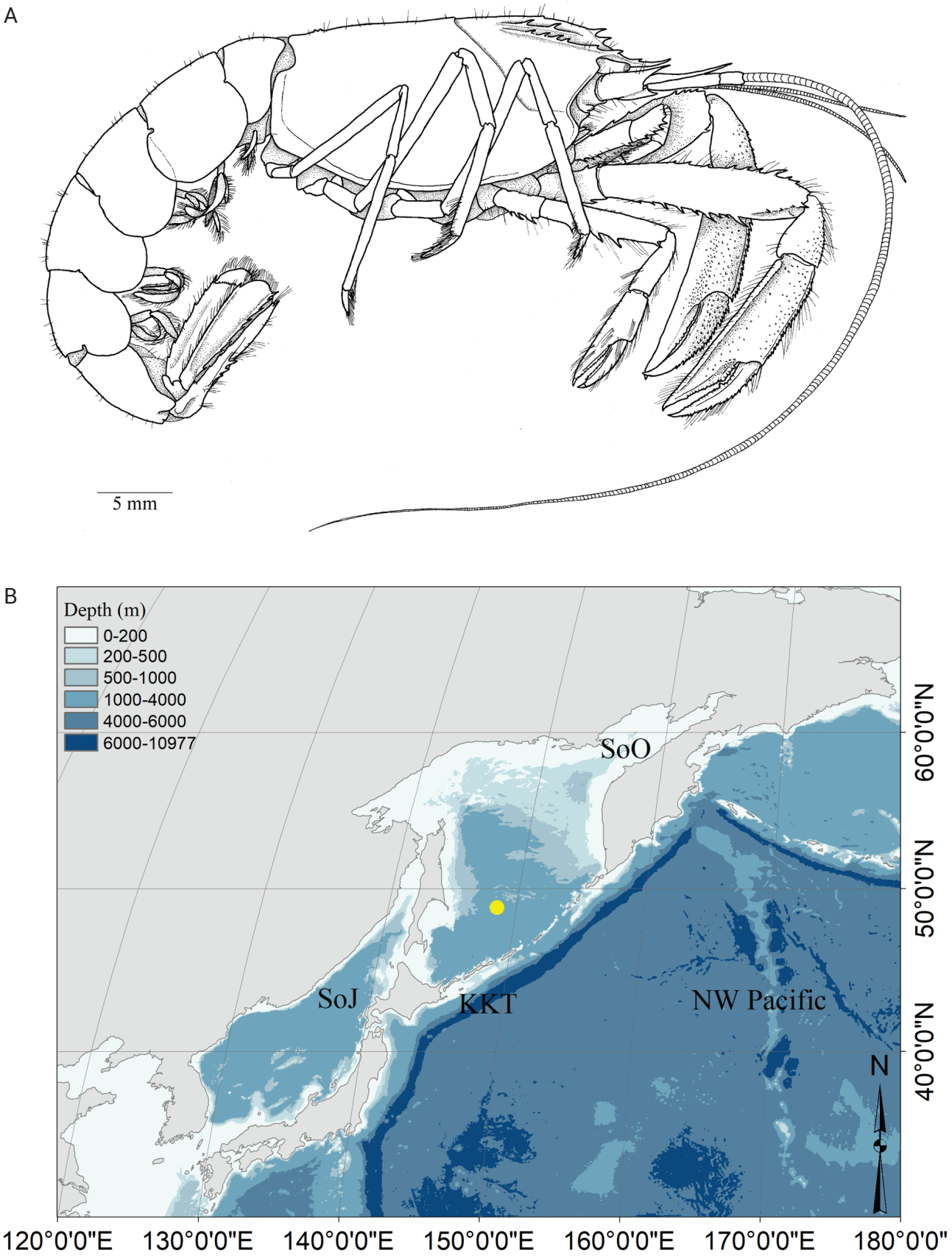


Figure 8. (A) General view of *Calocarides okhotskensis* Sakai, 2011 and (B) its distribution in the NW Pacific.

Suborder Pleocyemata Burkenroad, 1963
Infraorder Anomura

Family Parapaguridae Smith, 1882

***Parapagurus benedicti* de Saint Laurent, 1972**
(Figure 9)
Asakura (2006) recorded this species off Sanriku coast, northeastern Honshu, at a depth of 2,350 m. The species is widespread in the North Pacific, from northern Japan to Baja California, at the depths of 757–2,400 m (Birštein & Vinogradov, 1951 (as *P. pilosimanus*); Lemaitre 1999; Asakura 2006; Komatsu & Komai 2009).

Family Lithodoidea Samouelle, 1819

***Paralomis verrilli* (Benedict, 1895)**
(Figure 10)
Widely distributed in the northern part of the North Pacific, from Sea of Okhotsk and Komandor Islands to Kuril Islands, Pacific coast of Japan southward to Tokushima Prefecture, recorded from California, at the depths of 850–2,515 m (Sakai 1976, 1987; Komatsu & Komai 2009).

Family Munidopsidae Ortmann, 1898

***Munidopsis petalorhyncha* Baba, 2005**
(Figure 11)
This species was originally described from the Kuril–Kamchatka Trench off Urup Island (45°18'N 156°00'E), at depths of 5,060–5,130 m (type locality) (Birštein & Zarenkov 1970 (as *M. subsquamosa latimana*)), and in the Japan Trench off northern Japan (37°03.3'N 145°32.3'E to 37°03.1'N 145°31.0'E), at the depths of 5,353–5,382 m (Komai et al. 2017).

***Munidopsis beringana* Benedict, 1902**
This species is known from the Bering Sea based on samples obtained by RV "*Albatross*" (55°23′00"N 170°31′00"W) at a depth of 3,241 m (Benedict 1902), and the specimens described from the western part of the Bering Sea (without exact locality), at depths of 2,995–3,940 m (Birštein & Vinogradov 1953). The available records of the species in the Bering Sea are not in the borders of the studied area, but the species can be more widely distributed than is presently known.

***Munidopsis kurilensis* Marin, 2020**
(Figure 12)
The species is presently known from the deepest south-eastern part (the Derjugina Basin and bathyal slopes of the Kuril Basin) of the Sea of Okhotsk, at depths of 3,296–3,350 m (Marin 2018 (as *Munidopsis antonii*; Marin 2020a).

***Munidopsis* cf. *subsquamosa* Henderson, 1885**
(Figure 13)
A single specimen of the species was collected from the Kuril Basin of the Sea of Okhotsk, 48°18'08.5"N 151°48'41.0"E, at depths of 2,450–2,700 m (see Marin 2020a). Originally, this species was described by Henderson (1885, 1888) based on the specimens collected off Boso Peninsula, Japan, at the depth of 3,431 m, and is also found near the Izu Islands, Japan, at the depths of 2,670–3,960 m (Baba 1982).

Infraorder Brachyura

Family Oregoniidae Garth, 1958

***Chionoecetes angulatus* Rathbun, 1924**
(Figure 14)
This species is recorded off Kinkazan, Miyagi Prefecture of Honsu, at the depths of 2,034–

2,021 m (Takeda 1995); off Kamchatka, at the depth of 1,440–3,330 m (Birštein & Vinogradov 1953). Known from Japan, Kamchatka, Bering Sea, and British Columbia to Oregon, at depths of 90–3,330 m (Garth 1958; Sakai 1976; Komatsu & Komai 2009).

***Chionoecetes japonicus* Rathbun, 1932**
(Figure 15)
Restricted to East Asian waters: Sea of Japan southward to off Matsue, Shimane Prefecture, Pacific coast of northern Japan southward to Sagami Bay, Sea of Okhotsk; at depths of 450–2,500 m (Vinogradov 1950; Sakai 1976; Takeda & Miyauchi 1992; Ikeda 1998) (after Komatsu & Komai 2009).

Infraorder Caridea

Family Crangonidae Haworth, 1825

***Sclerocrangon zenkevitchi* Birštein & Vinogradov, 1953**
(Figure 16)
This species is known from the Kuril Basin of the Sea of Okhotsk, off northeastern Japan and the Bering Sea, at depths of 2,995–4,070 m (Birštein & Vinogradov 1953; Zarenkov 1993; Kim et al. 2000).

***Neocrangon abyssorum* (Rathbun, 1902)**
(Figure 17)
This species is known from the Bering Sea, Pacific side of Kuril Islands and northern Japan (off eastern Hokkaido to Iwate Prefecture), at depths of 887–4,000 m (Birštein & Vinogradov 1951; Birštein & Zarenkov 1970; Butler 1980; Komai 1991; Kim et al. 2000).

***Metacrangon ochotensis* (Kobjakova, 1955)**
(Figure 18)
This species is recorded in the Sea of Okhotsk, off Kunashir Island, at a depth of 2,850 m (Kobjakova 1955).

Family Glyphocrangonidae Smith, 1884

***Glyphocrangon caecescens* Wood-Mason, 1891**
(Figure 19)
This species is known from along the Pacific coasts of Japan from Miyagi Prefecture to Tosa Bay, at the depths of 2,698–2,814 m (see Komai & Komatsu 2016). Also known from the Bay of Bengal, Mid-Indian Basin, Philippines (Davao Bay, Mindanao) (see Komai & Komatsu 2016).

Family Thoridae Kingsley, 1879

***Eualus biungius* (Rathbun, 1902)**
(Figure 20)
This species is widely distributed in the North Pacific: Bering Sea to Oregon (Rathbun, 1904), Sea of Okhotsk (Kobjakova 1937) and the Sea of Japan (Yokoya 1933; Miyake & Hayashi 1967; Hayashi 1993; Tsuchida et al. 2008), at depths of 90–2,090 m (Vinogradov 1950).

***Lebbeus lamina*, Komai 2013**
(Figure 21)
This species is known from a heterosexual pair of specimens collected northeast of Miyake Island, Izu Islands, at the depths of 1,988–2,007 m (Komai 2013).

***Lebbeus sokhobio*, Marin 2020**
(Figure 22)
This species is recorded from the Kuril Basin of the Sea of Okhotsk, at depths of 3,303–3,366 m (Marin 2018; 2020b).

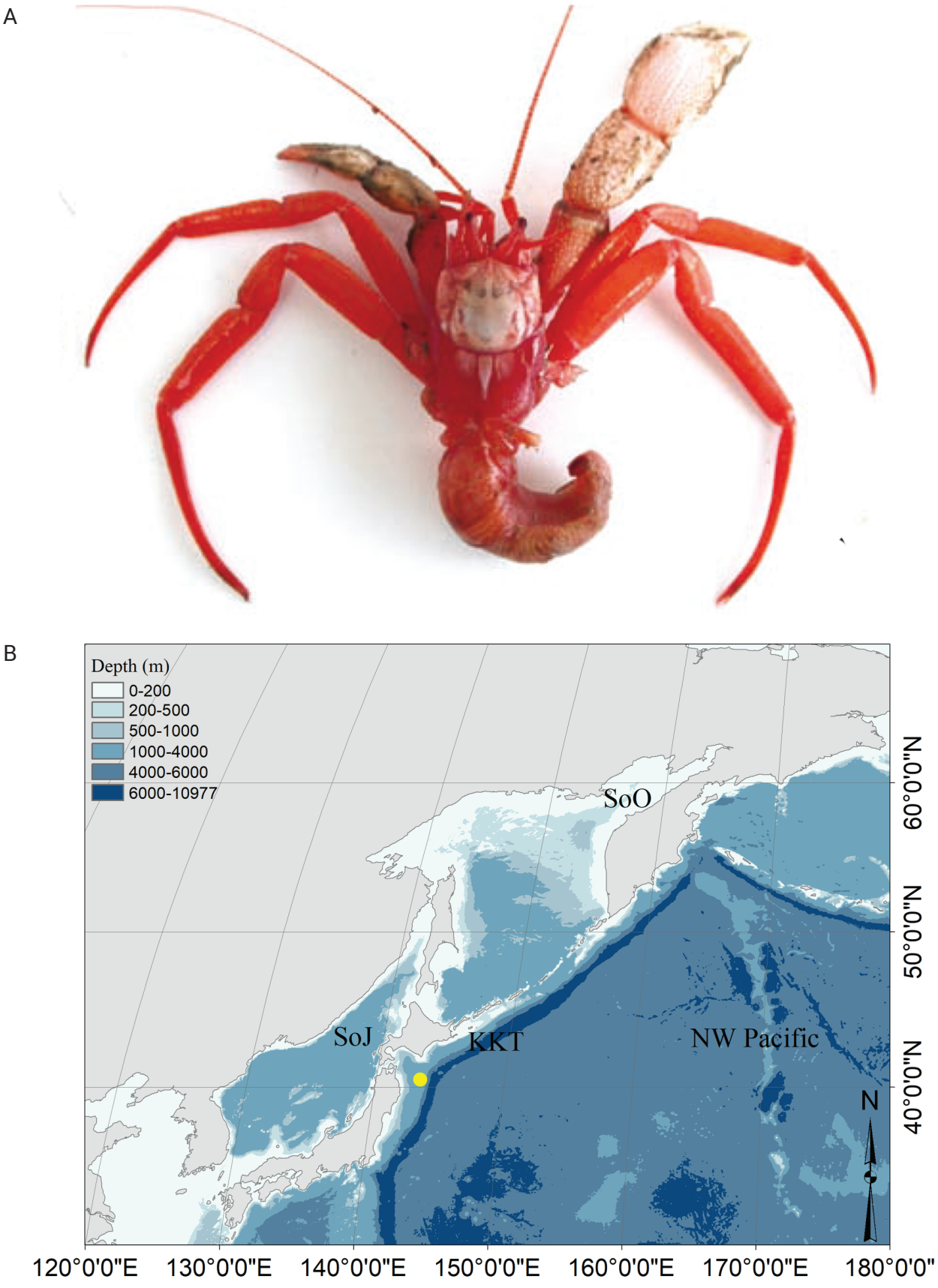
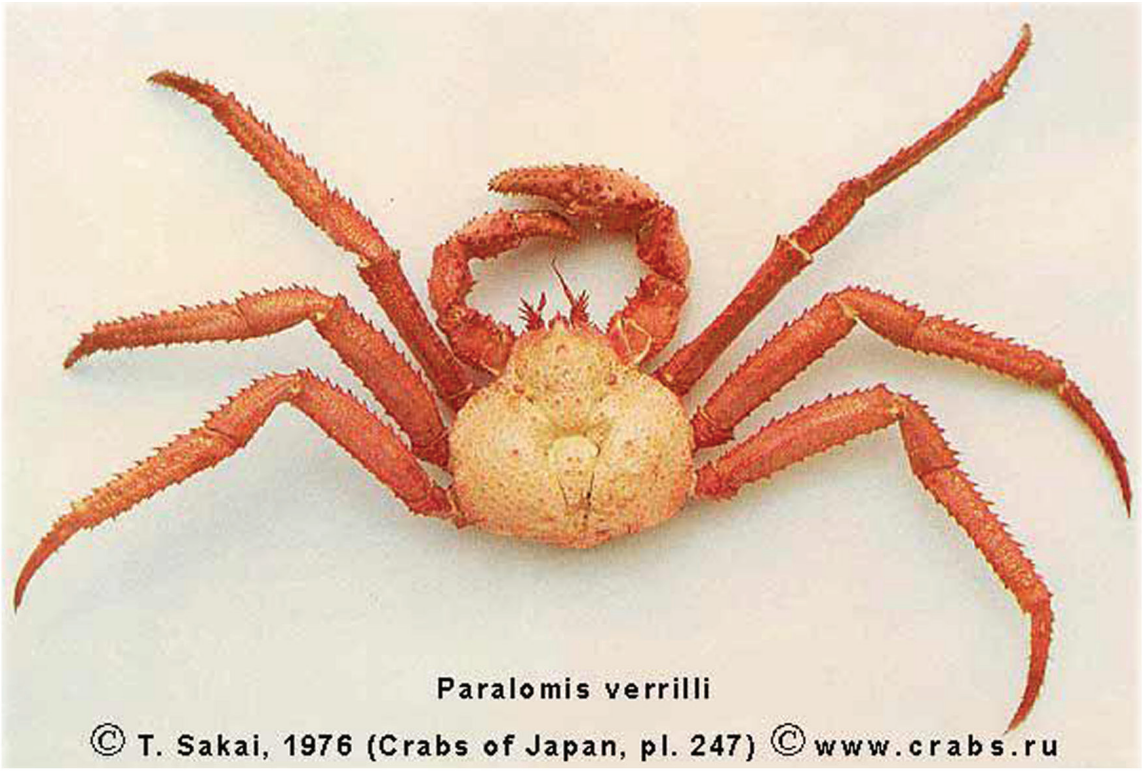


Figure 9. (A) Alive coloration of *Parapagurus benedicti* de Saint Laurent, 1972 (photo credit –Komatsu & Komai, 2009) and (B) the locality of its record deeper than 2000 m in the NW Pacific. The species in also widely distributed in shallower waters in the NE Pacific (see the text).

A



B

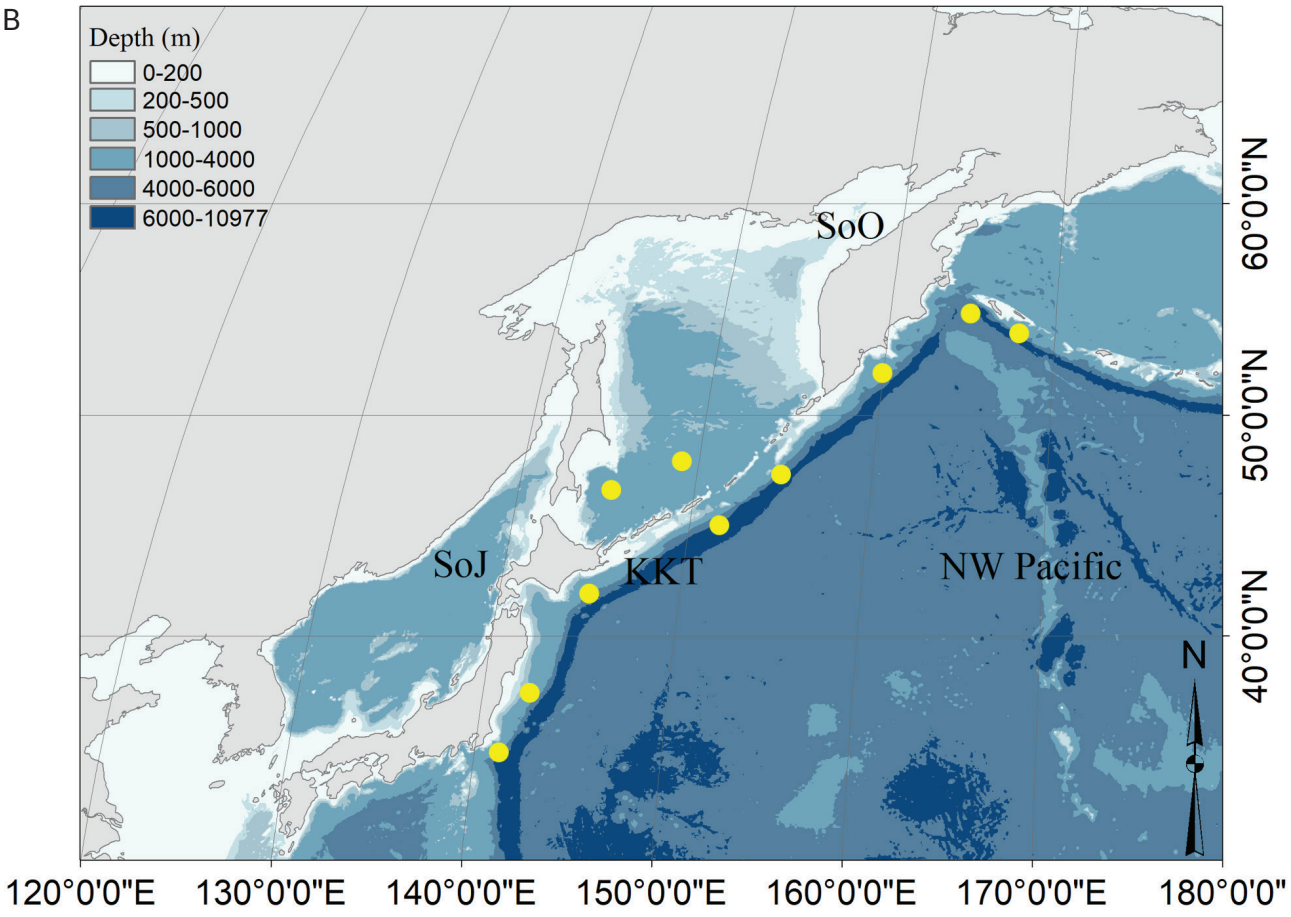


Figure 10. (A) Alive coloration of *Paralomis verrilli* (Benedict, 1895) and (B) its distribution in the NW Pacific.

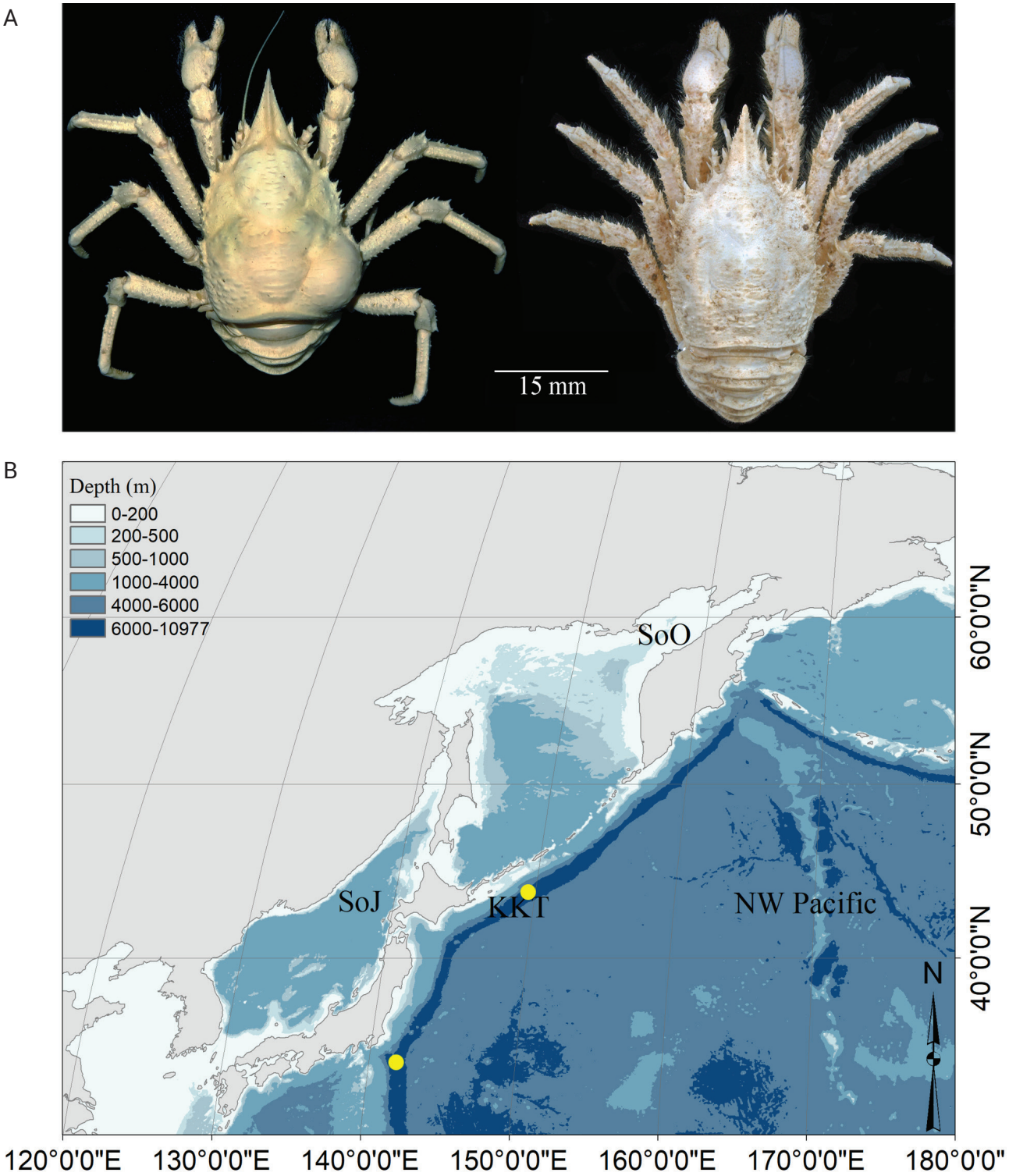


Figure 11. (A) General view of *Munidopsis petalorhyncha* Baba, 2005 (after Komai et al., 2017) and (B) its distribution in the NW Pacific.

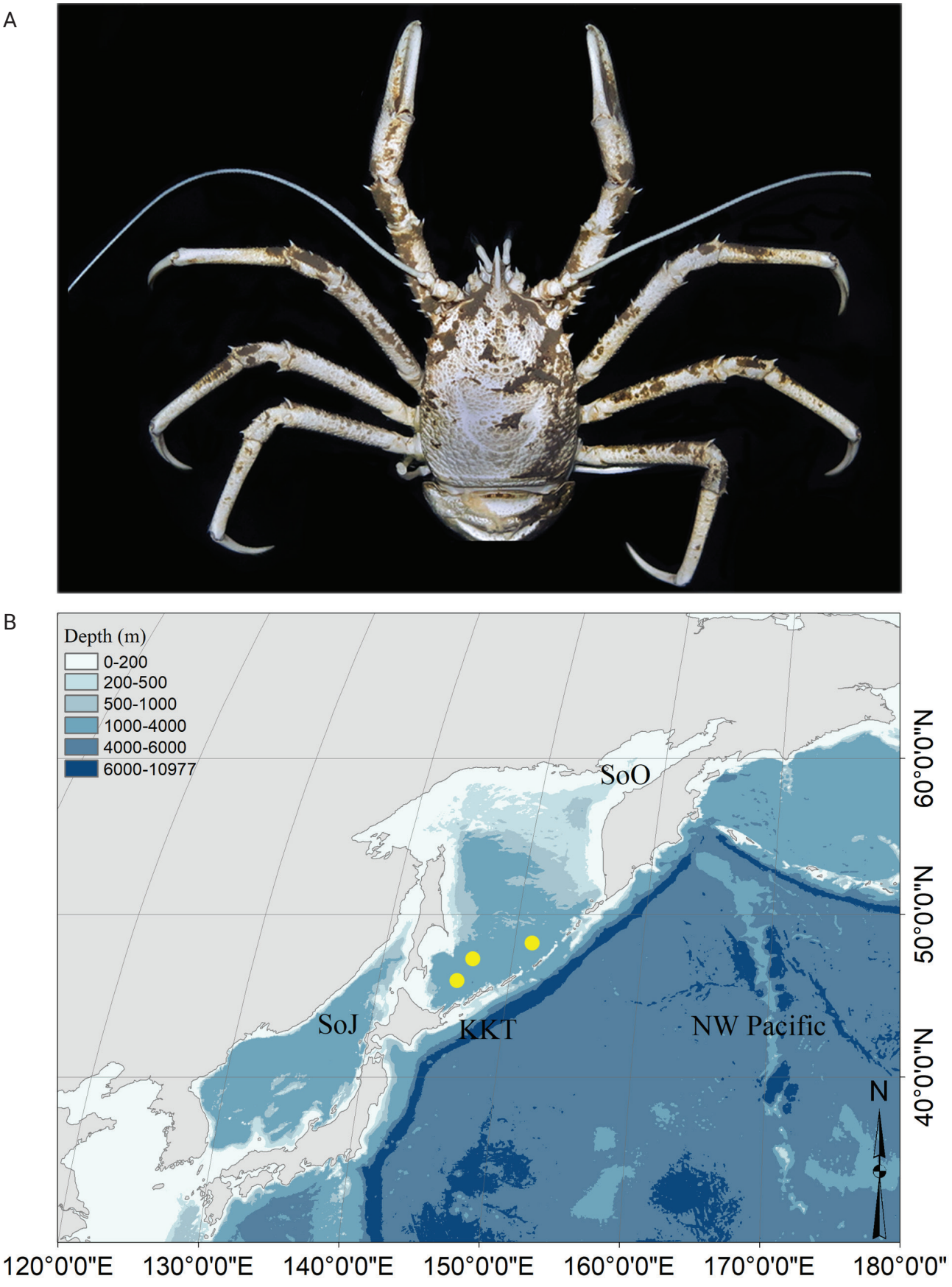


Figure 12. (A) General view of *Munidopsis kurilensis* Marin 2020 and (B) its distribution in the NW Pacific.

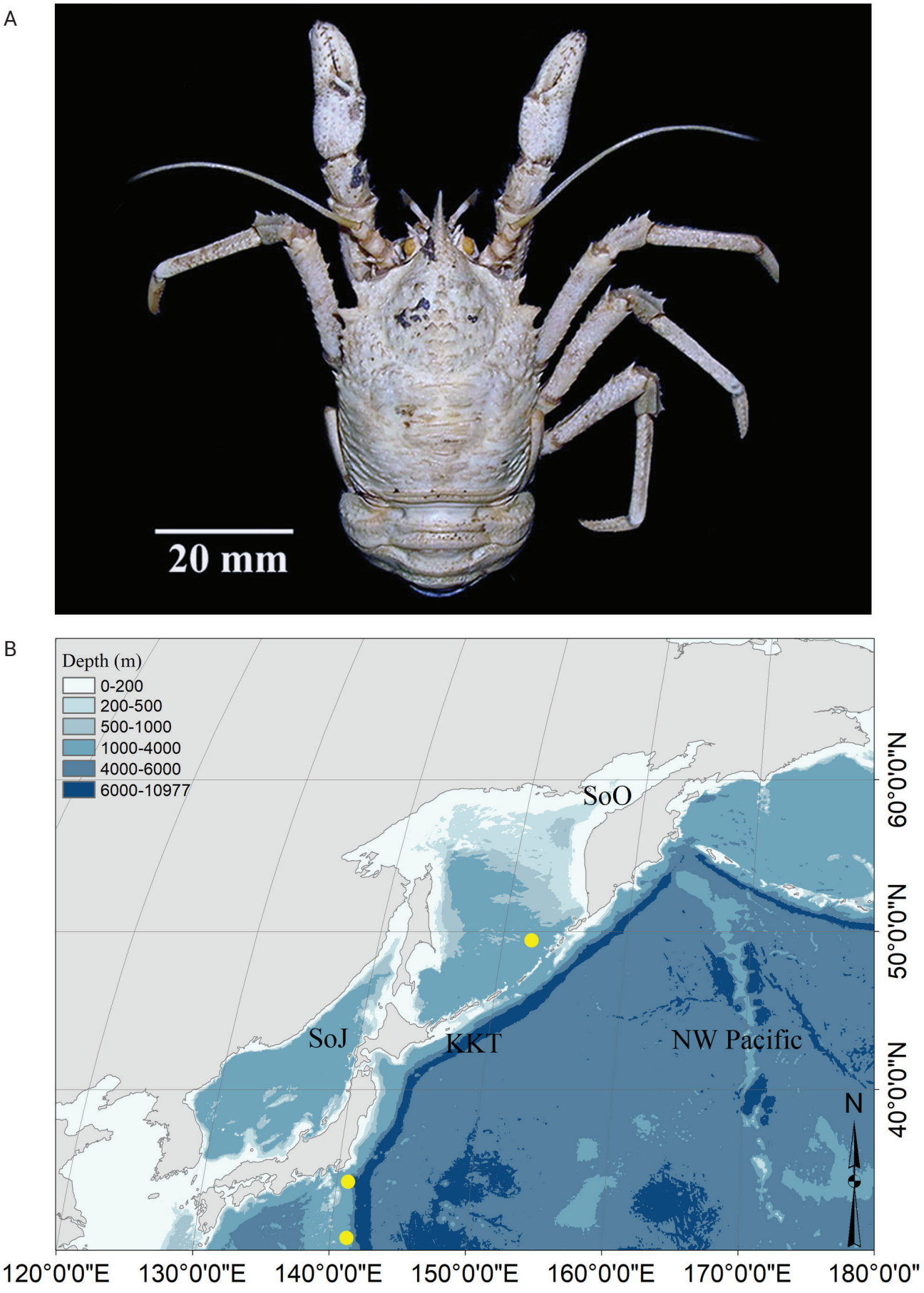


Figure 13. (A) General view of *Munidopsis* cf. *subsquamosa* Henderson, 1885 and (B) its distribution in the NW Pacific.

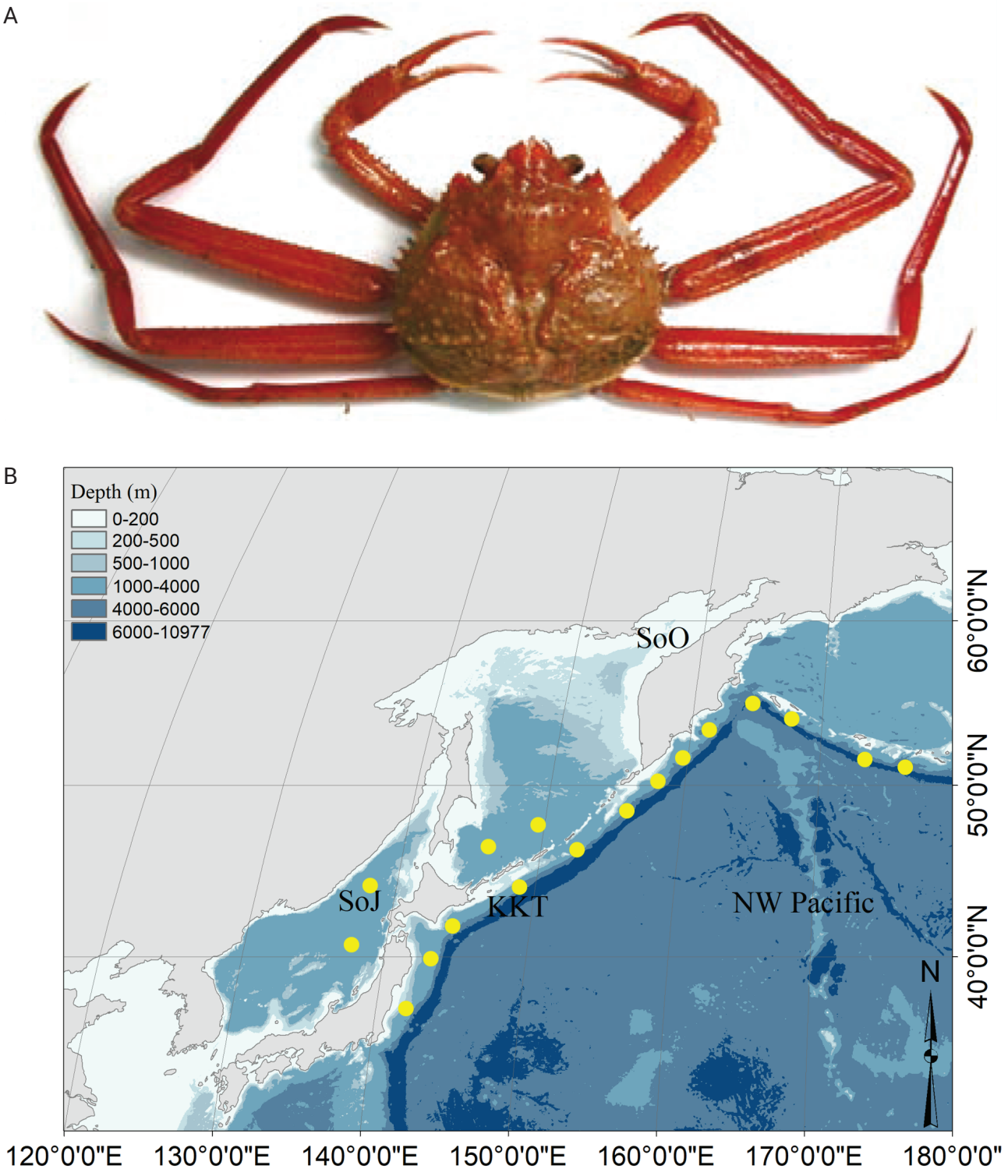


Figure 14. (A) Alive coloration of *Chionoecetes angulatus* Rathbun, 1924 (photo credit – Komatsu & Komai, 2009) and (B) its distribution in the NW Pacific.

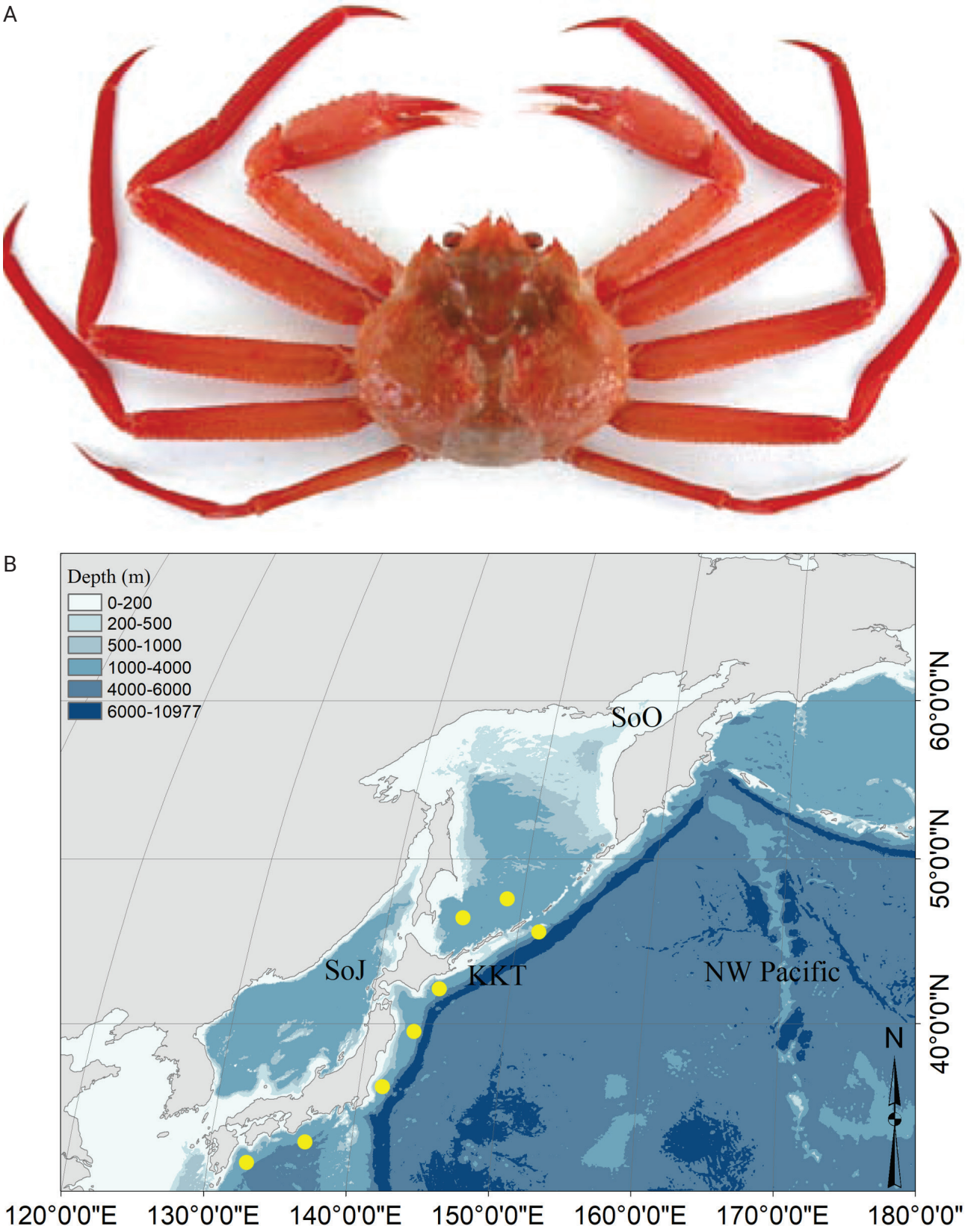


Figure 15. (A) Alive coloration of *Chionoecetes japonicus* Rathbun, 1932 (photo credit – Komatsu & Komai, 2009) and (B) its distribution in the NW Pacific.

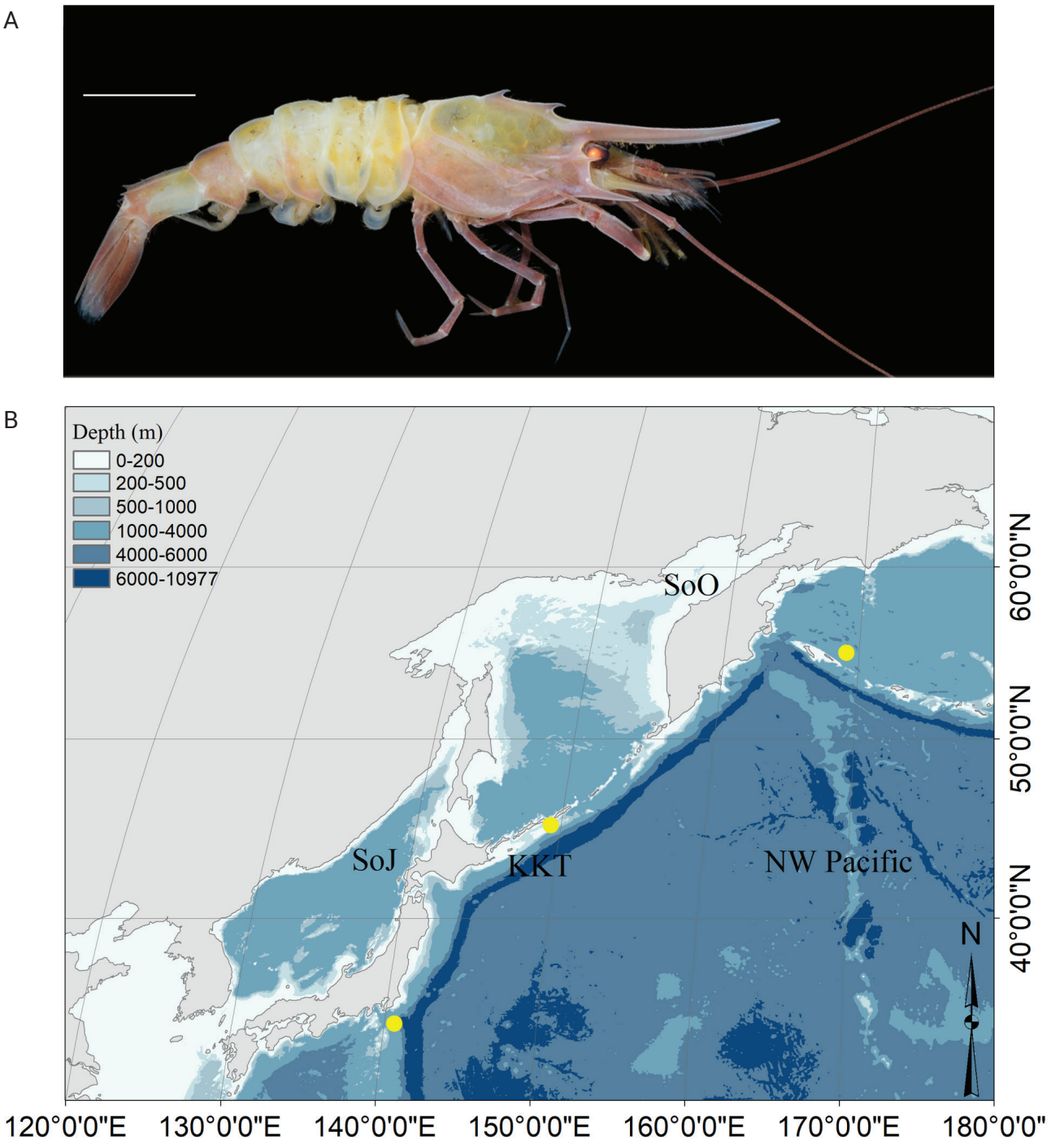


Figure 16. (A) Alive coloration of *Sclerocrangon zenkevitchi* Birštein & Vinogradov, 1953 and (B) its distribution in the NW Pacific (photo credit – Anna Lavrentjeva).

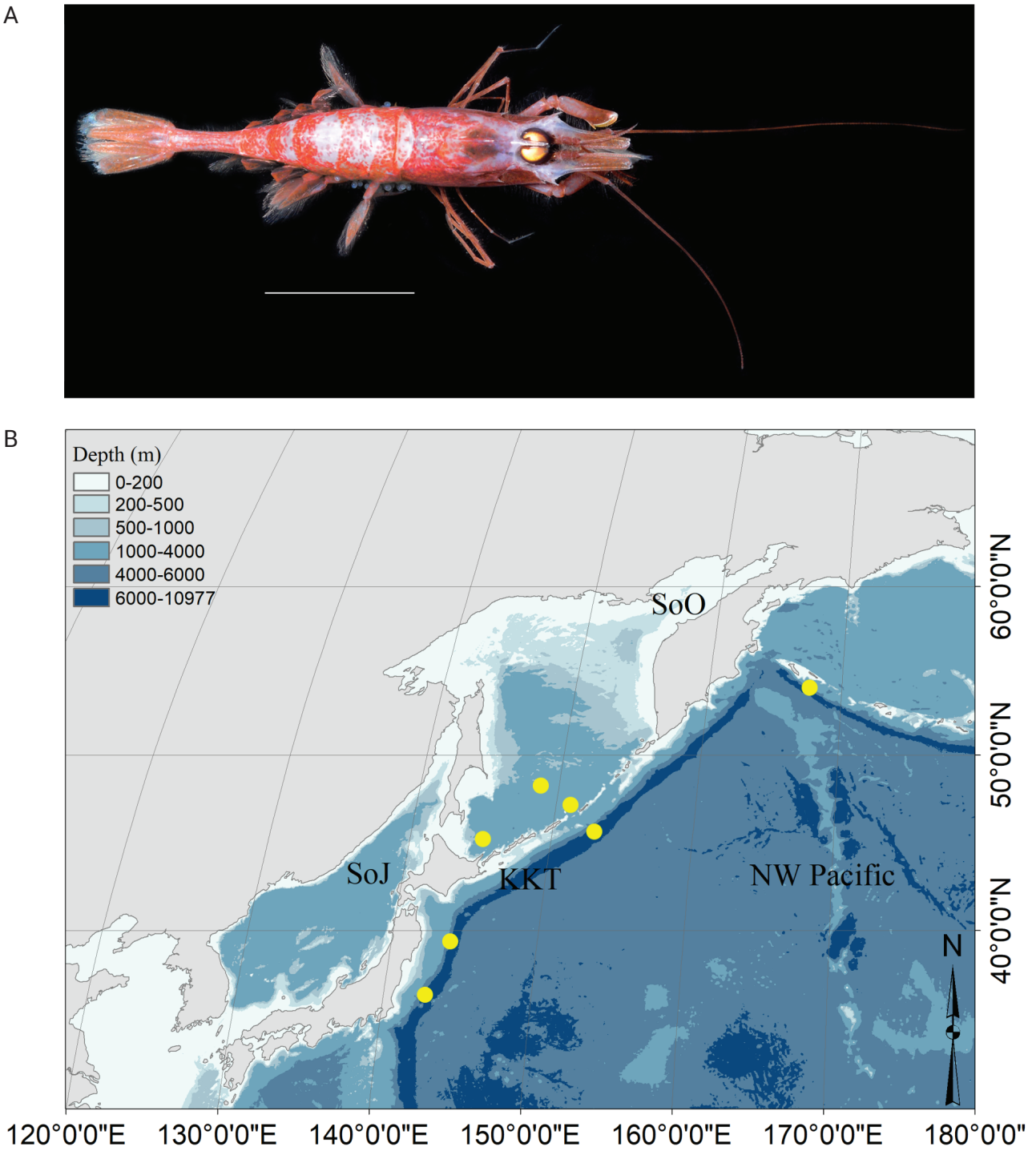


Figure 17. (A) Alive coloration of *Neocrangon abyssorum* (Rathbun, 1902) and (B) its distribution in the NW Pacific (photo credit – Anna Lavrentjeva).

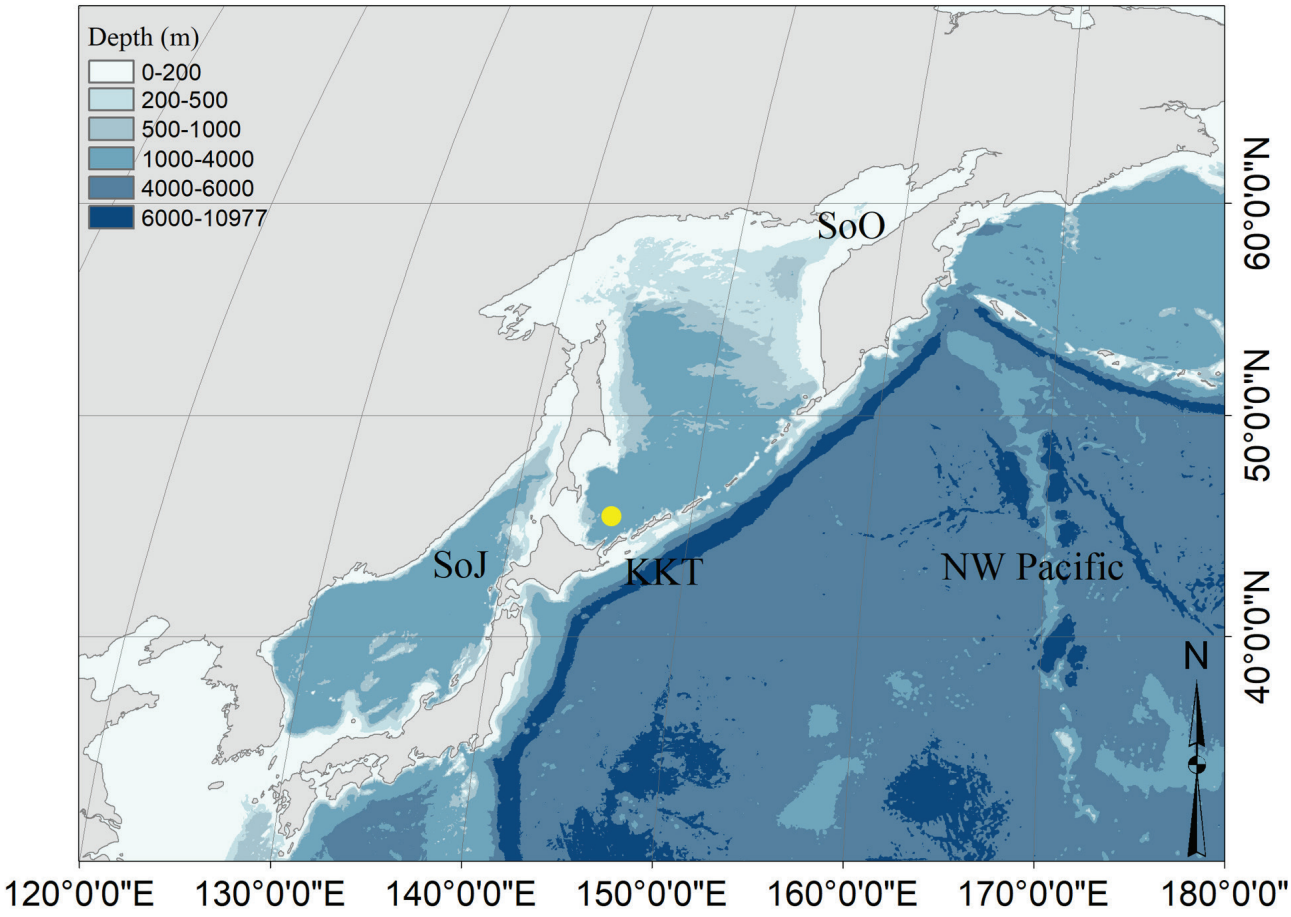


Figure 18. Distribution of *Metacrangon ochotensis* (Kobjakova, 1955) (after Kobjakova, 1955) in the NW Pacific.

Family Nematocarcinidae Smith, 1884

Nematocarcinus longirostris Bate, 1888

(Figure 23)

This species is known from the Pacific coasts of Japan, from Aomori to Boso Peninsula, at the depths of 2,698–3,470 m (Burukovsky 2000, 2003, as *Nematocarcinus batei* Burukovsky, 2000; Komai & Komatsu 2016).

Nematocarcinus tenuipes Bate, 1888

(Figure 24)

Widely distributed in the Indo–West Pacific; 518–3,429 m. In Japanese waters, recorded from off Izu Islands (Bate 1888 (as N. *parvidentatus*)) and Suruga Bay (Ohta 1983). Newly recorded from northeastern Honshu.

Family Pasiphaeidae Dana, 1852

Pasiphaea cf. *tarda* Krøyer, 1845

(Figure 25)

This species was recorded from the Sea of Okhotsk and Pacific coast of northeastern Japan (Hayashi 1986b; Komai 1991; Komai & Komatsu 2009; Marin 2018). Meso- and bathypelagic species widely distributed in the North Pacific from Unalaska to Oregon (Rathbun 1904) to southern Japan as well as known from the Ecuadorian coast (Faxon 1895), North Atlantic

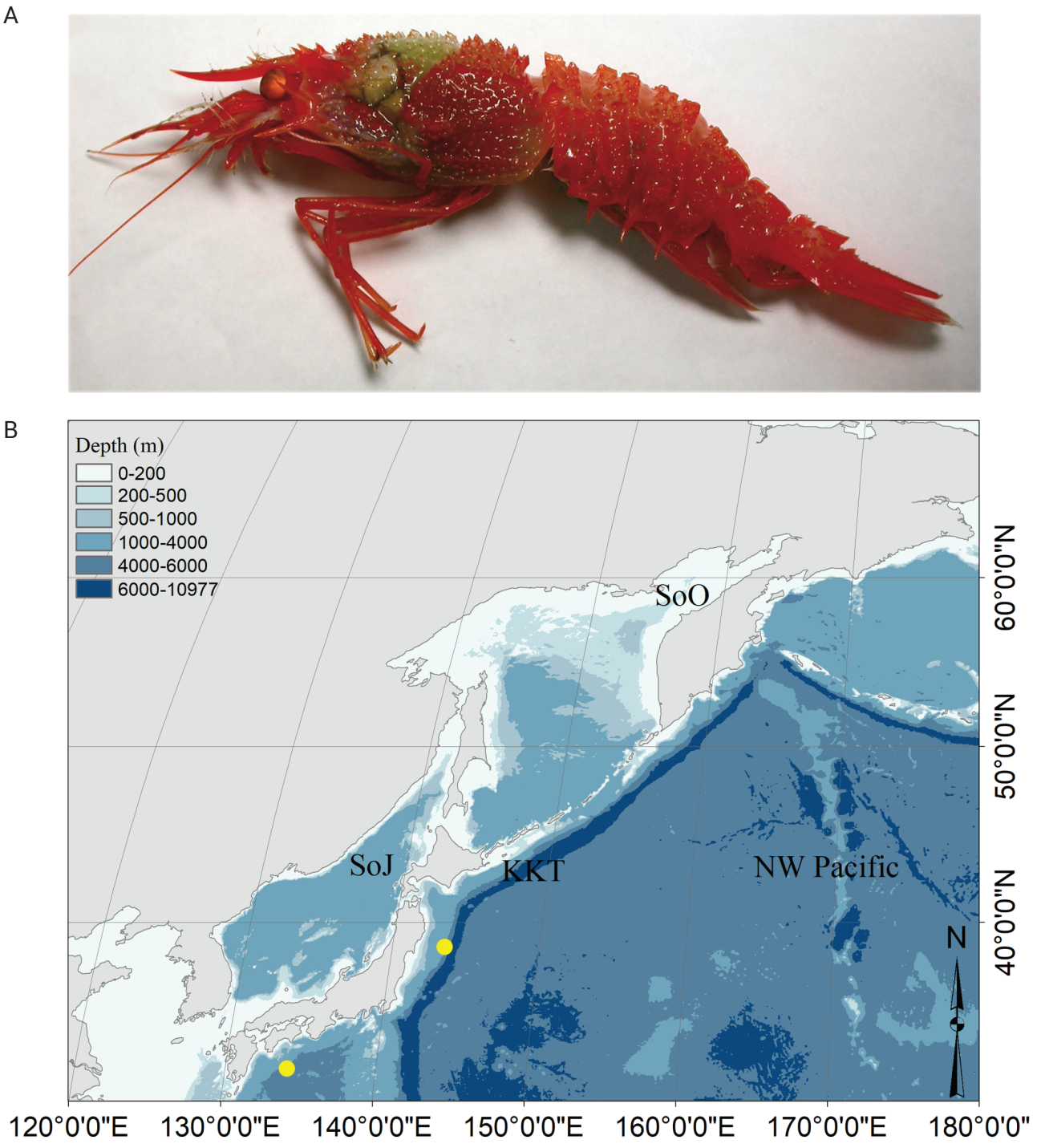


Figure 19. (A) Alive coloration of *Glyphocrangon caecescens* Anonymous, 1891 (photo credit – Komai & Komatsu, 2016) and (B) its distribution in the NW Pacific.

Ocean from Greenland to Bay of Biscay (Sivertsen & Holthuis 1956), south of Canary Islands (Maurin 1968), American coast south to South Carolina (Sivertsen & Holthuis 1956), and off Angola (Crosnier & Forest 1973); the depth range is 250–2,500 m (Sivertsen & Holthuis 1956).

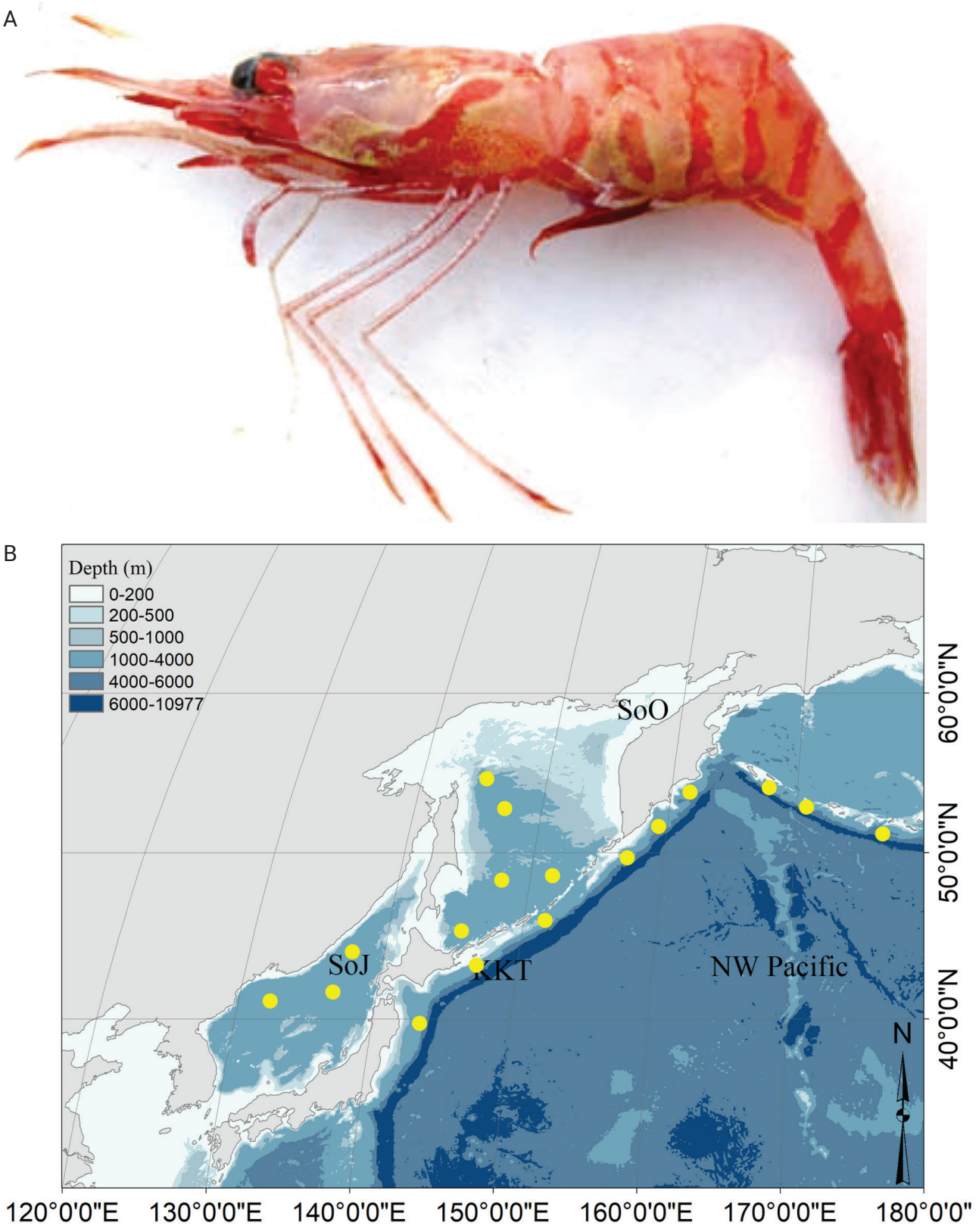


Figure 20. (A) Alive coloration of *Eualus biungius* (Rathbun, 1902) (photo credit – Komai & Komatsu, 2016) and (B) its distribution in the NW Pacific.

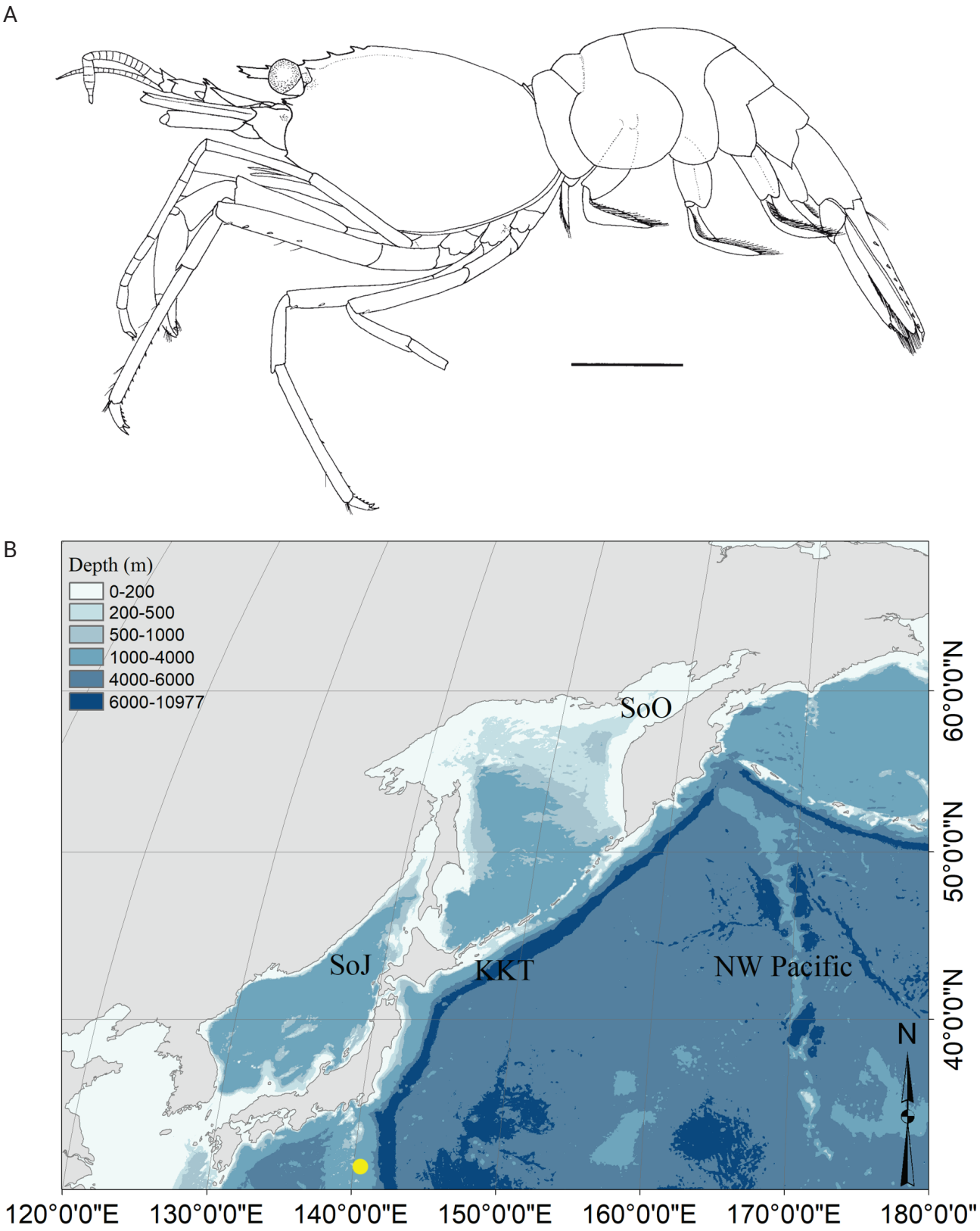


Figure 21. (A) General view of *Lebbeus lamina* Komai 2013 (after Komai, 2013) and (B) its distribution in the NW Pacific.

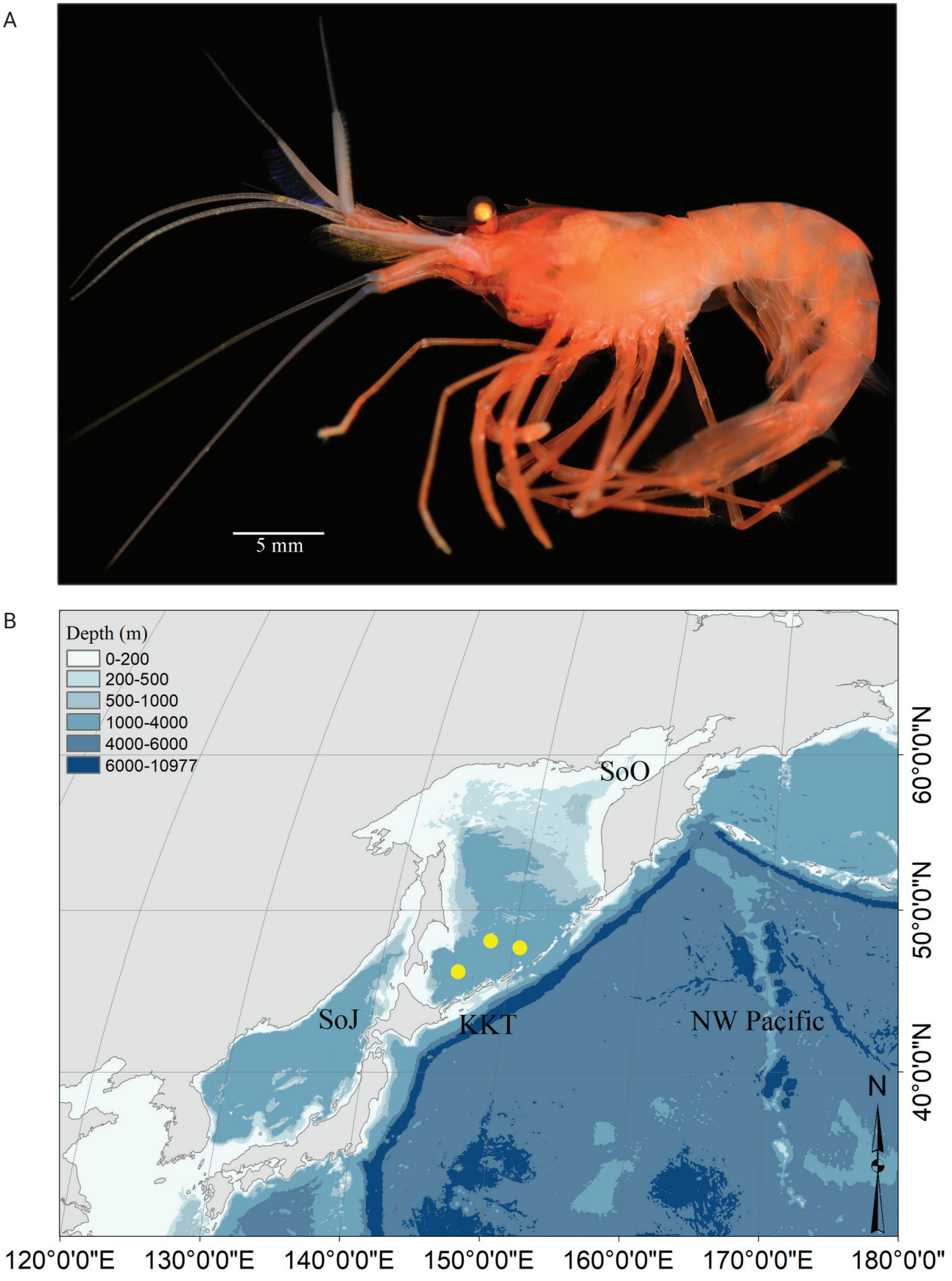


Figure 22. (A) Alive coloration of *Lebbeus sokhobio* Marin 2020 and (B) its distribution in the NW Pacific (photo credit – Anna Lavrentjeva).

Family Parapasiphae Smith, 1884

***Parapasiphae sulcatifrons* Smith, 1884**
(Figure 26)
A single specimen was collected off Hachinohe, Aomori Prefecture of Honshu (40˚00.0′N 143˚31.4′E to 41˚00.8′N 143˚30.2′E), at the depths of 2,055–2,032 m (Komai & Komatsu 2009). Cosmopolitan; meso- and bathypelagic, living deeper than 1,000 m (Komai & Komatsu 2009).

Family Oplophoridae Dana, 1852

***Systellaspis paucispinosa* Crosnier, 1988**
(Figure 27)
The species is rarely recorded from the Pacific side of Honsu, Japan (Hayashi 1987, 2007; Komai et al. 1999; Komai & Komatsu 2009). Widely distributed bathypelagic species also recorded from Indonesia and the NE Pacific from Vancouver Island to Los Angeles at the depths of 200–4,000 m (Butler 1980; Crosnier 1987; Hanamura 1983).

Family Acanthephyridae Spence Bate, 1888

***Acanthephyra eximia* Smith, 1884**
This species was recorded from Pacific coasts of Japan from Hokkaido to Ryukyu Islands (Komai 1991; Hayashi 2007). Meso- and bathypelagic species widely distributed in tropical and temperate waters of the World Ocean; 200–4,700 m (Chace 1986).

***Acanthephyra quadrispinosa* Kemp**, 1939
This species was collected off eastern Hokkaido, at the depths of 1,997–2,043 m (Komai & Komatsu 2009).

***Hymenodora frontalis* Rathbun, 1902**
(Figure 28a)
Widely distributed meso- and bathypelagic species known through the North Pacific, at depths of 0–4,432 m. (e.g., Vinogradov 1950; Aizawa 1974; Hayashi 2007; Kobjakova 1937; Marin 2018; Komai & Komatsu 2009).

***Hymenodora glacialis* (Buchholz, 1874)**
(Figure 28b)
Widely distributed meso- and bathypelagic species known throughout the North Pacific, from surface to the depth of 3,300 m (e.g., Vinogradov 1950; Kobjakova 1937; Marin 2018; Komai & Komatsu 2009).

5. Discussion

This new list collates a total of 31 decapod species, recorded from the area between 40–60°N and 120–180°E in the NW Pacific, including 17 benthic and 14 meso- and bathypelagic species. Among the latter, some species are probably eurybate and also can be caught by trawls or dredges in upper-water layers, when they were hauled up from bathyal depth. Such species, as *B. borealis*, *A. eximia*, *A. quadrispinosa*, *H. frontalis*, *Hymenodora glacialis*, are rather common in the higher latitudes of the NW Pacific, from Pacific coast of Japan to the Bering Sea, while *S. prehensilis*, *S. japonica*, *P. sulcatifrons*, *P. cf. tarda* and *S. paucispinosa*, are reported from the region of interest, only occasionally, and known mostly from it southern part. Large dendrobrachite bathypelagic species, such as, *C. monstrosus*, *H. spinidorsalis*, *Hepomadus gracialis*, *B. crenatus*, are usually recorded near the bottom by underwater cameras from a ROV

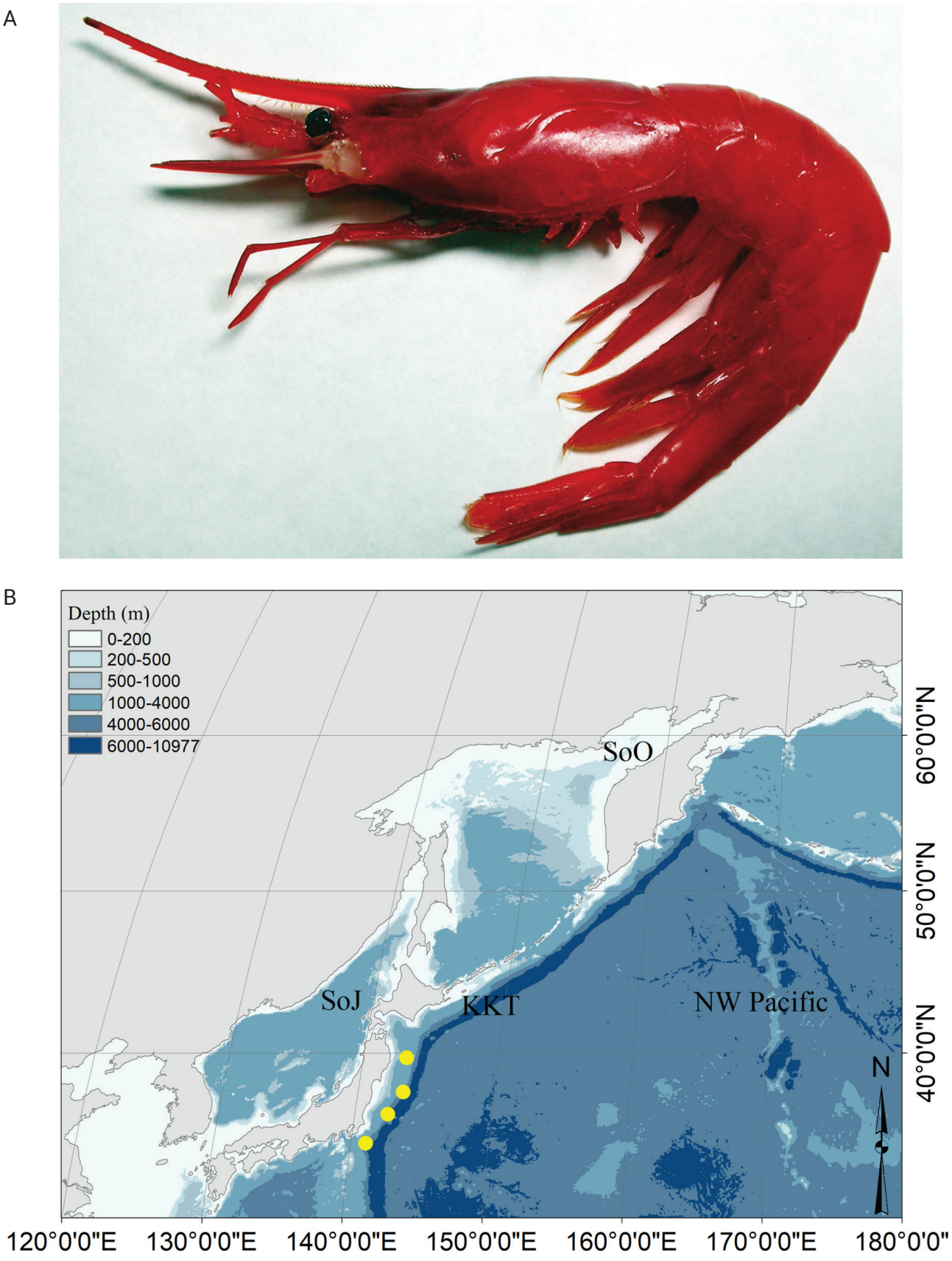


Figure 23. (A) Alive coloration of *Nematocarcinus longirostris* Spence Bate, 1888 (photo credit – Komai & Komatsu, 2016) and (B) its distribution in the NW Pacific.

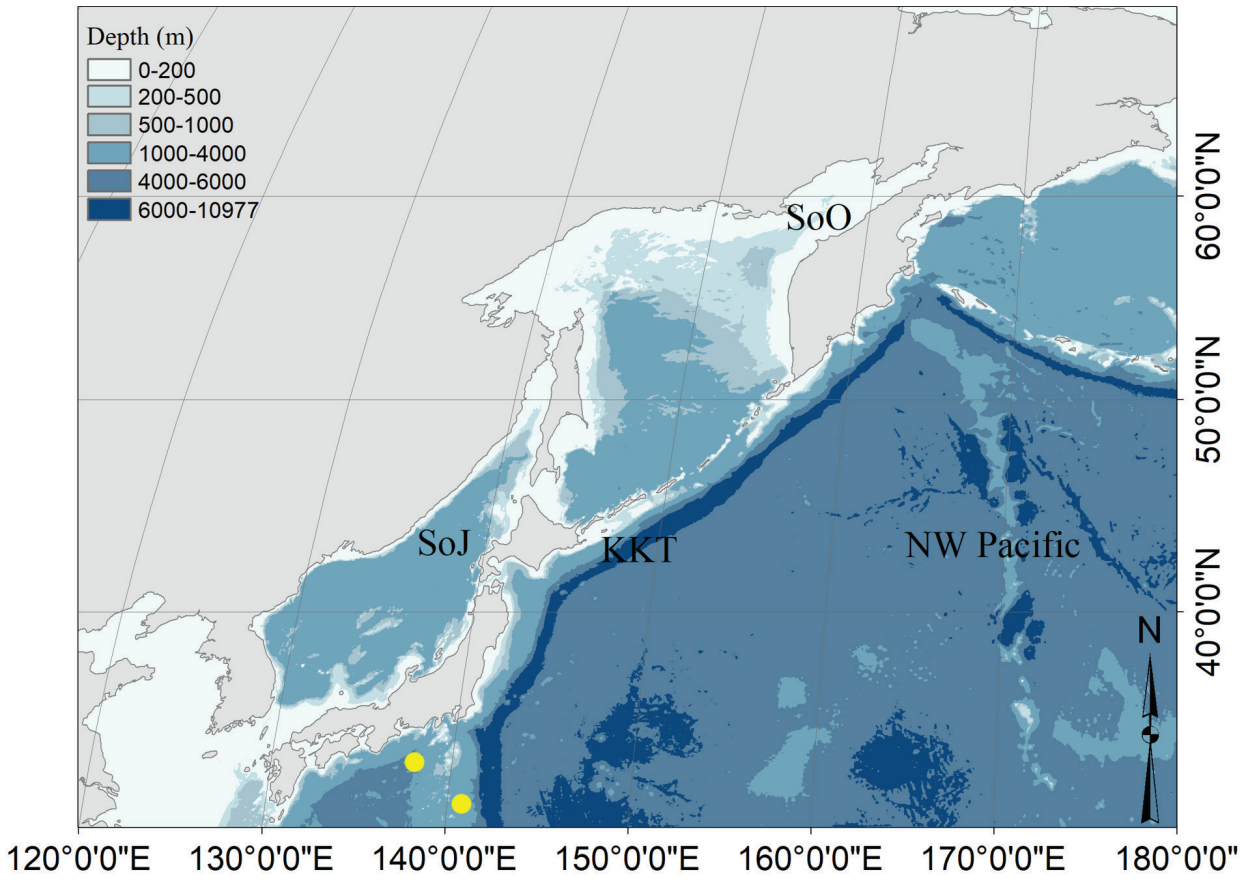


Figure 24. Distribution of *Nematocarcinus tenuipes* Bate, 1888 in the NW Pacific.

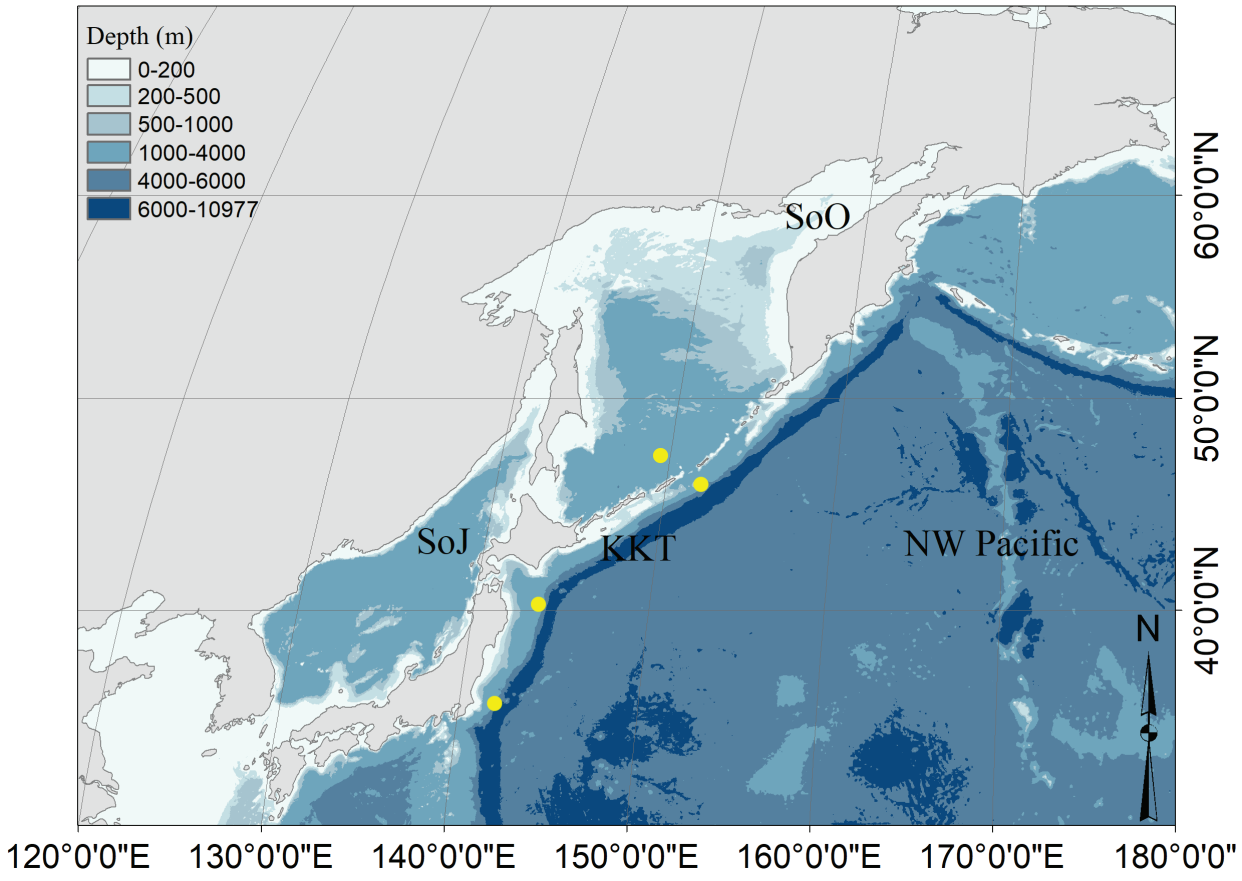


Figure 25. Distribution of *Pasiphaea cf. tarda* Krøyer, 1845 in the NW Pacific.

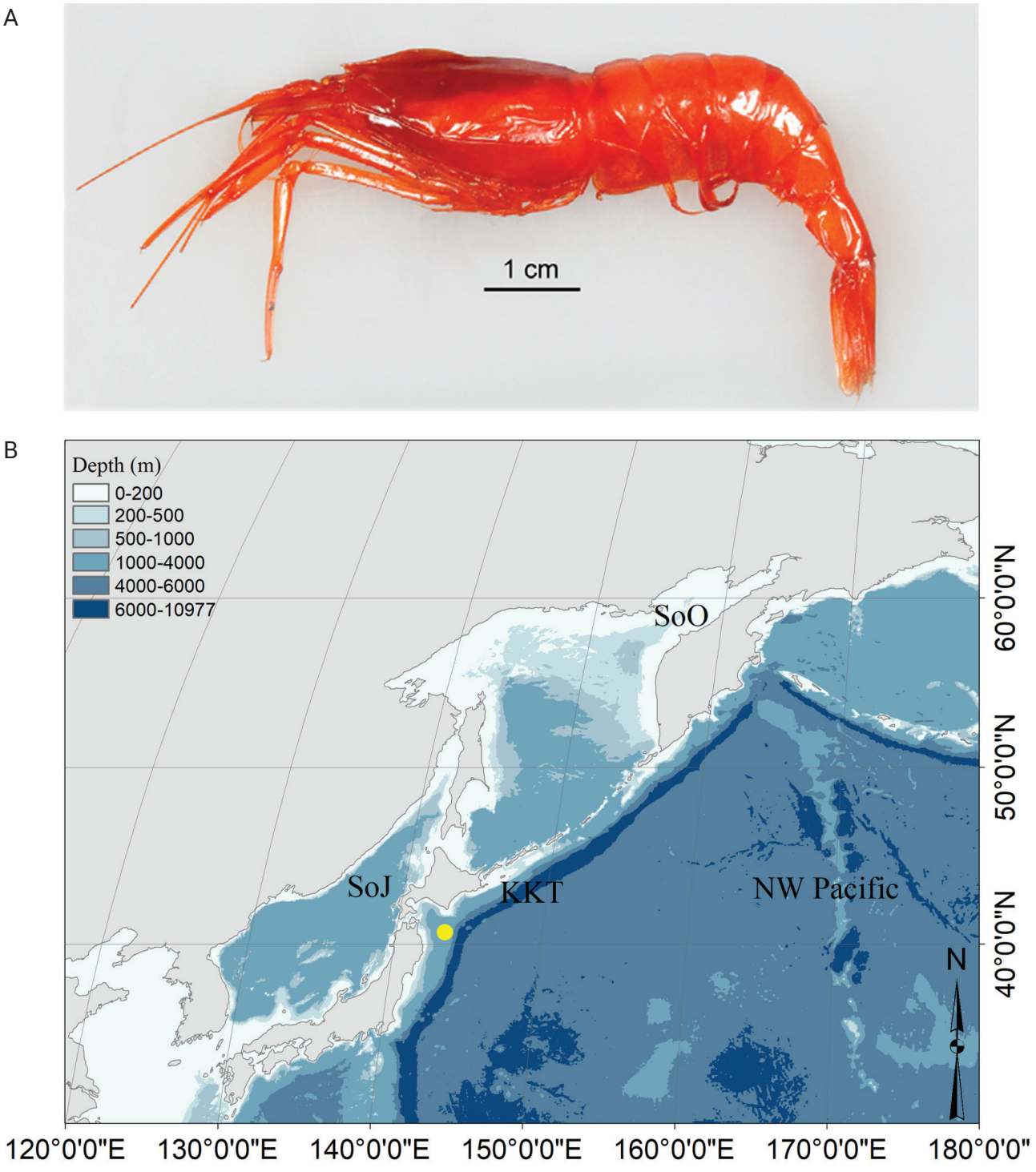


Figure 26. (A) Alive coloration of *Parapasiphae sulcatifrons* Smith, 1884 (photo credit – MacIsaac et al., 2014) and (B) its distribution in the NW Pacific.

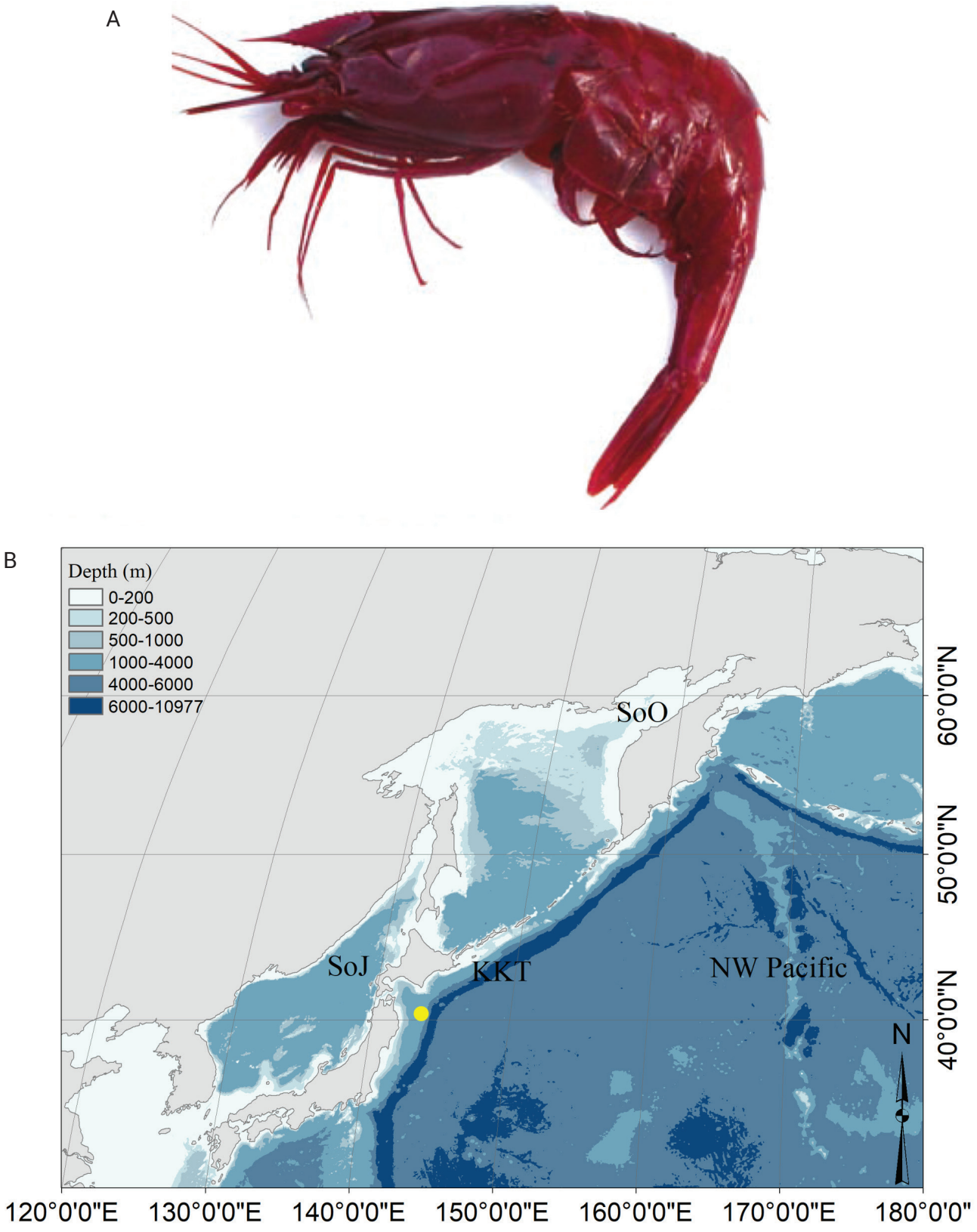


Figure 27. (A) Alive coloration of *Systellaspis paucispinosa* Crosnier, 1988 (photo credit – Komai & Komatsu, 2009) and (B) its distribution in the NW Pacific.

in the NW Pacific, and can be considered as a part of the benthic community.

Most of the known species, living deeper than 2,000 m, were recorded from the Pacific side of the Japan and Kuril Islands, adjacent to the North Pacific abyssal Plain. The deeper parts of the Sea of Okhotsk, the Kuril and Derjugina Basins, are inhabited by 13 species, including nine benthic species, showing a wide diversity of deep-water fauna and it close connection to other regions of NW Pacific. Only two benthic deep-water species are known from the deep parts of the Sea of Japan – *C. angulatus* and *E. biungiuis*. These species can live in relatively shallow waters, which have likely determined their ability to penetrate into the deep parts of the Sea of Japan.

Benthic species, such as *L. lamina* and *N. tenuipes*, were collected close to the southern border of the considered area between 40–60°N and 120–180°E in the NW Pacific, and probably can be collected north of the presented records with a lower probability. Benthic and bathypelagic species, such as *C. monstrosus*, *H. spinidorsalis*, *B. crenatus*, *P. benedicti* and *N. tenuipes*, are widely distributed in the North Pacific and adjacent areas; moreover, *C. monstrosus* and *H. spinidorsalis* are known as cosmopolitan bathypelagic species. Other reported benthic species, such as *C. okhotskensis*, undescribed *Lebbeus* sp. and *Munidopsis kurilensis* from the Kuril Basin of the Sea of Okhotsk, *C. angulatus*, *C. japonicus*, *Hepomadus glacialis*, *S. zenkevithchi*, *N. abyssorum*, *M. ochotensis*, *M. petalorhyncha*, *M. beringana* and *N. longirostris*, appear to be endemic of the bathyal depths greater than 2,000 m of the area between 40–60°N and 120–180°E in the NW Pacific.

Conclusion

This new list contains 31 decapod species (17 benthic and 14 meso-/bathypelagic species), recorded from the area between 40–60°N and 120–180°E in the NW Pacific. Most of known species, living deeper than 2,000 m, were recorded from the Pacific side of the Japan and Kuril Islands, and adjacent to the North Pacific abyssal plain. The deep parts of the Sea of Okhotsk, the Kuril and Derjugina Basins, are inhabited by 13 species, including nine benthic species, showing a wide diversity of deep water fauna and its close connection to other regions of NW Pacific. Only two benthic deep-water species are known from the deep parts of the Sea of Japan.

Acknowledgements

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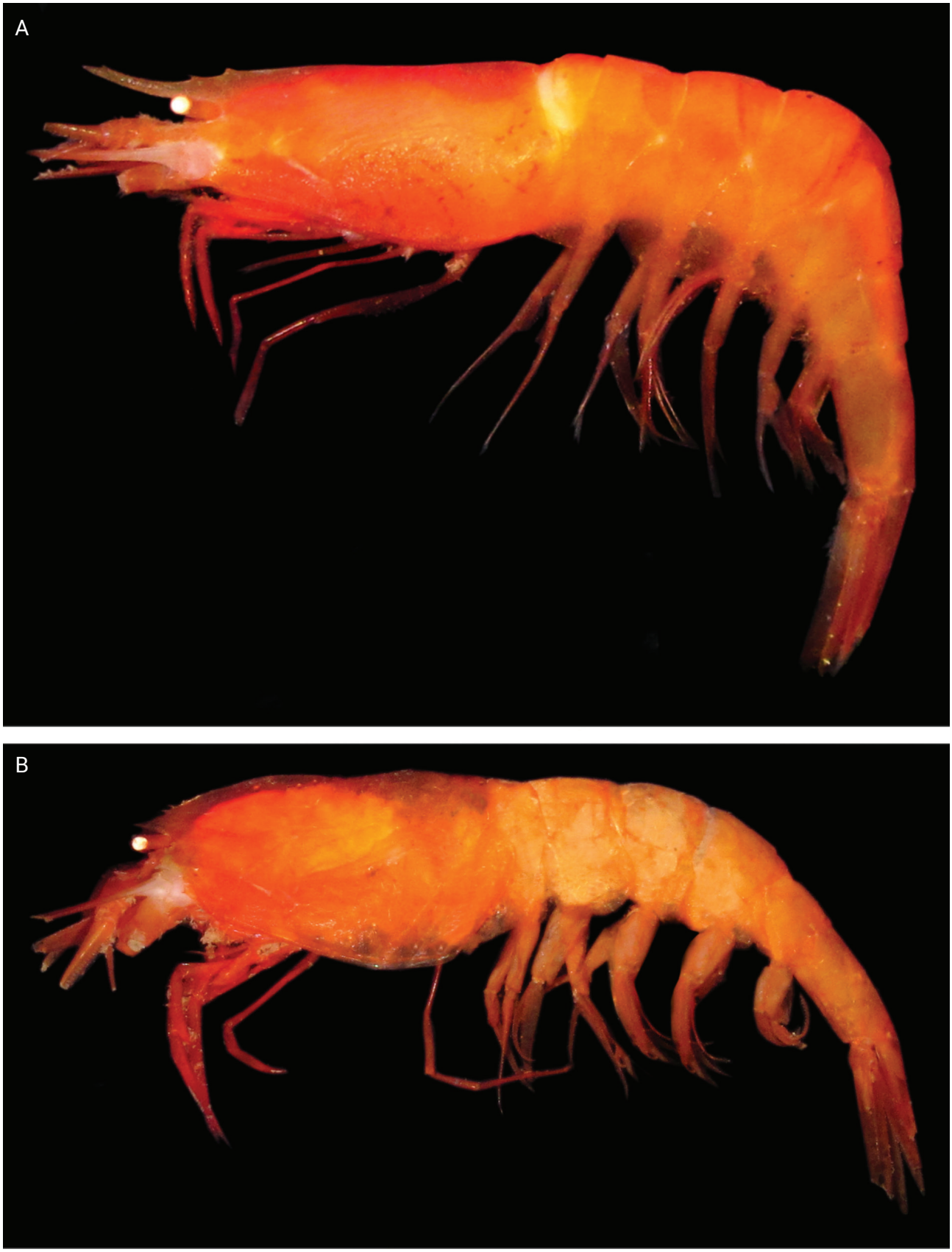


Figure 28. (A) Alive coloration of *Hymenodora frontalis* Rathbun, 1902 and (B) *Hymenodora glacialis* (Buchholz, 1874).

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CHAPTER 18

AMPHIPODA

DISTRIBUTION OF DEEP-SEA BENTHIC AMPHIPODA ALONG THE NW PACIFIC

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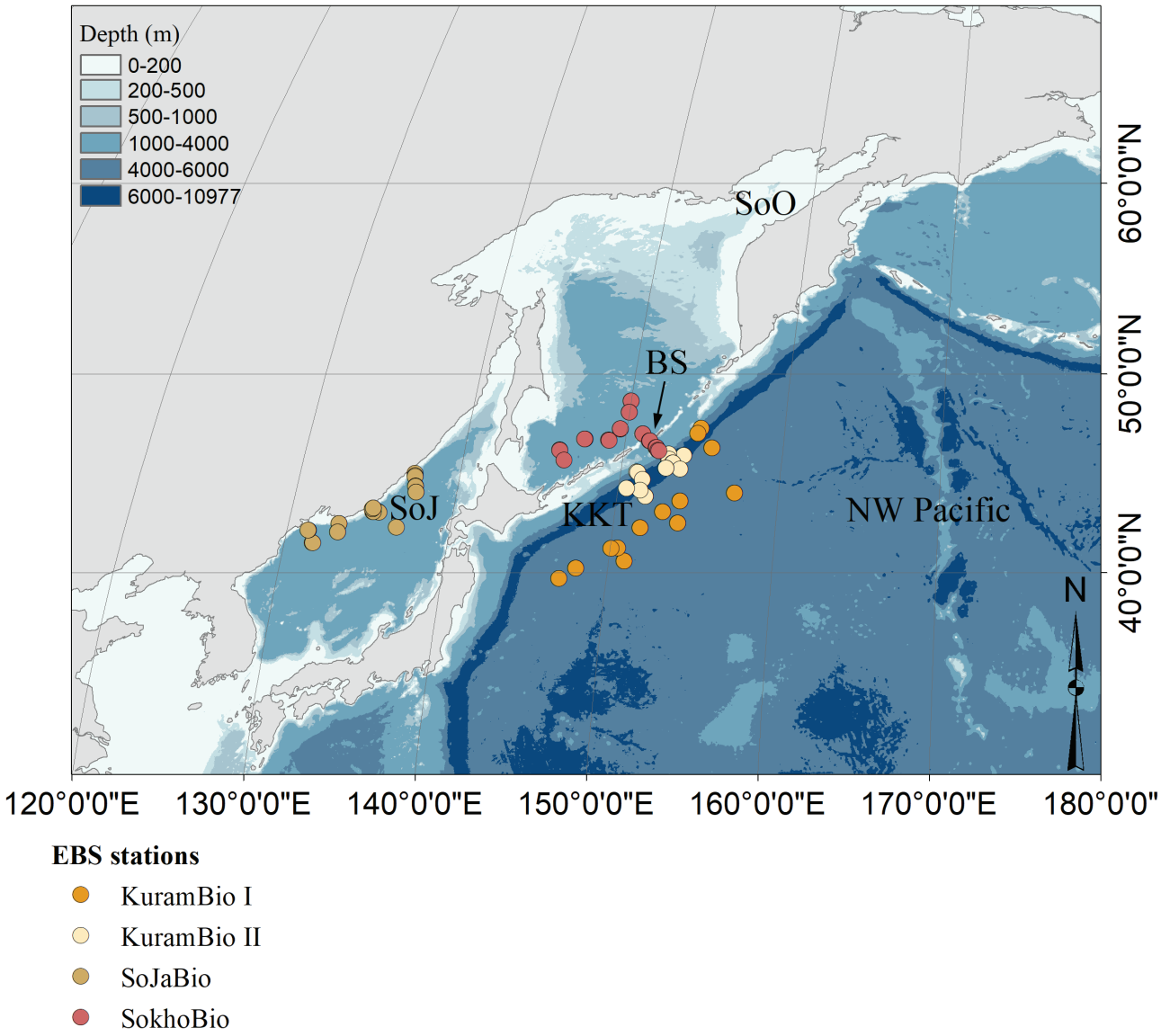
1. Introduction

The Order Amphipoda belongs to the crustacean Superorder Peracarida and contains 10,241 described species grouped in six suborders and 229 families (Horton et al. 2020, accessed 2019-04-11). A majority of species occur in the marine environment but about 20% of taxa live in freshwater and about 3% occupy supralittoral or terrestrial habitats (Richardson 2001; Väinölä et al. 2008; Lowry & Myers 2017; Horton et al. 2020). Marine species can be found at all latitudes and from the intertidal to the deepest parts of the ocean (e.g. Jazdzewski et al. 2001; Plaisance et al. 2009, Kobayashi et al. 2012). Marine Amphipoda are predominantly benthic, with just 4%, mainly representatives of the Suborder Hyperiidea, that are exclusive to the pelagic realm (Thurston 2001). Amphipods can occur at high densities and high abundances and are an important element of the oceanic food web (Dauby et al. 2001, 2003). Various ecological adaptations can be observed in benthic Amphipoda from tube building infaunal Ampeliscidae, through rather sedentary Corophiida that construct their "houses" on many organic and inorganic substrates, sediment-dwelling Oedicerotidae or Phoxocephalidae, epibenthic Eusiridae, to highly mobile, free-swimming Eurytheneidae, Hirondelleidae and some other lysianassoids (e.g. Barnard 1962; Barnard and Karaman 1991; Brix et al. 2018). The large variation in mobility is associated with different feeding types found among amphipods. They can be suspension-feeders, detritivores, herbivores, predators, omnivores or scavengers and a small proportion appear to be at least partially parasitic (e.g. Barnard 1962; Barnard and Karaman 1991; Brix et al. 2018; Horton et al. 2020). Amphipods brood eggs and young and do not go through a planktonic larval stage so that apart from pelagic species, large predators and scavengers, and a few other highly mobile species, dispersal abilities are restricted.

In the deep-sea amphipods constitute an abundant and diverse component of the zoobenthos at all latitudes (Frutos et al. 2017). Abundance and diversity are usually highest in the bathyal and decrease towards abyssal and hadal depths where they tend to be outnumbered by another peracarid order – the Isopoda (Frutos et al. 2017). Nevertheless, they may constitute up to one quarter of all peracarids collected in the deep sea (Brandt et al. 2019). The number of hitherto known benthic and bentho-pelagic amphipod species recorded below 2,000 m is 400 (Jażdżewska 2015).

Deep-sea studies in the NW Pacific were conducted intensively from the early 1950s to the 1970s during cruises of RV *Vityaz* (Monin 1983) resulting in the area becoming one of the best studied regions of the World Ocean (Brandt et al. 2019). Even at that time it was noted that the collecting gears used did not sample smaller size fractions of the fauna resulting in a major underestimate of biodiversity (Birstein 1963).

Based on material from the RV *Vityaz* expeditions and subsequent studies in the NW Pacific region a list of 52 benthic and bentho-pelagic amphipod species from depths greater than 2,000 m) was compiled (Supplementary Table 1: https://doi.org/10.3897/ab.e51315.suppl-2). In recent years four Russian-German and German-Russian expeditions to the region have taken place (Brandt et al. 2019). They were focused on the



Map 1. The area considered in the present study with indication of the stations sampled with epibenthic sled (EBS) during the four recent expeditions to the NW Pacific. SoO – Sea of Okhotsk, SoJ – Sea of Japan, BS – Bussol Strait, KKT Kuril-Kamchatka Trench. Abbreviations of the expedition names: KuramBio I and II – Kuril-Kamchatka Biodiversity Study I and II, SoJaBio – Sea of Japan Biodiversity Study, SokhoBio – Sea of Okhotsk Biodiversity StudyI.

study of the biodiversity, biogeography, and the trophic characteristics of the deep-sea benthic organisms in three areas (Map 1). In 2010 the first expedition within the project entitled Sea of Japan Biodiversity Study (SoJaBio) to the Sea of Japan took place. The Sea of Okhotsk was sampled during the Sea of Okhotsk Biodiversity Study cruise in 2015 (SokhoBio), while in 2012 and 2016 two expeditions to the Kuril-Kamchatka Trench (KKT) area Kuril-Kamchatka Biodiversity Study I and II (KuramBio I and KuramBio II) were conducted (Brandt et al. 2019). Amphipoda formed a very abundant and diverse component of the zoobenthos in the studied region (Golovan et al. 2013, 2019; Brandt et al. 2019; Frutos and Jażdżewska 2019).

2. Objectives

To provide a summary of the biogeography of NW Pacific Amphipoda based on all available literature.

3. Material and Methods

3.1. Study Area

For the purpose of this study the geographic limits of the NW Pacific were set at 40°N and 60°N latitude and from the east coastline of Asia (ca. 130°E) to longitude 180°E. The upper depth limit was set at 2,000 m.

3.2. Data collection

Distributional records of species were extracted from the available literature (Bulycheva 1936; Gurjanova 1952, 1955, 1962, 1972; Birstein and Vinogradov 1955, 1958; Birstein and Vinogradova 1960; Margulis 1967; Kamenskaya 1981, 1997; Golovan et al. 2013; Ritchie et al. 2015; Shimomura and Tomikawa 2016; Lörz et al. 2018a, 2018b; Jażdżewska and Mamos 2019; Jażdżewska and Ziemkiewicz 2019). Most of the results presented by Birstein and Vinogradov (1955, 1958) were from samples collected with non-closing nets so in case of these two publications only those species known also from benthic samples were considered. Distribution data for higher taxa (genera and families) were compiled from the above-mentioned papers and from additional publications where the identification was left at higher taxonomic level (Jażdżewska 2015; Schwabe et al. 2015; Frutos and Jażdżewska 2019; Golovan et al. 2019). All species, genera and families were checked against the most recent amphipod classification (Lowry and Myers 2017), available online in the World Amphipoda Database (WAD) (Horton et al. 2020), to ensure their correct systematic position. The single case when the classification of Lowry and Myers (2017) is not followed is the family Lepechinellidae which in the cited work is treated as a subfamily of Atylidae.

Stations positions of the material collected recently were determined using the Global Positioning System (GPS), so are very precise but earlier records are less so. Archive records from *Vityaz* cruises were cross-checked in different publications (including those dealing with other deep-sea animal groups) and some inconsistencies were found. We have made every effort to check the position of each station to confirm its coordinates, but the localities of the old records should be treated with caution. Additionally, for political reasons explained by Vinogradov and Vinogradov (2006) among others, in the former times it was forbidden to provide detailed geographic positions for samples, so certain species reported in the oldest publications cannot be associated with exact localities.

The distribution maps were created in ArcGIS. In case of species that were recorded also shallower than 2,000 m only the deep (>2,000 m) records have been presented on the maps.

3.3. Depth Range

The depth ranges of species recorded below 2,000 m in the studied region were defined using the shallowest and deepest records

of each individual taxon in the World Ocean. This was the base for counting the number of NW Pacific species for 1,000 m depth intervals starting from 2,000 m (in these counts only the ranges in studied area were considered). In the case of data coming from the publications based on material from non-closing nets it was impossible to determine the exact depth distribution of the species, so these records were excluded from the analysis. On the contrary, records of species without precise locality but for which the depth was given (Bulycheva 1936; Gurjanova 1955, 1962, 1972) were taken into account in this part of the work. A similar approach was used for genera and families with the restriction that only the records from below 2,000 m and from the studied area were used to present the depth ranges. Because identification of the representatives of the families Lysianassidae, Tryphosidae and Uristidae can be troublesome, in some recent papers they were treated as a single unit – Lysianassoidea (Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019) – we have done the same here. A similar situation arose with representatives of families within the Corophiida which were combined in one group (except for the families Caprellidae and Dulichiidae). The composition of genera/families in different depth intervals was also studied.

3.4. Latitudinal Range

Although the northern limit of the studied region was set at 60°N there were no georeferenced records of Amphipoda north of 51°30'N, so latitudinal ranges have not been considered.

4. Results

4.1. Richness Patterns

4.1.1. Family level

In the study area 34 families and two higher groupings, Lysianassoidea and Corophiida, occurring below 2,000 m were recorded from 109 stations (Table 1). The highest frequency of occurrence was the Pardaliscidae, present at 52% of stations. The Lysianassoidea and the families Eusiridae, Oedicerotidae and Phoxocephalidae were reported from more than 40% of stations and the Corophiida and the Synopiidae from more than 30%. The remaining 28 families occurred less frequently.

4.1.2. Generic level

The number of genera reported was 50 in 28 families occurring at 93 stations. The highest number of genera found was in the Pardaliscidae (six), followed by the Oedicerotidae (five). Three genera were recorded in the families Ampeliscidae, Phoxocephalidae and Stegocephalidae. The remaining families were represented by either two or one genus. The most common genera were *Rhachotropis* S.I. Smith, 1883 (Eusiridae), *Caleidoscopsis* G. Karaman, 1974 (Pardaliscidae), and *Halice* Boeck, 1871 (Pardaliscidae) represented at 38%, 21%, and 18% of stations, respectively. No other genus was found at more than 15% of stations.

4.1.3. Species level

At 64 localities 39 described species (from 28 genera and 21 families) were collected. The most

speciose family was the Ampeliscidae (three genera, seven species) followed the Eusiridae (one genus, four species), the Pardaliscidae (two genera, three species), and Lepechinellidae (one genus, three species). In all other cases families were represented by one or two species only. Most species (28) were recorded from very few stations (1–3) and seven taxa were collected at 4–5 localities. The frequency of four taxa exceeded 10% – *Princaxelia abyssalis* Dahl, 1959 and Uristidae *incertae sedis derjugini* (Gurjanova, 1962) (11%, 7 stations), *Rhachotropis saskia* Lörz & Jażdżewska, 2018 (16%, 10 stations) and *Hirondellea gigas* (Birstein & Vinogradov, 1955) (17%, 11 stations).

4.2. Biogeographic patterns – depth gradient

The number of families within pre-defined depth intervals varied from two in the deepest zone (>9,000 m) to a maximum of 28–30 in the depth range between 3,000–5,999 m (Table 1, Figure 1). Two peaks in the number of genera were observed – 23 at 2,000–2,999 m and 27 at 5,000–5,999 m (Table 1). Below 6,000 m this number decreased gradually and only nine genera were recorded between 3,000–3,999 m. The highest number of described species was observed in the depth range of 2,000–2,999 m (Table 1, Figure 1) with a secondary peak of 10–11 species at 6,000–7,999 m. In the zones 3,000–5,999 m and below 7,000 m the number of species did not exceed ten.

Table 1. Number of families, genera and species identified as well as the number of samples where they were found in each predefined depth interval. In brackets the number considering the stations lacking coordinates but possessing depth information. * one station sampled (4,903-5,266 m) crossed the border of the predefined zones that is why it was counted in both 4,000-4,999 and 5,000-5,999 m zones. + the genus *Eurythenes* was included in the total number of genera but it was found only in plankton samples, so its depth range could not be determined.

Depth interval	No of families	No of samples with family ID	No of genera	No of samples with generic ID	No of species	No of samples with species ID
2,000-2,999	21	12 (23)	23	10 (21)	23	10 (21)
3,000-3,999	28	16	9	4	3	2
4,000-4,999	28	8	18	6	2	3
5,000-5,999	30	27*	27	27*	8	11*
6,000-6,999	19	9	15	9	11	7
7,000-7,999	15	7	15	7	10	6
8,000-8,999	9	9	7	9	7	8
> 9,000	2	4	3	4	4	4
plankton samples		7		7		3
total	35	98 (109)	50+	82 (93)	39	53 (64)

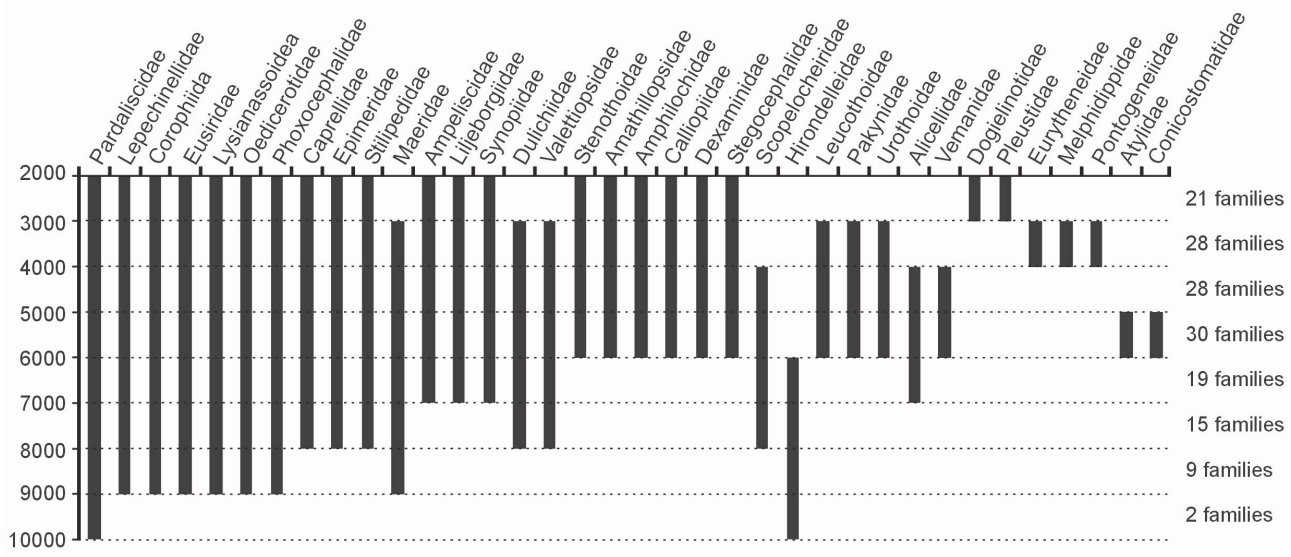


Figure 1. Distribution of the families recorded deeper than 2,000 m in the NW Pacific. The families are organized from the most widely distributed to the least common. The number of families in each depth zone are listed.

5. Discussion

5.1. Review of the taxa reported from the studied area

Suborder Amphilochidea Boeck, 1871

Parvorder Amphilochidira Boeck, 1871

Superfamily Amphilochoidea Boeck, 1871

Family Amphilochidae Boeck, 1871

The family is represented by 14 genera and 91 species (Lowry and Myers 2017; Horton et al. 2020) and is known from wide geographic and depth range (0–5,228 m) (Barnard and Karaman 1991; Golovan et al. 2019). In the deep sea of the NW Pacific it was recorded at six stations in the Bussol Strait and in the abyss adjacent to the KKT from the depth range 2,327–5,228 m (Frutos and Jażdżewska 2019; Golovan et al. 2019). No data about the generic and species composition of this material is available as yet.

Family Pleustidae Buchholz, 1874

There are 140 pleustid species belonging to 35 genera known from the sublittoral to 3,479 m (Barnard and Karaman 1991; Lowry and Myers 2017; Horton et al. 2020). Several species were reported and described from NW Pacific (Gurjanova 1972), but only one, *Pleustostenus displosus* Gurjanova, 1972, was recorded below 2,000 m depth.

Pleustostenus displosus Gurjanova, 1972

The species was described based on a single ovigerous female. The description of the locality states "found in north-western part of the Pacific Ocean, 57°45'8" N, 151°14' E at the depth 2,300 m" (Gurjanova 1972, p. 175) suggesting that the type locality is situated in the open ocean. However, the captions of the drawings state "the Sea of Okhotsk" and the coordinates indicate a locality within this sea at a depth not exceeding 200 m. Although the final decision how to treat this record cannot be definitive we decided to include this species among species

occurring below 2,000 m. The species has not been reported since its description.

Family Stenothoidae Boeck, 1871

This geographically widely distributed family consists of 46 genera and 271 species (Barnard and Karaman 1991; Lowry and Myers 2017; Horton et al. 2020). The deepest record of the family comes from NW Pacific where it was found at 5,379 m (Golovan et al. 2019). In the studied part of the NW Pacific deep sea the family was recorded at 19 stations in the depth range 2,300–5,379 m (in the Bussol Strait, the Sea of Okhotsk and in the abyss adjacent to the KKT) (Gurjanova 1952; Frutos and Jażdżewska 2019; Golovan et al. 2019). Only one species has been identified from this region and bathymetric range.

***Metopa mirifica* Gurjanova, 1952**

The species is known only from the type series consisting of six individuals collected in the vicinity of Kuril Islands at the depth 2,300 m (Gurjanova 1952). No exact sampling locality is provided for this species.

Superfamily Iphimedioidea Boeck, 1871

Family Amathillopsidae Pirlot, 1934

The Amathillopsidae consists of three genera and 19 species) recorded from various geographic localities over a wide depth range down to 5,045 m (Barnard 1961; Kamenskaya 1997; Lowry and Myers 2017; Horton et al. 2020). In the study area it was found at five stations in the Bussol Strait, the Sea of Okhotsk and in the abyss of the open Pacific Ocean at a depth range of 2,327 to 5,045 m (Kamenskaya 1997; Frutos and Jażdżewska 2019). One described species has been reported from this area.

***Amathillopsis pacifica* Gurjanova, 1955**

The description is based on a single individual collected in the Kuril Basin in the Sea of Okhotsk at a depth of 2,850 m but no exact position was provided (Gurjanova 1955). Barnard (1967) found an individual in the Cedros Trench (Baja California) at 3,481–3,518 m and established a new subspecies (*Amathillopsis pacifica margo*) for it.

Family Epimeriidae Boeck, 1871

The family Epimeriidae consists of 89 species ascribed to two genera (Lowry and Myers 2017; Horton et al. 2020). The genus *Epimeria* Costa, 1851 with 86 described species is particularly diverse in the Southern Ocean (Verheye et al. 2016; d'Udekem d'Acoz and Verheye 2017). The deepest record of the family comes from 7,230 m (Kamenskaya 1997). In the studied region benthic epimeriids were collected at four stations from the depths 2,430–7,230 m (Kamenskaya 1997; Shimomura and Tomikawa 2016). Two species were recorded in Northwest Pacific deep sea.

***Epimeria abyssalis* Shimomura & Tomikawa, 2016**
(Map 2)

This species is known only from the type series. It was described from the abyss adjacent to KKT from the depths 5,473–5,695 m (Shimomura and Tomikawa 2016).

***Uschakoviella echinophora* Gurjanova, 1955**
(Map 2)

Describing the species Gurjanova (1955) differentiated two subspecies *Uschakoviella echino-*

phora echinophora and *U. echinophora abyssalis*. The first of them was collected at a depth of 291 m east of Iturup island, and the second in the Sea of Okhotsk west of Iturup island at the depth 2,550 m. The species was reported subsequently from five shelf stations (99–247 m) in the Bering Sea (Shoemaker 1964), a single station on the continental side of the KKT at the depth 2,430–2,670 m (Kamenskaya 1997) and a single station in the Antarctic (Watling and Holman 1981). Taking into account that *U. echinophora echinophora* was found on the shelf, while *U. echinophora abyssalis* in the bathyal one cannot exclude the possibility that these are two valid sibling species that have different depth distribution. Additionally, the record from the Antarctic may represent another species.

Family Stilipedidae Holmes, 1908

The family consists of four genera and 24 species (Lowry and Myers 2017; Horton et al. 2020) recorded from all latitudes and wide depth range (60–7,300 m) (Barnard and Karaman 1991; Jażdżewska and Mamos 2019). In the studied region it was present at 16 stations from the Sea of Okhotsk, the Bussol Strait and the Kuril-Kamchatka Trench area at the depths from 2,327–7,300 m (Birstein and Vinogradova 1960; Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). A single species has been reported from the NW Pacific deep sea.

Alexandrella carinata (Birstein & Vinogradova, 1960)

(Map 2, Figure 2 A)

The species was described from the KKT (7,210–7,230 m) on the basis of a single male specimen (Birstein and Vinogradova 1960). During two KuramBio expeditions seven additional individuals were collected at four stations in the abyss adjacent to the KKT and the trench itself (5,223–7,300 m). A molecular analysis of the new collection revealed the existence of two genetic lineages, one grouping the abyssal individuals and the other the specimens from hadal stations (Jażdżewska and Mamos 2019). The limited number of individuals and the use of mitochondrial genes only provides insufficient evidence to determine whether two species are present or only a single one that shows high genetic variation.

Superfamily Leucothoidea Dana, 1852

Family Leucothoidae Dana, 1852

The family groups five genera and 194 described species widely distributed geographically and bathymetrically (to 5,379 m) (Barnard and Karaman 1991; Lowry and Myers 2017; Golovan et al. 2019; Horton et al. 2020). In the area of study leucothoids were found at nine stations in the Sea of Okhotsk and the abyss adjacent to the KKT (3,299–5,379 m) (Kamenskaya 1997; Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). No further identification of this material has been made as yet.

Parvorder Eusiridira Stebbing, 1888

Superfamily Eusiroidea Stebbing, 1888

Family Eusiridae Stebbing, 1888

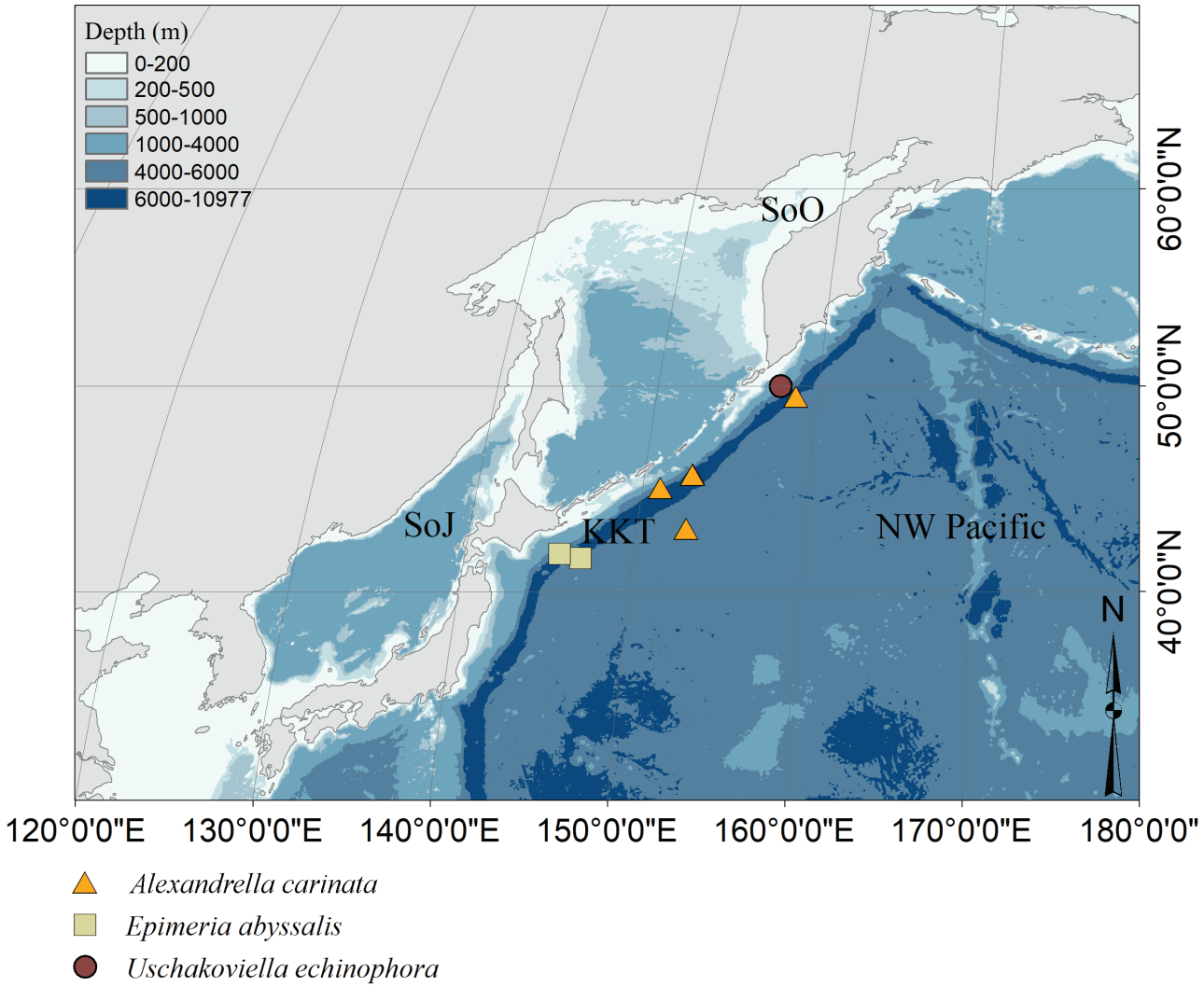
This geographically and bathymetrically widely distributed family (to 9,460 m) includes 11 genera

and 121 species (Barnard and Karaman 1991; Lowry and Myers 2017; Horton et al. 2020). It was one of the most frequently recorded families in the area of study being found at 48 stations in the Sea of Okhotsk, Bussol Strait, KKT and adjacent abyssal areas at depths of 2,327–8,193 m (Kamenskaya 1997; Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). Four species, all from the genus *Rhachotropis*, have been reported from the deep sea of the NW Pacific.

***Rhachotropis aculeata* (Lepechin, 1780)**

(Map 3)

This widely distributed species has been found in the North Atlantic, North Pacific and Arctic Oceans at shelf and upper bathyal depths (Gurjanova 1951; Bousfield and Hendrycks 1995; Lörz et al. 2018a, c). In the area in focus it has been recorded from a single station deeper than 2,000 m on the continental side of the KKT at 2,430–2,670 m (Kamenskaya 1997).



Map 2. Distribution of species of Epimeriidae and Stilipedidae in the NW Pacific. SoJ - Sea of Japan, SoO - Sea of Okhotsk, KKT - Kuril-Kamchatka Trench.

***Rhachotropis flemmingi* Dahl, 1959**

(Map 3)

This deep-sea species was described from Sunda (= Java) Trench at the depth 7,160 m (Dahl 1959). In the deep sea of NW Pacific it was found at a single station in the KKT (6,090–6,135 m) (Kamenskaya 1997).

***Rhachotropis marinae* Lörz, Jażdżewska & Brandt, 2018**

(Map 3)

A single individual of this species was reported from the Sea of Okhotsk (near Iturup island at 2,850 m) by Gurjanova (1955) under the name *Rhachotropis grimaldii* (Chevreux, 1887). During the SokhoBio expedition more specimens of this taxon were collected from a station in the Kuril Basin at 3,299 m. This new material allowed differentiation from *R. grimaldii* and validation as a new species (Lörz et al. 2018a).

***Rhachotropis saskia* Lörz & Jażdżewska, 2018**

(Map 3, Figure 2 B)

Rhachotropis saskia is a predatory species found at ten stations in a very wide depth range (4,987–8,192 m) in the KKT area. This unusually wide bathymetric distribution (over 3,000 m vertically) has been confirmed by molecular studies (Lörz et al. 2018b).

Superfamily Liljeborgioidea Stebbing, 1899

Family Liljeborgiidae Stebbing, 1899

This family comprising three genera and 120 species is distributed in all oceans and depths from 0 to 6,561 m (Barnard and Karaman 1991; Lowry and Myers 2017; Horton et al. 2020; Jażdżewska and Mamos 2019). In the area in focus representatives of this family were recorded at 15 stations situated in the Sea of Okhotsk, the Bussol Strait and in the KKT area at the depths from 2,327 to 6,561 m (Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). No species identification is available at the moment.

Parvorder Haustoriidira Stebbing, 1906

Superfamily Haustorioidea Stebbing, 1906

Family Phoxocephalidae G.O. Sars, 1891

This family of infaunal species constitutes an abundant and diverse component of the zoobenthos at all latitudes and at depths down to 8,744 m) (Dahl 1959; Brix et al. 2018; Jażdżewska and Mamos 2019). It consists of 79 genera and 362 species (Lowry and Myers 2017; Horton et al. 2020). In the studied area and at depths greater than 2,000 m it has been found at 43 stations in the Sea of Japan, the Sea of Okhotsk, the Bussol Strait and the open Pacific Ocean in the depth range 2,333–8,744 m (Kamenskaya 1997; Golovan et al. 2013, 2019; Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019). Although so common and abundant only two species of the genus *Harpiniopsis* have been identified to date.

***Harpiniopsis orientalis* (Bulycheva, 1936)**

(Map 3)

This species was described from the northern part of the Sea of Japan at depths of 59–145 m, but no exact locality was provided (Bulycheva 1936). It has been reported from the Sea of Okhotsk (Sirenko 2013). Recently it was collected during the SoJaBio expedition at two bathyal

stations (517 and 2,534 m) in the Sea of Japan (Golovan et al. 2013).

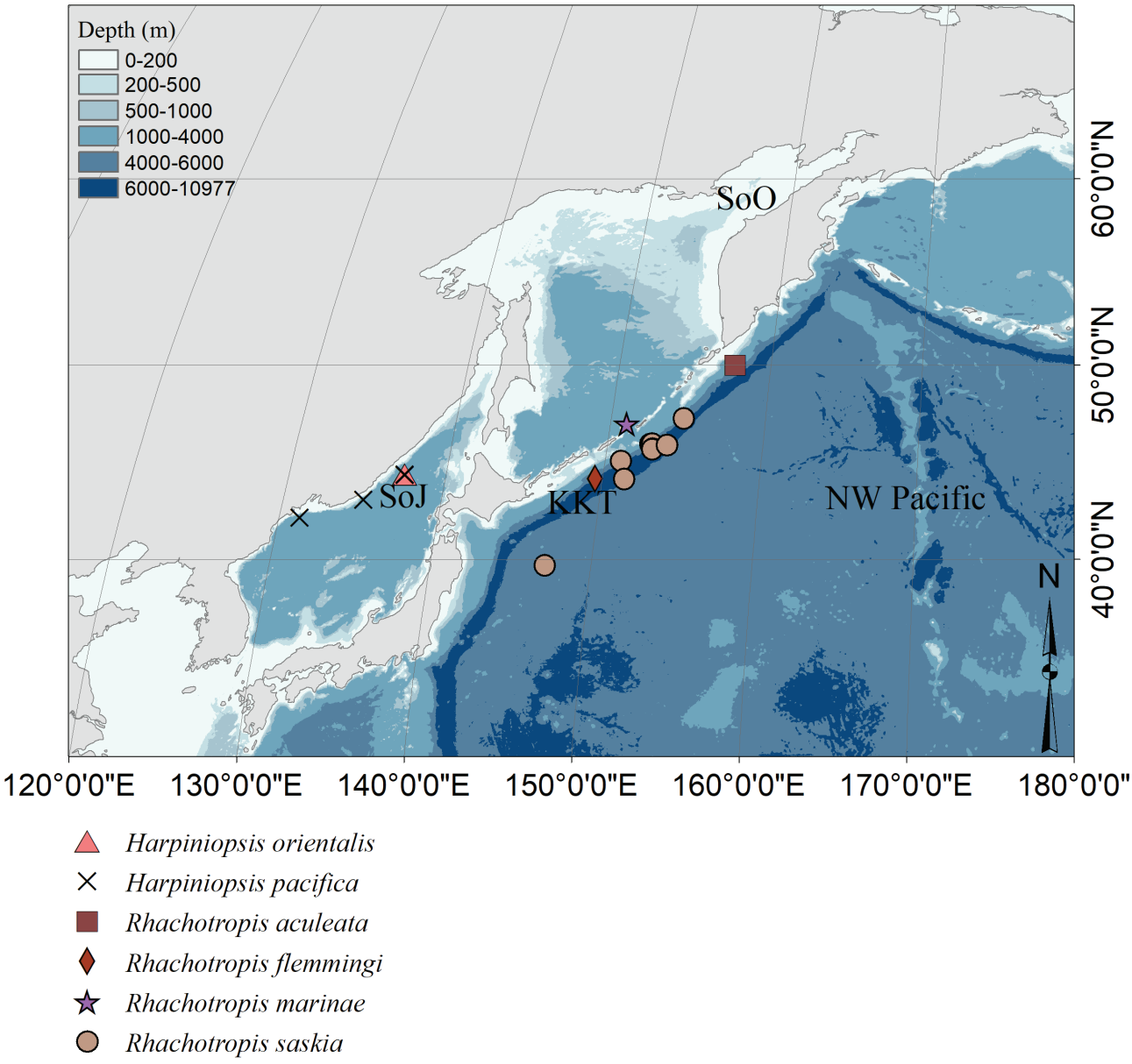
***Harpiniopsis pacifica* (Bulycheva, 1936)**

(Map 3)

Harpiniopsis pacifica was described from a single station situated in the Gulf of Peter the Great at the depth of 1,800–2,300 m and has been reported from the Sea of Okhotsk (Sirenko 2013). Further records of the species come from the SoJaBio expedition when it was collected at four stations in the depth range 2,511–2,683 m (Golovan et al. 2013).

Family Urothoidae Bousfield, 1979

This family groups 64 relatively small-sized, infaunal species distributed in six genera



Map 3. Distribution of species of Eusiridae and Phoxocephalidae in the NW Pacific. Only records deeper than 2,000 m are included on the map. SoJ - Sea of Japan, SoO - Sea of Okhotsk, KKT - Kuril-Kamchatka Trench.

(Lowry and Myers 2017; Brix et al. 2018; Horton et al. 2020). The family has a cosmopolitan distribution and is found from shallow water to abyssal depths (5,780 m) (Barnard and Karaman 1991; Brix et al. 2018; Golovan et al. 2019). In the deep sea of the NW Pacific it was recorded at 19 stations in the depth range from 3,371 to 5,780 in the abyss adjacent to the KKT (Frutos and Jażdżewska 2019; Golovan et al. 2019). No species were reported from the studied area and depth.

Parvorder Lysianassidira Dana, 1849

Superfamily Alicelloidea Lowry & De Broyer, 2008

Family Alicellidae Lowry & De Broyer, 2008

This primarily deep-sea family found down to 8,480 m) consists of six genera and 16 species (Lowry and De Broyer 2008; Lowry and Myers 2017). They are epifaunal, strong-swimming scavengers (Lowry and De Broyer 2008). Apart from being caught in the baited traps (e.g. Shulenberger and Barnard 1976) they were collected also in plankton samples (Birstein and Vinogradov 1955, 1958; Thurston 1990). In the study area individuals have been found in five trawls at abyssal depths (4,859–5,379 m) in the KKT area (Golovan et al. 2019), three plankton samples in the KKT collected from 5,000, 5,500 and 8,000 m to the surface (Birstein and Vinogradov 1955, 1958) and a baited trap deployed in the northernmost part of the Japan Trench (Ritchie et al. 2015). Three species of the genus *Paralicella* Chevreux, 1908 were identified from these samples. Two of them, *P. fusiformis* (Birstein & Vinogradov, 1955) and *P. microps* (Birstein & Vinogradov, 1958), were caught only in plankton samples so they are not considered here. It should be noted that in the recent checklist of NW Pacific invertebrate species (Sirenko 2013) *P. fusiformis* and the family were erroneously reported from the Sea of Okhotsk. A check of original data sources confirmed that this species is found only at hadal depths.

***Paralicella tenuipes* Chevreux, 1908**

(Map 4)

The species was described from the abyss of the Atlantic Ocean and later collected in different deep-sea Atlantic and Pacific localities (e.g. Chevreux 1908; Barnard and Shulenberger 1976; Ingram and Hessler 1983; Thurston 1990; Duffy et al. 2012; Ritchie et al. 2015). In the area considered by present study the species was reported from one baited trap set in the northernmost part of the Japan Trench at a depth of 6,945 m (Ritchie et al. 2015).

Family Valettiopsidae Lowry & De Broyer, 2008

This small family comprises of two genera and 12 species found mainly in the deep sea (183–7,300 m) (Lowry and De Broyer 2008; Lowry and Myers 2017; Horton et al. 2020; Jażdżewska and Mamos 2019). Like species of the Alicellidae these amphipods are epibenthic scavengers possessing good swimming abilities (Lowry and De Broyer 2008). In our area the family was found at three stations in the Sea of Okhotsk and the KKT area at the depths from 3351 to 7,300 m (Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). No species identification is available as yet.

Family Vemanidae Lowry & Myers, 2017

This family consists of a single genus (*Vemana* Barnard, 1964) and four deep-sea species occurring down to 4,077 m (Barnard 1964, 1967; Ledoyer 1986; Lowry and Myers 2017; Horton et al 2020). The family has been recorded from the western Indian Ocean, Northeast Pacific Ocean and the tropical western Atlantic (Lowry and Myers 2017) so the eight records from the abyssal (4,859–5,379 m) of KKT area constitute the first records of this taxon in NW Pacific (Golovan et al. 2019; Jażdżewska and Mamos 2019). The species identification awaits an on-going review of the family (Ed Hendrycks pers. comm.).

Superfamily Aristioidea Lowry & Stoddart, 1997

Family Conicostomatidae Lowry & Stoddart, 2012

This taxon consists of six genera and 19 shelf species (occurring till 232 m) distributed mainly in the southern hemisphere (Lowry and Stoddart 2012; Lowry and Myers 2017; Horton et al. 2020). In our study area it was collected at a single station in the abyss adjacent to the KKT (5,216–5,223 m) (Golovan et al. 2019; Jażdżewska and Mamos 2019). No more detailed identification is available at the date.

Family Pakynidae Lowry & Stoddart, 2012

This cosmopolitan family groups 12 genera and 38 species (Lowry and Myers 2017; Horton et al. 2020). The family has been recorded from shallow waters down to 5,305 m (Lowry and Stoddart 2012; Golovan et al. 2019). In the deep sea of the NW Pacific it was collected at seven stations in the Sea of Okhotsk (3,210–3,352 m) and in the abyss adjacent to the KKT (5,216–5,305 m) (Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). The material awaits identification.

Superfamily Lysianassoidea Dana, 1849

Family Eurytheneidae Stoddart & Lowry, 2004

This family comprises a single genus (*Eurythenes* S. I. Smith in Scudder, 1882) and nine species (Havermans 2016; Lowry and Myers 2017; Horton et al. 2020). Eurytheneids are scavengers and strong swimmers that have been reported at depths down to 8,074 m (Havermans et al. 2013; Eustace et al. 2016) and they were found also in the pelagic realm. In the area in focus the family was recorded at eight localities in the Sea of Okhotsk (three trawls at the depth range 3,210–3,347 m) and in the open Pacific Ocean (five plankton samples from 3,000, 4,000, 4,700, 6,500 to the surface) (Birstein and Vinogradov 1958; Frutos and Jażdżewska 2019). A single species has been reported from the area.

***Eurythenes gryllus* s.l.**

This species has been reported from five stations: one in the Sea of Okhotsk and four in the open Pacific Ocean, all records coming from non-closing midwater trawls (Birstein and Vinogradov 1955, 1958). Additional records of this taxon come from the Bering Sea and the open North Pacific but no detailed geographic information is provided (Gurjanova 1951). It has to be noted that recent reviews of the genus that included morphological and molecular methodology

revealed that *E. gryllus* s.l. is a complex of at least eight species that have different bathymetric and geographic ranges (Havermans et al. 2013; Havermans 2016). As a result, all material from earlier studies requires re-examination.

Family Hirondelleidae Lowry & Stoddart, 2010

This family of scavengers consists of a single genus and 20 predominantly deep-sea species found from 65 to 10,897 m (Lowry and Stoddart 2010; Kobayashi et al. 2012; Lowry and Myers 2017; Horton et al. 2020). In the studied area it was recorded at 11 hadal stations in the KKT (6,000–9,474 m) and one in the northernmost part of the Japan Trench (6,945 m) (Birstein and Vinogradov 1955, 1958; Ritchie et al. 2015; Jażdżewska and Mamos 2019). One species is reported from the area in focus.

***Hirondellea gigas* (Birstein & Vinogradov, 1955)**
(Map 4, Figure 2 C)
The species was described from the Kuril-Kamchatka Trench (Birstein and Vinogradov 1955). It was later recorded in several hadal localities in various North Pacific trenches (Japan, Izu-Ogasawara [=Izu-Bonin], Volcano, Mariana, Yap, Palau, and Philippine trenches) (Kamenskaya 1981, 1997; Ritchie et al. 2015; Li et al. 2019) including the station in the Challenger Deep at 10,897 m (Kobayashi et al. 2012). In the area in focus it is recorded from 11 stations in the KKT at the depths 6,000–9,474 m and one in the Japan Trench (6,945 m) (Birstein and Vinogradov 1955, 1958; Kamenskaya 1997; Ritchie et al. 2015; Jażdżewska and Mamos 2019). The wide geographic distribution of this hadal endemic is confirmed by molecular data because the intraspecific variation of all available COI sequences of this species (from the KKT, Japan, Izu-Ogasawara and Mariana trenches) (Ritchie et al. 2015; Jażdżewska and Mamos 2019) is a p-distance of 0.013, far below the threshold used to separate different amphipod species (e.g. Costa et al. 2009). It should be underlined that Sirenko (2013) in the recent checklist of NW Pacific invertebrate species erroneously included this species and the family in the Sea of Okhotsk. A check of original data sources confirmed that this species has been found only at hadal depths.

Lysianassoidea (Lysianassidae Dana, 1849, Tryphosidae Lowry & Stoddart, 1997, Uristidae Hurley, 1963)
The above listed families that for the purpose of the present study are treated together comprise of 98 genera and 696 species (Lowry and Myers 2017; Horton et al. 2020). They represent various ecological groups and are found at all depths (0–8,744 m) and latitudes (Dahl 1959; Brix et al. 2018; Jażdżewska and Mamos 2019). In the deep sea of the NW Pacific material was found at 46 stations ranging from 2,327 to 8,744 m and worked in the Sea of Japan, the Sea of Okhotsk, the Bussol Strait and the KKT area (Golovan et al. 2013, 2019; Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019). Although common and diverse only four species have been identified from the study area and depth up to the present time.

Family Tryphosidae Lowry & Stoddart, 1997

***Abyssorchomene chevreuxi* (Stebbing, 1906)**
This scavenging species has been recorded from a wide depth range (2,080–6,173 m) in the North Atlantic and South Pacific (Barnard 1961;

Thurston 1990; Horton et al. 2013; Lacey et al. 2016). The only records from NW Pacific come from three samples collected using non-closing plankton nets (Birstein and Vinogradov 1955, 1958). The species was assigned by these authors to *Orchomenella affinis* Holmes, 1908 (= *O. obtusa* Sars, 1891). Shulenberger and Barnard (1976) considered this material to be *Abyssorchomene gerulicorbis* (Shulenberger & Barnard, 1976) however, Thurston (1990) argued that it is more likely to be *A. chevreuxi*. Taking into account uncertainties in the identification of the material from the NW Pacific and its presence in plankton samples only this taxon is not considered in our calculations.

***Schisturella pulchra* (Hansen, 1887)**

This species was described from south of Greenland from the depth range 27–180 m (Hansen 1888) and has been recorded mainly in North Atlantic and the Arctic (Vader and Johnsen 2001). In the NW Pacific it was collected east of Iturup Island (110 m), in the La Pérouse Strait (150 m) and in the Sea of Okhotsk (2,440 m) (Gurjanova 1962) but no exact localities are available. Such disjunct geographic and depth distribution suggests that it could be a complex of species but further investigations are required to confirm this.

Family Uristidae Hurley, 1963

***Anonyx eous* Gurjanova, 1962**

The species was described from the NW Pacific and was regarded as common in the Sea of Okhotsk, the Bering Sea and in the vicinity of the Kuril Islands (no exact localities given). The species was recorded from the depths between 1,000 and 3,000 m in the two studied seas, while in the straits between the Kuril Islands it was collected from 200–380 m depths (Gurjanova 1962).

Uristidae *incertae sedis derjugini* (Gurjanova, 1962)

(Map 4)

This species was described under the name *Anonyx derjugini* from the Sea of Japan from wide depth range (from 2,000 m to the maximal depth of the sea). In the north part of the Sea of Japan it was collected at the depths 250–300 m (Gurjanova 1962). Sirenko (2013) indicated the records of this species in the south part of the Sea of Okhotsk and along northern Kuril Islands. None of these records has detailed coordinates provided. The species was reported recently from six stations (2,511–2,725 m) in the Sea of Japan sampled during SoJaBio cruise (Golovan et al. 2013).

Family Scopelocheiridae Lowry & Stoddart, 1997

This family comprises of 12 genera and 25 mostly scavenging species that have been found in shallow waters and the deep sea (30–9,104 m) (Kilgallen and Lowry 2015; Lowry and Myers 2017; Horton et al. 2020). In our area scopelocheiriss have been found at 15 stations (including three deep plankton samples) in and around the KKT at 4,987–7,120 m (Birstein and Vinogradov 1958; Kamenskaya 1997; Golovan et al. 2019; Jażdżewska and Mamos 2019). Only one species has been identified to date.

***Bathycallisoma schellenbergi* (Birstein & Vinogradov, 1958)**

(Map 4, Figure 2 D)

The species was described from material collected by ring trawl in the Kuril-Kamchatka and Japan Trenches at the depths of 6580, 7,000 and 8,000 m to the surface (Birstein and Vinogradov 1958). Later, in the area in focus, it was reported from a

single trawl (6,435–6,710 m) by Kamenskaya (1997) and recently from an epibenthic sledge sample at 7,111–7,120 m depth (Jażdżewska and Mamos 2019). The species has been recorded from several deep-sea locations in all three oceans (Japan, Tonga, Kermadec, New Hebrides, Sunda [=Java], Puerto Rico, South Orkney trenches) at depths of 5,600 to 9,104 m (Kilgallen and Lowry 2015). This apparent cosmopolitan distribution is confirmed by molecular data. Available COI sequences of specimens from the Puerto Rico Trench are very similar to those from specimens collected in the Kermadec, New Hebrides and Kuril-Kamchatka trenches (Ritchie et al. 2015; Jażdżewska and Mamos 2019). The overall variation of these sequences is covered by a p-distance of 0.008, while the p-distance between sequences derived from Atlantic and Pacific sources is 0.013. Both values are much below the threshold used to delimitate species within the Amphipoda (e.g. Costa et al. 2009).

Superfamily Stegocephaloidea Dana, 1852

Family Stegocephalidae Dana, 1852

This family of mainly benthopelagic species consists of 26 genera and 110 species that are found from intertidal to 8,015 m (Berge and Vader 2001; Lowry and Myers 2017; Brix et al. 2018; Horton et al. 2020; Jażdżewska and Mamos 2019). The family has been found at 22 deep-sea localities in the Sea of Japan, the Sea of Okhotsk, the Bussol Strait, the Bering Sea and the open Pacific Ocean (Gurjanova 1962; Golovan et al. 2013, 2019; Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019). The depth range of these localities is 2,440–8,015 m. Only a single species has been identified from the area.

***Stegocephalus longicornis* (Gurjanova, 1962)**

The species description was based on two individuals collected in the Bering Sea at the depth of 2,440 m, but no exact locality was provided (Gurjanova 1962).

Parvorder Oedicerotidira Ledoyer, 1973

Superfamily Oedicerotoidea Lilljeborg, 1865

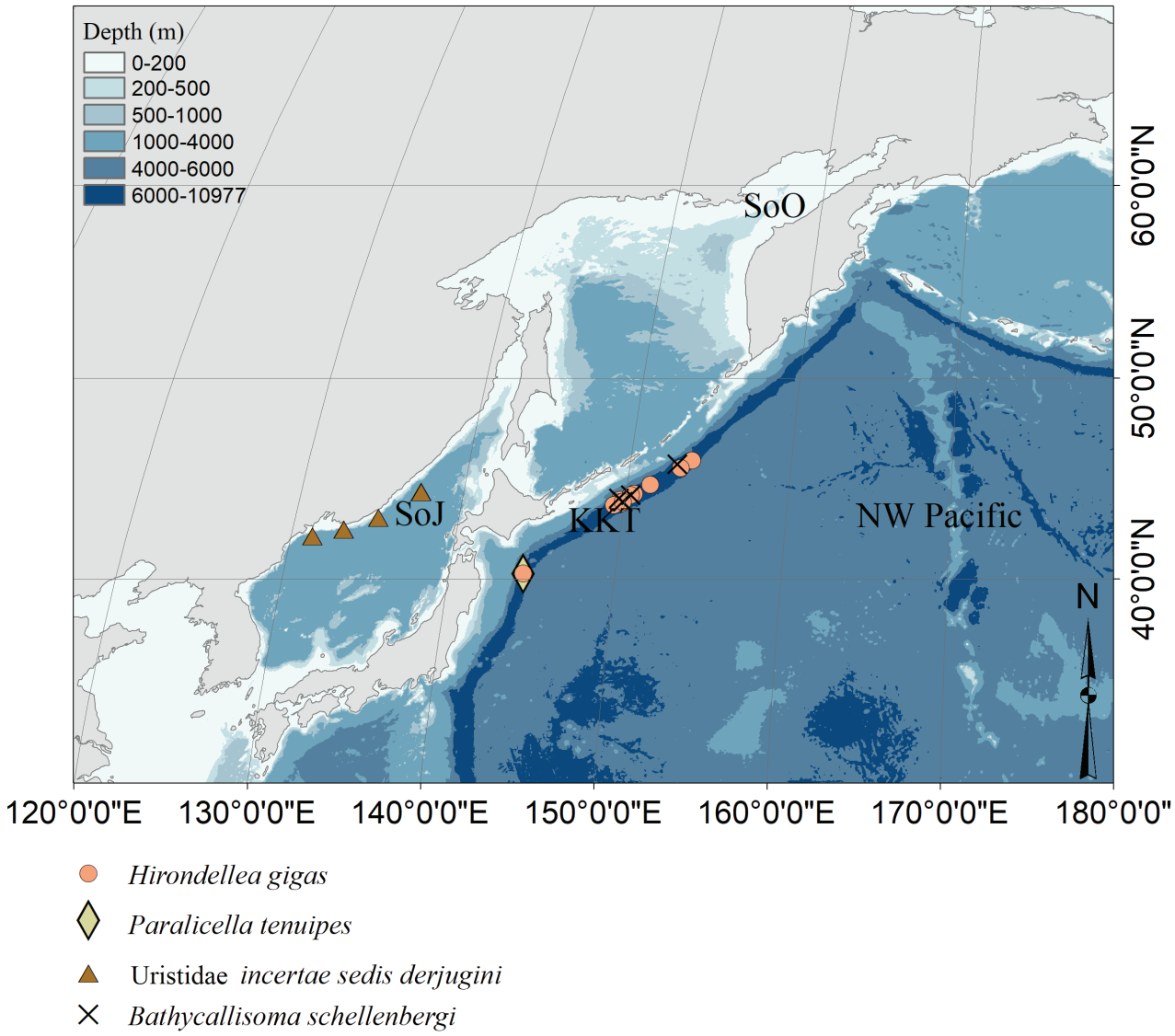
Family Oedicerotidae Lilljeborg, 1865

(Figure 2 E)

The family consists of 46 genera and 246 infaunal species (Lowry and Myers 2017; Brix et al. 2018; Horton et al. 2020). Oedicerotids constitute an abundant and diverse component of benthic communities at all latitudes and have been recorded as deep as 8,186 m (Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019). In the deep sea of the NW Pacific the family was recorded at 47 stations in the Sea of Okhotsk, Bussol Strait, the Sea of Japan and the KKT area at the depth range from 2,327 to 8,186 m (Kamenskaya 1997; Golovan et al. 2013, 2019; Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019). Only one species occurring below 2,000 m has been identified to date from the area in focus.

***Westwoodilla abyssalis* Gurjanova, 1951**

This species was described from a single station in the Bering Sea at the depth 2,900 m but no exact locality data were provided (Gurjanova 1951). The presence of this species at shelf depths in the south-eastern Bering Sea was recorded by Coyle et al. (2007).



Map 4. Distribution of species of Alicellidae, Hirondelleidae, Scopelocheiridae, and Uristidae in the NW Pacific. Only the records deeper than 2,000 m are included on the map. SoJ - Sea of Japan, SoO - Sea of Okhotsk, KKT - Kuril-Kamchatka Trench.

Parvorder Synopiidira Dana, 1852

Superfamily Dexaminoidea Leach, 1814

Family Atylidae Lilljeborg, 1865

This family comprises six genera and 40 species distributed worldwide and reaching beyond abyss (6,330 m) (Barnard and Karaman 1991; Kamenskaya 1997; Horton et al. 2020). In the KKT area one species from this family has been reported from one abyssal station (5,200 m) (Kamenskya 1997).

Aberratylus aberrantis (J.L. Barnard, 1962)

(Map 5)

The species was described from the Cape Basin at 4,893 m (Barnard 1962). Records come from a wide geographic range: North and South Atlantic, North Indian Ocean, Northwest and Southwest

Pacific (Barnard 1964, 1973; Kamenskaya 1997) and a depth range of 1,421 to 6,330 m. In the NW Pacific it has been collected once in the abyss adjacent to the KKT at a depth of 5,200 m (Kamenskaya 1997). The wide geographic and bathymetric distributions suggest that the species should become the focus of more detailed study to confirm or reject its cosmopolitanism.

Family Lepechinellidae Schellenberg, 1926

This family includes five genera and 41 species distributed worldwide and reaching hadal depths (8,015 m) (Kamenskaya 1997; Lowry and Myers 2017; Horton et al. 2020; Lörz et al. 2020). The family has been reported from 16 stations in the Sea of Okhotsk and the KKT area from the depths 2,770–8,015 m (Birstein and Vinogradova 1960; Kamenskya 1997; Frutos and Jażdżewska 2019 [as Atylidae]; Golovan et al. 2019; Jażdżewska and Mamos 2019 [as Atylidae]). Three species in one genus are known to occur in the area in focus.

Lepechinella arctica Schellenberg, 1926

(Map 5)

The species description was based on a single individual collected in the Arctic Ocean at 1,000 m depth (Schellenberg 1926) and subsequently has been reported from various North Atlantic localities in the depth range 301–2,567 m (Lörz et al. in review). It was also recorded at 140–200 m depth during ecological studies conducted in the Barents Sea (Zimina and Lyubina 2016). The record from NW Pacific comes from the single station at 2,770–2,820 m depth where it was collected with another *Lepechinella* species (Kamenskaya 1997). The recent review of North Atlantic lepechinellids underline that during the description *L. arctica* was not properly illustrated because the drawings of habitus, mouthparts and telson were missing (Johansen and Vader 2015; Lörz et al. in press). The latter authors show that some of the characters used for species identification are subject to ontogenetic variation thus complicating correct identification. These issues suggest that the identification of *L. arctica* from the KKT area requires confirmation.

Lepechinella uchu J.L. Barnard, 1973

(Map 5)

The species was described from the central East Pacific (Barnard 1973). The only additional record comes from the NW Pacific where it was collected at single station (2,770–2,820 m) together with above mentioned *L. arctica* (Kamenskaya 1997). The coexistence of different lepechinellid species in the same localities has been noted in the North Atlantic (Thurston 1980; Lörz et al. in press).

Lepechinella ultraabyssalis Birstein & Vinogradova, 1960

(Map 5, Figure 2 F)

The species was described from a hadal station (6,475–6,571 m) in the KKT (Birstein and Vinogradova 1960) and later reported again, also from the KKT at 7,795–8,015 m (Kamenskaya 1997). During the KuramBio II expedition it was collected at three stations in the KKT area at the depths from 5,119 to 7,300 m (Jażdżewska and Mamos 2019).

Family Dexaminidae Leach, 1814

The family consists of 12 genera and 127 species that generally are recorded from shelf or shallow bathyal depths (to 548 m) (Barnard and Karaman 1991; Lowry and Myers 2017; Horton et al. 2020). In the area in focus dexaminids were found at

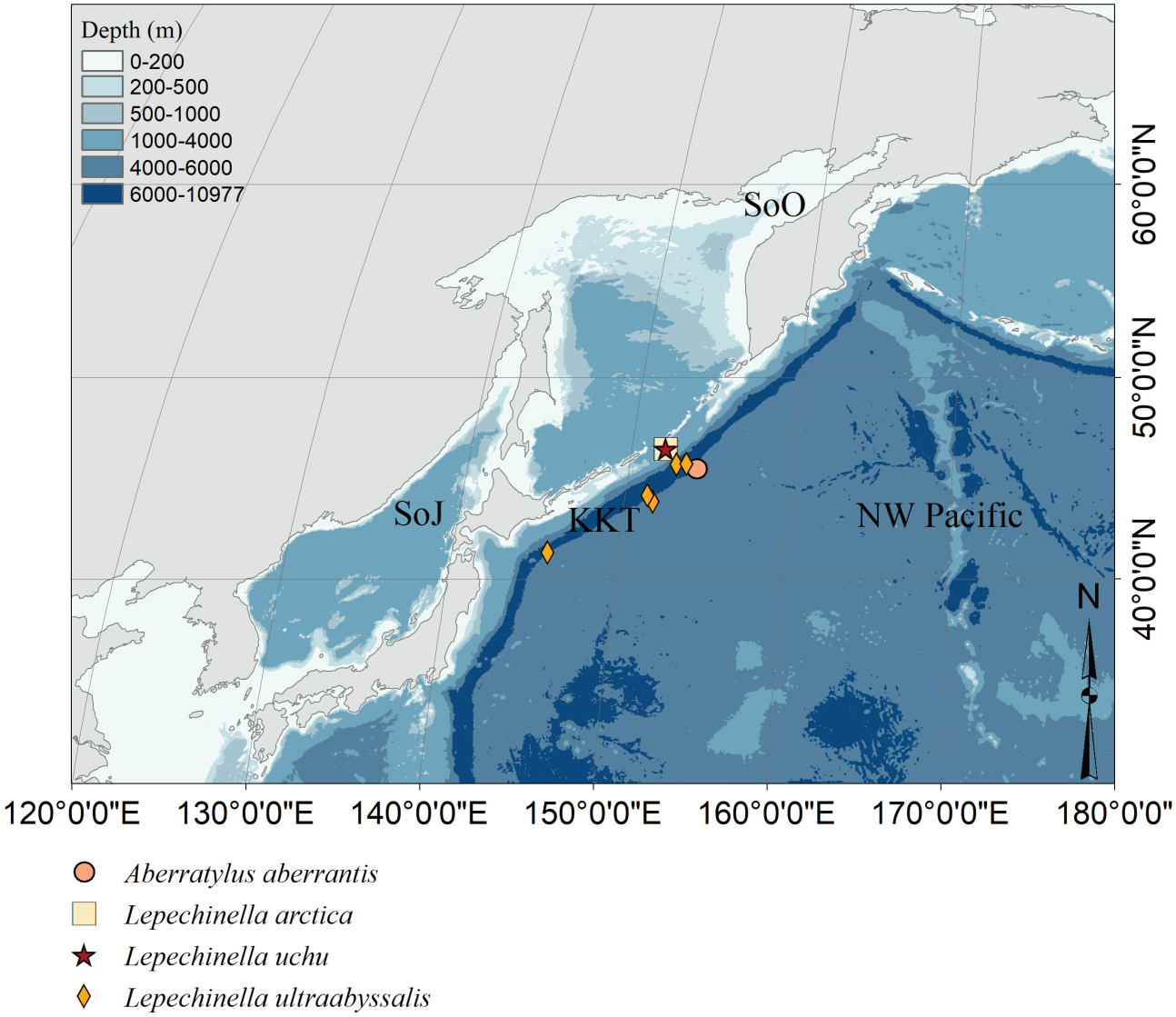
two stations in the Bussol Strait at the bathyal depths (2,327–2,336 m), considerably extending the known depth range of the family (Frutos and Jażdżewska 2019). No further identification has been undertaken to date.

Family Melphidippidae Stebbing, 1899

Only four genera and 18 species are recognized in the family Melphidippidae (Lowry and Myers 2017; Horton et al. 2020). The family has been recorded down to 3,377 m (Frutos and Jażdżewska 2019). In the area of study melphidippids were collected at three stations in the Sea of Okhotsk and on the continental side of the KKT at 3,210–3,377 m (Frutos and Jażdżewska 2019) but more detailed identification remains to be completed.

Family Pardaliscidae Boeck, 1871

This family groups 22 genera and 73 species that present clear deep-sea preferences (Birstein and



Map 5. Distribution of species of Atylidae and Lepechinellidae in the NW Pacific. SoJ - Sea of Japan, SoO - Sea of Okhotsk, KKT - Kuril-Kamchatka Trench.

Vinogradov 1962; Lowry and Myers 2017; Horton et al. 2020). The deepest record of the family comes from Mariana Trench from 10,911 m (Li et al. 2019). Pardaliscids are common in our area of focus, having been obtained at 56 stations sampled at depths of 2,327 to 9,583 m in the Sea of Japan, the Sea of Okhotsk, the Bussol Strait and the KKT area (Birstein and Vinogradov 1955, 1958; Kamenskaya 1997; Golovan et al. 2013, 2019; Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019). Three species from two genera have been identified so far.

***Halice quarta* Birstein & Vinogradov, 1955**

(Map 6, Figure 2 G)

The species was described from the KKT from a sample collected at 6,400–9,000 m (Birstein and Vinogradov 1955). Subsequently it has been reported from plankton catches in the KKT, Izu-Ogasawara (=Izu-Bonin), Mariana and Tonga trenches sampled from hadal depths to the surface (Birstein and Vinogradov 1958, 1960). Further records of the species come from three stations sampled during KuramBio II expedition (8,193–9,582 m) (Jażdżewska and Mamos 2019). In addition, *H. quarta* was reported recently from the Mariana Trench as *Halice* sp. MT-2017 where it was found at eight stations worked at 10,893–10,911 m (Li et al. 2019) confirming its hadal nature.

***Princaxelia abyssalis* Dahl, 1959**

(Map 6)

This species was described from Kermadec Trench from depths of 6,620–8,300 m (Dahl 1959) and subsequently recorded from the Aleutian, Kuril-Kamchatka, Japan, Izu-Ogasawara (=Izu-Bonin), Yap, Philippine and Bougainville trenches (Kamenskaya 1981, 1997). In the KKT it was found at seven stations at 6,435 to 9,530 m (Kamenskaya 1997).

***Princaxelia jamiesoni* Lörz, 2010**

(Map 6, Figure 2 H)

The species was described from the Japan and Izu-Ogasawara (=Izu-Bonin) trenches at depths of 7,703–9,316 m and observed *in-situ* in these two trenches (Lörz 2010; Jamieson et al. 2012). During the KuramBio II expedition it was collected at four stations in the depth range 7,055–9,583 m (Jażdżewska and Mamos 2019). Both *Princaxelia abyssalis* and *P. jamiesoni* have many similarities and show similar distribution in the KKT. Therefore, it cannot be excluded that they represent single species; however, more analyses are required to confirm this assumption.

Superfamily Synopioidea Dana, 1852

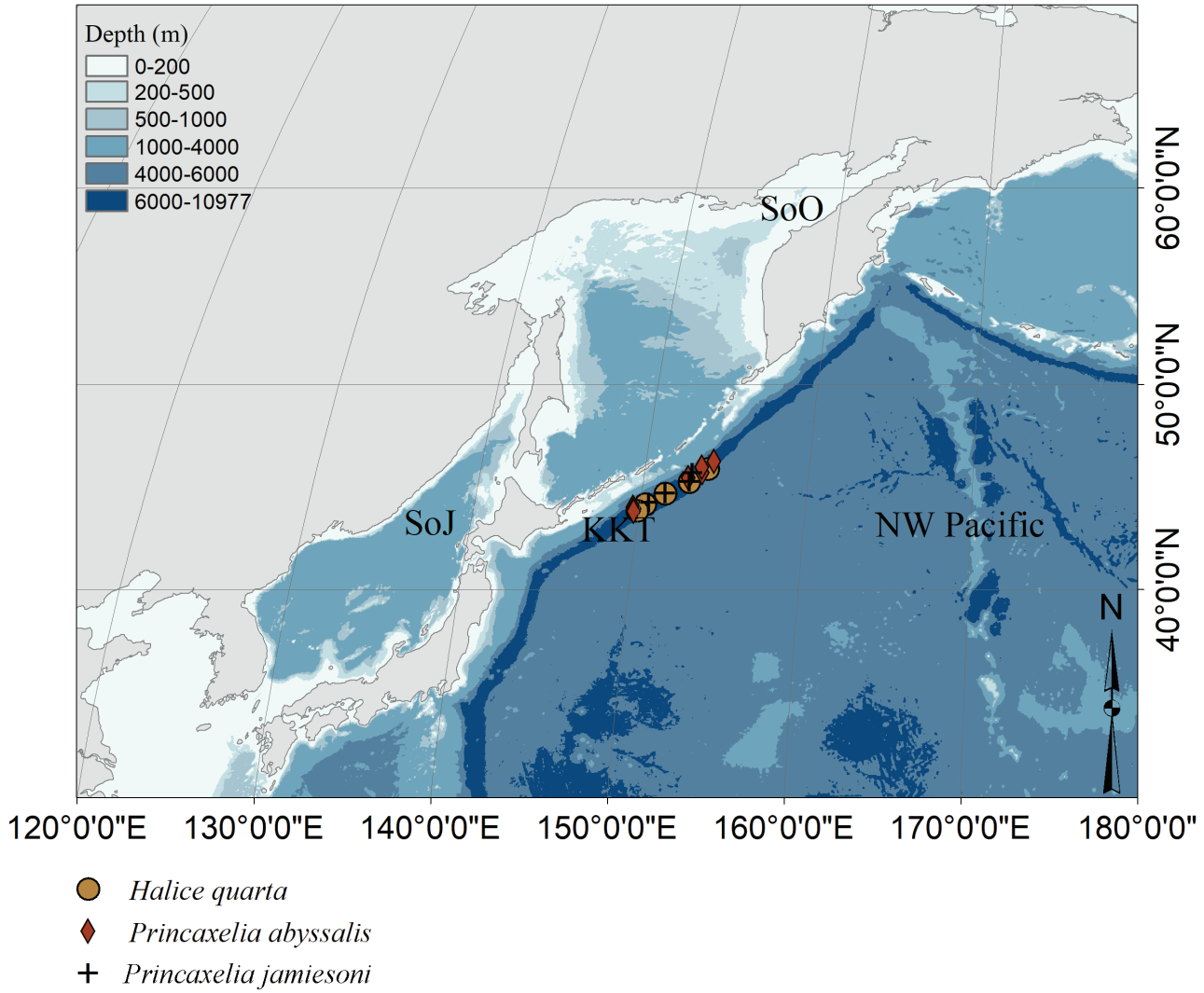
Family Ampeliscidae Krøyer, 1842

This family consists of 312 generally tube-dwelling and suspension-feeding species grouped in four genera (Lowry and Myers 2017; Brix et al. 2018; Horton et al. 2020). The family is known from sublittoral to abyssal depths (to 6,571 m) (Barnard and Karaman 1991; Kamenskaya 1997). In the deep sea of the NW Pacific ampeliscids were collected at 16 stations in the Sea of Okhotsk, the Bussol Strait and the open Pacific Ocean at 2,327 to 6,571 m (Margulis 1967; Kamenskaya 1997; Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). Seven species from three genera have been reported from this area.

***Ampelisca eoa* Gurjanova, 1951**

(Map 7)

The species was described from the Bering Sea at the depth of 1,000 m (Gurjanova 1951) and later recorded in Baja California from the depth range 421–3,178 m (Barnard 1967). It was



Map 6. Distribution of species of Pardaliscidae in the NW Pacific. SoJ - Sea of Japan, SoO - Sea of Okhotsk, KKT - Kuril-Kamchatka Trench.

also found at shelf depths in the Sea of Okhotsk (Budnikova and Bezrukov 2003, 2015). In the NW Pacific, below 2,000 m, it was recorded from a single station at 2,940 m on the continental side of the KKT (Margulis 1967).

***Ampelisca furcigera* Bulycheva, 1936**

(Map 7)

It was described from the shelf of the northern Sea of Japan (60–205 m) (Bulycheva 1936) and later it was reported from various shelf and upper bathyal localities in the Sea of Japan, the Sea of Okhotsk, the Bering Sea, and California (60–1,248 m) (Gurjanova 1951; Barnard 1967; Budnikova and Bezrukov 2003, 2015). There is only a single record of this species below 2,000 m, which comes from the continental side of the KKT (2,795 m) (Margulis 1967).

***Ampelisca plumosa* Holmes, 1908**

(Map 7)

The species was described from the East Pacific from 1,130–1,220 m (Holmes 1908). Further records come from Baja California and Cedros Trench at 813–2,667 m (Barnard 1967). In the area of this study *H. plumosa* has been recorded at three sta-

tions deeper than 2,000 m (2,795–3,388 m) and five above this depth (1,376–1,693 m) (Margulis 1967).

***Ampelisca unsocalae* J.L. Barnard, 1960**

(Map 7)

The species was described from South California at 764 m as a subspecies of *Ampelisca macrocephala* Liljeborg, 1852 and later recorded from California at the depth range 403–2,745 m (Barnard 1960, 1967). In the deep-sea area of the NW Pacific it was found at three stations in the depth range 2,430–4,927 m and one at 1,640 m (Margulis 1967).

***Byblis erythrops* Sars, 1883**

(Map 7)

This species was described from Norwegian waters at depths of 146–183 m (Sars 1883). It was recorded subsequently from different North Atlantic shelf and upper bathyal localities (e.g. Dauvin 1996). The Pacific records also come form rather shallow stations (e.g. Margulis 1963; Budnikova and Bezrukov 2003, 2015). The deep-water records of the species come from three stations in the NW Pacific, but only one of them was below 2,000 m in the studied area (2,430–2,670 m) (Margulis 1967).

***Byblis nana* Margulis, 1967**

(Map 7)

This species was described based on a single ovigerous female collected at the depth 2,795 m on the continental side of the KKT (Margulis 1967). It remains the only record of this taxon.

***Byblisoides arcillis* (J.L. Barnard, 1961)**

(Map 7)

The species was described from the Makassar Strait between Borneo and Sulawesi from 1,560–2,000 m (Barnard 1961). It was also reported from California at 3,315–3,340 m (Margulis 1967). In the area of study it was found at two stations in the open Pacific Ocean (5,005–6,571 m) (Margulis 1967).

Family Synopiidae Dana, 1852

This typical deep-sea family of 17 genera and 108 species has a worldwide distribution and has been found down to 6,228 m (Lowry and Myers 2017; Brix et al. 2018; Horton et al. 2020; Jażdżewska and Mamos 2019). In the area in focus it was collected at 35 stations in the Sea of Okhotsk, the Bussol Strait and the open Pacific Ocean in the depth range 2,327–6,228 m (Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). Species identifications have not been undertaken so far.

Suborder Senticaudata Lowry & Myers, 2013

Parvorder Caprellidira

Superfamily Caprelloidea Leach, 1814

Family Caprellidae Leach, 1814

This family groups 95 genera and 441 species many of which are epibionts or even commensals (Brix et al. 2018; Horton et al. 2020). Caprellids are known from both shallow and deep waters (to 7,322 m) (Takeuchi et al. 2016; Brix et al. 2018). In the deep sea of the NW Pacific specimens have been recorded at nine stations in the Sea of Okhotsk, the Bussol Strait as well as in the Japan Trench and the KKT area at the depths from 2,327 to 7,322 m

(Takeuchi et al. 2016; Frutos and Jażdżewska 2019; Golovan et al. 2019). One species has been identified from the studied area so far.

***Abyssododecas styx* Takeuchi, Tomikawa & Lindsay, 2016**

This species was described recently from five stations in the northernmost part of Japan Trench at depths of 5,313–7,322 m (Takeuchi et al. 2016). These are the only records of the species so far.

Family Dulichiidae Dana, 1849

This family consists of 30 species grouped in seven genera (Myers and Lowry 2003; Horton et al. 2020). The family is widely distributed in the World Ocean found down to 7,300 m (Jażdżewska and Mamos 2019). In our region dulichiids were collected at 19 stations in the Sea of Okhotsk, abyss adjacent to KKT and the trench itself from the depth range 3,299–7,300 m (Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019). No species identifications are available as yet.

Corophiida (includes superfamilies: Aoroidea, Corophioidea, Photoidea)

The above listed superfamilies that for the purpose of the present study are treated together comprise of 163 genera and 1,254 species (Horton et al. 2020). Although the deepest record of the Corophiida is 8,193 m (Jażdżewska and Mamos 2019), they are mainly shelf or bathyal, weakly motile amphipods often building tubes in which they live (Barnard 1964; Brix et al. 2018). In the deep sea of the NW Pacific they have been found at 37 stations ranging from 2,430 to 8,193 m in the Sea of Japan, the Sea of Okhotsk, the Bussol Strait and the KKT area (Kamenskaya 1997; Golovan et al. 2013, 2019; Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019). Only one species has been reported from the area in focus so far.

Superfamily Aoroidea

Family Unciolidae

***Neohela pacifica* Gurjanova, 1953**

The species was described from the shelf of the Sea of Japan and the Sea of Okhotsk (140–200 m) without exact locations (Gurjanova 1953). Later it was reported from a single station on the continental side of the KKT at the depth 2,430–2,670 m (Kamenskaya 1997). It is the only record of this species below 2,000 m. The wide bathymetric range attributed to this species suggests that a re-examination of the deep-sea material should be undertaken (cf d'Udekem d'Acoz 2007).

Parvorder Hadziidira S. Karaman, 1943

Superfamily Calliopioidea Sars, 1895

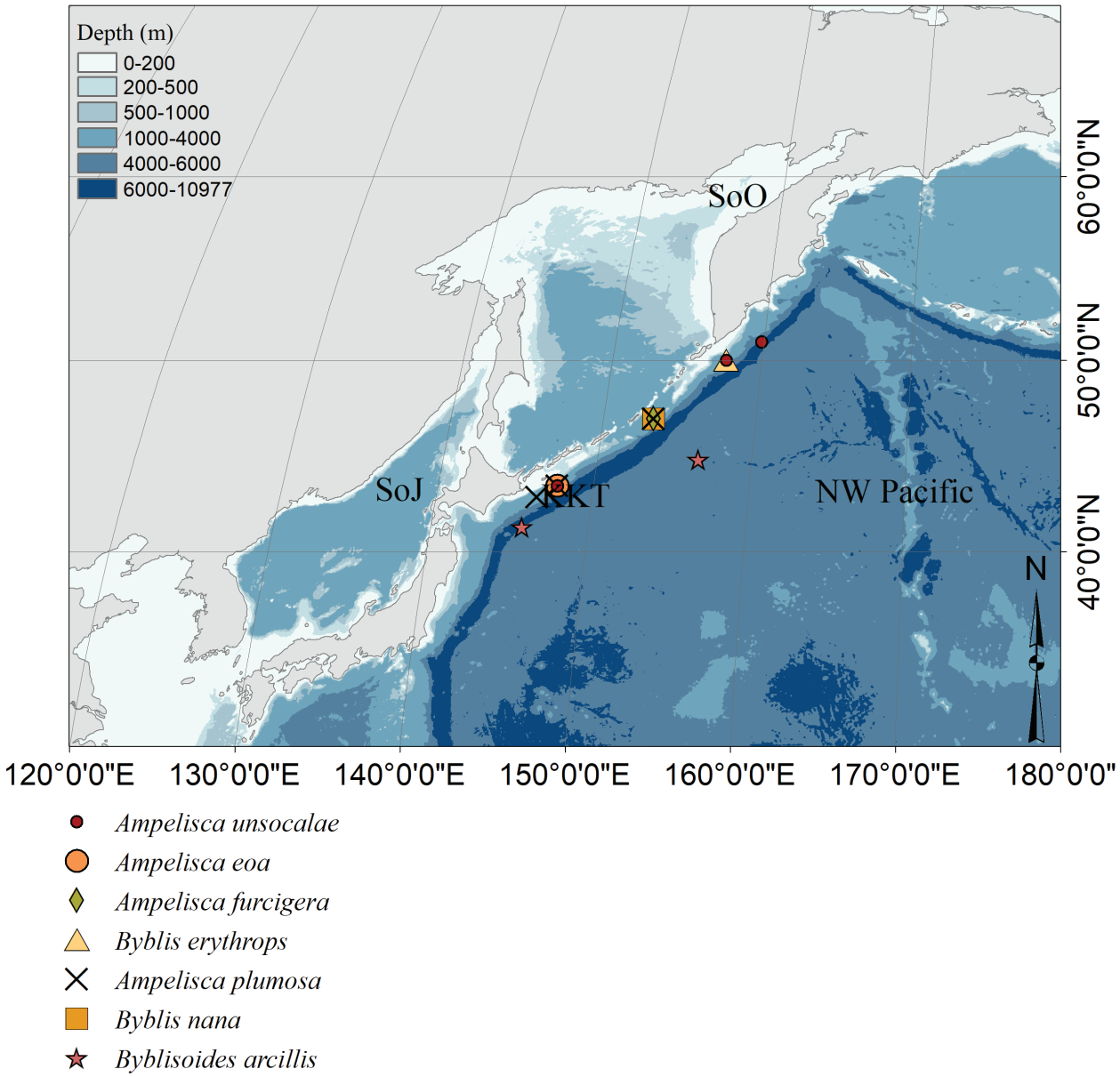
Family Calliopiidae Sars, 1895

This cosmopolitan family, found down to 5,119 m, includes 28 genera and 104 species (Lowry and Myers 2013; Horton et al. 2020; Jażdżewska and Mamos 2019). In the studied area it was collected at seven stations in the Sea of Japan, the Sea of Okhotsk, the Bussol Strait and the KKT area from the depth range 2,545-5,119 m (Golovan et al. 2013, 2019; Frutos and Jażdżewska 2019; Jażdżewska and Mamos 2019). Only one species has been reported from the area in focus so far.

***Leptamphopus sarsi* Vanhöffen, 1897**

(Map 8)

The species was described from the Norwegian coast from the depths of 274–732 m (Sars, 1893). In the North Atlantic it has been recorded from the depth range 200–1,500 m (Vader 1972). In the NW Pacific area it was collected at two stations in the Sea of Japan (517 and 2,545–2,555 m) (Golovan et al. 2013) and reported under the name *Leptamphopus longimanus* (Boeck, 1871). This name is not used anymore. The species described by Boeck (1871) was moved to the genus *Oradarea* Walker, 1903 (Shoemaker 1930). Sars (1893) reported and illustrated additional material from Norway that he assigned to *Amphithopsis longimana* Boeck, 1871 and created the new genus *Leptamphopus* to accommodate it. Vanhöffen (1897) recognized that two separate species were involved and applied



Map 7. Distribution of species of Ampeliscidae in the NW Pacific. Only records deeper than 2,000 m included on the map. SoJ - Sea of Japan, SoO - Sea of Okhotsk, KKT - Kuril-Kamchatka Trench.

the name *Leptamphopus sarsi* Vanhöffen, 1897 to the Sars material. Based on the probability that the Golovan material was identified using Sars (1893) rather than Boeck (1871) it is more likely that the species from the Sea of Japan is *L. sarsi*.

Family Pontogeneiidae Stebbing, 1906

This family groups together 30 genera and 167 species. It has a cosmopolitan distribution and is known to occur down to 9,990 m (Lowry and Myers 2013; Horton et al. 2020). In the deep sea of the NW Pacific it was reported at a single station in the Sea of Okhotsk at 3,330 m (Frutos and Jażdżewska 2019).

Superfamily Hadzioidea S. Karaman, 1943

Family Maeridae Krapp-Schickel, 2008

This family consists of 48 genera and 393 species (Lowry and Myers 2013; Horton et al. 2020). The family has a cosmopolitan distribution but occurs mainly in shallower waters (Krapp-Schickel 2008). The deepest record comes from 8,900 m (Kamenskaya 1981). In the area in focus this taxon was recorded at eight stations at the depths from 3,366 to 8,345 m in the Sea of Okhotsk and the KKT area (Kamenskaya 1997; Schwabe et al. 2015; Frutos and Jażdżewska 2019; Golovan et al. 2019; Jażdżewska and Mamos 2019; Jażdżewska and Ziemkiewicz 2019). Two deep-sea species were cited from the studied area.

***Bathyceradocus hawkingi* Jażdżewska & Ziemkiewicz, 2019**

(Map 8)

This wood-associated species was described from a single station in the abyss adjacent to the KKT (5,217–5,229 m) (Jażdżewska and Ziemkiewicz 2019). The record is unique.

***Metaceradocoides vitjazi* Birstein & Vinogradova, 1960**

(Map 8)

This species was described from KKT and later recorded in the Japan, Izu-Ogasawara (=Izu-Bonin), Yap and Mariana Trenches (Kamenskaya 1997). In the NW Pacific it has been collected at four hadal stations in the KKT (7,210–8,345 m) (Birstein and Vinogradova 1960; Kamenskaya 1981, 1997).

Parvorder Talitridira Rafinesque, 1815

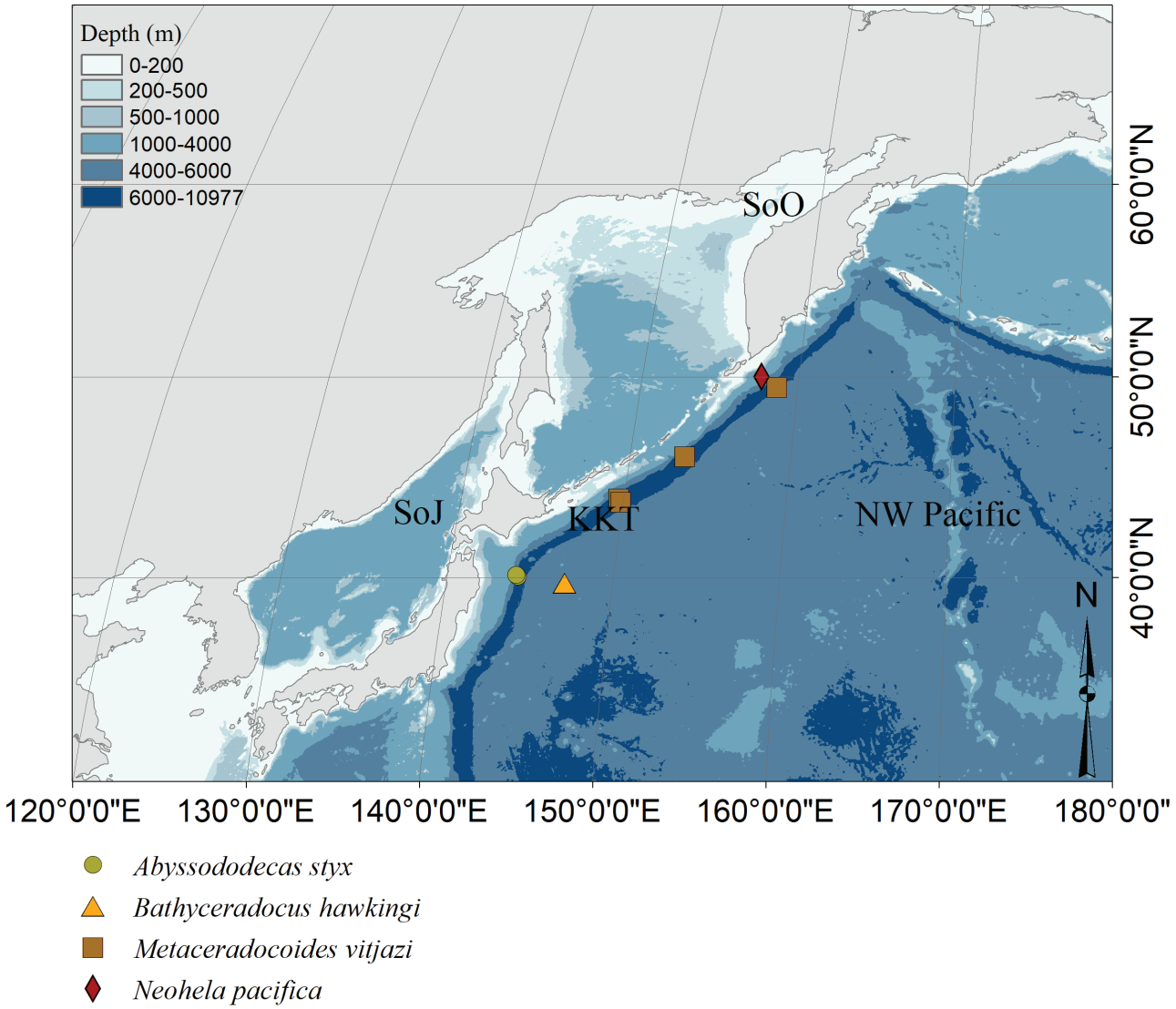
Superfamily Talitroidea Rafinesque, 1815

Family Dogielinotidae Gurjanova, 1953

This family comprises of 11 genera and 38 species (Lowry and Myers 2013; Horton et al. 2020). They are mainly shallow water amphipods (Bousfield 1982). In the studied area the family has been reported from the Sea of Japan from two stations at the depths 470–528 m and one at the depth 2,545–2,555 m (Golovan et al. 2013). The latter is the deepest known record of the family but it should be noted that the identification was treated by authors as uncertain.

5.2. Richness and bathymetric patterns at the family, genus and species level

The 35 amphipod families listed here are in most cases widespread in the deep sea (Brandt 1997; Brandt et al. 2005; Brix et al. 2018). Almost half of them occur in the list of the most speciose



Map 8. Distribution of the species of Caprellidae, Unciolidae and Maeridae in the NW Pacific. Only records deeper than 2,000 m are included on the map. SoJ - Sea of Japan, SoO - Sea of Okhotsk, KKT - Kuril-Kamchatka Trench.

amphipod families (Arfianti et al. 2018). Material collected by the four expeditions has added considerably to knowledge of amphipod bathymetry in the deep ocean, both in the NW Pacific and at a wider scale. The distributions of some families have been extended to greater depths, in some cases by a considerable amount. For example, the extension of the depth range in case of the Stenothoidae was 3,000 m, while for the Amphilochidae it was more than 2,500 m. Many families proved to have very wide bathymetric ranges: 16 being present in the study area from middle bathyal to hadal depths and another 10 extending down to abyssal depths. Four families (Scopelocheiridae, Hirondelleidae, Alicellidae, and Vemanidae) showed strong deep-sea affinities (Barnard 1964, 1967; Ledoyer 1986; Lowry and De Broyer 2008; Lowry and Stoddart 2010; Kilgallen and Lowry 2015). These results show that the main amphipod families can occur over very wide depth ranges. Maximum family diversity in the NW Pacific occurred at abyssal

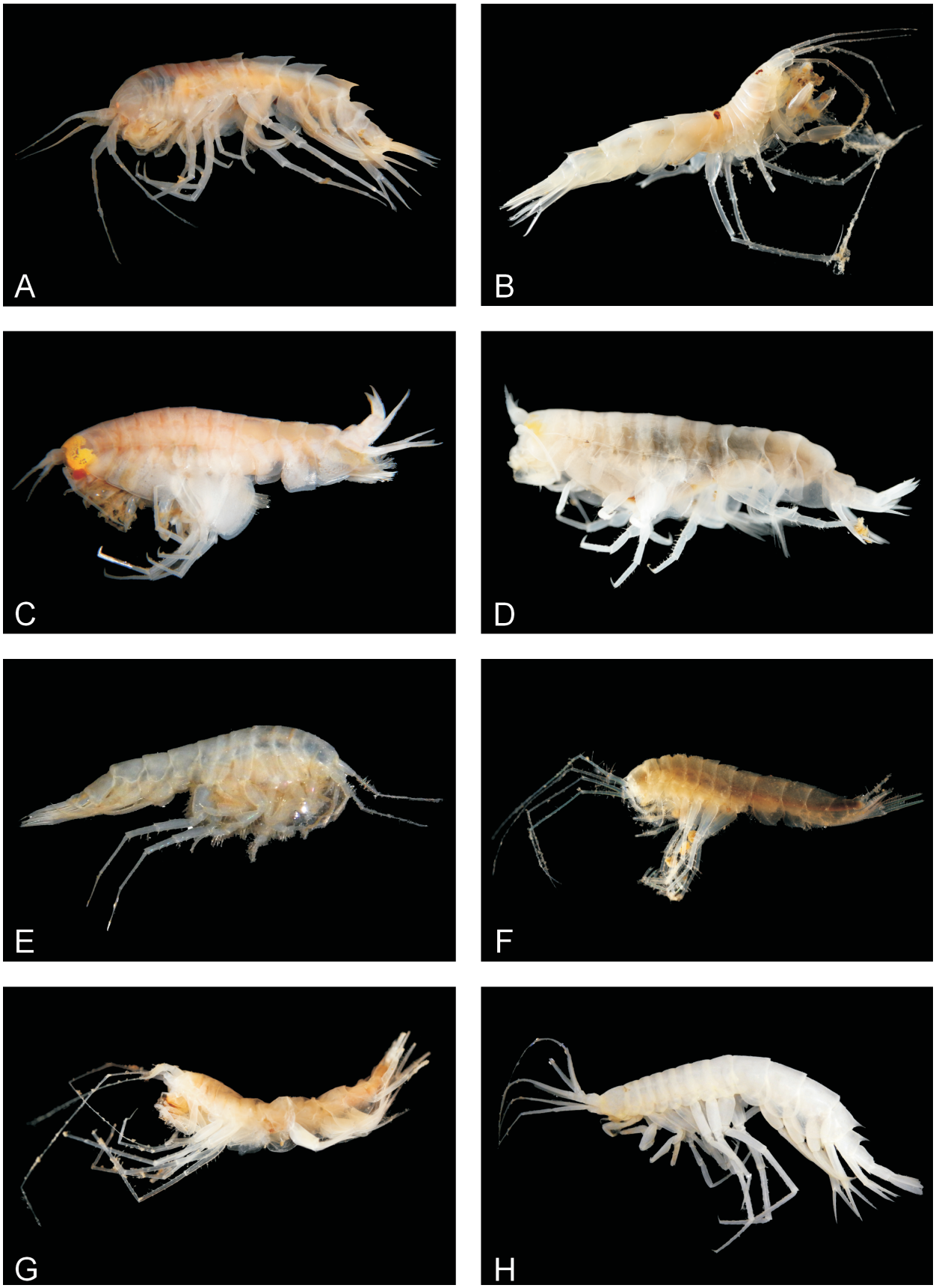


Figure 2. Photographs of freshly collected Amphipoda from the KKT area. (A) *Alexandrella carinata*, (B) *Rhachotropis saskia*, (C) *Hirondellea gigas*, (D) *Bathycallisoma schellenbergi*, (E) Oedicerotidae, (F) *Lepechinella ultraabyssalis*, (G) *Halice quarta*, (H) *Princaxelia jamiesoni*. Pictures A, C, E, H taken by A.M. Jażdżewska, B, D, F, G taken by Ulrike Minzlaff.

depths below which a clear decrease into the hadal zone is evident (Table 1, Figure 1). This pattern is thought to be real but should be treated with a degree of caution. The processing of samples from the four expeditions is incomplete. The largest number of samples where the identification to family level has been undertaken came from 5,000–5,999 m (Table 1), whereas below 6,000 m fewer samples have been studied. More samples from the deepest part of the KKT area remain to be processed (pers. obs.), so an increase in the number of families present in the trench may be expected. The unimodal trend in numbers at the family level parallels that found at the species level in several S Pacific trenches (Lacey et al. 2016). The marked decline in the number of families present at or around 6,000 m, the abyssal-hadal transition zone, suggests that the ecotone established for necrophages across this boundary in the Kermadec Trench (Jamieson et al. 2011) and which appears to exist in the NW Pacific may be a world-wide phenomenon. The bottom topography on the almost flat abyssal plain bottoms differs from that found in trench environments (Jamieson et al. 2011) and is likely to reflect differences in deposition of organic and inorganic material. In a potentially food-poor environment, necrophagy combined with other feeding strategies (Blankenship and Levin 2007; Kobayashi et al. 2012) may be the key to existence at hadal depths.

The 39 species reported from the studied region (Figure 3) constitute almost 10% of all deep-sea species reported from the World Ocean (Jażdżewska 2015). The number of species identified so far is much lower than expected because a morphological study of the amphipods in abyssal samples from the KKT area recognized 79 morphospecies (Golovan et al. 2019) and a molecular study of this collection and some additional samples from the trench revealed 133 Molecular Operational Taxonomic Units (Jażdżewska and Mamos 2019) indicating high diversity in the region. The data on deep-sea species richness are patchy despite a number of circumnavigating expeditions and regional studies. Analyses of the distribution of individual species show that many appear to have wide bathymetric ranges, often exceeding 2,000 m, especially when records from other parts of the world are included (Figure 2). The existence of such apparently eurybathic species has been noted previously (e.g. Thurston 2001; Brandt et al. 2012; Lörz et al. 2018b). The wide bathymetric range of *Rhachotropis saskia* (>3,000 m) has been confirmed genetically (Lörz et al. 2018b); however in case of another amphipod species, *Eurythenes gryllus* s.l. with a depth range of 0–8,074 m, the use of molecular markers has shown it to be a complex of species with narrower depth ranges (Havermans et al. 2013; Havermans 2016). Contrasting resolution of apparent eurybathic distributions emphasizes the need for detailed morphological, and if possible molecular, studies of species reported from shelf to mid-bathyal depths.

This analysis of bathymetric patterns is incomplete and is strongly affected by under-sampling. Sorting of all available samples and full identification of all the resulting material will be required before detailed conclusions can be drawn regarding the general bathymetric distribution of amphipod genera and species in the NW Pacific.

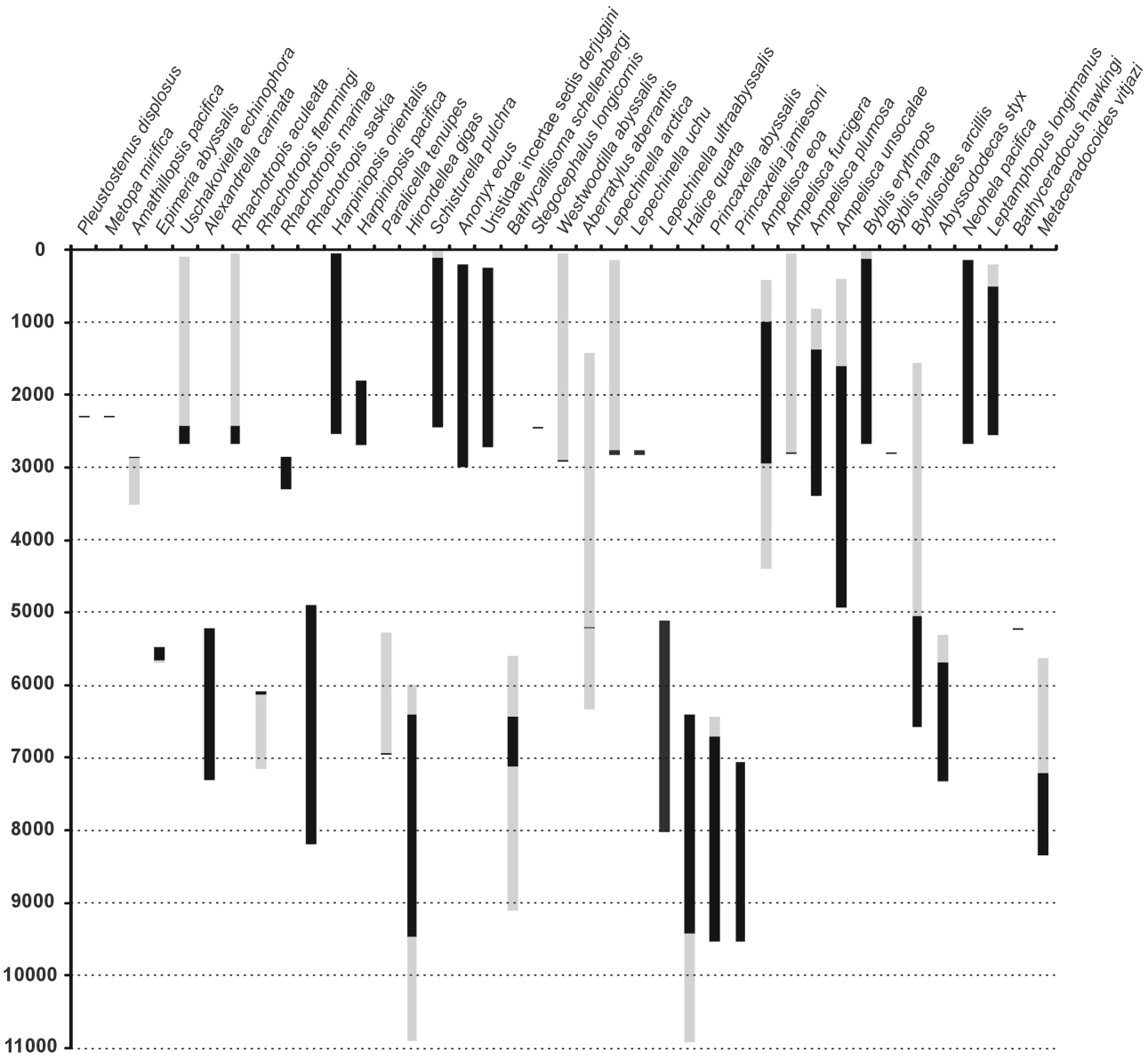


Figure 3. Depth ranges of species recorded deeper than 2,000 m in the NW Pacific. Black bars indicate depth ranges recorded in the study area, grey bars ranges reported from other parts of the World. The species organized according to the classification of Myers and Lowry (2017) and following the order of presentation in the Discussion (subchapter 5.1).

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CHAPTER 19

ISOPODA

A REVIEW ON DISTRIBUTION AND SPECIES-RICHNESS PATTERNS OF ISOPODS ALONG THE NW PACIFIC

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1. Introduction

The Northwest Pacific (NWP), including its marginal seas, used to be amongst the best-studied deep-sea regions worldwide, thanks to the immense effort of Russian scientists who participated in ten expeditions with RV *Vityaz* between 1949 and 1966 (Brandt and Malyutina 2015). These studies targeted mostly abyssal, but also hadal and bathyal benthos. They were the first to collect samples from the Kuril-Kamchatka Trench (KKT), one of the deepest oceanic trenches worldwide (Dreutter et al. 2020), as well as neighbouring trenches from the Aleutian in the north to the Mariana Trench in the south. The Russian work represented a milestone upon which today's deep-sea researchers build. Their historic zoological accounts (Birstein 1963, 1970, 1971; Zenkevich 1963; Kussakin 1971; Belyaev 1972, 1989) represented a major proportion of the globally known species for many deep-sea taxa at that time. Still today, the fauna of this region is thus well studied.

Beginning with the Russian-German joint expedition "SoJaBio" with the Russian RV '*Akademik M.A. Lavrentyev*' in 2010 to the Sea of Japan (Malyutina et al. 2010; Malyutina and Brandt 2013), this deep-sea region received new attention. Altogether, four joint campaigns have since been conducted to the NWP and adjacent marginal seas with support from both the German and Russian governmental research-funding agencies (Map 1). After SoJaBio, the abyssal Northwest Pacific Basin near the KKT and the slopes of the KKT were studied during "KuramBio" in 2012, with the German RV '*Sonne*' (Brandt and Malyutina 2012, 2015). In 2015, the RV '*Akademik M.A. Lavrentyev*' set out to study the deepest, southernmost part of the Sea of Okhotsk, the Kuril Basin and the Bussol Strait, featuring a bathyal connection to the open Pacific during the SokhoBio expedition (Malyutina et al. 2015); and in 2016, again on RV '*Sonne*', the KKT itself as well as its neighbouring abyssal areas were studied (Brandt et al. 2016; Brandt et al. 2020). These projects investigated the diversity and distribution of the benthic fauna in each studied area, and in what way various factors of isolation, including hadal depths of the trench, determine distribution patterns.

The crustacean order Isopoda Latreille, 1817 is one of the most frequent and diverse taxa at all depths of world oceans from the intertidal to hadal zones. Their contribution to overall diversity is especially important at great depths where they represent one of the dominant macrobenthic taxa. This is mostly due to the contribution of the suborder Asellota and its superfamily Janiroidea Sars, 1897, which is remarkably diverse and includes 20 deep-sea families (Menzies 1962; Wolff 1962; Hessler 1970; Kussakin 1988, 1999, 2003). Within the Isopoda, two opposing depth-diversity trends have been observed: the diversity of the suborder Asellota increases with depth while the diversity of other higher taxa decreases (Wilson 1998). In many deep-sea basins almost the entire isopod fauna consists of the Asellota (Thistle and Wilson 1987; Brandt et al. 2004, 2007; Wilson 2008b; Kaiser et al. 2009; Meyer-Löbbecke et al. 2014; Elsner et al. 2015; Golovan et al. 2019).

The dominant families of the deep-sea Asellota belonging to the superfamily Janiroidea are cosmopolitan and common throughout the world oceans. They have diversity and abundance

maxima at bathyal and abyssal depths. Some species are also found on the continental shelves up to the intertidal zone in the cold waters of both hemispheres and in hadal depths down to 10,687 m (Munnopsidae, Haploniscidae) and 10,710 m (Macrostylidae) (Hessler 1970; Hessler et al. 1979; Hessler and Wilson 1983; Wilson 1983c, 1989; Belyaev 1989; Svavarsson et al. 1993; Malyutina and Kussakin 1996; Brandt et al. 2004).

Isopods are, like all Peracarida, crustaceans that lack a planktonic developmental stage (with the exception of specialized parasitic taxa). Isopod females carry their developing offspring (from eggs via embryos through an early juvenile stage) in a brood chamber on the ventral side of the anterior pereon (the isopod trunk featuring the legs are dedicated to locomotion). The post-larval juveniles released from the brood chamber are referred to as manca. These mancae differ from adults in their small size, the underdeveloped or sometimes absent seventh pereonite, as well as missing seventh limbs. Because a dispersive larval stage is lacking, this developmental biology is generally considered to impede the isopods' dispersal capacities and, consequently, their gene flow, when compared with taxa that have a dispersive planktonic stage. Considering this, the wide distribution of deep-sea isopods is of interest for studying the mechanisms of dispersal of the abyssal benthic fauna.

1.1. Deep-sea isopods of the Northwest Pacific

At least 15 families of the isopod superfamily Janiroidea have been recorded for the NWP (Birstein 1963, 1970, 1971; Golovan et al. 2013, 2019; Elsner et al. 2015; Golovan 2018). Although in the abyss of the NWP, like in other regions, almost the entire isopod fauna (>90% ind.) was represented by Asellota (Golovan et al. 2019), some representatives of other isopod suborders have also been collected from the NWP deeper than 2,000 m. Thirteen species of Valvifera, one of Sphaeromatidea and four of Cymothoida are known from the NWP.

In the NWP below 2,000 m isopods are represented by >120 described species. One hundred and six species were described or identified based on the *Vityaz* collections and 19 species were described based on the materials of the recent Russian-German expeditions (Gurjanova 1933; Birstein 1963, 1970, 1971; Kussakin 1982, 1988, 1999, 2003; Brandt et al. 2015b; Elsner et al. 2015; Golovan 2015a, 2015b; Malyutina 2015; Bober et al. 2018c; Golovan et al. 2018a; Malyutina and Brandt 2018; Golovan and Malyutina 2019). Moreover, about 80% of about 300 species collected during the recent expeditions were new to science and still undescribed. In total they comprise 70 genera, in 18 families and four suborders. The suborder Asellota comprised 98% of isopod specimens and 90% of described species. Part of the material from previous expeditions has not yet been identified to species level, and further expeditions are planned. Therefore, the list of species will likely be expanded in the future.

Herein, we deal with the families Dendrotionidae Vanhöffen, 1914, Desmosomatidae Sars, 1897; Macrostylidae Hansen, 1916, as well as Munnopsidae Lilljeborg, 1864. While the former family is rather small, the latter three belong to the most abundant isopod groups in the NWP (Elsner et al. 2015; Malyutina and Brandt 2015, 2018,

2020; Golovan et al. 2019). Due to the enormous abundance and diversity of the Isopoda, not all groups could be treated here.

Dendrotionidae Vanhöffen, 1914

Biology/Ecology & Habitat

Dendrotionidae is a small family of asellotes with a peculiar morphology. They have been hypothesized to be commensals of sponges (Hansen 1916; George 2004).

Geographic Distribution

Dendrotionids are usually not frequently encountered; however, in the abyss of the equatorial Atlantic Ocean they have been collected in high abundance (dozens of individuals per epibenthic-sledge sample) in the Vema Fracture Zone (Brandt et al. 2015a). The family includes 25 described species distributed across three genera: *Dendrotion* G.O. Sars, 1872 (11 species); *Acanthomunna* Beddard, 1886 (10 species), and *Dendromunna* Menzies, 1962 (six species). The family is known from the North Atlantic (10 species), the South Atlantic (two species), the Southern Ocean (1 species), the South Pacific (10 species), and the North Pacific (three species). Representatives of the family have been found at a depth range of 130–6,568 m, while most species occur at bathyal depths (Golovan et al. 2018b).

Within Dendrotionidae, the eye-bearing and rather eurybathic and speciose genus *Acanthomunna* is assumed to have a basal phylogenetic position, while the eyeless deep-sea genus *Dendromunna* is considered to be more derived (Wilson 1976; Raupach et al. 2009). Only two species of the family have been found at shelf depths until now, both of them eurybathic species of the genus *Acanthomunna*, which also occurs at bathyal depths. Two dendrotionid species have been described from abyssal depths, namely *Acanthomunna beddardi* Menzies, 1962 from the South Atlantic (at 4,885 m) and *Dendromunna mirabile* Wolff, 1962 from the South Pacific (Kermadec Trench, at 5,230–5,340 m). In addition, unidentified representatives of the family have been collected in the abyss of the equatorial Atlantic Ocean (at depths up to 6,568 m) during the Vema-TRANSIT expedition (Brandt et al. 2015a).

Desmosomatidae Sars, 1897

General information

Desmosomatidae is one of the largest janiroidean families primarily inhabiting the deep sea. Currently, this group is comprised of over 140 described species distributed across 19 genera (Boyko et al. 2008b; Brix et al. 2015). In several recently studied deep-sea regions, Desmosomatidae were the second-most abundant and speciose isopod family after the Munnopsidae (see below), and in some cases, even dominated the isopod fraction of the macrofauna (Golovan 2015b). Its members are small (usually less than 4 mm) benthic isopods, with a slender and flexible body. They are adapted to living in soft sediments and a predominantly burrowing lifestyle. For burrowing, desmosomatids use their anterior four pairs of pereopods (especially pereopods II and III), which usually bear stout composite setae. When disturbed, desmosomatids use pereopods V–VII to swim backwards. These limbs possess slightly or moderately extended and

flattened carpi and propodi that are equipped with long composite setae (Hessler 1970; Hessler and Strömberg 1989; Kussakin 1999). Little information is available on the general biology of these isopods besides rather limited information about their postmarsupial development (Hessler 1970) and the behaviour of a single species observed under experimental conditions (Hessler and Strömberg 1989). Even basic information, such as their feeding preferences, remains undescribed.

Taxonomic history

The family Desmosomatidae was erected by G.O. Sars (1897) who initially included genera *Desmosoma* G.O. Sars, 1864, *Echinopleura* G.O. Sars, 1897, *Eugerda* Meinert, 1890, *Ischnosoma* G. O. Sars, 1866, *Macrostylis* G.O. Sars, 1864, and *Nannoniscus* G. O. Sars, 1870. The last three genera were separated by Hansen (1916) into three different groups (currently considered families). Hansen also established a group named Pseudomesini for the genus *Pseudomesus* Hansen, 1916. Hessler (1970) described ten new genera of Desmosomatidae in his monograph and provided an extensive revision of the family. As a result, it was divided into two subfamilies, Desmosomatinae Hessler, 1970 and Eugerdellatinae Hessler, 1970, comprising all the genera except *Torwolia* Hessler, 1970. The genus *Torwolia* remained *incertae sedis*, but later it was reassigned to the Desmosomatinae by Brix (2007). The genus *Thaumastosoma* Hessler 1970 was transferred to the family Nannoniscidae Hansen, 1916 by Siebenaller and Hessler (1981). After Hessler's work, four new desmosomatid genera, *Chelibranchus* Mezhov, 1986, *Reductosoma* Brandt, 1992, *Chelantermedia* Brix, 2006 and *Parvochelus* Brix and Kihara, 2015 were described. Later Brix et al. (2015) rejected the genus *Chelibranchus* Mezhov, 1986 as poorly defined and suggested that the type species *C. canaliculatus* Mezhov, 1986 should be considered a *nomen dubium*. Svavarsson (1984) rejected the family Pseudomesidae and transferred its two genera *Pseudomesus* Hansen, 1916 and *Micromesus* Birstein, 1963 to the Desmosomatidae and Nannoniscidae respectively.

Relationships

The family Desmosomatidae is closely related to the family Nannoniscidae, which has been discussed in a number of publications. Particularly, the taxonomic affiliation of the genus *Thaumastosoma* Hessler, 1970 (currently Nannoniscidae) and *Pseudomesus* Hansen, 1916 has been changed several times (Svavarsson 1984; Wägele 1989; Wilson 2008a; Brix et al. 2015).

Biogeography

Desmosomatidae has a global distribution and its members occur in a wide bathymetric range covering 4–6,675 m (Birstein 1970; Kussakin 1999; Boyko et al. 2008b). The largest number of species are concentrated at bathyal and abyssal depths, as well as in cold waters of both hemispheres where some species have secondarily colonized the continental shelves (Hessler 1970; Kussakin 1999; Brix and Svavarsson 2010; Stransky and Svavarsson 2010). Over 40% of the currently described desmosomatid species are known from the North Atlantic, whereas the rest of the known species have been reported from other deep-sea regions, namely from the South Atlantic, the North and South Pacific, and the

polar regions (Boyko et al. 2008b). Hessler (1970) suggested a cosmopolitan distribution of most desmosomatid genera and considered the absence of the family in some deep-sea basins (e.g., in the Indian Ocean) to be the result of insufficient sampling. The data obtained from the NWP during the recent expeditions confirm this conclusion. Thus, during the *Vityaz* expeditions only four desmosomatid species had been collected in this region at depths below 2,000 m (Birstein 1963; Kussakin 1965; Golovan and Malyutina 2010). Nevertheless, as a result of the recent expeditions SoJaBio, SokhoBio, KuramBio and KuramBio II, a rich desmosomatid fauna has been discovered using sampling gear especially developed for collecting macrofauna (e.g., C-EBS (Brandt et al. 2013)). More than 90% of the collected species were new to science.

Macrostylidae Hansen, 1916

The first species of this family recorded and described, *Macrostylis spinifera* G. O. Sars, 1864, was assigned to the Desmosomatidae (Sars 1864, 1899), before sufficient evidence had been uncovered to justify the erection of a distinct family for the genus *Macrostylis* G. O. Sars, 1964 (Hansen 1916). Meanwhile, Meinert (1890) described a second and rather similar species and allocated it to a separate genus named *Vana* Meinert, 1890, probably unaware of G. O. Sars' earlier description. G.O. Sars synonymized the only species of *Vana*, *V. longiremis* Meinert, 1890, with *M. spinifera*. However, it was reinstated as *Macrostylis longiremis* (Meinert, 1890) by Hansen (1916). The family remained monogeneric until Brandt (1992) described the genus *Desmostylis*, which was; however, subsequently synonymized with *Macrostylis* (Riehl and Brandt 2010). Until today, even though currently 89 species have been formally described, the family remains monogeneric (Riehl and Brandt 2010; Bober et al. 2018c). The genera *Vana* Meinert, 1890 and *Desmostylis* Brandt, 1992 are currently listed as junior synonyms of *Macrostylis* (Riehl and Brandt 2010).

Macrostylids are characterized by a relatively conservative morphology and a comparatively long list of apomorphic characters (Riehl et al. 2014b). The habitus of Macrostylidae is more or less elongate and cylindrical, often with a keel or ventral spines on one or several sternites. It has a peculiar tagmosis with both the anterior and posterior three pereonites forming distinct tagmata. Pereonites 1–3 form a compact and musculous tagma called fossosoma, which lacks functional articulations between pereonites. The fourth pereonite may resemble either the anterior ones, or those of posterior segments, but the fourth pereopods are distinctly different from preceeding or succeeding pereopods. Oostegites form internally in the preparatory stage compared with Desmosomatidae and Munnopsidae which have external buds. The prognathous cephalothorax lacks eyes. The antennal sockets are located dorsolaterally, and both antennulae and antennae have posterior orientation (Riehl et al. 2014b). The pleotelson is highly integrated and bears a pair of statocysts (Bober et al. 2018b). The anterior three pairs of pereopods have a peculiar and unique setation, especially the dactyli (Riehl et al. 2012; Riehl and Brandt 2013). The fourth walking legs are comparatively short and are dorsolaterally oriented alongside the body. The uropods are styliform and often long, which inspired the genus name. The uropod exopod is absent.

Amongst the Macrostylidae, species are best morphologically distinguished by their pereonite proportions and shapes (e.g., size, shape and distribution of posterolateral protrusions), shape and size of the pleotelson, as well as the shape and setation of the ischium of the third pereopod (Riehl and Kaiser 2012; Riehl and Brandt 2013).

Biology/Ecology

Macrostylids are small, enigmatic crustaceans of which only little is known. Feeding preferences, mating strategy, longevity, lifecycle and ecological interactions are all unknown. Direct behavioural observations of macrostylids are extremely rare. The single behavioural report published, described their behaviour rather briefly: specimens put into an aquarium were observed to sink to the sediment where they immediately dug themselves in and did not return to the surface (Hessler and Strömberg 1989). This single observation in conjunction with sampling evidence (Thistle and Wilson 1987, 1996) suggests that Macrostylids are sediment dwellers and burrowers.

Comparative anatomical observations of macrostylids with other Janiroidea suggest that it is unlikely that these isopods are active swimmers. In most macrostylid species the pereopods are medium-sized (ca. 0.3 body length), stick-like appendages positioned close to the sternites, which better supports the theory of a burrowing lifestyle as hypothesized by Hessler and Strömberg (1989).

Sex- and stage-specific infestation with certain protists suggests sexually dimorphic habitat preferences where adult males live epibenthically, while juveniles and adult females seem to prefer an endobenthic lifestyle (Kniesz et al. 2018). In certain populations macrostylids seem to be popular hosts for tantulocarid parasites (Boxshall and Lincoln 1987).

Recent population-based genetic studies suggest that despite the apparent lack of adaptations for swimming and a likely preferred burrowing lifestyle, some species attain large biogeographic ranges, crossing obstacles such as ridges (Bober et al. 2018a; Riehl et al. 2018) or trenches (Bober et al. 2018c).

A close affinity with Desmosomatidae has been hypothesized since the first macrostylids were reported. This was also supported by the first morphological phylogenetic studies on the Isopoda (Wägele 1989). More recently, molecular phylogenetic studies support a close relationship of these two families (Raupach et al. 2004, 2009). However, while a monophyletic origin of Macrostylidae is highly supported, the sister-group of Macrostylidae could not be clearly identified yet using traditional molecular methods. Amongst the potential candidates for the sister group of Macrostylidae, according to the latest original molecular study (Raupach et al. 2009), are the Desmosomatidae, Ischnomesidae, Janirellidae, Mesosignidae, Munnopsidae, Nannoniscidae, and the aberrant genus *Xostylus* Menzies, 1962. This group, referred to as munnopsoid radiation (Raupach et al. 2004, 2009), is statistically well supported, although internal nodes are partially ambiguous and not supported by morphological evidence. Molecular dating suggests that the munnopsoid radiation is the oldest of the deep-sea isopod lineages dating back to before the Permo-Triassic boundary ca. 250 million years ago (Lins et al. 2012).

The discovery of a new family of the Janiroidea has brought new insights but also more controversy into the debate of the macrostylid relationships. Urstylidae Riehl et al., 2014 has been identified as the potential sister group of Macrostylidae based on morphological analysis (Riehl et al. 2014b). Molecular data are still lacking for this taxon. An ancestral-state analysis of the depth distribution of the two families suggests an abyssal origin and diversification of the groups (Riehl 2014). Although Urstylidae has been reported from Pacific and Atlantic Oceans it has not yet been collected in the NWP.

Geographical Distribution

Macrostylid isopods have a worldwide distribution in cold water masses of the deep sea (Bober et al. 2018c). In cold-water Boreal and Austral regions, species have also been recorded in the upper bathyal and even at shelf depths, for instance in Norwegian Fjords or on the Antarctic continental shelf (Meinert 1890; Sars 1899; Hansen 1916; Malyutina and Kussakin 1996; Brandt 2002; Riehl and Kaiser 2012). Macrostylids frequently occur in trenches (Kniesz et al. 2018) and *Macrostylis mariana* Mezhov, 1993 from the deep Mariana Trench (Mezhov 1993) is one of the deepest ever recorded isopod species.

Munnopsidae Lilljeborg, 1864

General information

The family Munnopsidae was originally erected as a tribe by Lilljeborg (1864). G.O. Sars (1885) elevated it to family rank, including the type genus *Munnopsis* M. Sars, 1861 with the genera *Eurycope* G.O. Sars, 1864, *Ilyarachna* G.O. Sars, 1870, and *Desmosoma*. Later, G.O. Sars (1899) described the family Munnopsidae more precisely and delineated it from the family Desmosomatidae. Tattersall (1905a) described a separate family Lipomeridae for a new genus, *Lipomera* Tattersall, 1905b with similarities to juvenile *Ilyarachna*. Hansen (1916) subdivided the family Munnopsidae into the three tribes Ilyarachnini, Munnopsini and Eurycopini that were later recognized as subfamilies by Gurjanova (1932). Subsequently the Eurycopinae (Nierstrasz and Schuurmans Stekhoven Jr. 1930) and then the other subfamilies were elevated to family rank (Wolff 1962). In the latter work the family Eurycopidae constituted four subfamilies: the Eurycopinae besides the newly established Acanthocopinae Wolff, 1962, Bathyopsurinae Wolff, 1962 and Syneurycopinae Wolff, 1962. Furthermore the previously separate family Lipomeridae was included as a genus (*Lipomera*) within the Eurycopinae besides *Eurycope*, *Munneurycope* Stephensen, 1912, *Munnopsurus* Richardson, 1912 and *Storthyngura* Vanhöffen, 1914. Wilson and Hessler (1981) revised *Eurycope* and established four genera and subsequently several new species of the widely distributed genus were described (Wilson 1983a, 1983b, 1983c). In a cladistics analysis Wilson (1989) analysed characters of most of the genera of the munnopsids sensu lata and proposed to reduce all munnopsid families to subfamily rank included into one large family Munnopsidae, as it had been originally proposed by G.O. Sars (1899). He revised a problematic group of "ilyarachnid-like eurycopids", the Lipomeridae, and reduced it to subfamily rank (Lipomerinae), also adding four new genera to the subfamily (Wilson 1989). For some genera remaining *incertae sedis* according to Wilson's (1989) analysis, Kussakin

(2003) erected the subfamilies Betamorphinae Kussakin, 2003 and Storthyngurinae Kussakin, 2003. During the last two decades ten additional munnopsid genera have been described in the different subfamilies (Malyutina 1999, 2003, 2004, 2008; Malyutina and Brandt 2006, 2007a; Merrin 2009, 2011). In spite of numerous publications on the munnopsid phylogeny (Wilson 1989; Wägele 1989; Kussakin 2003; Osborn 2009; Raupach et al. 2009), the relationships within the Munnopsidae are still not well resolved and some genera (*Munneurycope*, *Munnopsurus*, *Munnicope* Menzies and George, 1972, *Microcope* Malyutina, 2008 and *Gurjanopsis* Malyutina and Brandt, 2007) are still *incertae sedis*.

Munnopsidae is a morphologically diverse family which can be distinguished from other Janiroidea mainly by their secondary adaptations for a swimming locomotion (Wilson 1989; Wilson et al. 1989; Hessler 1993; Kussakin 2003; Osborn 2009). These adaptations include a paddle-like appearance of the posterior three pairs of pereopods (V–VII), with broad carpi and propodi featuring fringes of plumose setae. The entire posterior body forms a natatory tagma, the natasome, with integrated pereonites 5–7 and pleotelson. This integration is also reflected in the nervous system (Hult 1941). Moreover, the basal article of the antennule is flattened and expanded, the antennal sockets have a dorsal position and both antennulae and antennae are anteriorly oriented – another adaptation possibly connected to swimming backwards.

Amongst Munnopsidae 42 genera of nine subfamilies are distinguished by various combinations of distinct character states of the body shape (with or without spines and cephalic rostrum), varied fusion of the segments of the natasome, and different morphologies of the anterior and posterior (natatory) pereopods. The habitus of the Munnopsidae is considerably variable between the subfamilies, ranging from elongate and stick-like in the case of the fossorial Syneurycopinae, to swollen, with thin, transparent integuments in the holopelagic Bathyopsurinae, some of Munnopsinae Lilljeborg, 1864, *Munneurycope*, and *Gurjanopsis*. Furthermore the different groups amongst the munnopsids can be distinguished from each other by their differing ambulosome and natasome proportions, as well as smooth (e.g. Eurycopinae Hansen, 1916) or spiny (Acanthocopinae, Storthyngurinae, some of Ilyarachninae Hansen, 1916) body outlines. The reduction of the seventh pereonite and its legs, the mandibular palps or uropod exopods, as well as the dactyli of pereopods V–VII in some genera, are interpreted as a trend of secondary simplifications.

Biology/Ecology

Munnopsidae is a highly specialized family, whose members, unlike most asellotes, are able to swim actively (Hessler 1993; Marshall and Diebel 1995). The swimming adaptations probably give the munnopsids advantages for colonizing new areas and habitats, and could explain their higher abundance and wider distribution in three-dimensional space in comparison with other families (Malyutina and Brandt 2007b). However, with the exception of a small number of truly pelagic species, most munnopsids are benthic and epibenthic crustaceans that are able to walk on the seafloor and swim short distances during feeding. Some munnopsids secondarily evolved a fossorial

lifestyle. Therefore, the distribution of most of the Munnopsidae, like other isopods, is probably more dependent on bottom currents or turbulence than on their own swimming abilities (Hessler and Strömberg 1989; Brandt et al. 2007).

Geographical Distribution

Munnopsidae is the largest family among the 20 deep-sea families of the Asellota. A total of over 320 species belonging to 42 genera occur in the deep sea worldwide bathymetrically covering depths from the upper bathyal to the hadal depth of 10,687 m (Boyko et al. 2008c). Some munnopsid species also occur at shallow depths in the high latitudes of both hemispheres, having been recorded from 4 m in the Arctic and 59 m in the Antarctic continental shelf (Sars 1899; Hansen 1916; Kussakin 2003; Malyutina and Brandt 2007b).

The highest biodiversity of Munnopsidae has been revealed in the Atlantic sector of the Southern Ocean, where 219 species from 31 genera were counted. About 60 species were reported in the North Atlantic (Wilson 1983a, 1983c; Kussakin 2003; Malyutina and Brandt 2007b; Schnurr and Malyutina 2014; Schnurr et al. 2014). The most speciose and abundant genera are *Eurycope*, *Disconectes* Wilson and Hessler, 1981, *Ilyarachna*, *Betamorpha* Hessler and Thistle, 1975, *Vanhoeffenura* Malyutina, 2004, *Rectisura* Malyutina, 2003, *Munnopsis*, *Munnopsurus*, *Munneurycope*, *Acanthocope* Beddard, 1885. These are also the most widely distributed genera in world oceans.

2. Objectives

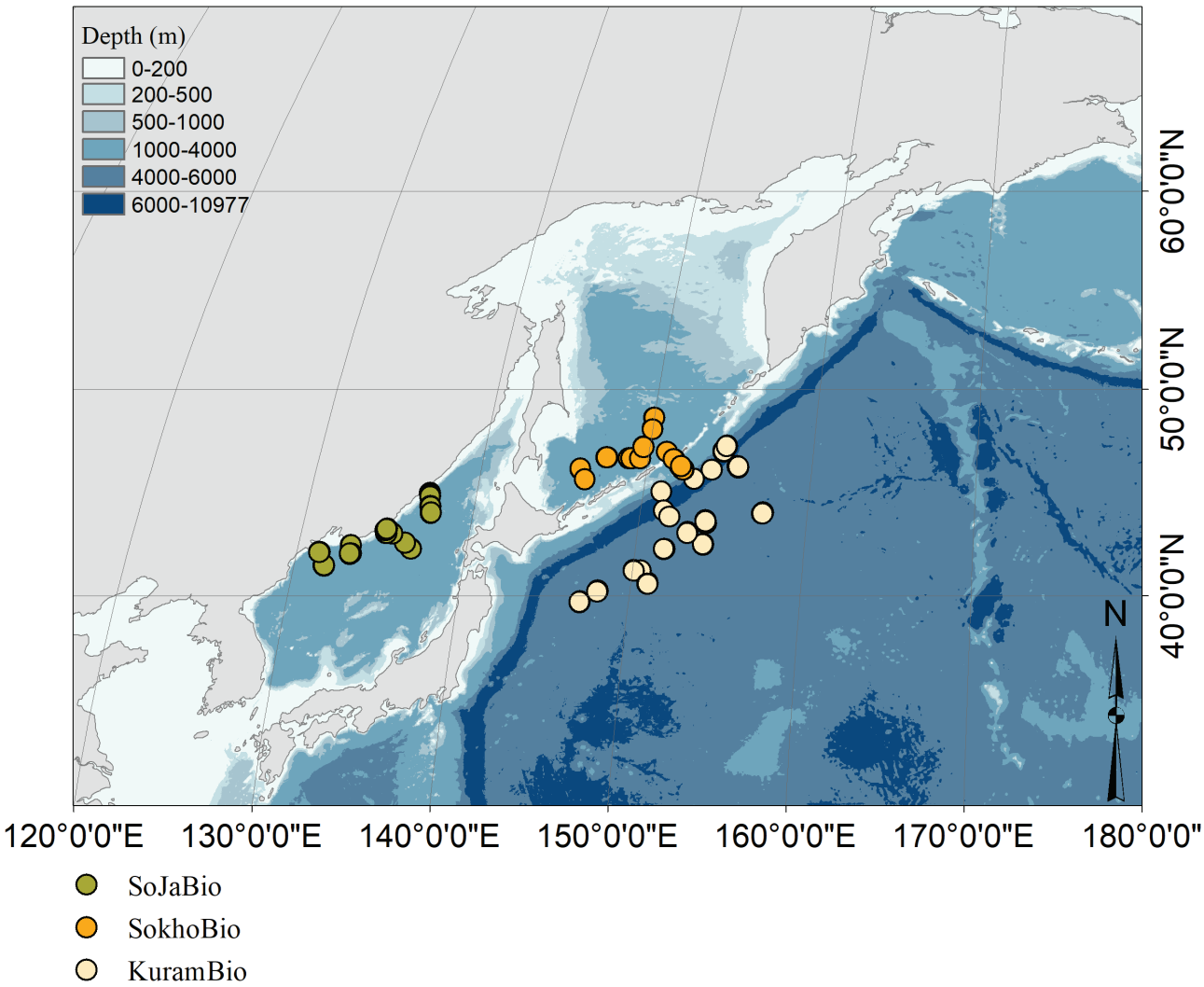
This chapter provides a review of the distribution and species-richness patterns of selected janiroid families in the deep NWP. The families Dendrotionidae, Desmosomatidae, Macrostylidae and Munnopsidae are treated herein (Figure 1), and a broad spectrum of lifestyles and biogeographic patterns is covered. For these families we provide an updated checklist of the NWP species. From this list, all Dendrotionidae and Macrostylidae are discussed, while a selection of the more diverse Desmosomatidae and Munnopsidae is reviewed. We review what is known about taxonomic histories, and also touch on lifestyles and adaptations as well as general worldwide distributions. This chapter presents a baseline for future studies on expected distributional changes in the NWP with continuing global climatic changes.

3. Material and Methods

Species distributions and richness patterns presented and discussed in this chapter are based on recent deep-sea sampling campaigns to the Northwest Pacific (NWP; Map 1) as well as a review of older records from the literature and the Ocean Biogeographic Information System (OBIS) from the same region. Recent collections were obtained during four Russian-German joint projects. “Sea of Japan Biodiversity Studies” (SoJaBio) was conducted with the Russian RV ‘Akademik M.A. Lavrentyev’ in 2010 (Malyutina et al. 2010; Malyutina and Brandt 2013). “Kuril-Kamchatka Biodiversity Studies I and II” (KuramBio I and II) with the German RV ‘*Sonne*’ in 2012 and 2016 targeted the abyssal

Northwest Pacific Basin near the KKT (Brandt and Malyutina 2012, 2015) and the KKT itself (Brandt and Fahrtteilnehmer der 250. Expedition des FS Sonne 2016; Brandt et al. 2020). The project "Sea of Okhotsk Biodiversity Study" (SokhoBio) set out in 2015 with the RV '*Akademik M.A. Lavrentyev*' to sample the Kuril Basin of the Sea of Okhotsk and the Bussol Strait (Malyutina et al. 2015). Samples were taken with various types of gear, including camera-equipped epibenthic sledge (Brandt et al. 2013), Agassiz trawl, giant box corer, multiple corer as well as multi-plankton net, and sampling details can be found in the cruise reports (Malyutina et al. 2010, 2015; Brandt and Malyutina 2012; Brandt and et al. Expedition des FS Sonne 2016).

From these expeditions, the collected material was fixed and preserved according to international standards, suitable for morphological and genetic analyses (Riehl et al. 2014a). It is or will be accessible from the respective museums. Permanent storage locations of type material may vary by taxon (please consult original descriptions).



Map 1. Sampling sites of the KuramBio (I and II), SoJaBio and SokhoBio campaigns in the Northwest Pacific, the Sea of Japan and the Sea of Okhotsk.

4. Results

4.1. Dendrotionidae Vanhöffen, 1914

Biogeographic Patterns

In the NWP two similar species of the genus *Dendromunna* were found recently during the expeditions KuramBio and SokhoBio (Table 1; Map 2). *D. kurilensis* Golovan and Malyutina 2018 (Figure 1A) was collected at two stations in the abyss of the Pacific Ocean to the east of the KKT at depths of 5,399–5,408 m. *Dendromunna okhotensis* Golovan and Malyutina 2018 was collected at two stations of one site in the Kuril Basin of the Sea of Okhotsk at depths of 3,299–3,300 m (Golovan et al. 2018b).

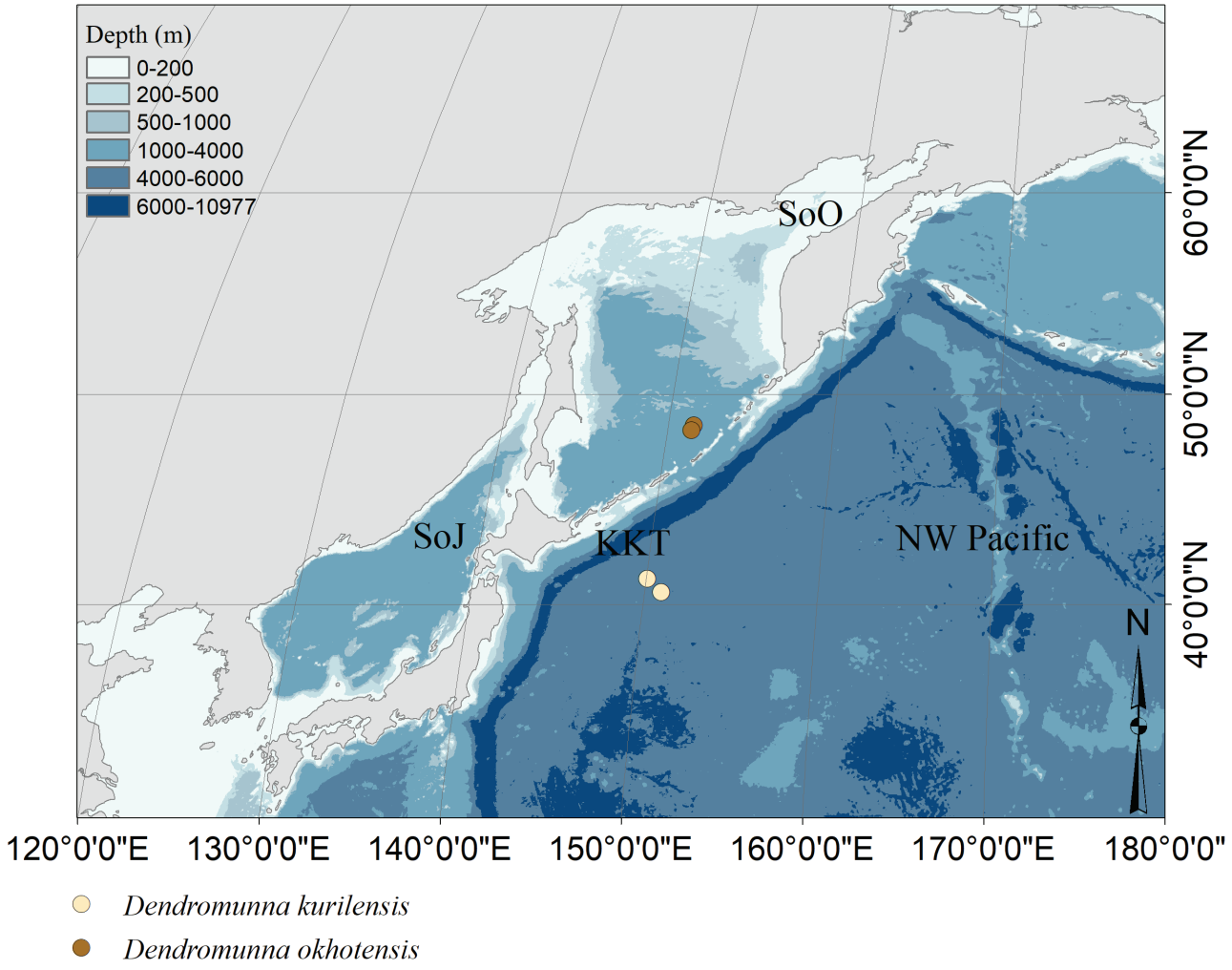
4.2. Desmosomatidae G.O. Sars, 1897

Richness Patterns

In the NWP 85 morphospecies of Desmosomatidae belonging to 13 genera are currently recognized from a depth range of 15–6,675 m (Birstein 1963, 1970; Kussakin 1965, 1999; Golovan 2007, 2015a, 2015b, 2018; Malyutina et al. 2010; Golovan et al. 2013; Jennings et al. 2020). Seventeen of them are described species, and the others await description. Among these, 70 morphospecies (including ten described species; see Table 1) belonging to twelve genera were collected at depths >2,000 m. Recent molecular studies based on KKT material have revealed morphologically similar species among the previous set of morphologically recognized species, and have also assigned sexually dimorphic conspecifics as well as morphologically different but nevertheless conspecific life stages (Jennings et al. 2020).

The richest genera (in terms of species richness per genus) of the NWP region were *Eugerda* (23 species, 27.1% of the Desmosomatidae species list), *Mirabilicoxa* Hessler, 1970 (19 species, 22.4%), *Desmosoma* G.O. Sars, 1864, and *Eugerdella* Kussakin, 1965 (each 9 species, 10.6%), followed by *Prochelator* Hessler, 1970 (5 species, 5.9%). These percentages are relatively similar to those of the global desmosomatid fauna. The most species rich genera are also the most eurybathic ones, occurring in the NWP from the shelf (*Desmosoma*, *Eugerda*) or bathyal (*Mirabilicoxa*, *Prochelator*) to abyssal or even hadal (*Mirabilicoxa*) zones (Map 3). The genus *Eugerdella* was found at abyssal and hadal depths in the NWP (Map 4), but in the Atlantic and Antarctic it has been reported from the shelf down to the abyss. The genus *Paradesmosoma* Kussakin, 1965 is known only from shelf and upper bathyal depths; in the NWP it seems to be restricted to the shelf. The remaining genera occurred at abyssal depths of the Pacific Ocean and/or the Sea of Okhotsk.

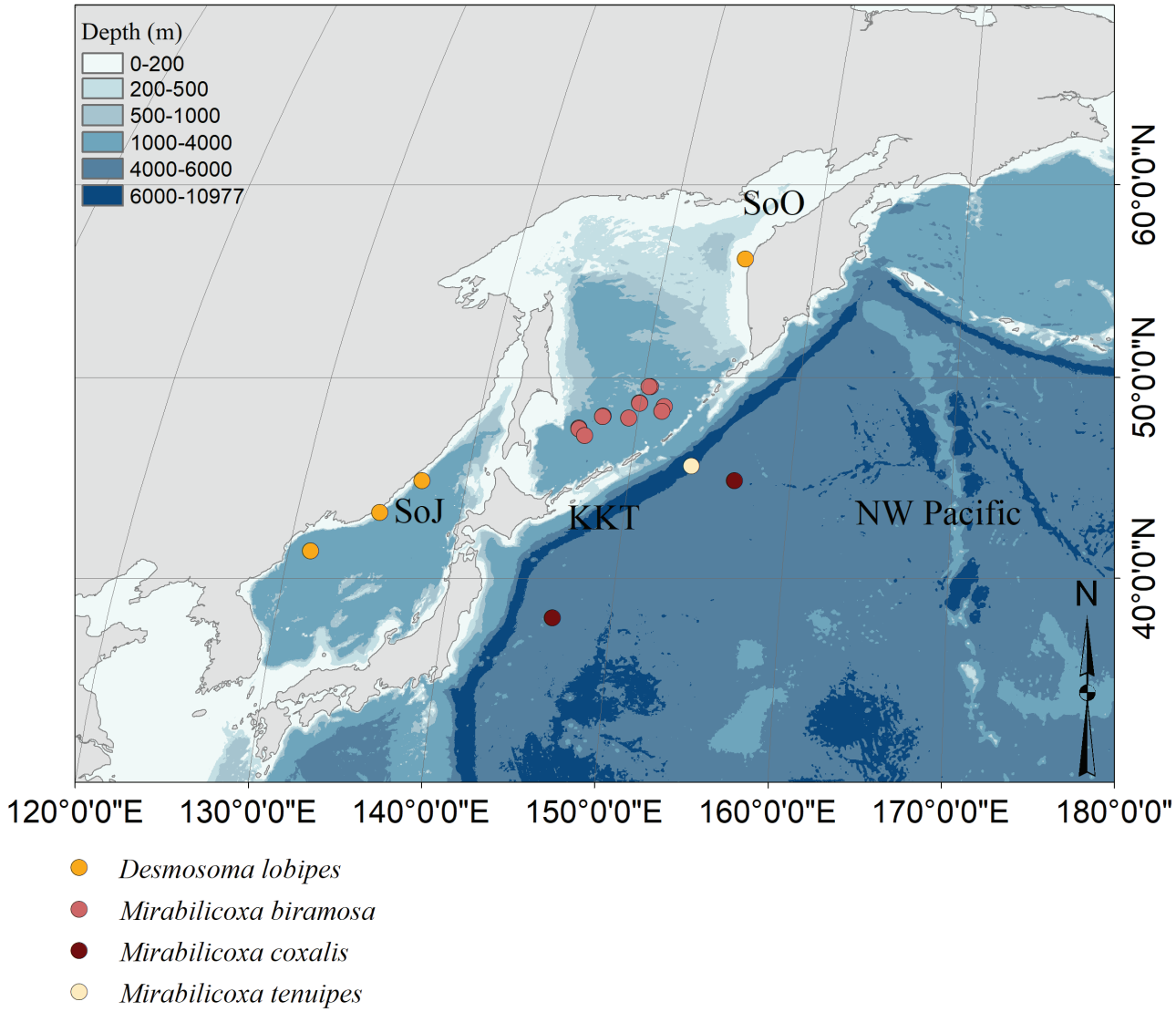
During the German-Russian NWP expeditions the Desmosomatidae diversity was highest at abyssal depths southeast of the KKT (Northwest Pacific Basin) (62 morphospecies, 11 genera) (Golovan et al. 2019; Jennings et al. 2020). The most species-rich genera were *Eugerda* (19 species) and *Mirabilicoxa* (17 species), followed by *Eugerdella* (seven species). Half of the species (31) were collected at more than one site. Ten species were collected at both sides of the trench. Four species occurred at the upper slope of the trench, reaching depths of about 6,200 m (*Mirabilicoxa* sp. 3, *Eugerdella* sp. 3) and 7,100 m (*Mirabilicoxa* sp. 1, *Eugerdella* cf. *kurabyssalis* Golovan, 2015). *Mirabilicoxa tenuipes* (Birstein,



Map 2. Records of the two currently known species of Dendrotionidae Vanhöffen, 1914 in the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

1970) was collected at the upper trench slope at depths of 6,675–6,710 m (Map 3). *Eugerdella hadalis* Golovan and Brix, 2020 was the only true hadal desmosomatid species, occurring exclusively in the KKT at a depth range of 7,111–8,744 m (Jennings et al. 2020) (Map 4). The latter currently represents the worldwide deepest record for the family and the only true hadal desmosomatid species.

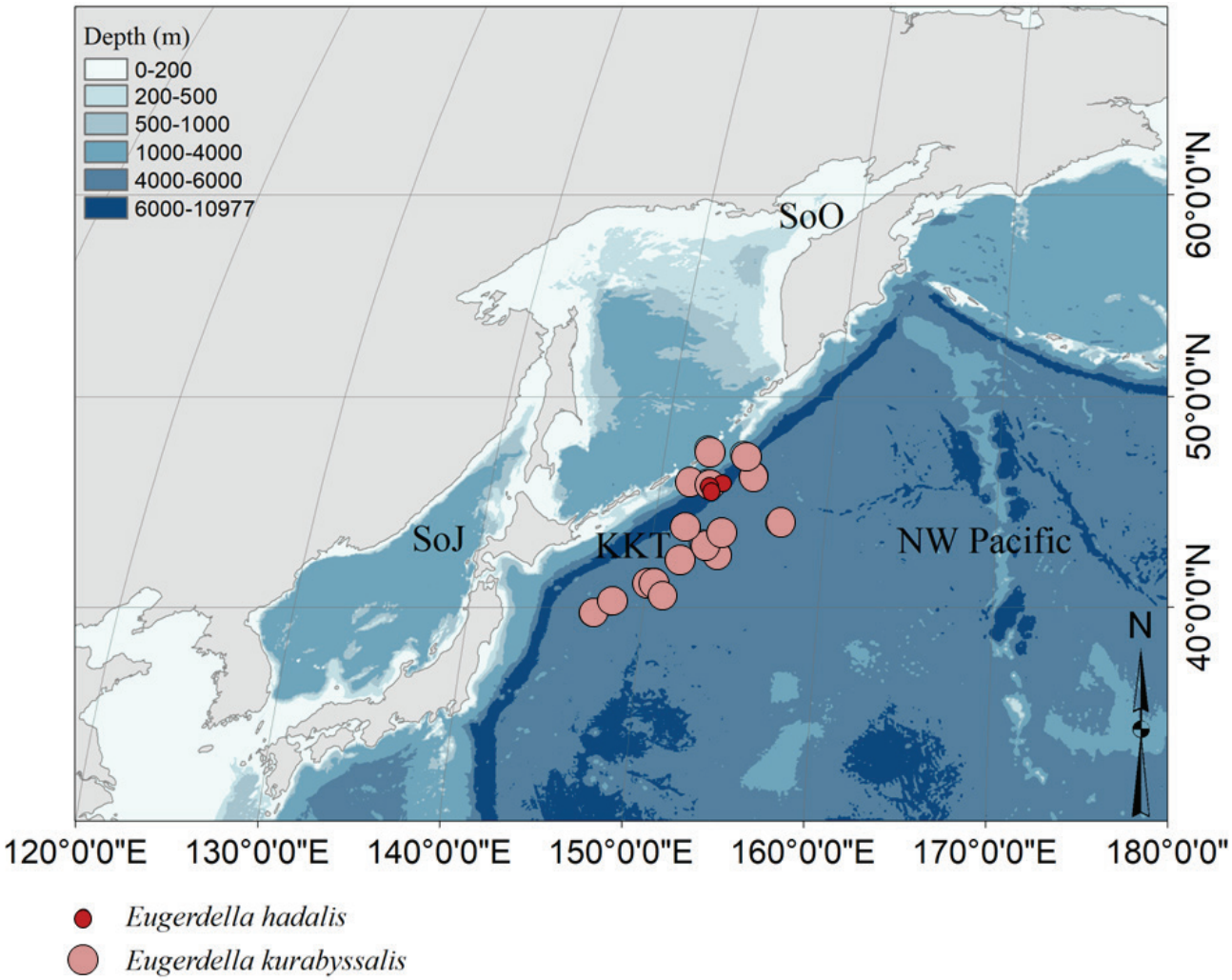
The abyssal fauna of the Sea of Okhotsk is comprised of 17 desmosomatid morphospecies in eight genera. It is linked with the Pacific abyssal fauna (Golovan 2018) as ten morphospecies (*Desmosoma* sp. 1, *D.* sp. 3, *Eugerda* sp. 2, *E.* cf. sp. 2–1, *E.* sp. 3, *E.* sp. 4, *E.* cf. sp. 7, *Mirabilicoxa* sp. 2, *Chelator michaeli* Golovan, 2015, *Eugerdella* sp. 2) and seven genera are shared between the Sea of Okhotsk and the abyssal KKT region (Map 5). In all NWP samples the genus *Oecidiobranchus* Hessler, 1970 was found only in abyssal depths of the Sea of Okhotsk. Other species of *Oecidiobranchus* are known from the Arctic (4 species) and the South Pacific (1 species, off New South Wales, Australia) where they occurred between shelf and abyssal depths.



Map 3. Records of selected genera *Desmosoma* G.O. Sars, 1864 and *Mirabilicoxa* Hessler, 1970 (Desmosomatidae G.O. Sars, 1897) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

Biogeographic Patterns

In the Sea of Japan, isolated from the adjacent deep-sea regions by straits with rather shallow sill depths, twelve desmosomatid species belonging to at least four genera (*Desmosoma*, *Eugerda*, *Mirabilicoxa* and *Paradesmosoma*) have been found at the shelf (e.g., *Paradesmosoma orientale* Kussakin, 1965) and at upper bathyal depths of up to about 500 m. Four of these species reach greater depths, reaching up to 1,011 m (*Mirabilicoxa kussakini* Golovan, 2007), 1,525 m (*Mirabilicoxa* sp.), 1,900 m (*Eugerda fragilis* (Kussakin, 1965)), and 3,420 m (*Desmosoma lobipes* Kussakin, 1965) (Map 3). Three species, *P. orientale*, *E. fragilis*, *D. lobipes* (Map 3), also occur at shelf depth of the Sea of Okhotsk. This principally confirmed previous assumptions that the deep-sea fauna of the Sea of Japan is relatively poor in species and mostly

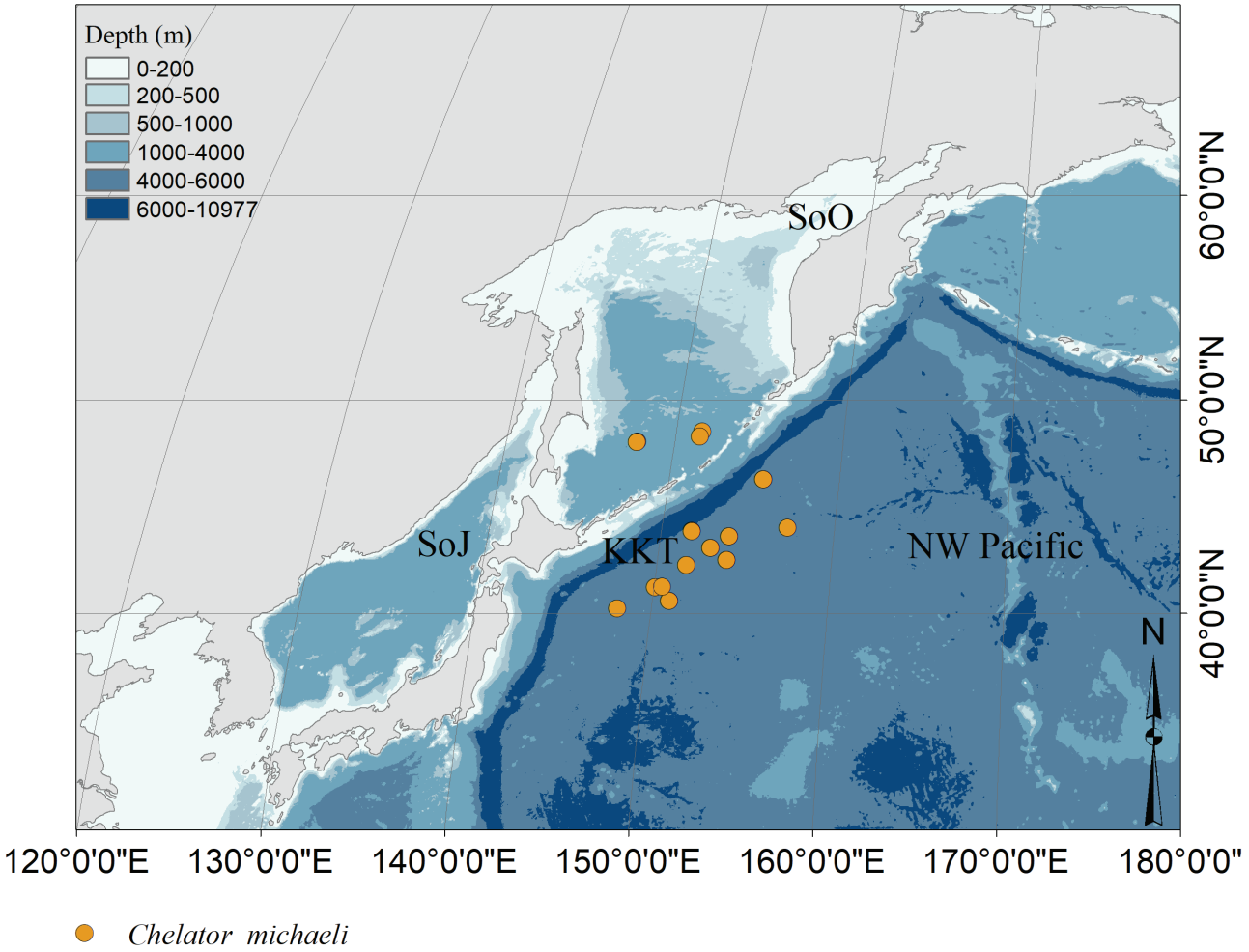


Map 4. Records of selected species of the genus *Eugerdella* Kussakin, 1965 (Desmosomatidae G.O. Sars, 1897) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

comprised of eurybathic cold-water species present also on the shelf of the adjacent high-boreal regions.

The distribution of the abyssal fauna in the Sea of Okhotsk is apparently limited to the abyssal zone of the Kuril Basin. This can be explained by the hydrology of the Sea of Okhotsk. Here, water exchange with the Pacific Ocean occurs via the deep (up to ca. 2,200 m) Kuril Strait while this cool and oxygenated water is overlain by a relatively warm and oxygen-depleted layer at bathyal depths (ca. 600–1,350 m).

Thus in summary, the desmosomatid fauna of all studied areas of the NWP is connected at the generic level, with the shelf and bathyal fauna of the Seas of Japan and Okhotsk also related at species level. The abyssal fauna of the Sea of Okhotsk seems to have originated in the Pacific, and the fauna of the Sea of Japan and the Sea of Okhotsk shelf fauna are highly similar. Most desmosomatid species encountered occurred exclusively in the abyssal Northwest Pacific Basin (see, e.g., Maps 6–7).



Map 5. Records of the species *Chelator michaeli* Golovan, 2015 (Desmosomatidae G.O. Sars, 1897) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

4.3. Macrostylidae Hansen, 1916

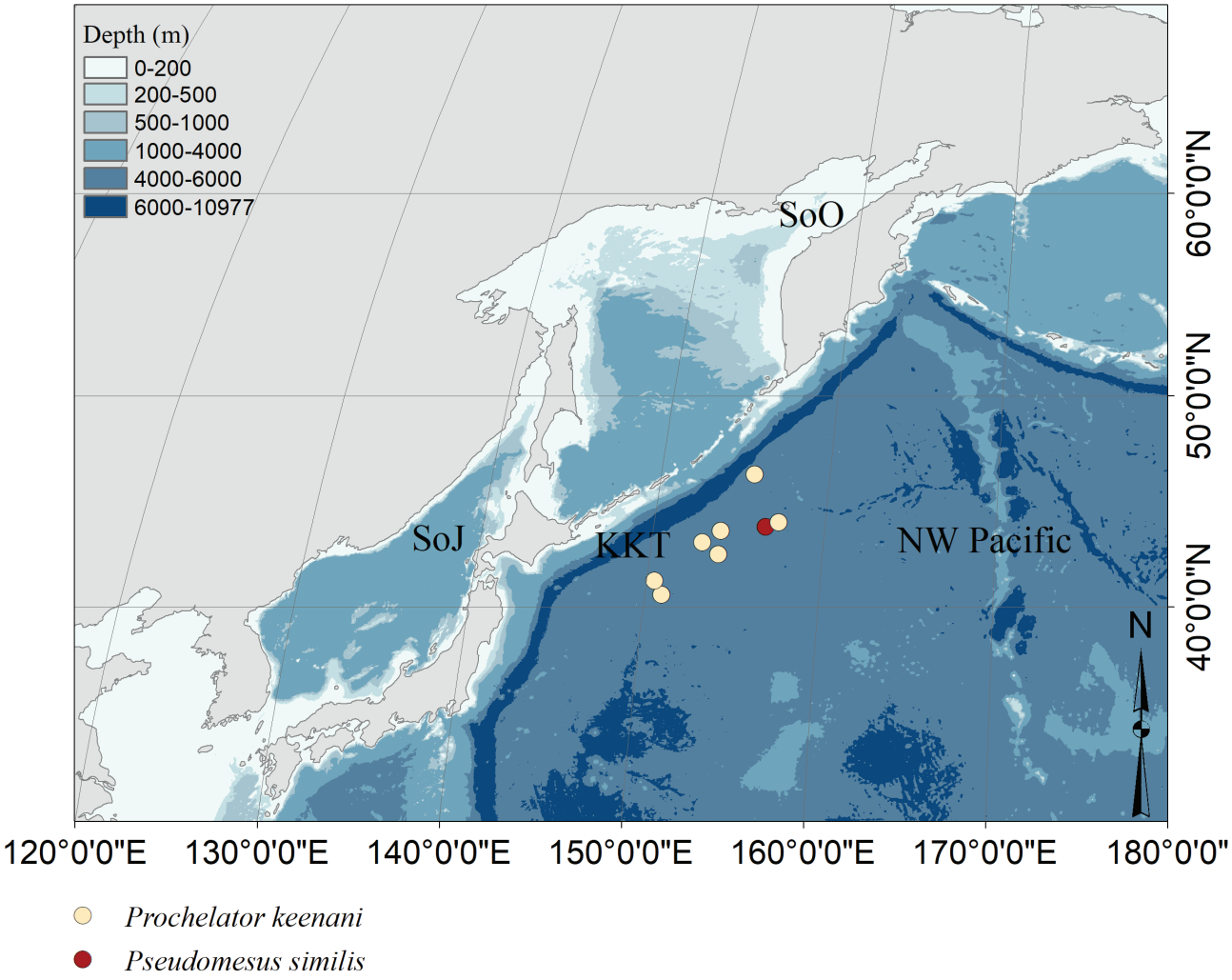
Richness Patterns

In the Northwest Pacific currently 18 species of Macrostylidae have been recognized (Elsner et al. 2015) of which 14 have been formally described and named (Table 1). All of these occur in the open NWP, including the Northwest Pacific Basin, the south-eastern slope of the Kuril Archipelago, as well as the KKT itself. Until now no macrostylids have been encountered in the Sea of Japan or the Sea of Okhotsk (Maps 8–11).

Biogeographic Patterns

***Macrostylis affinis* Birstein, 1963**

One of the first species of Macrostylidae to be described from the NWP, *M. affinis* was not found in recent expeditions. It was originally collected from the Northwest Pacific Abyssal Basin SE of the KKT co-occurring at abyssal depths with most of the other species known from this region (Map 8).



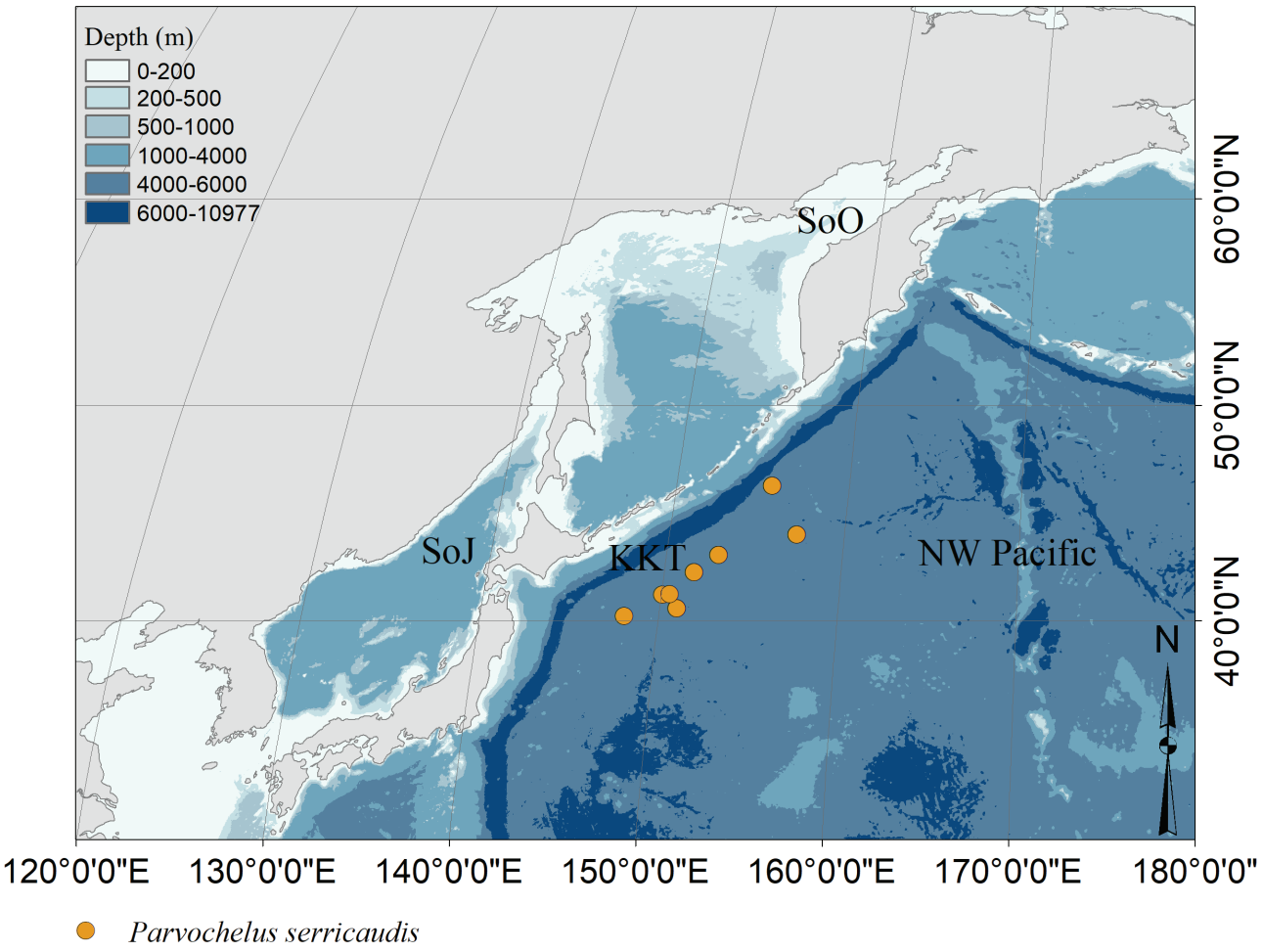
Map 6. Records of the species *Prochelator keenani* Golovan, 2015 and *Pseudomesus similis* Birstein, 1963 (Desmosomatidae G.O. Sars, 1897) from the abyssal Northwest (NW) Pacific Basin. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

Macrostylis amaliae/sabinae Bober et al. 2018

Macrostylis amaliae and *M. sabinae* were recently described as a complex of morphologically mostly indistinguishable species (Bober et al. 2018c). This species complex constituted 19.3% of all NWP macrostylid "morphospecies", second in abundance only to *M. curticornis*. Like *M. curticornis* (see below) this species complex has a wide occurrence on both sides of the KKT as well as in the hadal zone. Despite its wide distribution (Map 9), Bober et al. (2018c) identified a disproportionate increase in the genetic differentiation across the KKT indicating that gene flow is restricted across the KKT.

Macrostylis curticornis Birstein, 1963

Most numerous amongst the macrostylids of the KuramBio and KuramBio II expeditions was *M. curticornis* comprising ca. 60.5% of all collected macrostylids. *Macrostylis curticornis* is also one of the most widely distributed macrostylids in the NWP and occurs on both sides of the KKT at



Map 7. Records of the species *Parvochelus serricaudis* Golovan, 2015 (Desmosomatidae G.O. Sars, 1897) from the abyssal Northwest (NW) Pacific Basin. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

abyssal depths as well as in the hadal zone of the trench itself (Map 10). The depth range extends from less than 5,000 m to over 8,000 m and accordingly, for this species, the KKT does not seem to constitute a dispersal barrier. However, genetic confirmation of this assumption is still wanting, and furthermore, a distinctly bimodal size-distribution of both adult females and males was observed during shipboard examinations (Riehl et al. 2016) indicating another previously overlooked species.

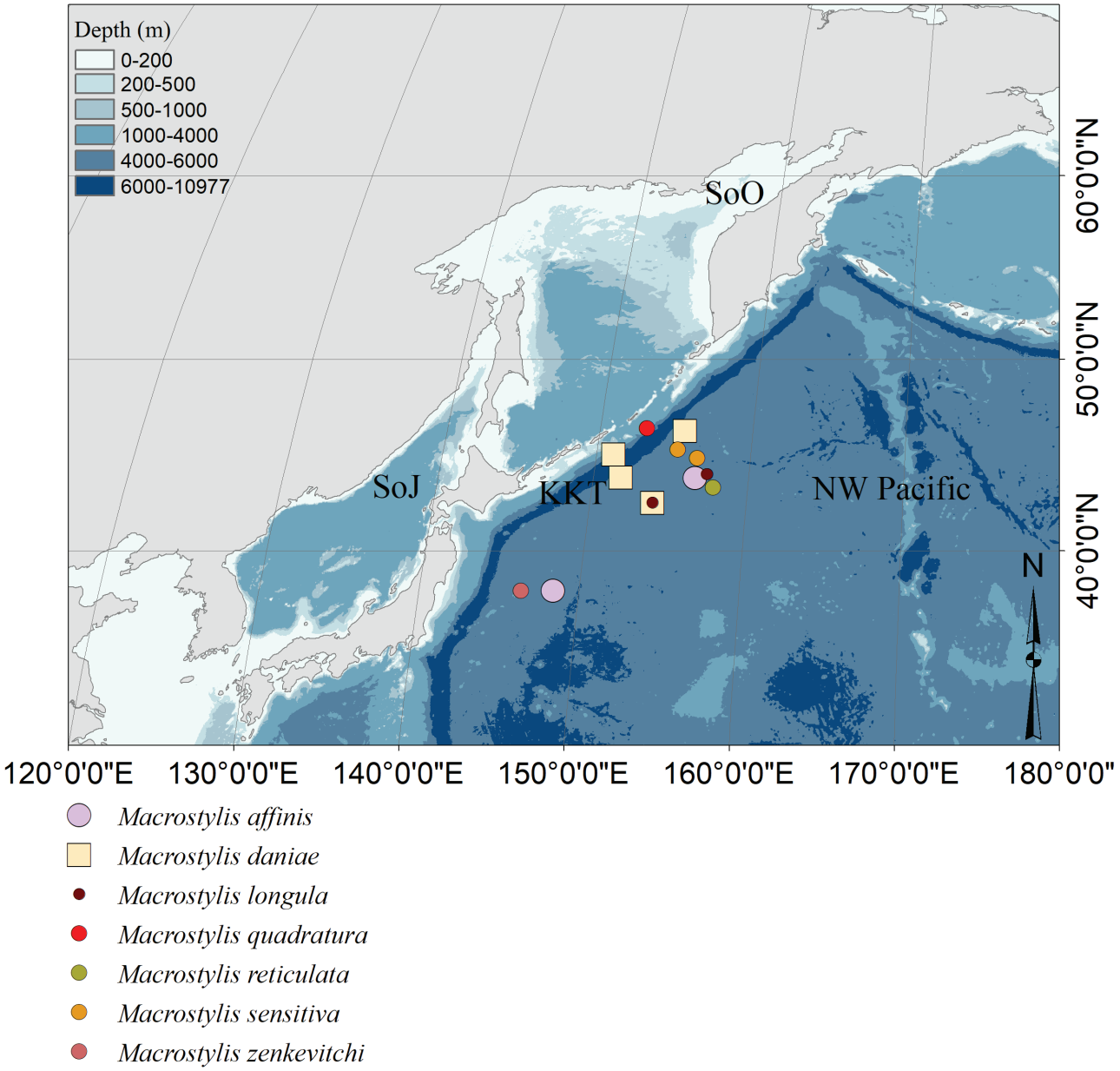
***Macrostylis daniae* Bober et al. 2018**

This species seems to be restricted in its occurrence to the Northwest Pacific Basin and abyssal depths (Map 8). Only two occurrences both from the KuramBio as well as the KuramBio II expeditions have been recorded.

***Macrostylis grandis* Birstein, 1970**

Junior synonym: *Macrostylis ovata* Birstein, 1970 (Riehl and Kühn 2020).

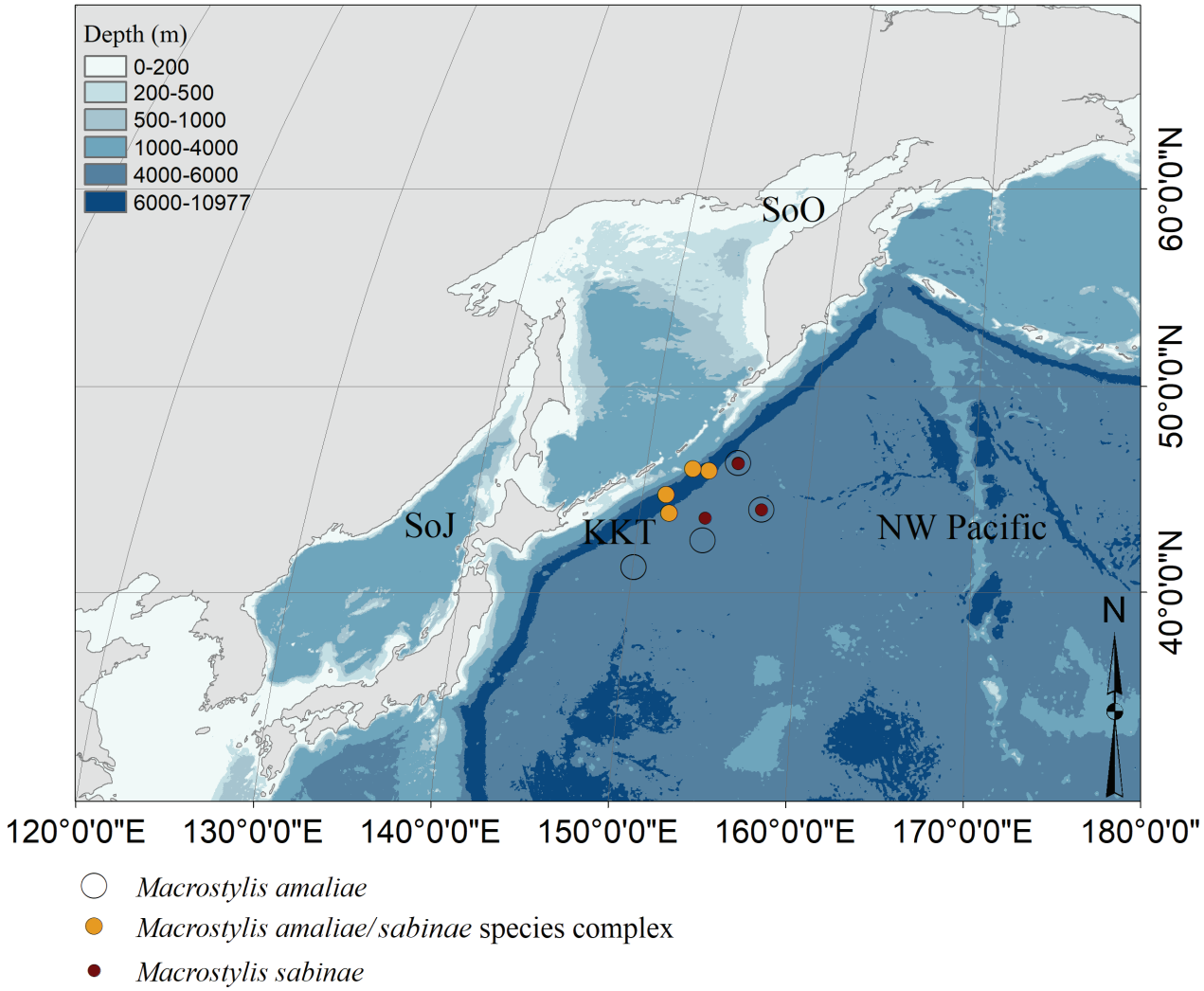
After failing to delineate *M. ovata* from *M. grandis*, Riehl et al. (2016) stated that *M. ovata*



Map 8. Records of various species of Macrostylidae Hansen, 1916 from the abyssal Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

was most likely a synonym of *M. grandis* and its description by Birstein (1970) was most certainly based on a manca-stage specimen, although this could not be confirmed as type material was not available upon request. However, a recent study led to the confirmation of the hypothesis based on molecular methods (Riehl and Kühn 2020).

However, a recent study led to the confirmation of the hypothesis based on molecular and ontogenetic data (Riehl and Kühn 2020). The species occurs across the KKT covering depths of 4,769–7,295 m. Taking into account the seafloortopography of the KKT with multiple deep pits separated by shallower sills, a



Map 9. Records of the *Macrostylis amaliae/sabinae* Bober et al. 2018 species complex (Macrostylidae Hansen, 1916) from the abyssal Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

continuous distribution of this species across the KKT (Map 11) can be assumed.

Macrostylis longissima Mezhov, 1981 & _M. longiuscula_ Mezhov, 1981

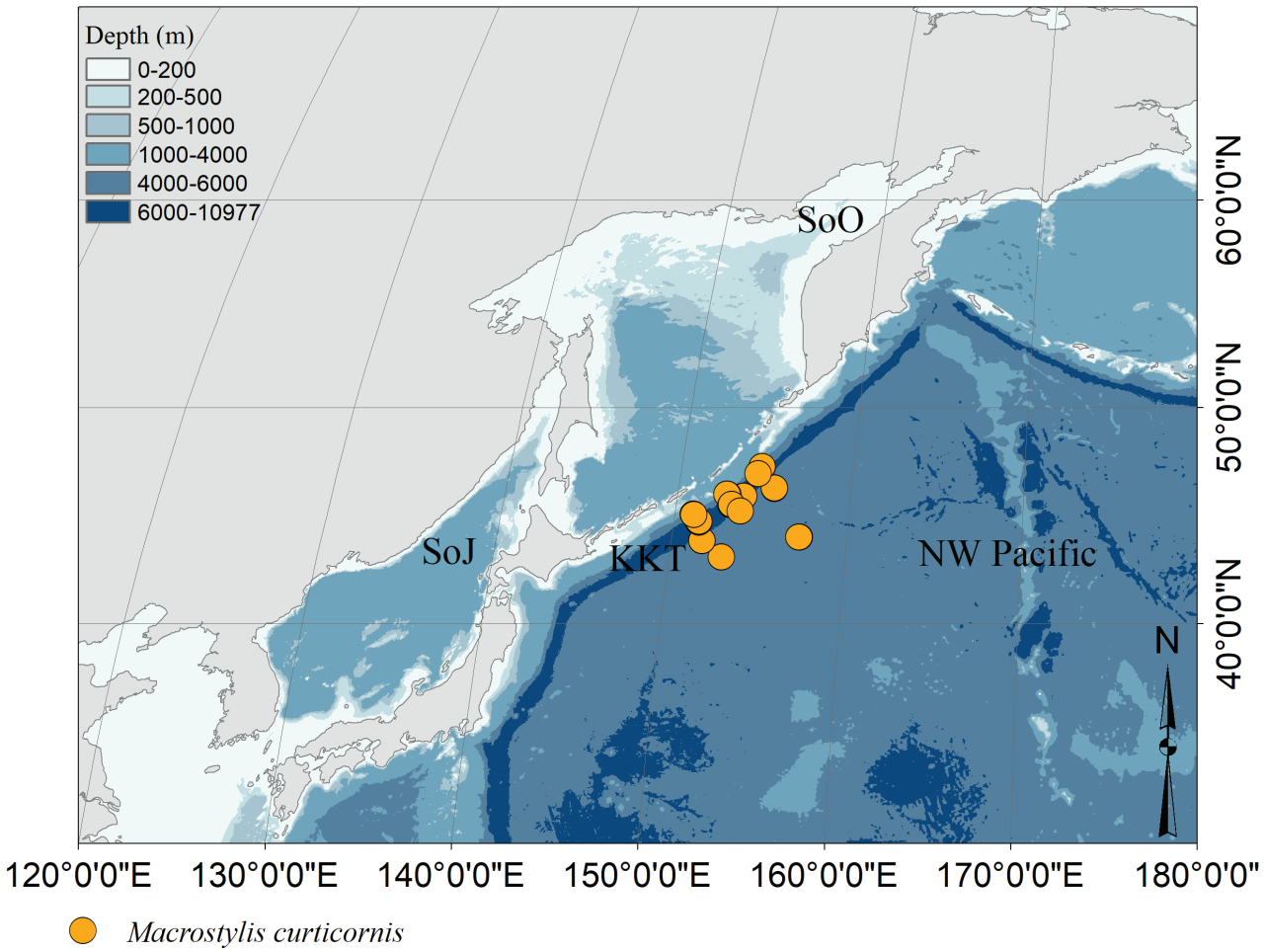
Macrostylis longissima and *M. longiuscula* are known only from their type localities at or near the Marcus-Necker range. They have not been collected near the KKT (Map 8).

Macrostylis longula Birstein, 1970

Described from the RV 'Vityaz' expeditions *M. longula* is among the species that were recently collected again. In all cases the records of this species are from abyssal depths (Map 8).

Macrostylis profundissima Birstein, 1970

Macrostylis profundissima is an exclusively hadal species. Its occurrence has been recorded solely from the KKT at depths between 8,183 m and 9,335 m (Birstein 1970; Riehl et al. 2016) (Map 11).



Map 10. Records of *Macrostylis curticornis* Birstein, 1963 (Macrostylidae Hansen, 1916) in the abyssal Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

Macrostylis quadratura Birstein 1970 & _M. reticulata_ Birstein 1963

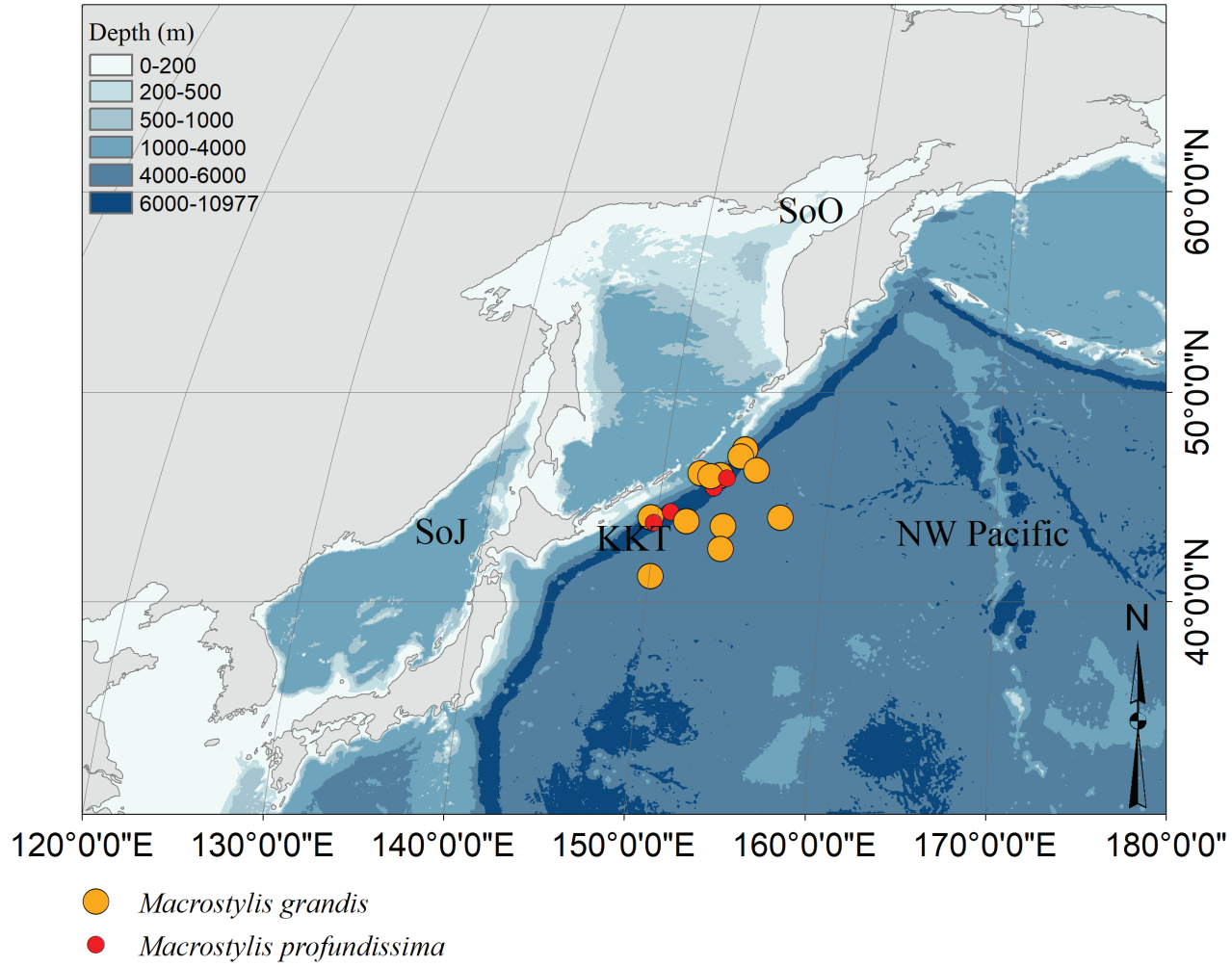
Known only from a single record, *M. quadratura* has never been found after its original discovery by Birstein. It is a bathyal species occurring at 3,175–3,250 m Similar to the previous species, *M. reticulata* is known only from a single record. The original discovery by Birstein occurred at an abyssal depth of the Northwest Pacific Basin (Map 8).

Macrostylis sensitiva Birstein, 1970

Since its original discovery by Birstein at two abyssal NWP stations, this species has never been recollected (Map 8).

Macrostylis zenkevitchi Birstein, 1963

After *Macrostylis zenkevitchi* was described from a single occurrence in the Northwest Pacific Basin, rather close to the Japanese island of Honshu (Birstein 1963), it was recently recorded for a second time during KuramBio II (Elsner et al. 2015), when it was collected from abyssal depths on the north-western slope of the KKT (Map 8).



Map 11. Records of the abyssohadal species *Macrostylis grandis* Birstein, 1970 and the hadal species *Macrostylis profundissima* Birstein, 1970 (Macrostylidae Hansen, 1916) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

4.4. Munnopsidae Lilljeborg, 1864

Richness Patterns

About one third of all described NWP isopods, 34 species (Table 1), belong to the family Munnopsidae (Gurjanova 1933; Birstein 1957, 1960, 1961, 1963, 1970, 1971; Kussakin 1971, 1999, 2003; Kussakin and Vasina 1993). During the Russian-German NWP expeditions only 16 of these known munnopsid species have been recollected.

In total, 157 species in 35 genera of the Munnopsidae have now been recorded for the studied NWP region. The greatest species richness was revealed in the abyssal area near the KKT – 106 species in 29 genera. In the KKT deeper than 6,000 m, 41 species in 15 genera were recorded. In the abyssal Kuril Basin 39 species in 19 genera were collected (Malyutina and Brandt 2015, 2018, 2020) Isopoda, Asellota. In the Sea of Japan, only four endemic munnopsid species from four genera *Eurycope*, *Ilyarachna*, *Munnopsurus* and *Baeonectes* were found at 455–3,435 m depths (Elsner et al. 2013; Golovan et al. 2013; Malyutina et al. 2013). Therefore, the regional species-richness declines from the abyssal Northwest

Pacific Basin to the marginal seas as well as into the KKT hadal zone.

Amongst the German-Russian samples, 87% of the collected species appear to be new to science, with multiple genera as well as the subfamily Lipomerinae being recorded from the NWP for the first time (*Lipomera*, *Hapsidohedra*, *Coperonus*, *Mimocopelates*, *Lionectes* (Lipomerinae), *Belonectes*, *Dubinectes*, *Tytthocope* (Eurycopinae), *Aspidarachna*, *Bathybadistes* (Ilyarachninae) *Bellibos* (Syneurycopinae), *Acanthomunnopsis*, *Munnopsoides*, *Paramunnopsis* (Munnopsinae)).

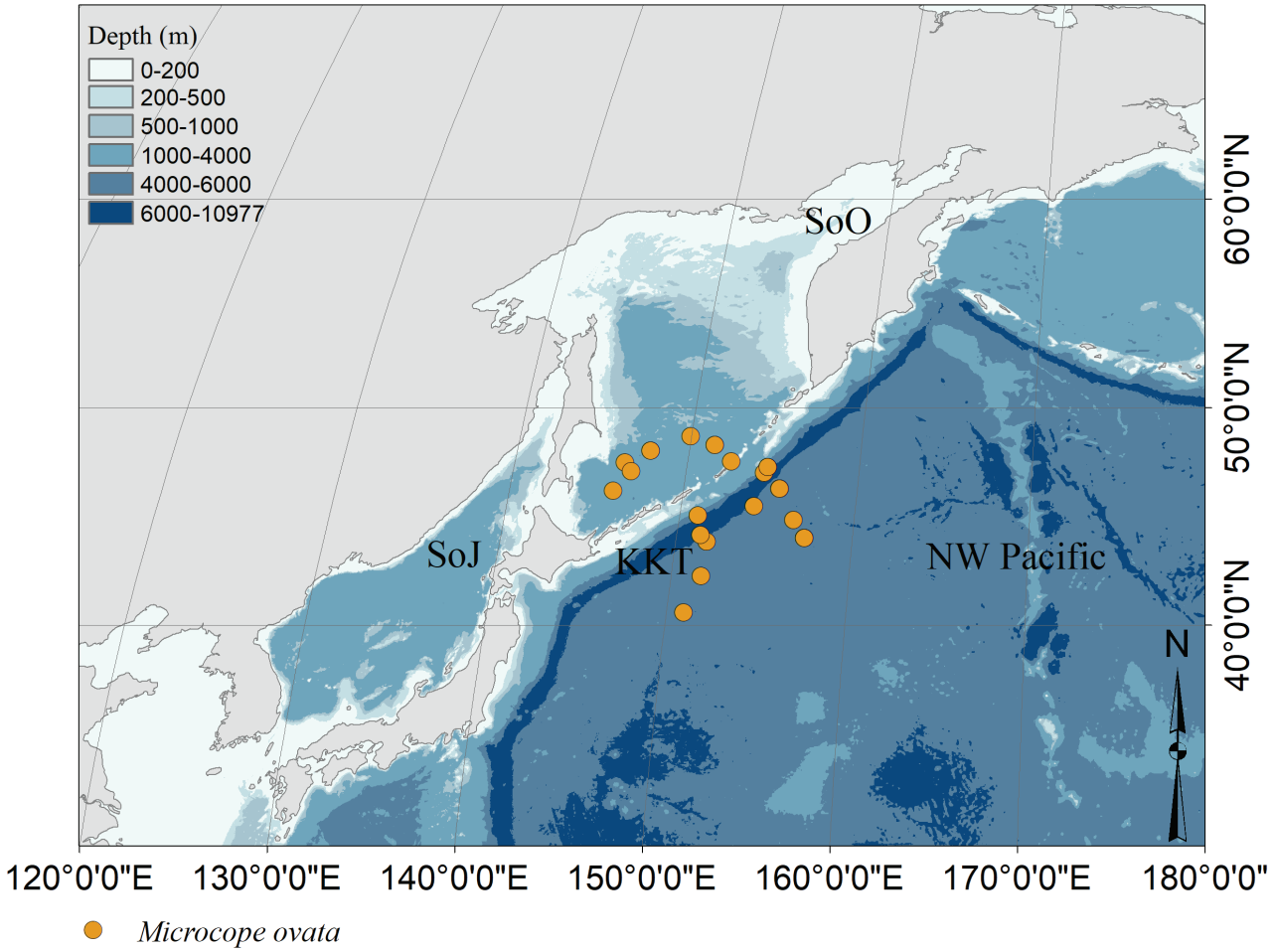
Biogeographic Patterns

Most of the recorded species for each studied area are rare, occurring at one or two stations with one or few specimens, many species are patchily distributed. The most widespread nine species (*Eurycope* sp. 1. *E.* sp. 1a, *E.* sp. 2., *Ilyarachna kussakini* Birstein, 1963, *Paramunnopsis* sp. 1, *Munnopsoides tattersalli* (Birstein, 1963), *Microcope ovata* (Birstein, 1970), "*Tytthocope-Munnopsurus*" sp. 1, "*T-M*" sp. 2) were found in all studied areas apart from the Sea of Japan (e.g., Map 12). Some of these (*Paramunnopsis* sp. 1, *Munnopsoides tattersalli*) were not abundant and distributed patchily (Map 13), while others were numerous and frequent, occurring at most stations.

Twenty-nine species occurred at both hadal and abyssal depths in the KKT region. The subfamily Eurycopinae with the main genus *Eurycope* dominated in all studied areas in terms of species richness and abundance. *Eurycope* species were the only munnopsids found at abyssal depths of the Sea of Japan at ca. 3,300 m (*E. spinifrons* Gurjanova, 1936), and at the deepest station in the KKT, at 9,584 m (*Eurycope* sp. 3) (Map 14). From 36 species of *Eurycope* recorded for the NWP only three species were found in all sampled areas besides the Sea of Japan.

In the KuramBio collection Eurycopinae comprised 56% of all abyssal munnopsids, followed by the genus *Microcope* (*incertae sedis*) (16%), Ilyarachninae (10%), Betamorphinae (4%), and Munneurycope (4%) (Malyutina and Brandt 2015). In the hadal zone the ratio of the subfamilies was reversed (Eurycopinae 43%, Betamorphinae 33%, Storthyngurinae 17%, and Ilyarachninae 3%) (Malyutina and Brandt 2020). Two subfamilies, Lipomerinae and Acanthocopinae were not found at hadal depths. At hadal stations only giant munnopsids (several cm length) of the subfamily Storthyngurinae and Betamorphinae that had previously been described were collected (Map 15): *Rectisura herculae* (Birstein, 1957) known from the KKT and Aleutean Trench at 6,475–9,346 m depths; *R. distincta* (Birstein, 1970) at 4,798–6,215 m; *R. kurilica* (Birstein, 1957) at 7,210–8,200 m; *Vanhoeffenura chelata* (Birstein, 1957) at 4,859–6,860 m (Map 13); and *Betamorpha acuticoxalis* (Birstein, 1963) (Map 16). The other species, collected for the first time, were of small size (few millimetres length).

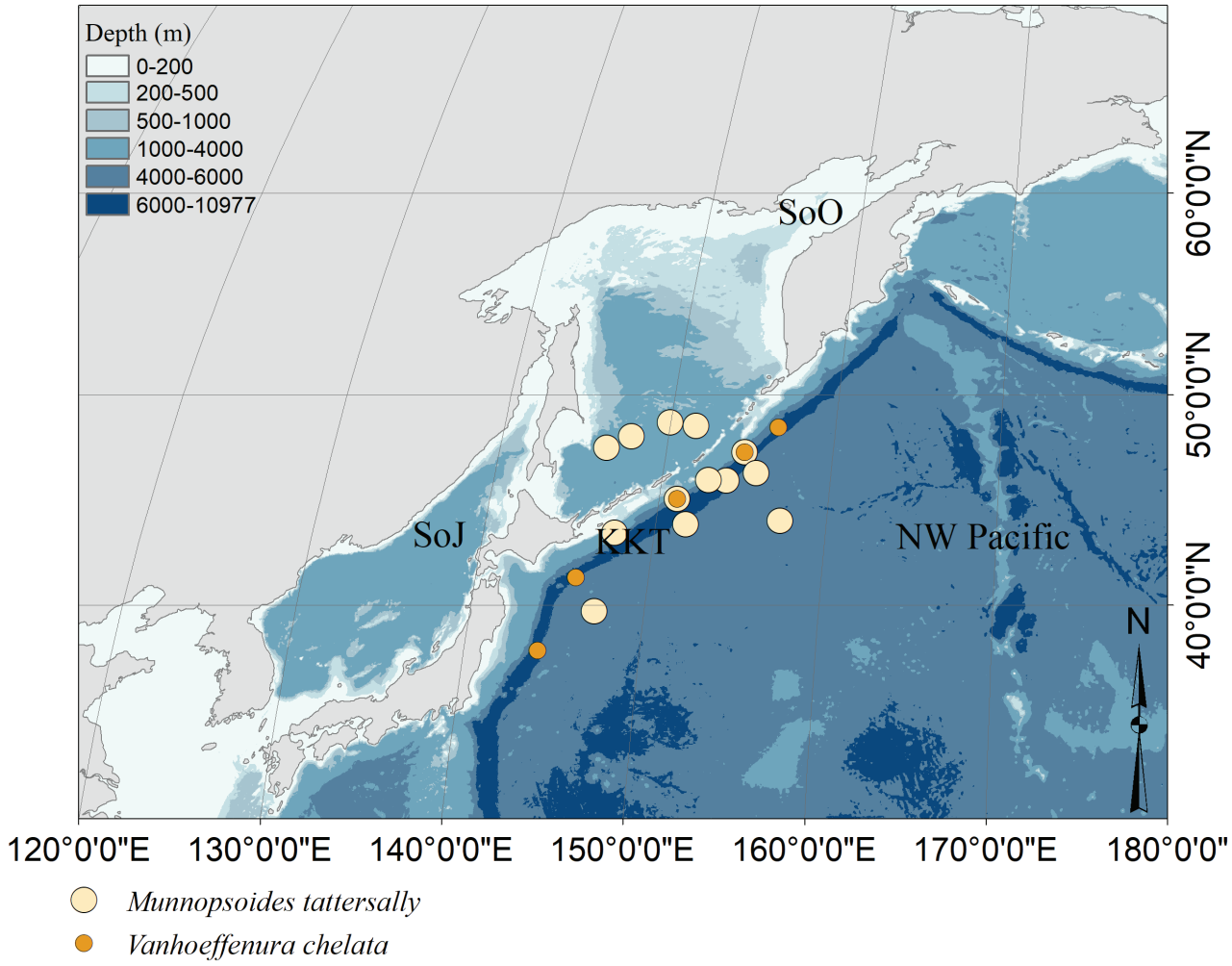
Besides the genera *Baeonectes*, *Echinozone*, *Microprotus*, and *Munnicope* whose distributions are restricted by the high latitudes of the Northern Hemisphere (Malyutina and Brandt 2007b; Boyko et al. 2008c), the other 31 genera found to be present are widely distributed. The most speciose and abundant genera *Eurycope*, *Disconectes*, *Ilyarachna* (Map 17), *Betamorpha*, *Vanhoeffenura*, *Munnopsis*, *Munneurycope*, and



Map 12. Records of *Microcope ovata* (Birstein, 1963) (Munnopsidae Lilljeborg, 1864) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

Acanthocope are the most widely distributed munnopsid genera in the World Ocean. Some rare genera also have wide distributions (Map 18). Thus, the recently described genus *Microcope* Malyutina, 2008, comprised of two Antarctic, two NWP abyssal species, and one SE Australian bathyal species, was first recorded at hadal depth in the KKT (6,575 m). *Microcope ovata* was the second most abundant and frequent munnopsid species in the KuramBio abyssal area and in the Kuril Basin. The second species of this rare genus described from the KuramBio material, *M. stenopigus* Malyutina, 2015 was recorded neither in the KKT nor in the Kuril Basin (Malyutina and Brandt 2018).

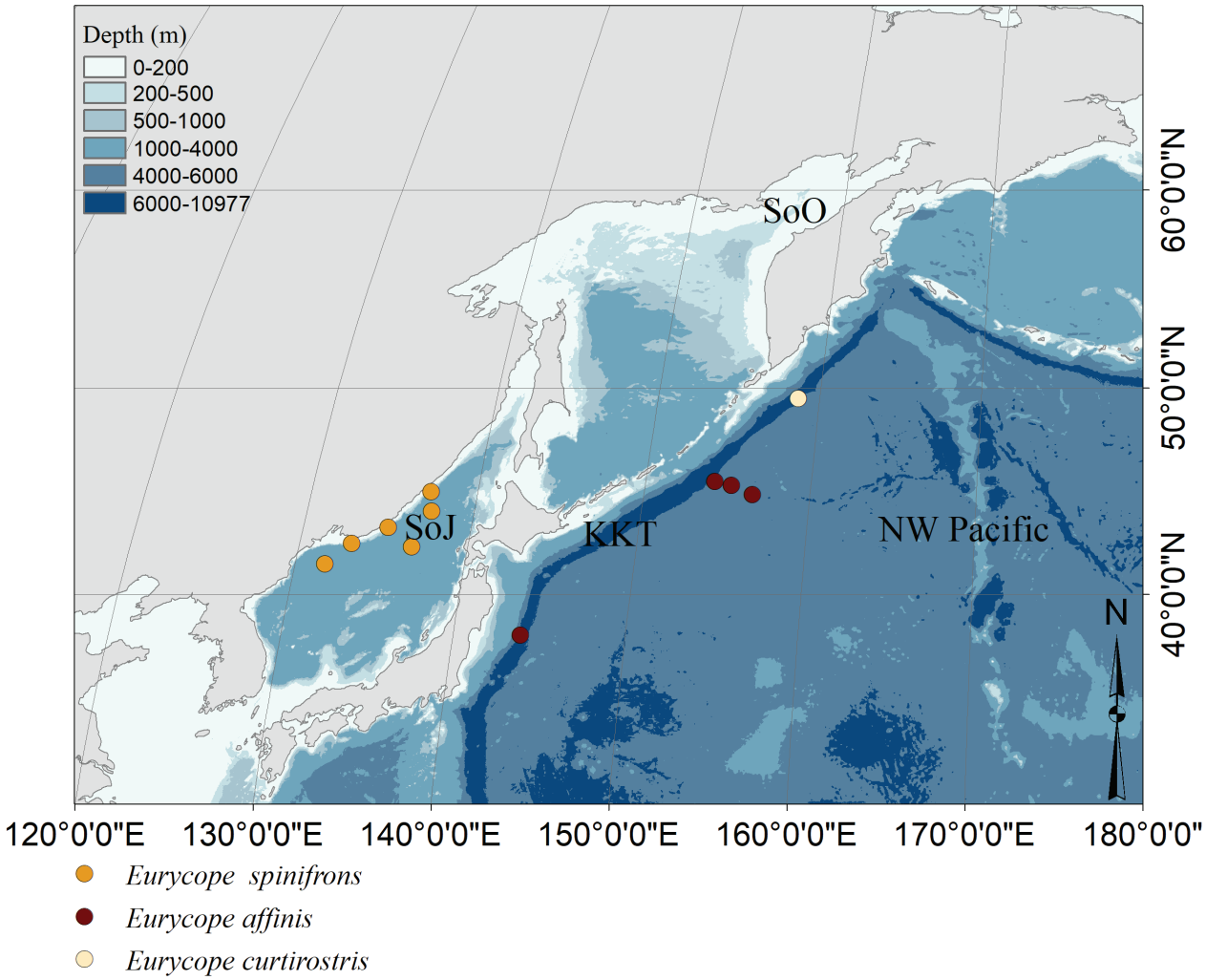
A new species from the abyssal Kuril Basin is noteworthy: *Gurjanopsis kurilensis* Malyutina and Brandt, 2018 is the third species of the rare nectobenthic genus *Gurjanopsis* Malyutina and Brandt, 2007. It has been known so far only from the deep Antarctic and Arctic. This is the first record of the genus for the Pacific Ocean (Map 18). *Gurjanopsis* has a unique morphology for the family. There is a notch on the posterior margin of the pleotelson. Furthermore the male



Map 13. Records of the abyssohadal species *Munnopsoides tattersalli* Birstein, 1963 and *Vanhoeffenura chelata* (Birstein, 1957) (Munnopsidae Lilljeborg, 1864) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

operculum is similar to that of the primitive shallow-water superfamilies Aselloidea and Stenetroidea whose the operculum is formed by reduced first and second (genital) pleopods as well as enlarged third pleopods (Malyutina and Brandt 2018). Normally in the superfamily Janiroidea the operculum is formed only by the first and second pleopods (Wilson 1987).

Another noteworthy new species belongs to the genus *Baeonectes* Wilson, 1982. *Baeonectes brandtae* Malyutina et al. 2013 was found in the Sea of Japan at depths of 455–1,525 m, which represented a new depth record for the genus. Moreover, a few years later the genus was recorded in the Kuril Basin at 3,300 m depth which is now the new depth record for the genus (Malyutina and Brandt 2018). Until then, this genus was comprised of seven species restricted in their distribution by the boreal zone and a depth range of 9–961 m (Golovan and Malyutina 2010; Malyutina et al. 2013). It had been known until then as the shallowest-living genus of Munnopsidae.

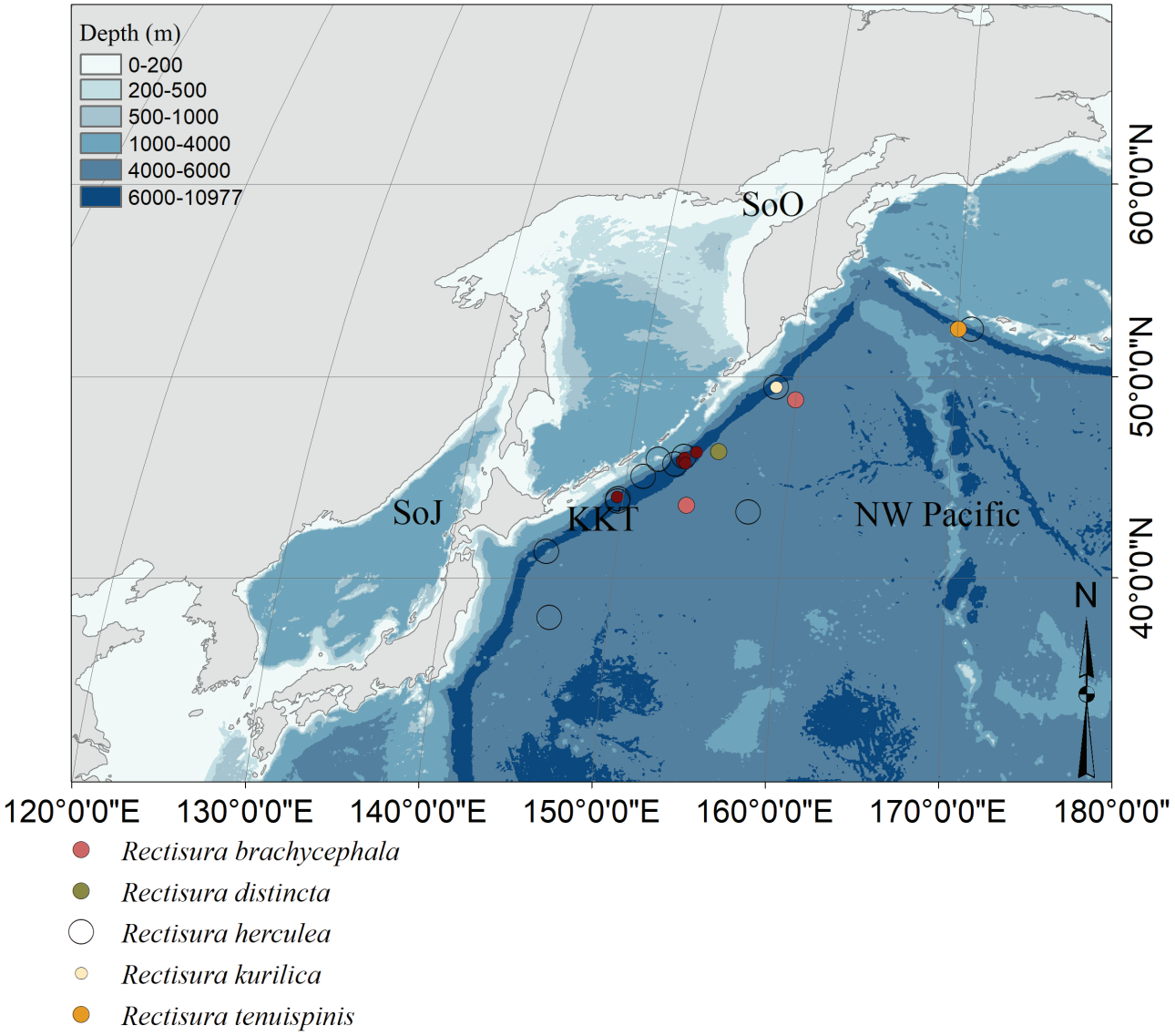


Map 14. Records of selected species of the genus *Eurycope* G.O. Sars, 1864 (Munnopsidae Lilljeborg, 1864) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

5. Discussion

In this chapter the biogeography of selected janiroid isopod families in the deep NWP is summarized, setting a baseline for future studies on their expected distributional changes with continuing climatic changes. Focussing on the families Dendrotionidae, Desmosomatidae, Macrostylidae and Munnopsidae, we also treat one rather uncommon family (Dendrotionidae) with relatively few known species, as well as three of the most abundant and diverse isopod groups of the deep sea.

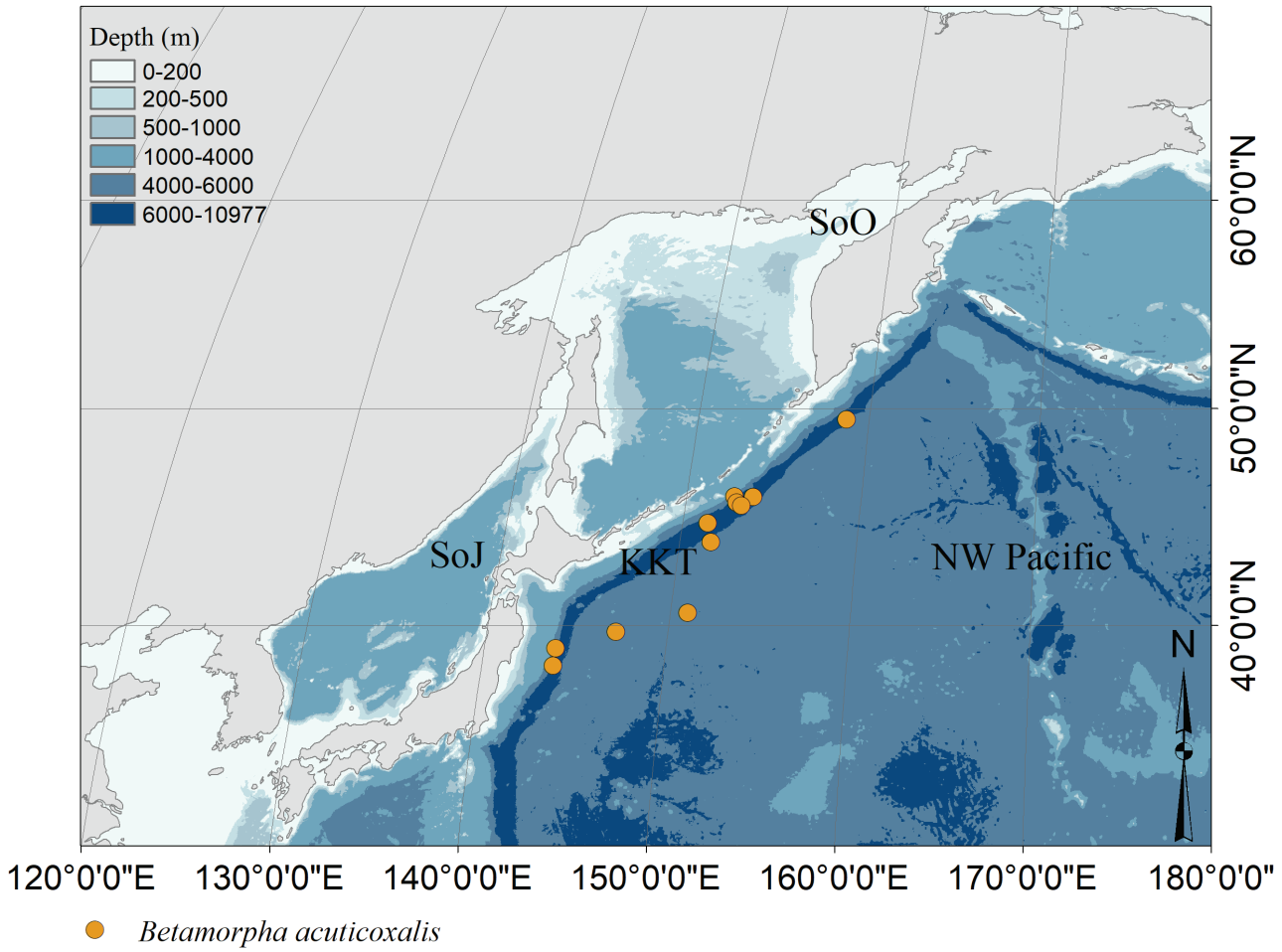
Both in the open NWP as well as in the Sea of Okhotsk dendrotionids are represented by one single species, but not in the Sea of Japan. These two occurred at lower bathyal and abyssal depths exclusively confirming a mainly abyssal distribution of the family (Boyko et al. 2008a; Golovan et al. 2018b).



Map 15. Records of the genus *Rectisura* Malyutina, 2003 (Munnopsidae Lilljeborg, 1864) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

For the other three families diversity was highest at abyssal depths southeast of the KKT (Northwest Pacific Basin). Desmosomatidae and Munnopsidae were recorded also for both the Seas of Okhotsk and Japan. However, their diversities were distinctly reduced in the Sea of Okhotsk and even more so in the Sea of Japan. Macrostylidae have not been recorded from any of the two marginal seas indicating their absence there. At hadal depths Munnopsidae was the most diverse group but also Desmosomatidae and Macrostylidae occurred there. The number of trench endemics was low.

The observed family distribution reflects the oceanographic characteristics and climatic history of the region, and may also be interpreted with regard to the swimming abilities of the families. The Sea of Japan, being the most isolated of the studied areas, is least inhabited

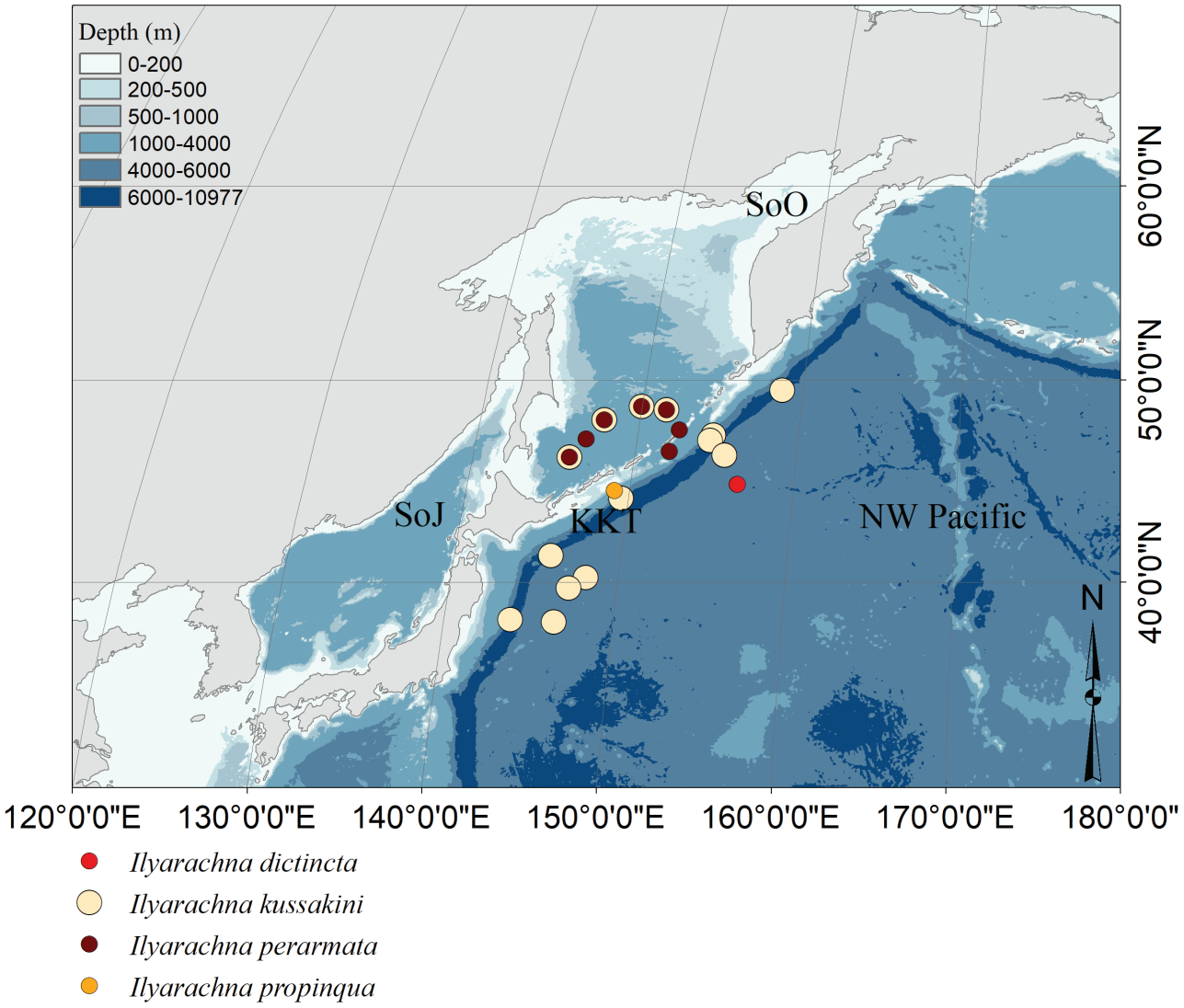


Map 16. Records of the species *Betamorpha acuticoxalis* (Birstein, 1963) (Munnopsidae Lilljeborg, 1864) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

by these typical deep-sea groups, followed by the Sea of Okhotsk and the open NWP. Given that Macrostylidae have been collected at rather shallow sites of cold boreal and austral regions (Sars 1899; Brandt 1992; Riehl and Kaiser 2012; Brix et al. 2018) the apparent absence of this family from the NWP marginal seas seems surprising. Yet this may be a reflection of the lack of swimming adaptations by the Macrostylidae as opposed to Desmosomatidae and Munnopsidae (Bober et al. 2018a) and their preferred endobenthic lifestyle (Hessler and Strömberg 1989; Wägele 1989; Bober et al. 2018b) in spite of their importance – as judged from faunal diversity and numerical abundance.

Interestingly, the abyssal plain of the Northwest Pacific Basin appears to support the highest number of janiroidean isopod species. This finding contradicts the depth-differentiation hypothesis which predicts that highest diversity occurs on bathyal slopes (Rex and Etter 2010).

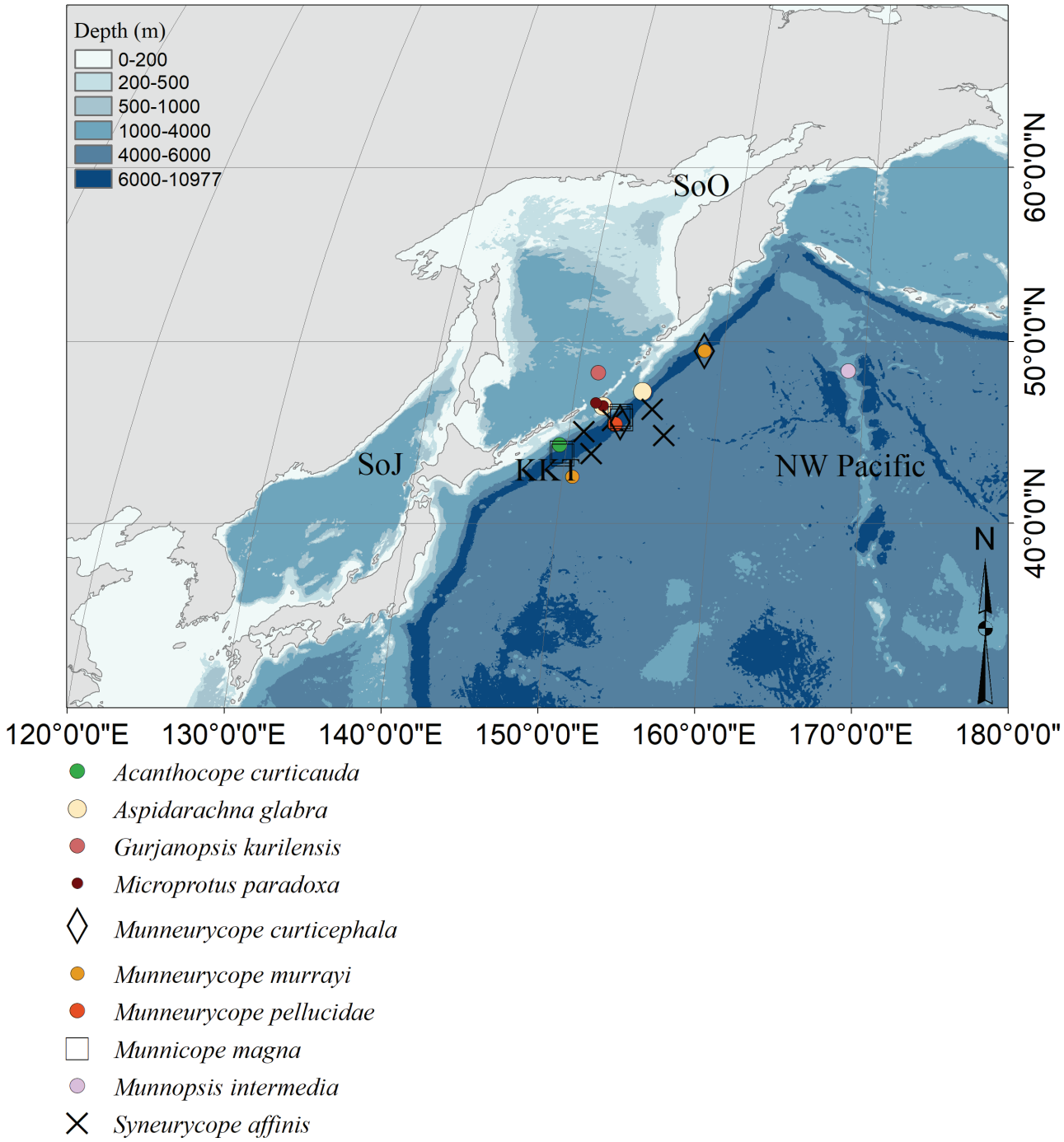
Only few species have been recorded at hadal depths alone – most species encountered there occurred at abyssal depths as well, reflecting the low degree of isolation and extreme conditions.



Map 17. Records of selected species of the genus Ilyarachna G.O. Sars, 1869 (Munnopsidae Lilljeborg, 1864) from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

Acknowledgements

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Map 18. Records of selected rare species of the Munnopsidae Lilljeborg, 1864 from the Northwest (NW) Pacific. Abbreviations: KKT = Kuril-Kamchatka Trench; SoJ = Sea of Japan; SoO = Sea of Okhotsk. See Table 1 for localities.

her organisational effort with writing grants and managing projects, without which none of the recent NWP deep-sea campaigns would have been possible. Captains and crews of RVs '*Akademik M.A. Lavrentyev*' and '*Sonne*' deserve a big thank you for their fantastic work. Many people contributed to sample management and sorting and deserve the authors' gratitude.



Figure 1. Northwest Pacific deep-sea isopod species. (A) *Dendromunna kurilensis* Golovan and Malyutina 2018 (Dendrotionidae). (B) *Macrostylis amaliae / sabinae* Bober et al. 2018 (Macrostylidae). (C) *Rectisura herculae* (Birstein, 1957) (Munnopsidae). (D) *Mirabilicoxa* sp. (Desmosomatidae).

Table 1. Updated checklist of the families Dendrotionidae, Desmosomatidae, Macrostylidae and Munnopsidae (Crustacea, Isopoda, Janiroidea) from the deep Northwest Pacific.

Family	Subfamily	Genus	Species	Taxonomic authority, date of description	Depth range (m)	Data sources
Dendrotionidae				Vanhöffen, 1914		
		Dendromunna		Menzies, 1962		
			D. okhotensis	Golovan and Malyutina, 2018	3,299–3,300	Golovan et al., 2018
			D. kurilensis	Golovan and Malyutina, 2018	5,399–5,408	Golovan et al., 2018, 2019
Desmosomatidae				Sars, 1897		
	Desmosomatinae			Hessler, 1970		
		Desmosoma		Sars, 1864		
			D. lobipes	Kussakin, 1965	220–3,420	Kussakin, 1965,1999, Golovan and Malyutina, 2010, Golovan et al., 2013
		Mirabilicoxa		Hessler, 1970		
			M. biramosa	Golovan, 2018	3,210–3,366	Golovan, 2018
			M. coxalis	(Birstein, 1963)	5,005–54,95	Birstein 1963, 1970, Kussakin, 1999
			M. tenuipes	(Birstein, 1970)	6,675–6,710	Birstein 1970, Kussakin, 1999
		Pseudomesus		Hansen, 1916		
			P. similis	Birstein, 1963	5,441	Birstein 1963, Kussakin, 1999
	Eugerdellatinae			Hessler, 1970		
		Chelator		Hessler, 1970		
			C. michaeli	Golovan, 2015	3,300–5,408	Golovan, 2015b, Golovan, 2018, Golovan et al., 2019, Jennings et al., 2020
		Eugerdella		Kussakin, 1965		
			E. hadalis	Golovan and Brix, 2020	7,111–8,744	Jennings et al., 2020
			E. kurabyssalis	Golovan, 2015	4,830–5,429	Golovan, 2015a, 2018, Golovan et al., 2019, Jennings et al., 2020
		Parvochelus		Brix and Kihara, 2015		
			P. serricaudis	Golovan, 2015	4,830–5,429	Golovan, 2015a, Golovan et al., 2019
		Prochelator		Hessler, 1970		
			P. keenani	Golovan, 2015	4,830–5,408	Golovan, 2015b, Golovan et al., 2019

Family	Subfamily	Genus	Species	Taxonomic authority, date of description	Depth range (m)	Data sources
Macrostylidae				Hansen, 1916		
		Macrostylis		Sars, 1864		
			M. affinis	Birstein, 1963	4,690–5,554	Birstein 1963, 1970, Bober et al. 2018
			M. amaliae	Bober et al. 2018	5,251–5,429	Birstein 1963, 1970, Bober et al. 2018
			M. daniae	Bober et al. 2018	4,830–5,380	Birstein 1963, 1970, Bober et al. 2018
			M. curticornis	Birstein, 1963	5,680–6,670	Birstein 1963, 1970, Bober et al. 2018
			M. grandis	Birstein, 1970	6,435–7,295	Birstein 1963, 1970, Bober et al. 2018, Riehl and Kühn 2020
			M. longula	Birstein, 1970	5,291–5,429	Birstein 1970
			M. longissima	Mezhov, 1981	6,043–6,051	Mezhov 1981
			M. longiuscula	Mezhov, 1981	4,400	Mezhov 1981
			M. profundissima	Birstein, 1970	8,185–9,530	Birstein 1963, 1970, Bober et al. 2018
			M. quadratura	Birstein, 1970	3,175–3,250	Birstein 1963, 1970, Bober et al. 2018
			M. reticulata	Birstein, 1963	5,502	Birstein 1963, 1970, Bober et al. 2018
			M. sabinae	Bober et al. 2018	4,830–5,429	Birstein 1963, 1970, Bober et al. 2018
			M. sensitiva	Birstein, 1970	5,005–5,100	Birstein 1963, 1970, Bober et al. 2018
			M. zenkevitchi	Birstein, 1963	4,690–6,135	Birstein 1963, 1970, Bober et al. 2018
Munnopsidae				Lilljeborg, 1864		
	Acanthocopinae			Wolff, 1962		
		Acanthocope		Beddard, 1885		
			A. curticauda	Birstein, 1970	4,690–4,720	Birstein 1970
	Betamorphinae					
		Betamorpha		Hessler and Thistle, 1975		
			B. acuticoxalis	(Birstein, 1963)	4,942–7,587	Birstein 1963, 1970, Malyutina and Brandt 2015, 2020
	Eurycopinae			Hansen, 1916		
		Eurycope		S.O. Sars, 1864		
			E. affinis	Birstein, 1970	5,005–5,495	Birstein 1963, 1970

Family	Subfamily	Genus	Species	Taxonomic authority, date of description	Depth range (m)	Data sources
			E. linearis	Birstein, 1963	4,000–4,150	Birstein 1963
			E. curtirostris	Birstein, 1963	7,210–7,230	Birstein 1963
			E. spinifrons	Gurjanova, 1933	308–3,665	Gurjanova, 1933
	Ilyarachninae			Hansen, 1916		
		Ilyarachna		S.O. Sars, 1869		
			I. dictincta	Birstein, 1971	4,681–5,780	Birstein 1971, Malyutina and Brandt 2015, 2020
			I. kussakini	Birstein, 1963	3,299–7,230	Birstein 1963, 1971, Malyutina and Brandt 2015, 2018, i2020
			I. perarmata	(Birstein, 1971)	2,770–4,863	Birstein 1971, Malyutina and Brandt 2015, 2020
			I. propinqua	(Birstein, 1971)	2,665–3,015	Birstein 1971, Malyutina and Brandt 2015, 2020
		Aspidarachna		S.O. Sars, 1899		
			A. glabra	(Birstein, 1971)	2,915–4,863	Birstein 1971, Malyutina and Brandt 2015, 2020
		Echinozone		S.O. Sars, 1899		
			E. longipes	(Birstein, 1963)	2,940	Birstein 1963, 1970
			E. tuberculata	Birstein, 1971	2,665–3,015	Birstein 1971
			E. venusta	Birstein, 1971	2,770–2,820	Birstein 1971
			E. scabra	Birstein, 1971	2,770–2,820	Birstein 1971
	Munnopsinae			S.O. Sars, 1869		
		Munnopsis		M. Sars, 1861		
			M. intermedia	Birstein, 1963	3,015–2,865	Birstein 1963
		Munnopsoides		Tattersall, 1905		
			M. tattersalli	Birstein, 1963	2,940–8,255	Birstein 1963, Malyutina and Brandt 2015, 2018, 2020
	Storthyngurinae			Kussakin, 2003		
		Vanhoeffenura		Malyutina, 2004		
			V. chelata	(Birstein, 1957)	4,859–9,346	Birstein 1957, 1963, Malyutina and Brandt 2015, 2020
			V. bicornis	(Birstein, 1957)	6,156–8,430	Birstein 1957, 1963
		Rectisura		Malyutina, 2003		
			R. herculea	(Birstein, 1957)	6,475–9,346	Birstein 1957, 1963, 1970, 1971, Malyutina and Brandt 2020

Family	Subfamily	Genus	Species	Taxonomic authority, date of description	Depth range (m)	Data sources
			R. distincta	(Birstein, 1970)	4,798–6,215	Birstein 1970, Malyutina and Brandt 2020
			R. kurilica	(Birstein, 1957)	7,210–8,200	Birstein 1957, 1963, 1970, 1971, Malyutina and Brandt 2020
			R. brachycephala	(Birstein, 1957)	5,461–5,680	Birstein 1957, 1963, 1970, 1971,
			R. tenuispinis	(Birstein, 1957)	7,246–7,286	Birstein 1957, 1963, 1970
			R. vitjazi	(Birstein, 1957)	6,435–8,430	Birstein 1957, 1963, 1970
		Microprotus		Richardson, 1910		
			M. paradoxa	(Birstein, 1970)	2,327–2,872	Birstein 1970, Malyutina and Brandt 2020
	Syneurycopinae			Wolff, 1962		
		Syneurycope		Hansen, 1916		
			S. affinis	Birstein, 1970	5,005–6,228	Birstein 1970, Malyutina and Brandt 2015, 2018, 2020
incertae sedis		*Microcope*		Malyutina, 2008		
			M. ovata	(Birstein, 1970)	3,299–6,575	Birstein 1970, Malyutina 2015, Malyutina and Brandt 2015, 2018, 2020
			M. stenopigus	Malyutina, 2015	4,681–5,780	Malyutina, 2015; Malyutina and Brandt 2015, 2018, 2020
incertae sedis		*Munneurycope*		Stephensen, 1912		
			M. pellucidae	Birstein, 1970	5,900–8,400	Birstein 1970, Malyutina and Brandt 2020
			M. curticephala	Birstein, 1963	6,675–7,230	Birstein 1963, 1970
			M. murrayi	(Walker, 1903)	530–7,800 pelagic	Birstein 1963, 1970
incertae sedis		*Munnicope*		Menzies and George, 1972		
			M. magna	(Birstein, 1963)	7,600–8,345	Birstein 1963
incertae sedis		*Gurjanopsis*		Malyutina and Brandt, 2007		
			G. kurilensis	Malyutina and Brandt, 2018	3,300	Malyutina and Brandt 2018

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CHAPTER 20

TANAIDACEA

TANAIDACEAN DIVERSITY ON THE NW PACIFIC – STATE OF KNOWLEDGE AND FUTURE PERSPECTIVES

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1. Introduction

1.1. Biology/Ecology

Tanaidacea (Crustacea: Peracarida) is an order of marine benthic crustaceans represented mainly by brooders with low mobility and limited dispersal potential (Larsen 2005, Błażewicz-Paszkowycz et al. 2012). Tanaidacea are extremely diverse in morphology, ecology and lifestyles, including free living forms of Neotanaidae (Gardiner 1975), burrowers like most apseudomorph species or tube dwellers like the tanaidomorphs (Hassack & Holdich 1987, Kakui & Hiruta 2017) (Figure 1).

Feeding preferences have not been intensively studied for tanaidaceans, but they are considered to be mostly detritivores collecting food from the sea bottom (Johnson & Attramadal 1982, Kudinova-Pasternak 1991, Błażewicz-Paszkowycz & Ligowski 2002). To our knowledge, active preying on live animals seem to have been reported only once so far (Alvaro et al. 2011), but feeding on the sediment makes tanaidaceans potential opportunistic predators that could prey on a variety of meiofauna taxa. According to Larsen (2005), tanaidacean preys include echinoid larvae (Highsmith, 1982, 1983), polychaetes (Oliver & Slattery 1985), nematodes and harpacticoid copepods (Feller, 1978). The piercing mandible molar observed in some Pseudotanaidae or Leptognathiidae species suggest an active predatory behavior, whereas the reduced molars and modified setation of some Anarthruridae (Bird 2004, Gellert & Błażewicz 2018) suggest they could feed on soft tissue-organisms. The deep-sea species *Exspina typica* actively drills the body-walls of Molpadiida and Elasipodida holothurians (Alvaro et al. 2011) and it can be considered a parasite. Members of the Kalliapseudinae subfamily are suspension feeders, with chelipeds and maxillipeds modified into a specialized filtering apparatus (Lang 1956, Drumm 2005). One genus present in NW Pacific deep-sea waters (i.e. *Protanais* Sieg, 1980) is particularly known for being an active burrower and one of the firsts colonizers on sunken wood (McClain et al. 2011; Błażewicz-Paszkowycz, et al., 2015). On the other hand, tanaidaceans are known to host a wide range of taxa (Figure 2), including parasitic nematodes (Bamber & Błażewicz-Paszkowycz 2013), tantulocarids (Greve 1988, Kolbasov & Savchenko 2010) or epibiontic protists (Morales-Vela et al. 2008).

1.2. Habitat

Tanaidacea are considered eurytopic organisms, being present in all types of marine ecosystems, such as shallow coral and *Lophelia* reefs (Jakiel et al. 2015, Stępień et al. 2019a), estuarine marshes (Stępień & Błażewicz-Paszkowycz 2009a), mangrove swamps (Larsen et al. 2013), methane or sulfurous brine seeps and hydrothermal vents (Larsen et al. 2006, Błażewicz-Paszkowycz & Bamber 2011, Błażewicz-Paszkowycz et al. 2011, Esquete & Cunha 2018). Often associated with soft sediments, they are also found on coral rubles and rocks, particularly when overgrown by epibionts and algae. Few species are recorded from brackish waters, such as *Sinelobus vanhaareni* or *Heterotanais oerstedi* (Bückle-Ramirez 1965, Bamber 2014), or freshwater, like *Sinelobus stanfordi* and *Pseudohalmyrapseudes aquadulcis* (Larsen and Hansknecht 2004, Jaume and Boxshall 2007). *Sinelobus stromatoliticus* (Rishworth, Perissinotto & Błażewicz, 2018) is an important element of the fauna associated with temporary stromatolites (Rishworth et al.



Figure 1. Tanaidacea diversity present in NW Pacific deep-sea waters, with examples from the Kuril-Kamchatka Trench (KKT) and Sea of Okhotsk (SoO) areas. (A) *Leviapseudes* sp. (KKT); (B) *Agathotanais* sp. (SoO); (C) *Agathotanais* sp. (KKT); (D) *Paragathotanais* (KKT); (E) *Collettea* sp. (KKT); (F) *Leptognathia* sp. (SoO); (G) *Pseudotanais* sp.; (H) *Arthrura* sp. (KKT); I, *Tanaella* sp. (SoO); (J) *Typhlotanais* sp. (KKT); (K) *Typhlamia* sp. (SoO) and (L) *Typhlotanais* sp. (SoO). All scale bars represent 1 mm. a, for A; b, for B–D, G; c, E, F, H–L.

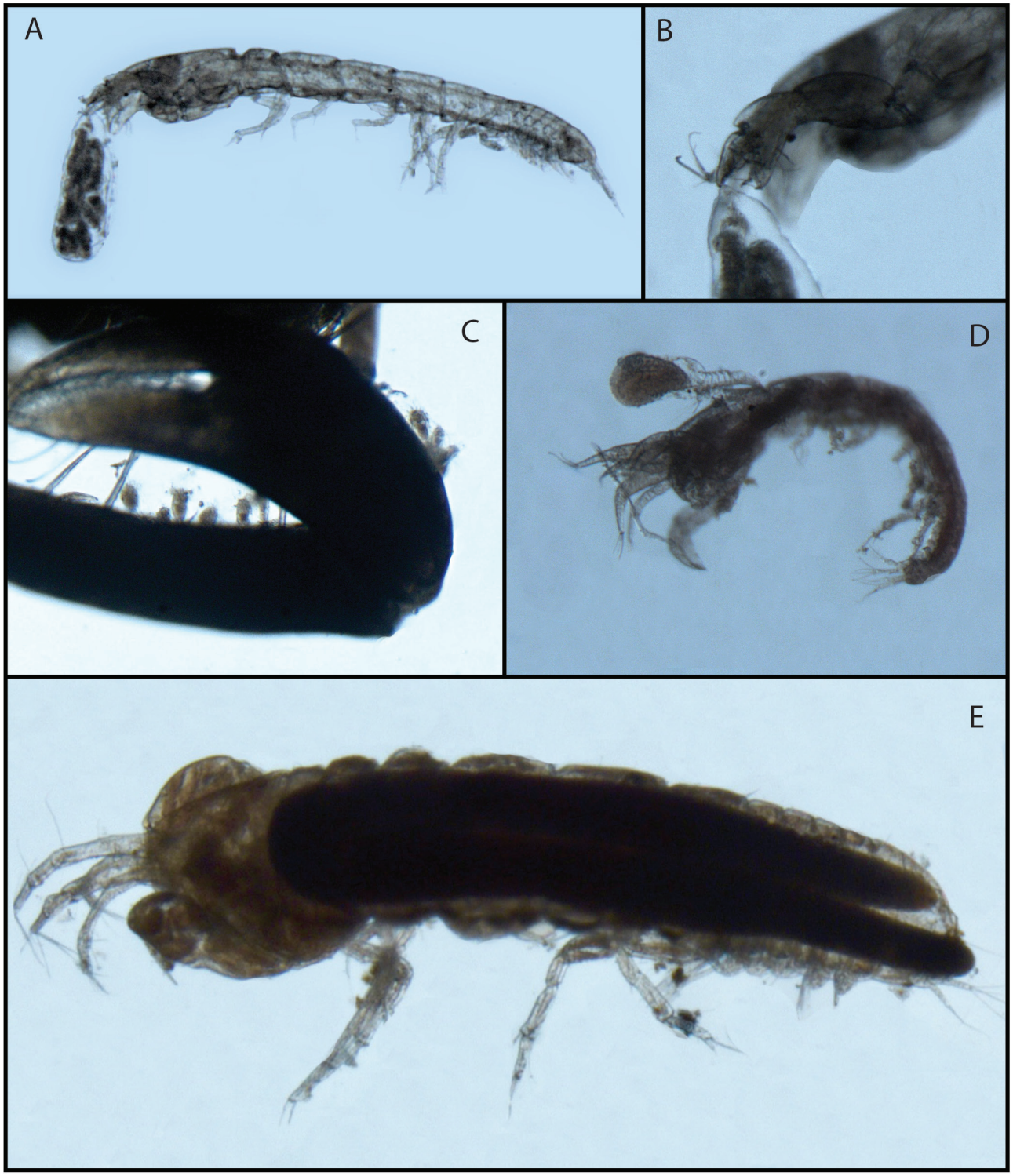


Figure 2. Fauna associated with Tanaidacea from NW Pacific deep-sea waters: (A, B) agathotanaid with mature parthenogenetic tantulocarid (?) female attached to chela; (C) ciliate epibiont on cheliped of *Leviapseudes* sp.; (D) typhlotanaid manca with tantulocarid (?) attached to articulation between pereonites 1–2; (E) parasitic nematode inside *Pseudotanais* sp.

2019). Tanaidaceans occupy interstitial habitats (Bird & Holdich 1985, Gellert & Błażewicz 2018), caves and groundwaters (Larsen & Hansknecht 2004). *Hexapleomera robusta* has been recorded

from shell crevices on manatees and sea turtles (Kitsos et al. 2005, Morales-Vela et al. 2008), and *Charbeitanais spongicola* (Bamber & Bird, 1997) can be found in sponge ostia (or oscula) or the buccal cavity of some polychaetes (Suárez-Morales et al. 2011).

Tanaidaceans are found across a very large depth range – from tidal to hadal (Kudinova-Pasternak 1973, Stępień & Błażewicz-Paszkowycz 2009). Tanaidacea densities can reach a few thousand individuals per square meter in the upper shelf (Delille et al. 1985, Błażewicz-Paszkowycz & Jażdżewski 2000), and they often outnumber polychaetes, amphipods or isopods in deep-sea waters (Błażewicz-Paszkowycz et al. 2012). The abundance of tanaidaceans in benthic communities drops along a depth gradient, although species diversity seems to increase for some families. Consequently, bathyal or deeper abyssal ecosystems may include fewer individuals but a larger number of species than shallower areas (Pabis et al. 2014, 2015, Błażewicz et al. 2019). This trend of diversity changes according to depth does not constitute a general pattern though, and studies on the deep part of the Sea of Okhotsk (SoO) show tanaidaceans to be diverse but as numerous as those on the shelf (Stępień et al. 2019b). Organic matter, as a proxy of ecosystem productivity, has been suggested to be a key factor shaping Tanaidacea distribution in marine ecosystems, but ecological constraints are far from being understood (McCallum et al. 2015, Woolley et al. 2016).

1.3. Geographical distribution

Tanaidaceans can be found in all latitudes, from the tropics to polar regions (Błażewicz-Paszkowycz et al. 2012). Many tanaidacean species are considered to have restricted zoogeographical ranges, but there are some interesting exceptions. For example, *Meromonakantha macrocephala* (Hansen, 1913) has been recorded from both polar regions (Sieg 1986a) and the holothurian parasite – *Exspina typica* – is considered a cosmopolitan species (Alvaro et al. 2011). *Sinelobus vanhaareni* (Bamber, 2014) is reported as worldwide invasive species, recorded in high abundances in the coasts of Netherlands (Van Haaren and Soors 2009) and the eastern part of the Baltic Sea (Brzana et al. 2019). Much of our understanding of how species change from tropics to poles comes from taxonomical papers, and so far a single study has focused on the latitudinal diversity gradient of Tanaidacea (Pabis et al. 2015). The results obtained are very sensitive to geographical sampling and some regions of the world ocean are better studied than others (Sars 1899, Hansen 1913, Bird and Bamber 2013, Błażewicz-Paszkowycz 2014). Contrary to what could be expected, tanaidaceans from both polar regions are better studied than temperate and warm-water taxa, while recent studies have focused mostly on deeper ocean regions rather than shallow waters (Brandt et al. 2005, 2015, 2018, Barnes et al. 2009, Fischer & Brandt 2015).

Wide distribution ranges are considered to be the common rule based on the concept of continuous and monotonous deep-sea benthic ecosystems (Rex and Etter 2010). This concept has been recently questioned though, proving that there is no simple pattern for how species are distributed or how population connectivity is sustained (Havermans et al. 2013). Poorly-swimming tanaidaceans, with no planktonic stages in their life history, show a restricted dispersal potential

(Jakiel et al. 2018). According to Błażewicz-Paszkowycz et al. (2012), about one third of all known apseudomorph genera (N = 109) occur in one ocean basin only, and 28 out of those (mainly shallow-water) genera were only recorded from the Indo-Pacific region. Apseudomorphs can have restricted zoogeographic ranges at the family level. The deep-sea Apseudidae genera, such as *Carpoapseudes* Lang, 1968, *Colobocladus* Gutu, 2006, *Eliomosa* Gutu, 2006, *Fageapseudes* Bâcescu & Gutu, 1971, *Glabroapseudes* Guerrero-Kommritz & Heard, 2003, *Langapseudes* Bacescu, 1987 and *Leviapseudes* Sieg, 1983, are distributed in two or more marine basins. The hard coral-associated Tanzanapseudinae (Stępień & Błażewicz-Paszkowycz 2009b) and shallow-water Metapseudidae occure exclusively in tropical areas (Stępień et al. 2019a), while Whiteleggidae are only present in Australia (Błażewicz-Paszkowycz & Bamber 2012). The Sphyrapodidae probably had a shallow-water origin and colonized the deep-sea only after isolation of Antarctica by the Antarctic Circumpolar Current (Błażewicz-Paszkowycz et al. 2012), because the family has not been recorded in the Southern Ocean.

Tanaidomorpha live inside self-constructed tubes and might have a lower dispersal capability than burrowing apseudomorphs. Nevertheless, recent results on the numerous and diverse abyssal genus P*seudotanais* suggest that some haplotypes can be distributed over a few hundred kilometers (Jakiel et al. 2019).

2. Objectives

Current knowledge on the diversity of deep-sea Tanaidacea occurring in the NW Pacific is summarized here based on information gathered from published literature. Taxonomic, geographic and bathymetric data was collected mostly from the series of studies resulting from the Russian expedition on RV *Vityaz* (Kudinova-Pasternak 1970, 1976, 1984), multiple Japanese expeditions (Bamber 2007a, Bird 2007b, 2007c, Błażewicz-Paszkowycz 2007, Larsen 2007, Larsen & Shimomura 2007, McLelland 2007, Błażewicz-Paszkowycz et al. 2013) and results of the recent German-Russian programs: Sea of Japan Biodiversity Studies – SoJaBio (Brandt et al. 2010), Sea Of Okhotsk Biodiversity Studies – SokhoBio (Malyutina, Brandt, & Ivin, 2015) and Kuril-Kamchatka Biodiversity Studies – KuramBio (Brandt & Malyutina 2012, Błażewicz-Paszkowycz et al. 2013, Jóźwiak 2016). The diversity of each family found in the area and their bathymetric and spatial distribution patterns are analyzed. The gradual change in tanaidacean family, genera and species diversity with depth and latitude are shown and discussed in detail.

3. Material and Methods

3.1. Coverage Area

For the purpose of this paper, we focused on the NW Pacific deep-sea (below 2,000 m) comprised between 40–60°N and 120–180°E. The list of taxa recorded in the studied area and reported in the literature is shown in Table 1. Taxonomical classification of species is based on the World Register of Marine Species (WoRMS; accessed 10/09/2019). For each nominal species all previous records have been compiled and information about latitude, longitude and bathymetry extracted whenever possible, so that spatial distribution and bathy-

metric patterns could be further analyzed. All taxa for which the type locality is placed outside Pacific are indicated with an asterisk (*). The list of nominal taxa is complemented with previously undescribed species and recently published: Stępień, Pabis & Błażewicz (2019), Bird (2007) and Jakiel, Palero & Błażewicz (2019), indicated with indexes 1–3 respectively (see List of Tanaidacea species in the Results section).

3.2. Depth Gradient

The original set of records obtained from the literature was curated and reduced by removing those cases where bathymetry could not be recovered directly from the text. Information about bathymetric ranges for each species, genera and families were estimated based on this final dataset (n = 474 records). The median depth and standard deviation was estimated for each family using the Median and StandardDeviation functions in Mathematica v11.3.0.0 (http://www.wolfram.com/mathematica/). Several histograms, chosen to approximate an underlying smooth distribution, were plotted for each tanaidacean family using the Histogram function in Mathematica v11.3.0.0. The variation in number of species, genera and families with depth, assuming the median depth as the preferred depth for each species, was assessed counting the taxa present every 100 m. Finally, in order to analyze how deep in the ocean do we need to go to observe a particular proportion of the total diversity, a cumulative curve was built using the FoldList function in Mathematica v11.3.0.0.

3.3. Latitudinal Gradient

The latitudinal gradient of decreasing richness from tropical to temperate and polar areas is known since the early days of ecology, but exceptions to the general rule exist and these patterns may be dependent on characteristics of spatial scale and taxonomy (Willig et al. 2003). The variation in the relative proportion of families, genera and species with latitude was assessed counting the taxa present every latitudinal degree from 40°N to 60°N and dividing by the total number of taxa observed in the final dataset (at the corresponding taxonomic level). A cumulative curve was then built using the FoldList function in Mathematica v11.3.0.0 (http://www.wolfram.com/mathematica/) in order to analyze how far north in the NW Pacific do we need to go to observe a particular proportion of the total diversity. Finally, the Jaccard distance was used to estimate the amount of differentiation between the tanaidacean fauna present on each of the marine ecoregions included in the review namely, the Sea of Okhotsk, the Oyashio Current, NE Honshu and the Sea of Japan. The JaccardDissimilarity function was used to measure the overlap between the presence/absence vectors of Tanaidacea.

4. Results

4.1. Richness patterns

A total of 14 families, comprising 41 genera and 115 tanaidacean species have been reported from the NW Pacific deep-sea waters in the literature. From these, 62 species (belonging to 32 genera) are already described, but as many as 53 species (from 23 genera) are new to science and await further morphological/molecular analyses (Bird 2007b,c, Jakiel et al. 2019, Stępień et al. 2019b). About 2/3 of the final 474 records

belong to four Tanaidomorpha families namely: Typhlotanaidae, Pseudotanaidae, Akanthophoreidae and Agathotanaidae (Figure 3). The most speciose family was Typhlotanaidae (20 species; seven genera) followed by Akanthophoreidae (16 species; five genera), Pseudotanaidae (14 species; two genera), Leptognathiidae (14 species; one genus), and Agathotanaidae (10 species; three genera). Each of the families Neotanaidae, Apseudidae and Anarthruridae were represented by seven species from one, five and two genera, respectively. The less diverse families include Colletteidae (five species; three genera), Cryptocopidae (four species, two genera), Tanaellidae (two species, two genera) and Paranarthrurellidae (two species, two genera). Heterotanoididae and Tanaidae were only represented by one species each. Additionally, the summary below is supplemented with five species with an *incertae sedis* family status.

The relative proportion of species, genera and families (over the total number of taxa observed at each taxonomic level) present every 100 m bathymetric interval, is shown in Figure 4. About 80% of the total family-level diversity recorded in NW Pacific can be already observed between 3,000 and 3,500 m, whereas the diversity of genera and species present at that depth is around 50% and 20%, respectively. A second peak of diversity can be observed between 5,000–6,000 m, with the cumulative curve showing that over 95% taxa are present above hadal depths (Figure 4). Histograms showing of the bathymetric distribution of the most abundant tanaidacean families are given in Figure 5 (notice the estimated median depth and standard deviation under each family name). Six of the families had an estimated median depth below 4,000 m namely, Akanthophoreidae, Agathotanaidae, Anarthruridae, Typhlotanaidae, Leptognathiidae and Colletteidae (Figure 5). The

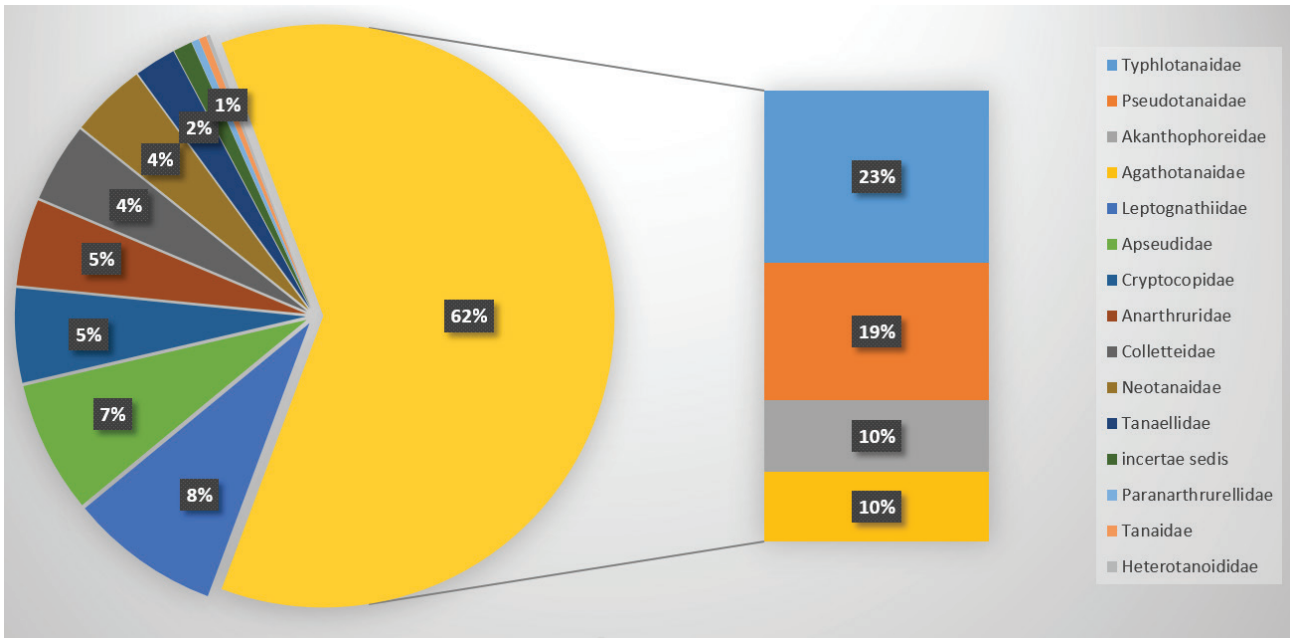


Figure 3. Expanded pie-chart showing the taxonomic distribution of Tanaidacea species diversity in NW Pacific deep-sea waters. Percentages obtained from the final dataset of literature records (N = 474 records).

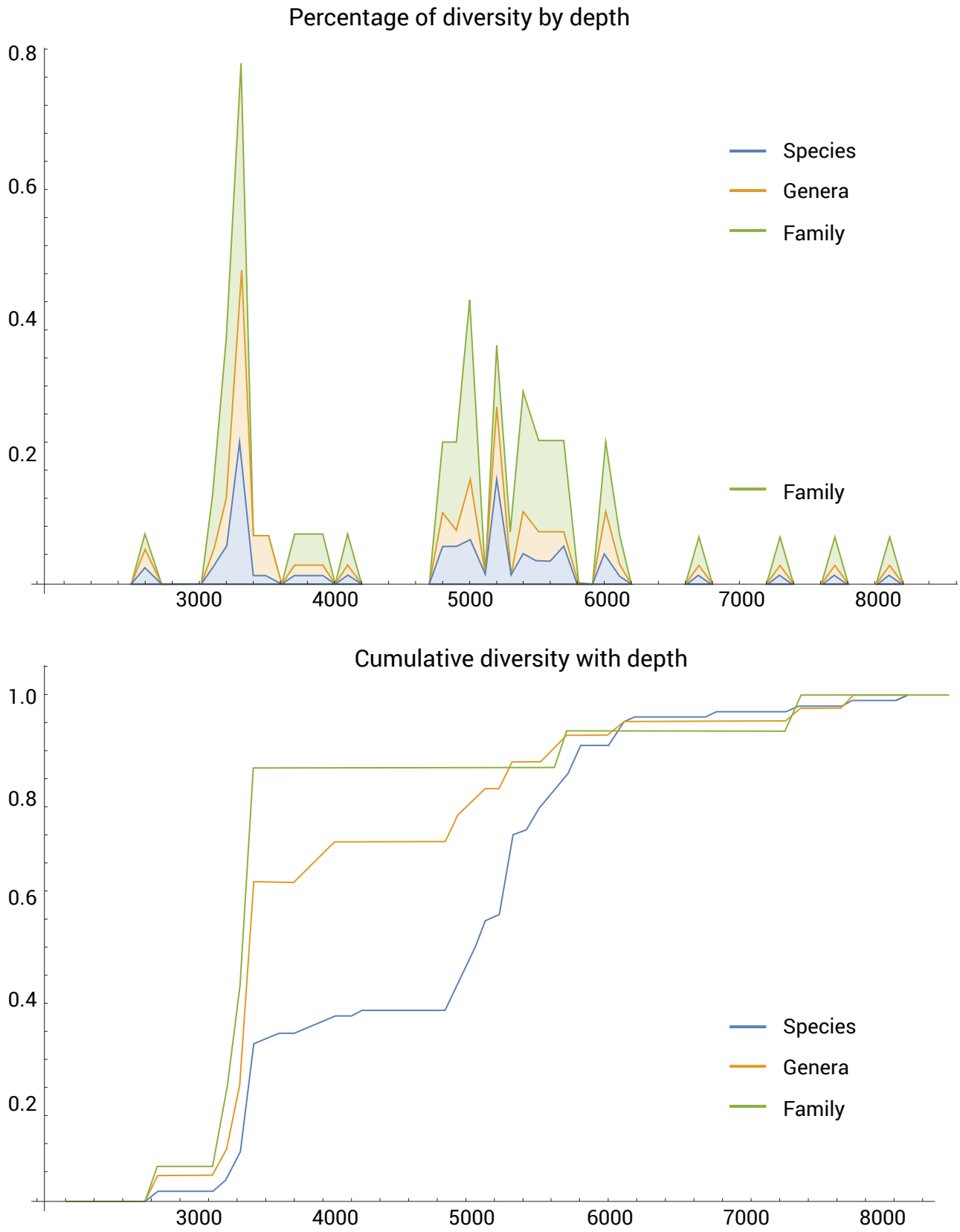


Figure 4. Diversity of tanaidacean families/genera/species as a function of depth. Both the percentage over the total diversity (top) and cumulative percentages (bottom) were estimated for every 100 m depth stratum, from 2,000 m to 8,000 m depth.

first three families are clearly more frequent around 3,000–4,000 m, but the last three approximating a multimodal distribution with another peak around 5,000 m. A second group of families, including Neotanaidae, Apseudidae, Cryptocopidae and Pseudotanaidae, had an

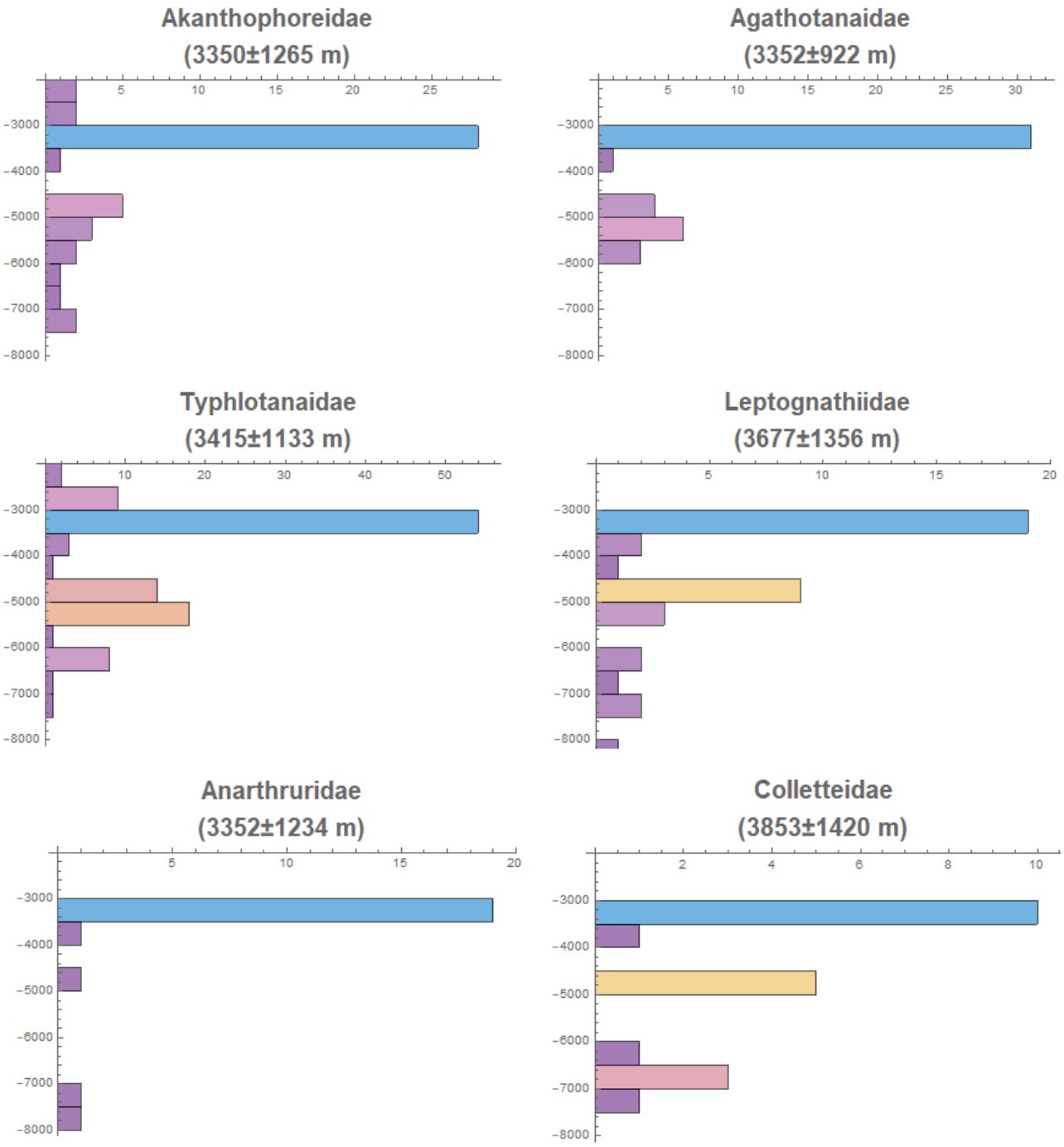


Figure 5. Depth distribution histograms for: Akanthophoreidae, Agathotanaidae, Anarthruridae, Typhlotanaidae, Leptognathiidae, and Colletteidae. Columns are colored as a function of the total number of records for each family, with light blue representing the depth stratum with the largest number of records. Median estimated depth and standard deviation are indicated under each family name.

estimated median depth around 5,000 m (Figure 6).

The latitudinal variation of diversity revealed a gradual increase in richness from southern to northern areas, with two main areas located around 41–43°N and 45–47°N (Figure 7). The proportion of families, genera or species present was highest around 45–47°N, corresponding to the area including the Sea of Okhotsk. The cumulative proportion of families, genera and species with latitude revealed that the diversity of families already present south of 42°N is as high as 80% of the total, whereas we need to get to 46°N in order to get a similar proportion of the total number of species and genera (Figure 7). More details on particular genera and/or species are given in the following taxonomical account.

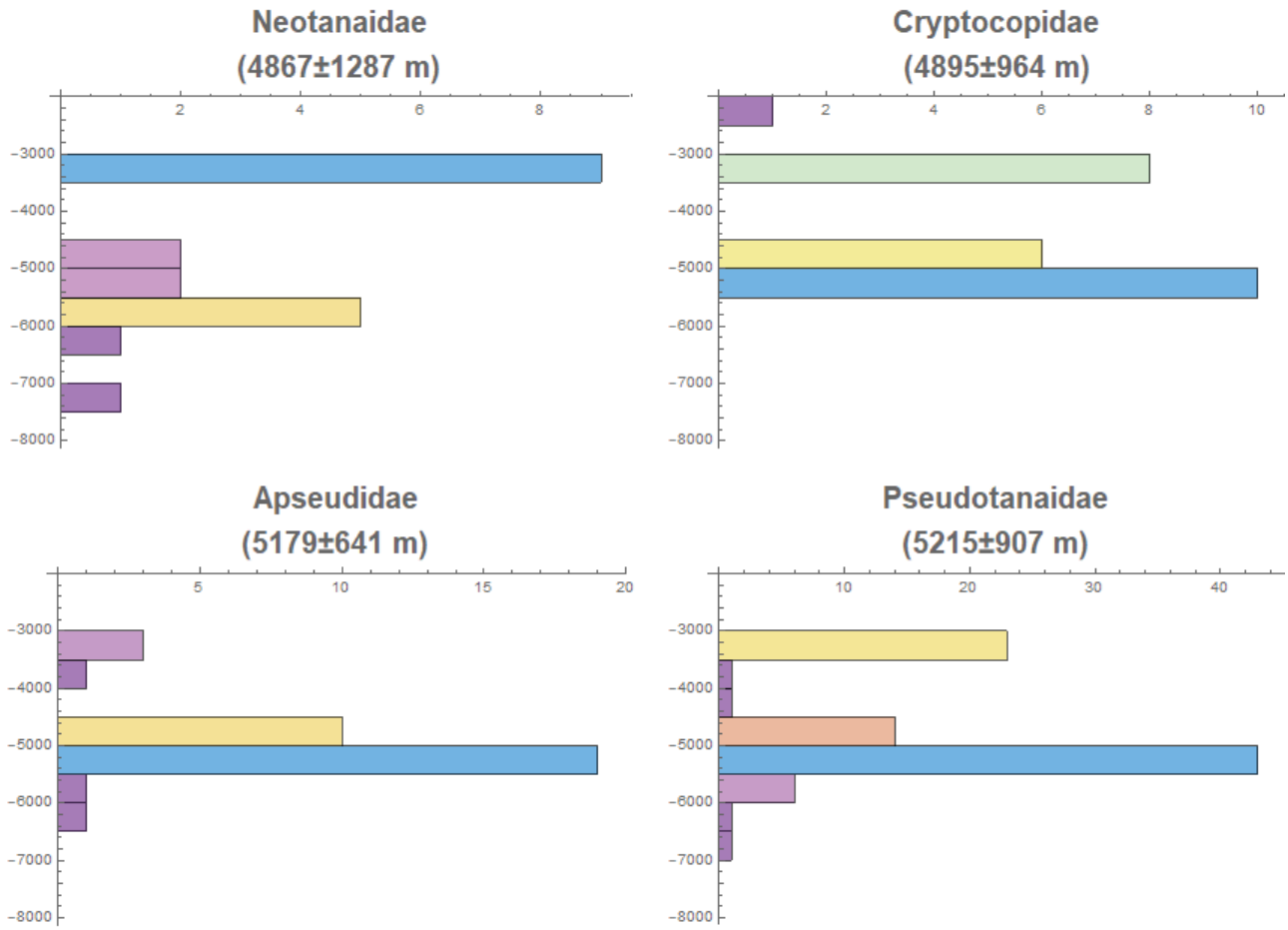


Figure 6. Depth distribution histograms for: Neotanaidae, Cryptocopidae, Apseudidae, and Pseudotanaidae. Columns are colored as a function of the total number of records for each family, with light blue representing the depth stratum with the largest number of records. Median estimated depth and standard deviation are indicated under each family name.

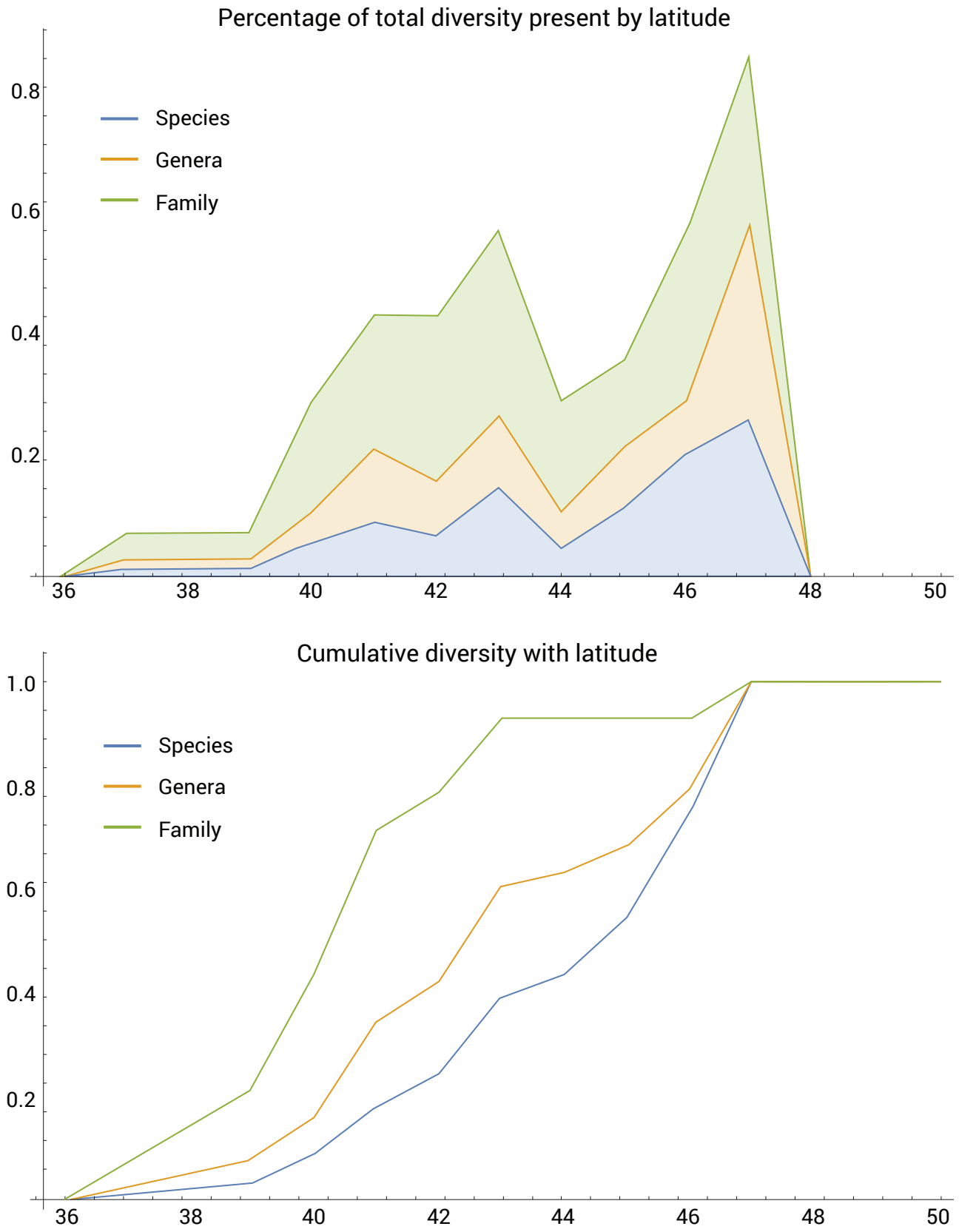


Figure 7. South to North latitudinal gradient of tanaidacean families/genera/species diversity. Both the percentage over the total diversity (top) and cumulative percentages (bottom) were estimated for every latitudinal degree, from 38 N to 50 N.

List of Tanaidacea species from NW Pacific deep sea waters (>2,000 m)

Suborder Apseudomorpha

Family Apseudidae Leach, 1814

Apseudes sp. 1[1]
Apseudopsis sp. [1]
Carpoapseudes varindex Bamber, 2007
Fageapseudes bicornis (Kudinova-Pasternak, 1973)
Fageapseudes brachyomos Bamber, 2007
Fageapseudes vitjazi (Kudinova-Pasternak, 1970)
Leviapseudes zenkevitchi (Kudinova-Pasternak, 1966)

Suborder Tanaidomorpha

Superfamily Neotanaoidea Sieg, 1980

Family Neotanaidae Lang 1956

Neotanais americanus Beddard, 1886*
Neotanais kuroshio Bamber, 2007
Neotanais oyashio Bamber, 2007
Neotanais sp. 1[1]
Neotanais sp. 2[1]
Neotanais tuberculatus Kudinova-Pasternak, 1970
Neotanais wolffi Kudinova-Pasternak, 1966

Superfamily Paratanaoidea Lang, 1949

Family Agathotanaidae Lang, 1971
Agathotanais hadalis Larsen, 2007
Agathotanais ingolfi Hansen, 1913
Agathotanais sp. 1[1]
Agathotanais splendidus Kudinova-Pasternak, 1970
Paragathotanais abyssorum Larsen, 2007
Paragathotanais sp. 1[1]
Paragathotanais sp. 2[1]
Paragathotanais zevinae Kudinova-Pasternak, 1970
Paranarthrura sp. 1[1]
Paranarthrura vitjazi Kudinova-Pasternak, 1970

Family Akanthophoreidae Sieg, 1986

Akanthophoreus crassicauda Bird, 2007
Akanthophoreus undulatus Bird, 2007
Akanthophoreus sp. 1[1]
Akanthophoreus sp. KK#1[2]
Akanthophoreus sp. KK#3[2]
Akanthophoreus sp. KK#5[2]
Chauliopleona armata (Hansen, 1913)*
Chauliopleona hansknechti Larsen & Shimomura, 2007
Chaulipleona sp. 1[1]
Parakanthophoreus gracilis (Krøyer, 1842)*
Parakanthophoreus imputatus (Bird, 2007)
Parakanthophoreus verutus (Błażewicz-Paszkowycz, Bamber & Jóźwiak, 2013)
Parakanthophoreus sp. 1[1]
Paraleptognathia sp. 1[1]
Paraleptognathia sp. 2[1]
Tumidochelia dentifera (Sars, 1899)*

Family Anarthruridae Lang, 1971

Anarthruridsae sp. [1]
Anarthruridae sp. 2[1]
Anarthruridae sp. 3[1]
Anarthruridae sp. 4[1]
Anarthruridae sp. 5[1]
Anarthruropsis langi Kudinova-Pasternak, 1976
Siphonolabrum tenebrosus Bird, 2007

Family Colletteidae Larsen and Wilson, 2002

Collettea cylindrata (Sars, 1882)*
Collettea sp. 1[1]
Leptognathiella aff. *abyssi*
Leptognathiopsis langi (Kudinova-Pasternak, 1970)
Leptognathiopsis sp. 1[1]

Family Cryptocopidae Sieg, 1977

Cryptocope sp.

Cryptocopoides arcticus (Hansen, 1887)*
Cryptocopoides pacificus McLelland, 2007
Cryptocopoides sp.1[1]

Heterotanoididae Bird, 2012
Heterotanoides ornatus Sieg, 1977

Leptognathiidae Sieg, 1976
Leptognathia aneristus Bird, 2007
Leptognathia birsteini Kudinova-Pasternak, 1965
Leptognathia breviremis (Lilljeborg, 1864)*
Leptognathia dentifera Sars, 1886*
Leptognathia greveae Kudinova-Pasternak, 1976
Leptognathia microcephala Kudinova-Pasternak, 1978
Leptognathia parelegans Kudinova-Pasternak, 1970
Leptognathia rotundicauda Kudinova-Pasternak, 1970
Leptognathia sp. 3[1]
Leptognathia sp. 1[1]
Leptognathia sp. 2[1]
Leptognathia tuberculata Hansen, 1913
Leptognathia vinogradovae Kudinova-Pasternak, 1970
Leptognathia zenkevitchi Kudinova-Pasternak, 1970

Paranarthrurellidae Błażewicz, Jóźwiak, Jennings & Frutos, 2019
Arthrura andriashevi Kudinova-Pasternak, 1966
Paranarthrurella sp. 1[1]

Pseudotanaidae Sieg, 1976
Mystriocentrus sp. 1[3]
Pseudotanais nipponicus McLelland, 2007
Pseudotanais sp. 1[1]
Pseudotanais sp. 3[1]
Pseudotanais sp. 4[1]
Pseudotanais sp. 5[1]
Pseudotanais sp. 5A[1]
Pseudotanais sp. 6[1]
Pseudotanais sp. 7[3]
Pseudotanais sp. 8[3]
Pseudotanais sp. 9[3]
Pseudotanais sp. 10[3]
Pseudotanais sp. 11[3]
Pseudotanais vitjazi Kudinova-Pasternak, 1966

Tanaellidae Larsen and Willson, 2002
Araphura sp. 1[1]
Tanaella sp. 1[1]

Tanaidae Dana, 1849
Protanais birsteini (Kudinova-Pasternak, 1970)

Typhlotanaidae Typhlotanaidae, 1984
Larsenotanais kamchatikus Błażewicz-Paszkowycz, 2007
Meromonakantha setosa (Kudinova-Pasternak, 1966)
Paratyphlotanais japonicus Kudinova-Pasternak, 1984
Peraeospinosus brachyurys (Beddard, 1886)*
Peraeospinosus magnificus (Kudinova-Pasternak, 1970)
Peraeospinosus rectus (Kudinova-Pasternak, 1966)
Torquella angularis (Kudinova-Pasternak, 1966)
Torquella grandis (Hansen, 1913)*
Torquella sp. 1[1]
Typhlamia mucronata (Hansen, 1913)*
Typhlamia sp. 1[1]
Typhlotanais compactus Kudinova-Pasternak, 1966
Typhlotanais kussakini Kudinova-Pasternak, 1970
Typhlotanais longicephala Kudinova-Pasternak, 1970

Typhlotanais sp. 1[1]
Typhlotanais sp. 3[1]
Typhlotanais sp. 4[1]
Typhlotanais sp. 5[1]
Typhlotanais sp. 6[1]
Typhlotanais sp. 7[1]

Family *incertae sedis*
Exspina typica Lang, 1968*
incertae sedis gen sp. 1[1]
incertae sedis gen sp. 3[1]
Leptognathioides sp.KK#1[2]
Pseudoarthrura sp. 1[1]

[1]Stępień et al. 2019, [2]Bird 2007a, *species with type locality outside Pacific.

Suborder: Apseudomorpha

Family Apseudidae

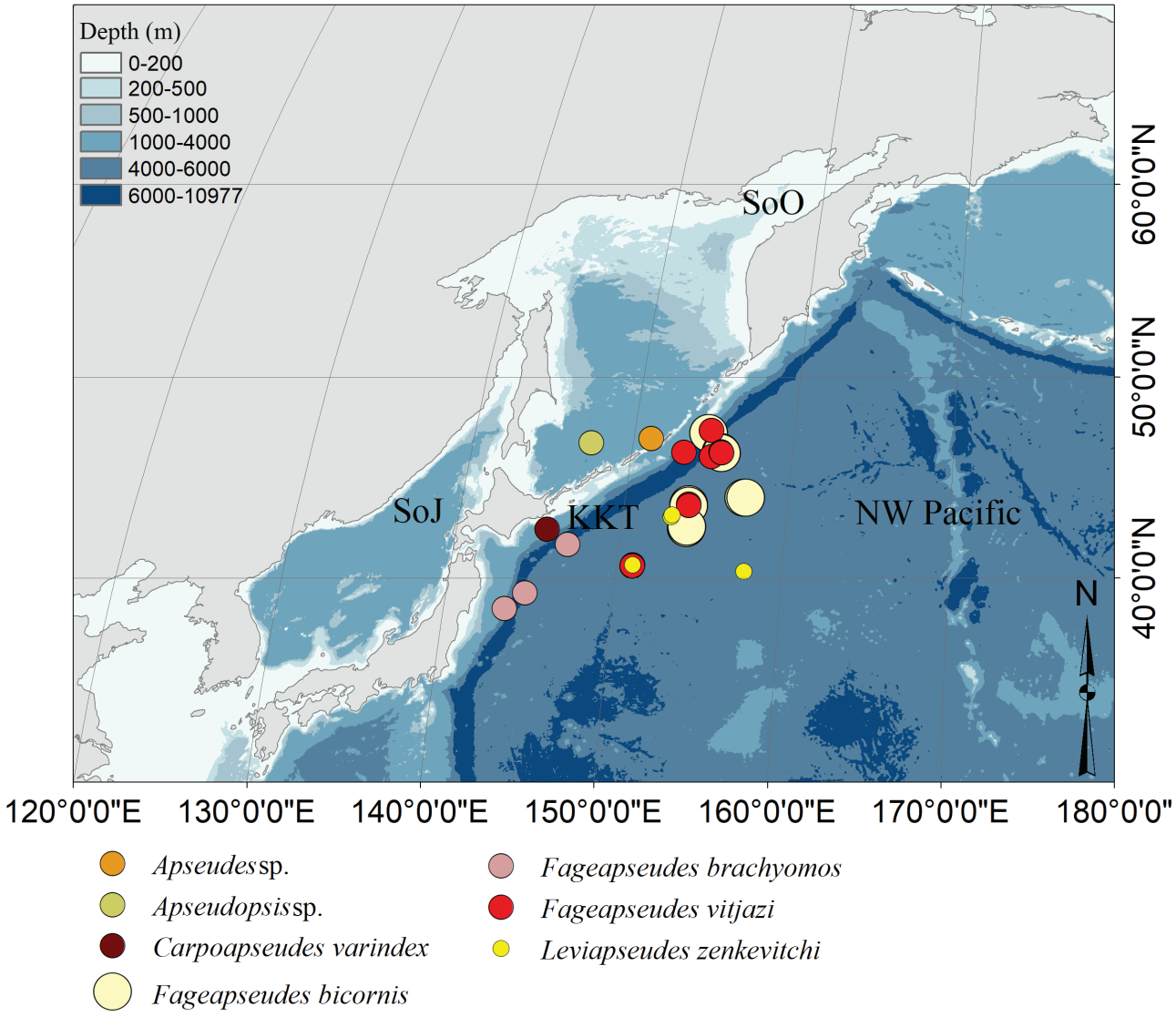
Seven species of Apseudidae, distributed among five genera, have been reported from the NW Pacific area covered in this review (Map 1). Five of them are described: *Carpoapseudes varindex*, *Fageapseudes bicornis*, *F. brachyomos*, *F. vitjazi* and *Leviapseudes zenkevitchi* (Figure 1A) (Kudinova-Pasternak 1966, 1970, Bamber 2007b, Kakui et al. 2011, Jóźwiak 2016), and two additional species, belonging to two genera, were recently recorded from the Sea of Okhotsk and remain undescribed (Stępień et al. 2019b). *F. bicornis*, *F. vitjazi* and *L. zenkevitchi* are among the most widespread taxa, being found at the Kuril-Kamchatka Trench within a relatively narrow depth range from 5,179 to 6,065 m (Kudinova-Pasternak 1966, 1970, Jóźwiak 2016), and outside NW Pacific, in the Gulf of Alaska at depths between 950–5,050 m (Kudinova-Pasternak 1973). *F. brachyomos* has been reported from the Japan Trench and adjacent area at depths between 3,990–5,762 m (Bamber 2007b, Kakui et al. 2011).

Suborder: Tanaidomorpha

The Tanaidomorpha is represented in the NW Pacific by a total of 107 species classified to 36 genera and 13 families; five species with *incertae sedis* family status.

Family Agathotanaidae

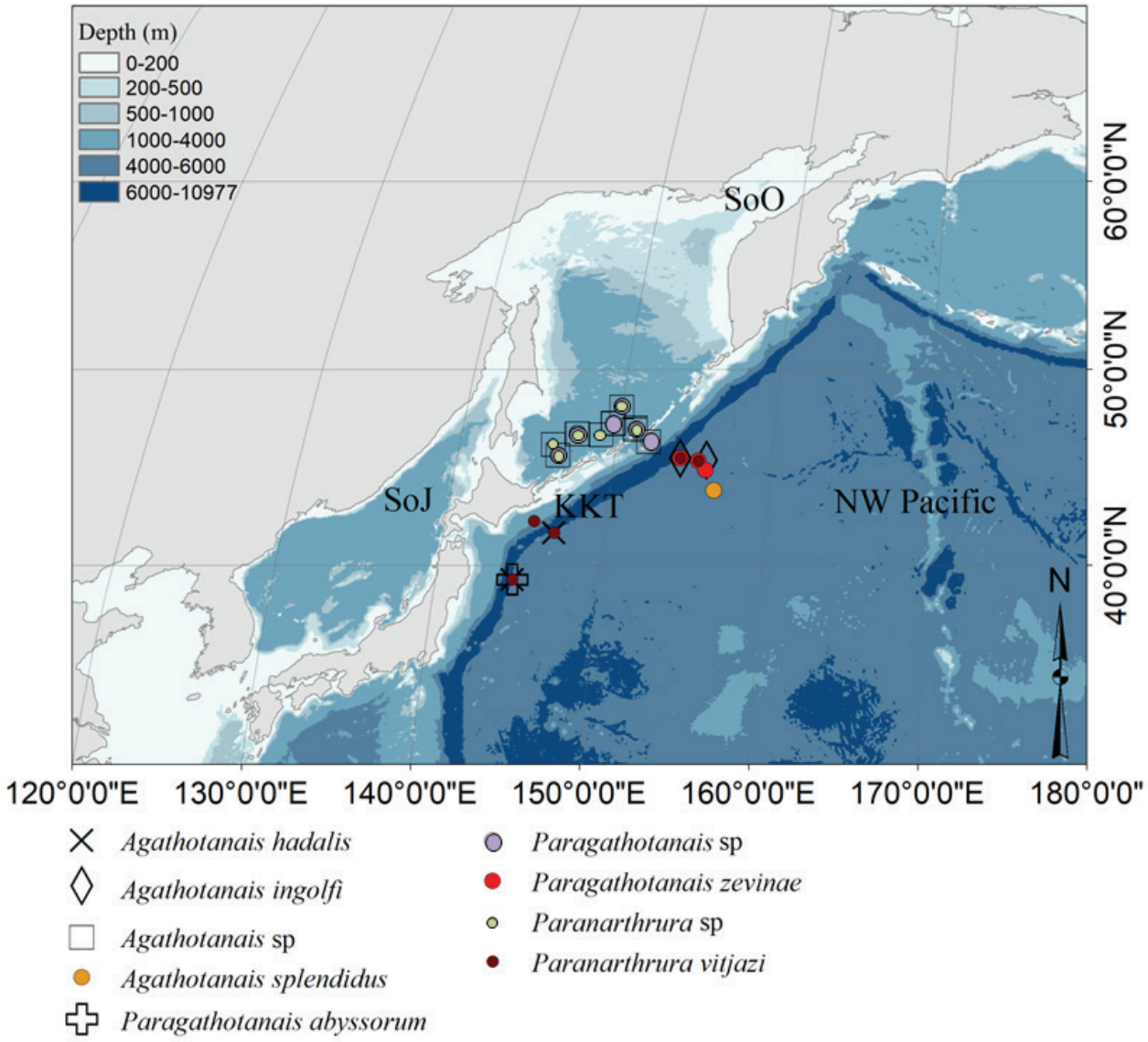
Ten species of Agathotanaidae, classified to three genera, have been described from NW Pacific below 2,000 m, such as *Agathotanais abyssorum*, *A. hadalis*, *A. ingolfi*, *A. spendidus*, *P. zevinae*, and *P. vitjazi* (Map 2) (Kudinova-Pasternak 1966, 1970, Larsen 2007). Several additional species, apparently new for science, were recently found in the Sea of Okhotsk (Stępień et al. 2019b) (Figure 1B-D). Two Agathotanaidae species have particularly restricted distribution and are known from single locality or from a few spots located in the Japan Trench (e.g. *A. hadalis* found at 5,433–5,762 m depth and *P. abyssorum* found at 5,733–5,762 m), while the others have been reported also outside the NW Pacific area. For example, *A. spendidus* is present both at the Kuril-Kamchatka Trench (5,441 m) and the Gulf of Alaska (3,450 m). *P. vitjazi* was collected near the Sea of Japan and Kuril-Kamchatka Trench (3,853–57,33 m), but also from the Gulf of Alaska (3,080 m) (Kudinova-Pasternak 1973). Finally, *A. ingolfi*, reported by Kudinova-Pasternak from the Kuril-Kamchatka Trench area (4,895–5,240 m) (Kudinova-Pasternak 1970), was originally described from the North Atlantic (Hansen 1913).



Map 1. Spatial distribution of Apseudidae in the NW Pacific (*Apseudes* sp., *Apseudopsis* sp., *Carpoapseudes varindex, Fageapseudes bicornis, F. vitjazi, Leviapseudes zenkevitchi*).

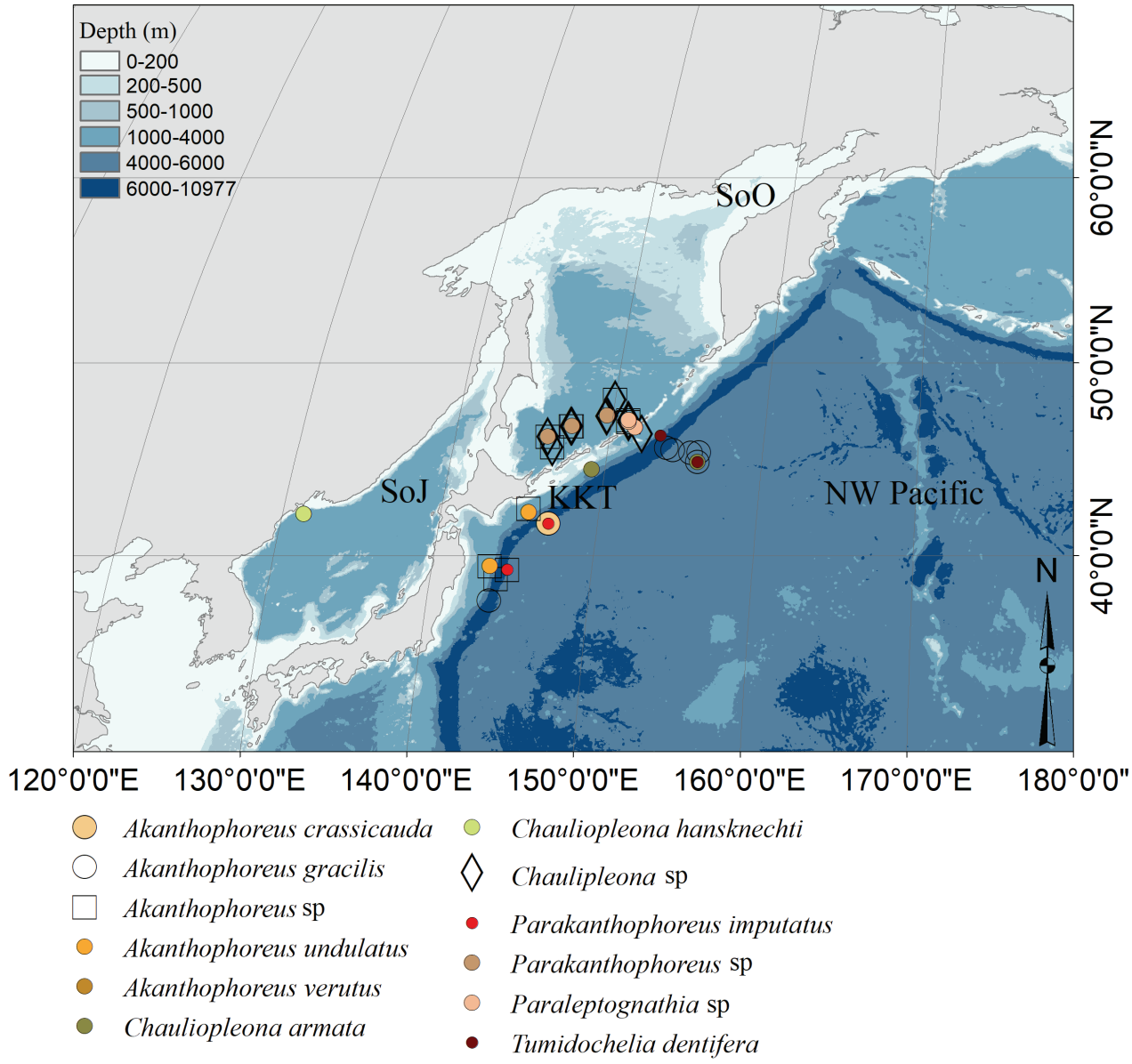
Family Akanthophoreidae

Sixteen species of Akanthophoreidae are known from the NW Pacific in waters deeper than 2,000 m (Map 3). Eight of them, belonging to four genera, are described: *Akanthophoreus crassicauda*, *A. undulatus*, *Chauliopleona armata*, *C. hansknechti*, *Parakanthophoreus gracilis*, *P. imputatus P. verutus* and *Tumidochelia dentifera* (Kudinova-Pasternak 1970, 1976, Bird 2007a, Larsen & Shimomura 2007), while another eight taxa are formally undescribed. Four of the known taxa were collected from a restricted geographical area, mostly near the Sea of Japan, and within narrow bathymetrical ranges. For example, *A. crassicauda* was recorded only in the Sea of Japan at 5,473–5,484 m (Bird 2007a), *A. undulates* in Japan Trench from 3,146–3,858 m (Bird 2007a) and *P. imputatus* from the Japan Trench at depths between 5,473–5,762 m (Bird 2007a). The other representatives of the family are recorded in a wider depth range. For example,



Map 2. Spatial distribution of Agathotanaidae species in the NW Pacific (*Agathotanais hadalis, A. ingolfi, A. splendidus, Agathotanais* sp., *Paragathotanais abyssorum, P. zevinae, Paragathotanais* sp., *Paranarthrura vitjazi, Paranarthrura* sp.).

P. verutus was found between 517 and 2,637 m in the Sea of Japan (Błażewicz-Paszkowycz et al. 2013) and *C. hansknechti* between 455 and 2,637 m in the same area (Błażewicz-Paszkowycz, Bamber & Jóźwiak 2013). Three species recorded in the NW Pacific have been originally reported from NW Atlantic (*P. gracilis*, *C. armata* and *T. dentifera*) (Krøyer 1842, Lilljeborg 1864, Sars 1899, Hansen 1913). Surprisingly, the same species have extremely wide bathymetric ranges covering several thousands of meters and are found in more than one locality across the Pacific Ocean. For example, *P. gracilis* was collected in the Kuril-Kamchatka Trench at 4,895–6,610 m (Kudinova-Pasternak 1970), in the Aleutian Trench at 180–4,260 m (Kudinova-Pasternak 1973), and in the Japan Trench at 7,370 m (Kudinova-Pasternak 1976); *C. armata* is known from the Aleutian Trench (1,550–6,520 m) (Kudinova-Pasternak 1973), but it has been reported also from the Kuril-



Map 3. Spatial distribution of Akanthophoreidae species in the NW Pacific (*A. gracilis, A. undulatus, Akanthophoreus* sp., *Chauliopleona armata, C. hansknechti, Chaulipleona* sp., *Parakanthophoreus crassicaudus, P. imputatus, P. verutus, Parakanthophoreus* sp., *Paraleptognathia* sp., *Tumidochelia dentifera*).

Kamchatka Trench (3,885–4,895 m) (Kudinova-Pasternak 1970). Finally, *T. dentifera* was found at the Kuril-Kamchatka Trench (4,895 m) and the Aleutian Trench (5,000 m) (Kudinova-Pasternak 1970, 1973).

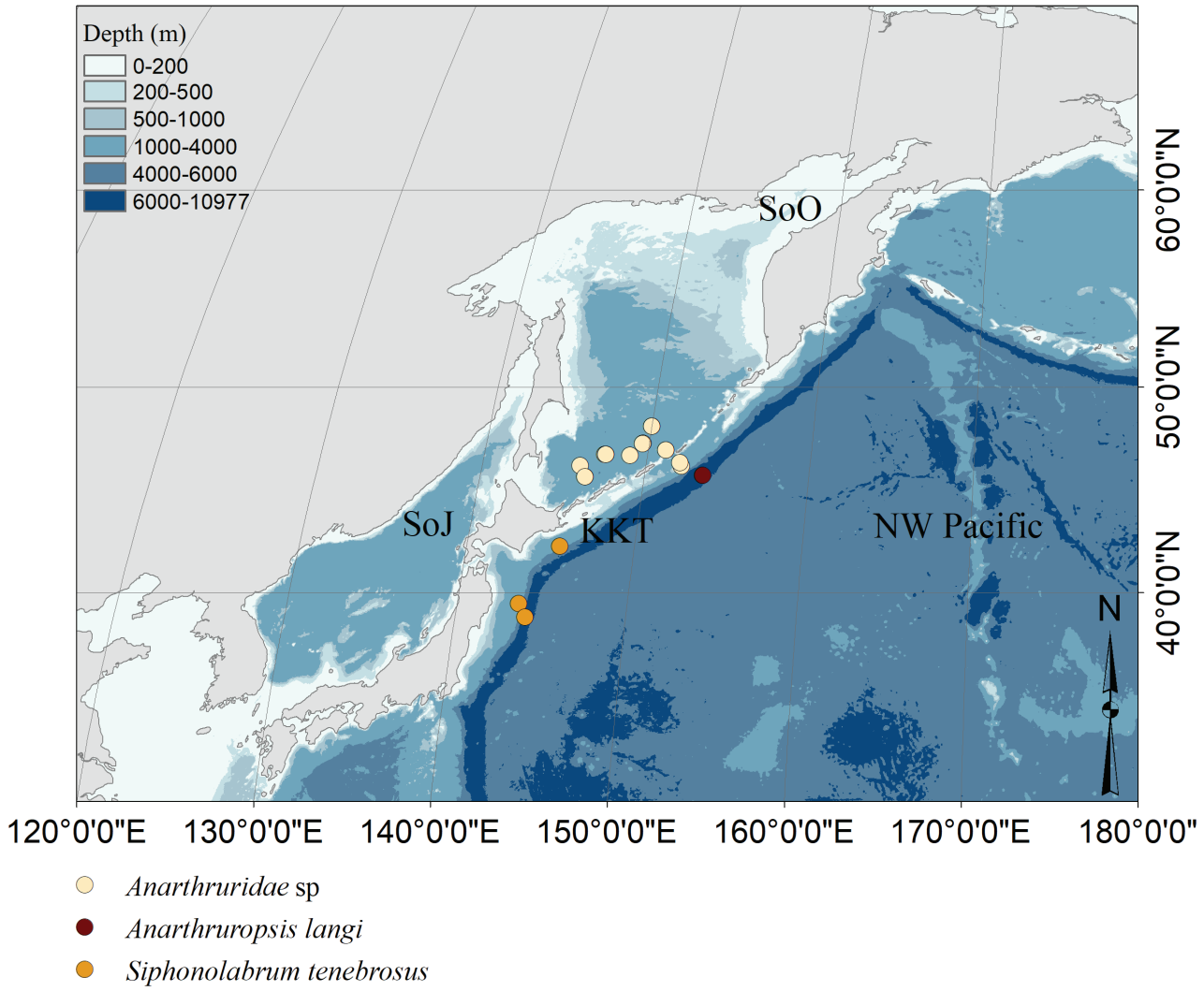
Family Anarthruridae

Two nominal species *Siphonolabrum tenebrosus* and *Anarthruropsis langi* represent Anarthruridae in the NW Pacific waters >2,000 m depth (Map 4) and up to five species putatively new for science have been reported from the Sea of Okhotsk (Stępień et al. 2019b) especially from deeper parts, remains virtually unexplored. The material for this study was collected in the Sea of Okhotsk, Bussol Strait, and from the northern

slope of the Kuril-Kamchatka Trench during SokhoBio. *Siphonolabrum tenebrosus* and *A. langi* are recorded from wide bathymetric ranges and hold the maximal depth records: *S. tenebrosus* was found in the Japan Trench between 3146 and 7,433 m (Bird 2007), and *A. langi* from the Kuril-Kamchatka Trench at 7,795 m (Kudinova-Pasternak, 1976).

Family Colletteidae

Two Colletteidae species, representing two different genera, have been reported from NW Pacific deep-sea waters: *Collettea cylindrata* and *Leptognathiopsis langi* (Kudinova-Pasternak 1970, Bird 2007b) (Map 5). A third genus is present with a high probability and could include another new species for science, *Leptognathiella* aff. *abyssi* (Stępień et al. 2019b) especially from deeper parts, remains virtually unexplored. The material for this study was collected in the Sea of Okhotsk, Bussol Strait, and from the northern slope of the Kuril-Kamchatka Trench, during SokhoBio. Additionally, two new species of *Leptognathiopsis* and a new species of *Collettea*

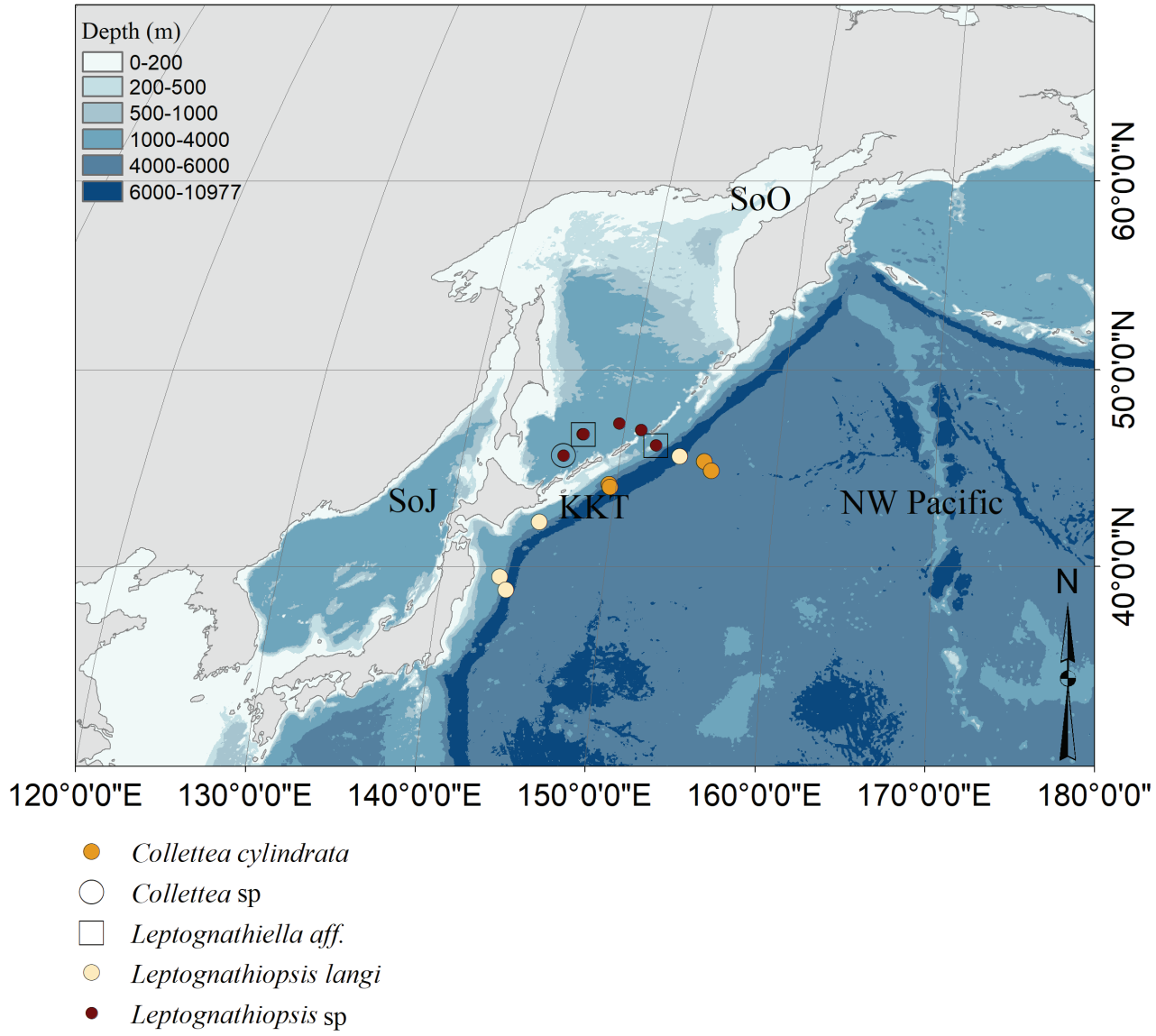


Map 4. Spatial distribution of Anarthruridae species in the NW Pacific (Anarthruridae sp., *Anarthruropsis langi, Siphonolabrum tenebrosus*)

were recently found in the Sea of Okhotsk (Figure 1E) (Stępień et al. 2019b). *L. langi* (3,722–7,340 m) and *C. cylindrata* (3,350–6,710 m) are known from wide depth ranges. Furthermore, the latter was originally described from North Atlantic waters by Sars (1882), thus individuals present in the Pacific might belong to a different species.

Family Cryptocopidae

Two *Cryptocopoides* species are known from NW Pacific waters >2,000 m so far (Kudinova-Pasternak 1970, 1978b; McLelland 2007): *C. arcticus* and *C. pacificus* (Map 6). *C. arcticus* has a wide geographical distribution, being also reported from the area adjacent to the Aleutian and Mariana Trench, and in North Atlantic waters (Hansen 1887, Błażewicz-Paszkowycz et al. 2014). Bathymetric ranges of both *Cryptocopoides* species overlap, being 1,950–4,895 m for *C. arcticus* and 3,154–5,484 m for *C. pacificus*.



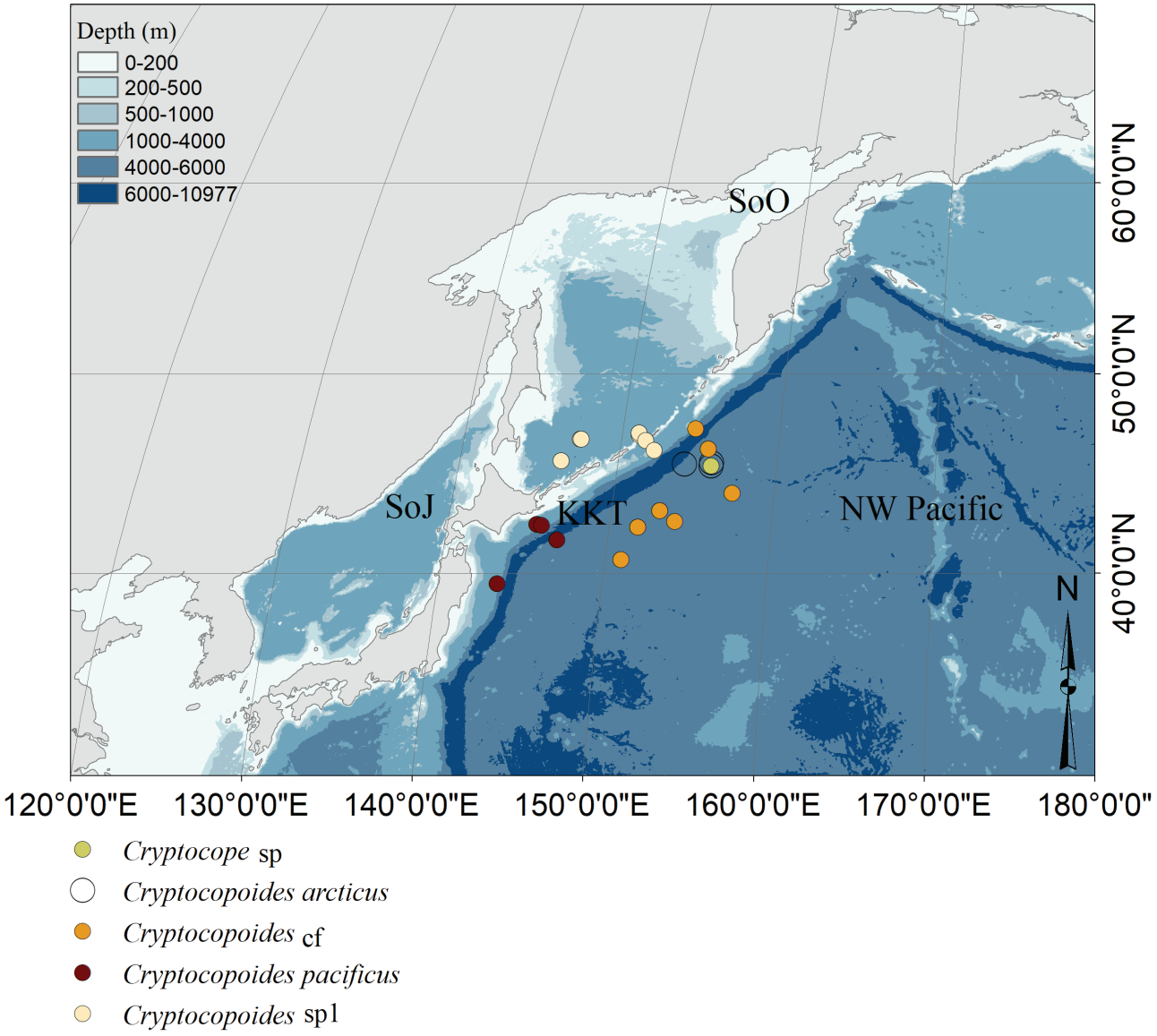
Map 5. Spatial distribution of Colletteidae species in the NW Pacific (*Collettea cylindrata, Collettea* sp., *Leptognathiella aff abyssi, Leptognathiopsis langi, Leptognathiopsis* sp.)

Family Heterotanoididae

This family is represented in the NW Pacific by one species only, *Heterotanoides ornatus*, for which one individual was found in the Japan Trench at about 7,370 m (Map 7) (Błażewicz-Paszkowycz & Bamber 2007). Considering that the species retains well-developed eyes, it seems likely that this individual is the result of contamination from shallow waters.

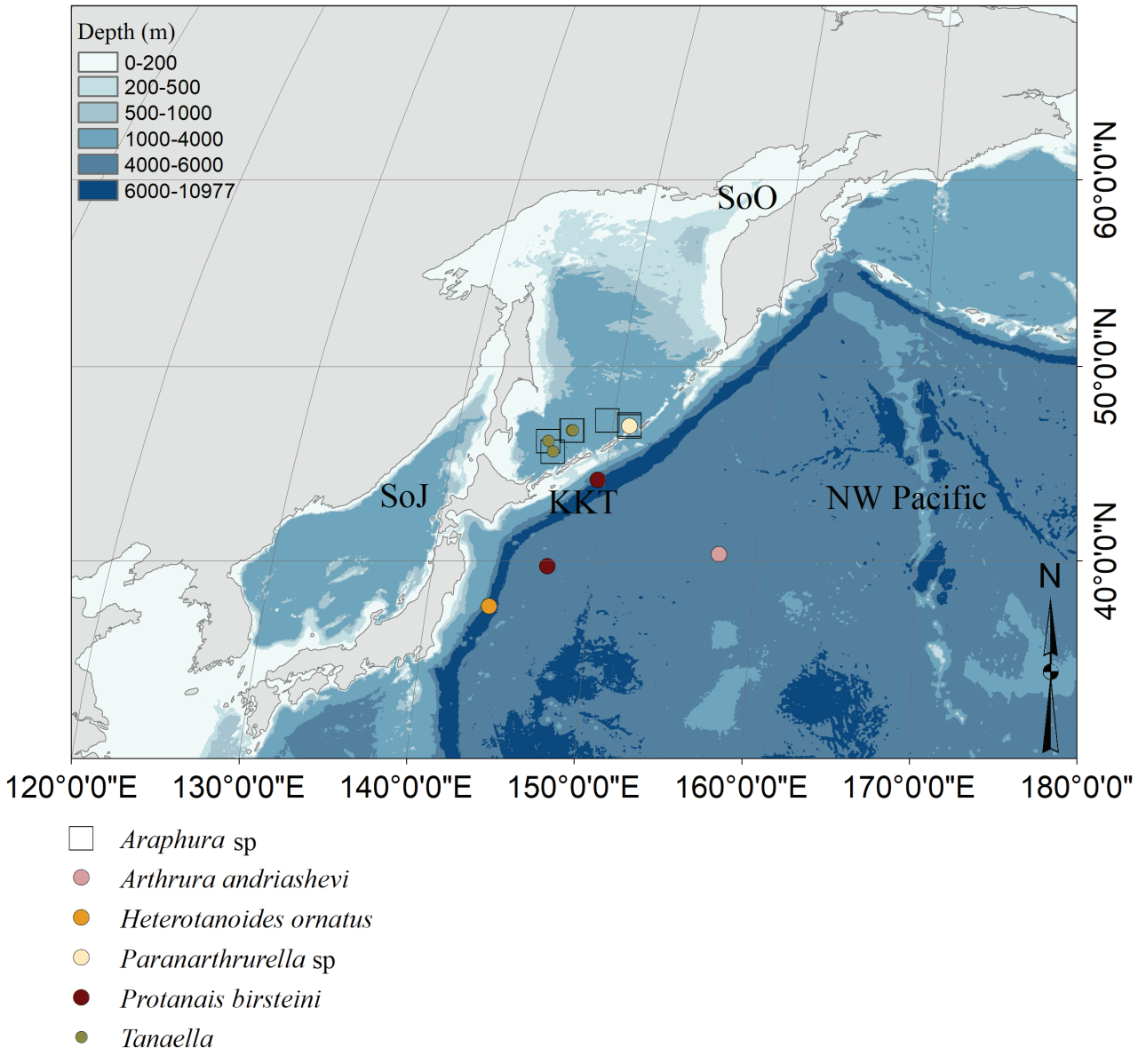
Family Leptognathiidae

Fourteen species belonging to one genus are known from deep NW Pacific: *Leptognathia aneristus*, *L. birsteini*, *L. breviremis*, *L. dentifera*, *L. greveae*, *L. microcephala*, *L. parelegans*, *L. rotundicauda*, *L. tuberculata*, *L. vinogradovae* and *L. zenkevitchi* (Kudinova-Pasternak 1970, 1976, 1978a, Bird 2007b) and putatively up to another three have been recently recorded from the Sea



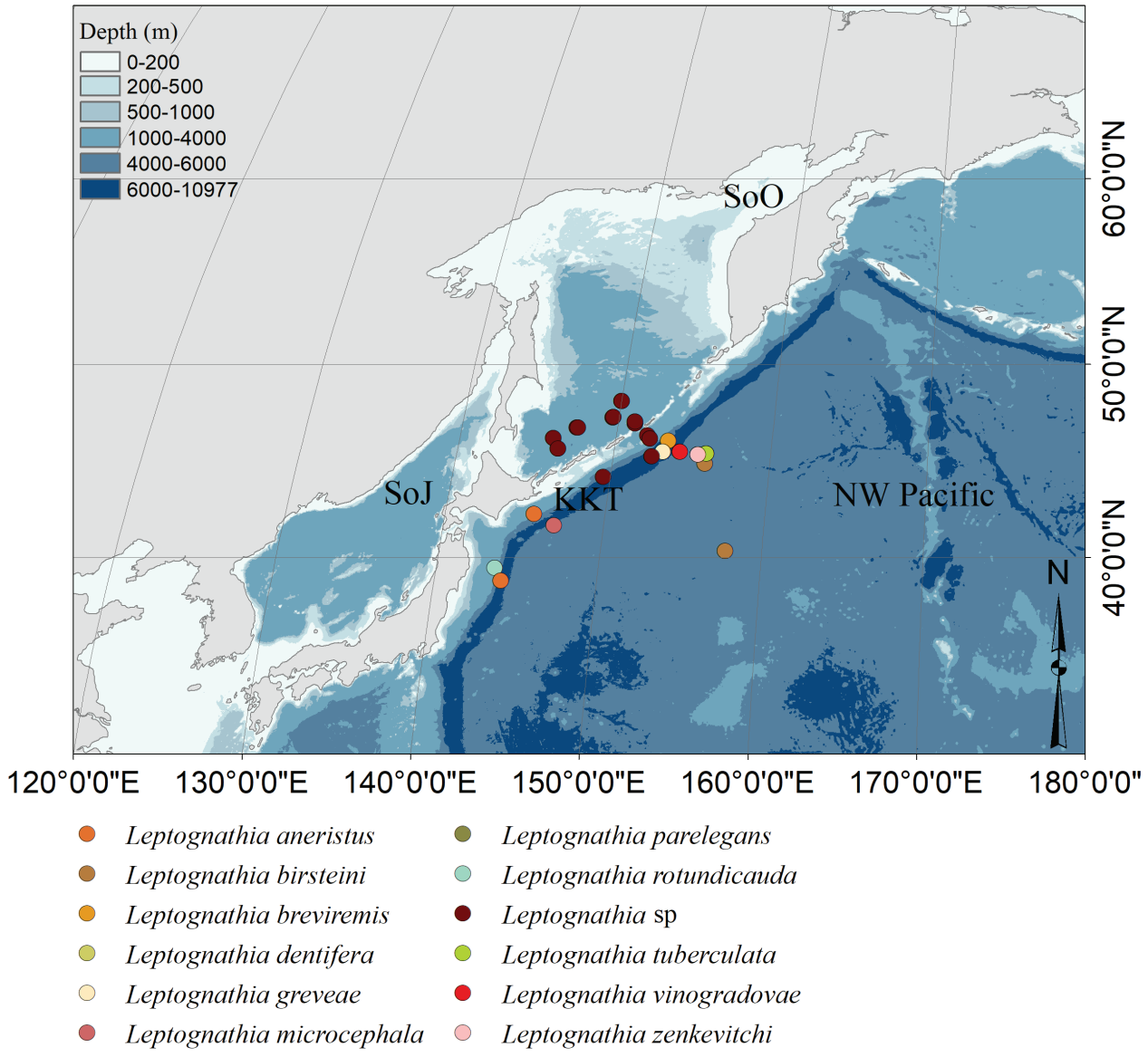
Map 6. Spatial distribution of Cryptocopidae species in the NW Pacific (*Cryptocope* sp., *Cryptocopoides arcticus*, *C. pacificus*, *Cryptocopoides* sp., *Cryptocopoides* cf. *pacificus*)

of Okhotsk (Stępień et al. 2019b). The material for this study was collected in the Sea of Okhotsk, Bussol Strait, and from the northern slope of the Kuril-Kamchatka Trench, during the Russian-German expedition Sea of Okhotsk Biodiversity Studies (SokhoBio (Map 8). A few taxa are known from a single locality and have narrow depth ranges. For example, *L. rotundicauda* is known from the Japan Trench from depths around 3,146–3,272 m (Bird, 2007) and *L. parelegans* was collected in the Kuril-Kamchatka Trench at 5,240 m (Kudinova-Pasternak 1970, 1978). Some species have wider distributions, with *L. greveae* being recorded from two trenches (e.g. South Salomon and Kuril-Kamchatka Trench at depths 7,974–8,185 m (Kudinova-Pasternak 1965, 1976), *L. birsteini* from Kuril Kamchatka Trench and Pacific abyssal plains from 4,895–7,656 m



Map 7. Spatial distribution of less-frequent tanaidacean taxa in the NW Pacific (*Araphura* sp., *Cryptocopoides arcticus, Heterotanaoides ornatus, Paranarthrurella* sp., *Protanais birsteini, Tanaella* sp.)

depth (Kudinova-Pasternak 1966, 1970); and *L. microcephala* from the Kuril-Kamchatka (5,473–5,484 m) and the Mariana Trench at 6,330 m (Kudinova-Pasternak 1978, Bird 2007). Finally, two species have depth ranges extending above one thousand meters. For example, *L. zenkevitchi* has been recorded from Aleutian and Kuril-Kamchatka Trenches with a bathymetric range from 1,550 to 4,945 m (Kudinova-Pasternak 1970, 1973) and *L. aneristus* was found at 3,858 and 7,340 m depth in Japan Trench (Bird 2007). *L. breviremis* and *L. tuberculata* were originally reported from North Atlantic waters (Sars G.O. 1886, Hansen 1913). In the NW Pacific these two species are truly abyssal taxa: *L. breviremis* was collected in the Kuril-Kamchatka Trench from 4,895 m and 7,265–7,295 m, and *L. tuberculata* was collected in the Kuril-Kamchatka Trench



Map 8. Spatial distribution of Leptognathidae species in the NW Pacific (*Leptognathia aneristus, L. birsteini, L. breviremis, L.dentifera, L. greveae, L. microcephala, L. paraelegans, L. rotundicauda, L. tuberculata, L. vinogaradovae, L. zenkevitchi, Leptognathia* sp.)

and the Pacific abyssal plain between 4,895 and 6,051 m depth (Kudinova-Pasternak 1970, 1976).

Family Neotanaidae

This exclusively deep-water family is represented in the NW Pacific by seven species, namely: *Neotanais americanus*, *N. kuroshio*, *N. oyashio*, *N. N. tuberculatus and N. wolffi* (Kudinova-Pasternak 1970, Bamber 2007b), beside of two other putative new species from the Sea of Okhotsk (Stępień et al. 2019b) (Map 9). The widest distribution has *N. americanus* that was collected from the Kuril-Kamchatka Trench (4,895–5,240 m), the Aleutian Trench (5,560–6,520 m), abyssal NW Pacific (5,057 m) and SE Pacific (6,920–7,657 m) (Kudinova-Pasternak 1965, 1970, 1973). *Neotanais kuroshio* and *N. oyashio* were found in the Kuril-Kamchatka Trench between 5,733–5,762 m, and *N. wolffi* was recorded in Japan Trench between 6,126–6,156 m. *Neotanais tuberculatus* was also reported from the Kuril-Kamchatka Trench but a wider depth range (4,840–7,295 m). *Neotanais americanus*, originally collected off Kerguelen Islands (Beddard 1886), has been reported at the Izu-Bonin Trench in the NW Pacific, from 6,770–6,850 m depth (Kudinova-Pasternak 1978a).

Family Paranarthrurellidae

The only Paranarthrurellidae species known from the NW Pacific so far is *Arthrura andriashevi* (Map 7). It was found in the Kuril-Kamchatka Trench and the Pacific abyssal plain at depths between 4,000 and 6,065 m (Kudinova-Pasternak 1966). In a recent paper, another putatively new species was reported from the Sea of Okhotsk (Stępień et al. 2019b).

Family Pseudotanaidae

Only two Pseudotanaidae species have been described from the NW Pacific: *Pseudotanais nipponicus* and *P. vitjazi* (Map 10). Nevertheless, the use of DNA barcoding methods has revealed the presence of up to twelve undescribed species in the Sea of Okhotsk and Kuril-Kamchatka Trench areas (Stępień et al. 2019b, Jakiel et al. 2020). The most shallow record for this family in the NW Pacific corresponds to *P. nipponicus* collected at 3,145–3,858 m (Kudinova-Pasternak 1970, McLelland 2007, Jakiel et al. 2020), but the new Pseudotanaidae taxa are recorded from relatively narrow ranges going from 4,987 m down to 6,065 m.

Family Tanaellidae

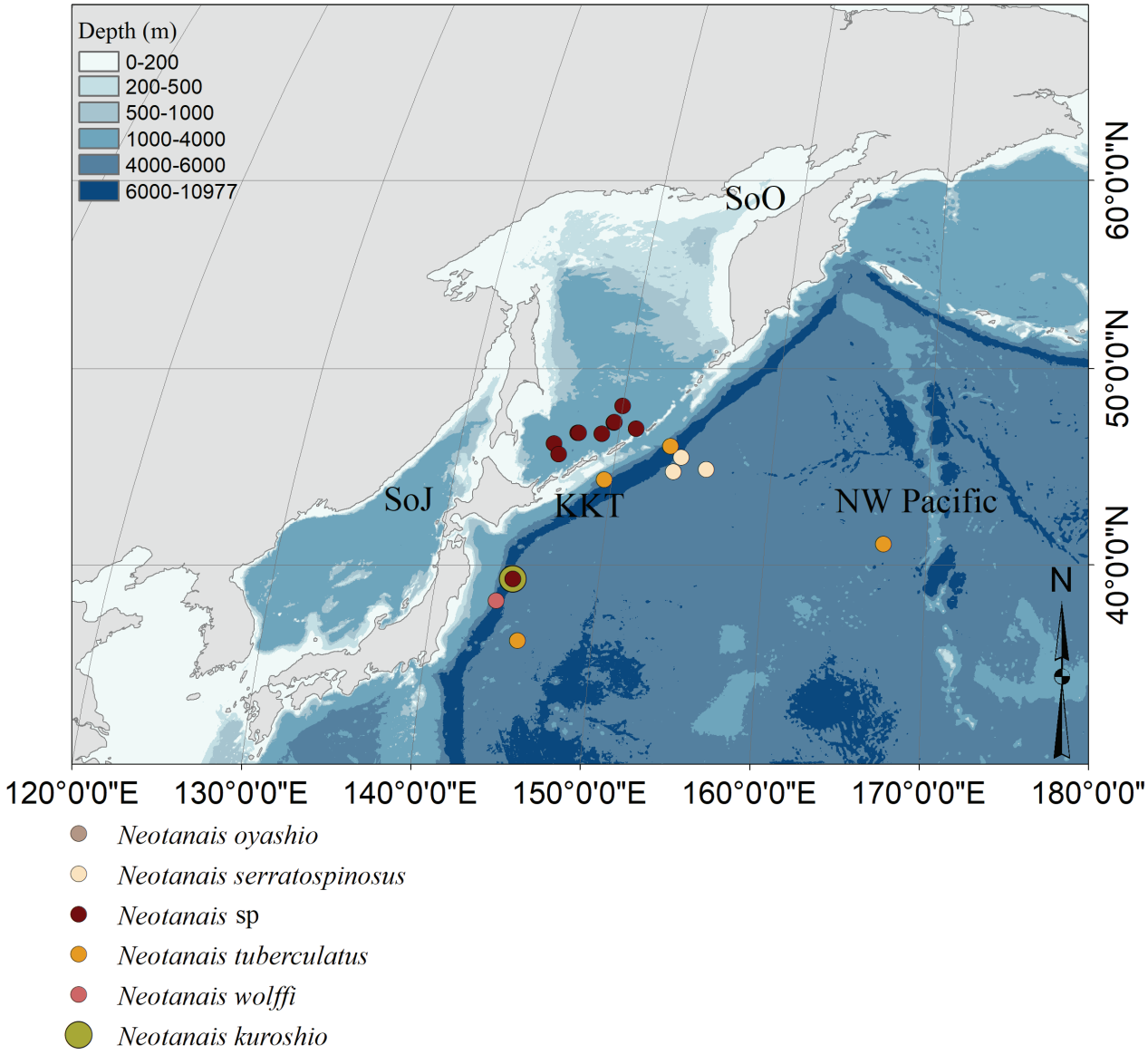
The Tanaellidae in deep NW Pacific include two new and still undescribed species recently collected from the Sea of Okhotsk (Stępień et al. 2019b) (Map 7).

Family Tanaidae

The only deep-water member of Tanaididae in the NW Pacific area is *Protanais birsteini*, which has been recorded twice from the area adjacent to the Kuril-Kamchatka Trench by Kudinova-Pasternak (1970) at 6,090 m depth, and by Błażewicz-Paszkowycz et al. (2015) at 5,017–5,020 m (Map 7). The second record confirmed the association of the species with sunken-wood (Duperron et al. 2013, Schwabe et al. 2015).

Family Typhlotanaidae

The Typhlotanaidae is one of the most diversified Paratanaoidea deep-sea families. As many as twelve species belonging to seven genera have been described from the NW Pacific so far, including *Larsenotanais kamchatikus*, *M. setosa*, *Paratyphlotanais japonicus*, *Peraeospinosus brachyurus*, *P. magnificus*, *P. rectus*, *Torquella an-*



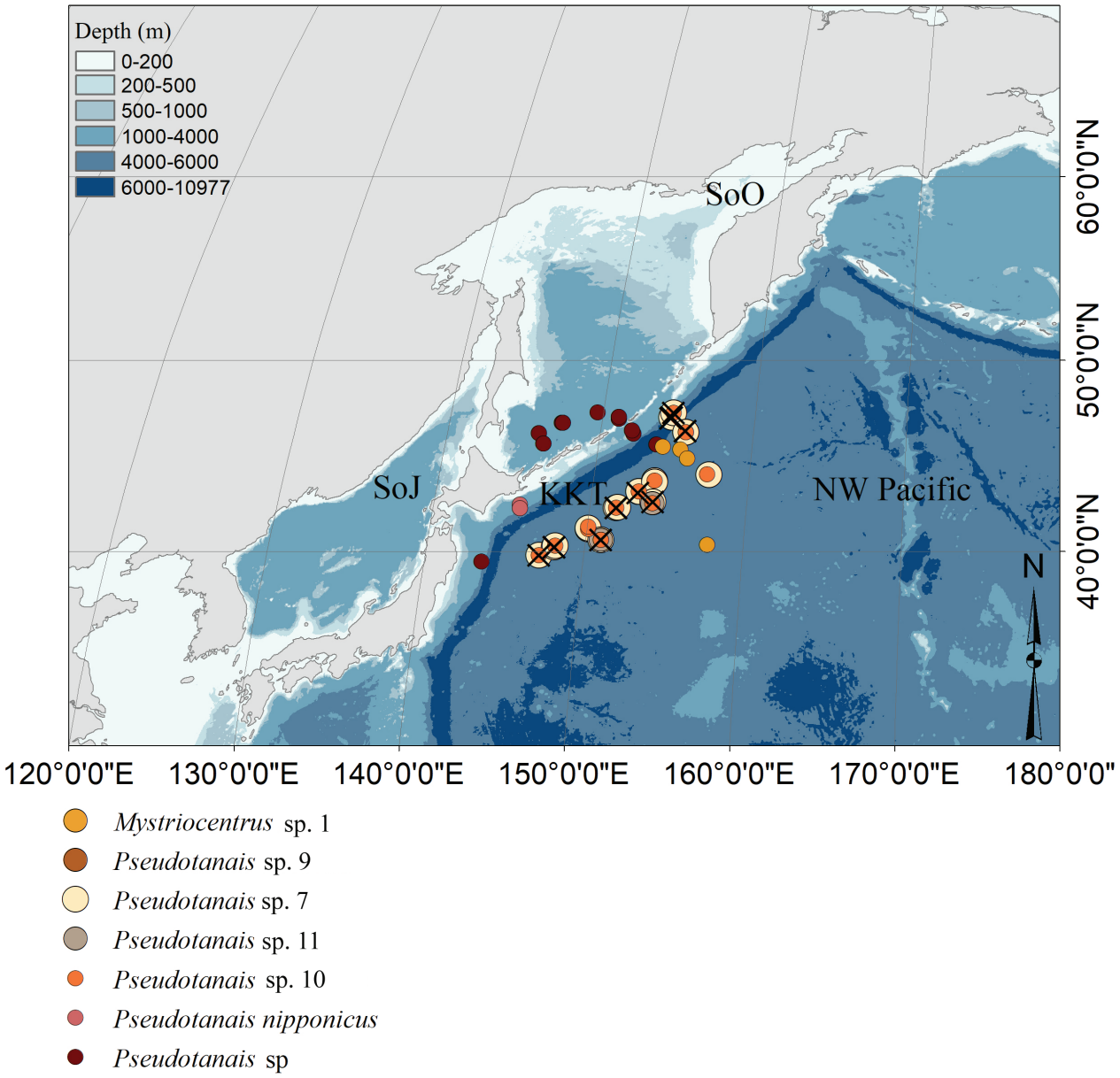
Map 9. Spatial distribution of Neotanaidae species in the NW Pacific (*Neotanais americanus, N. kuroshio, N. oyashio, N. tuberculatus, N. wolffi, Neotanais* sp.)

gularis, *Typhlamia mucronata*, *T. compactus*, *T. kussakini* and *T. longicephala* (Map 11). Additionally, eight undescribed species were recently collected from the Sea of Okhotsk (Stępień et al 2019b). Ten species have been recorded from the Kuril-Kamchatka Trench, but some of them with a single record only (e.g. *P. magnificus* from 4,895 m, *T. kussakini* from 6,090 m and *T. angularis* from 6,065 m) or rather with restricted bathymetric ranges, such as *T. mucronata* (4,840–6,710 m), *T. compactus* (4,895–6,090 m), *T. grandis* (4,895–6,065 m), *P. rectus* (4,895–6,065 m) and *T. longicephala* (4,895–5,240 m). Four species were recorded from the Sea of Japan: *P. japonicus* (1,130–3,666 m), *L. kamchatikus* (3,145–3,265 m), *T. angularis* (5,473–5,484 m) and *T. compactus* (3,146–5,484 m) (Kudinova-Pasternak 1984, Błażewicz-Paszkowycz 2007, Błażewicz-Paszkowycz et al. 2013). Some typhlotanaids have been recorded elsewhere in the Pacific Ocean. For example, *P. rectus* was found in the Mariana Trench at 6,330 m (Kudinova-Pasternak 1978a),

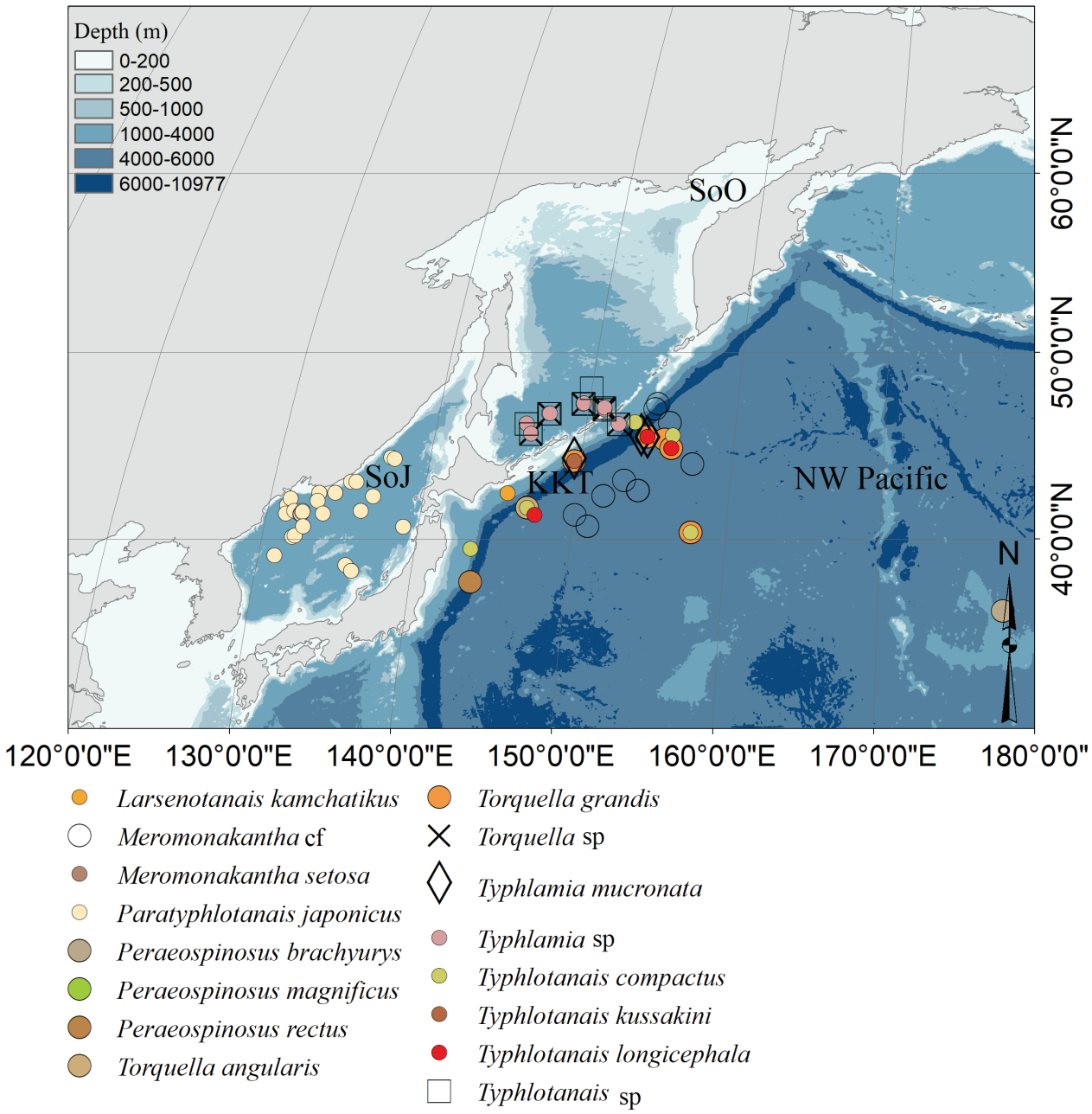
while *P. magnificus*, *P. rectus*, *T. mucronata* and *T grandis* were recorded in Gulf of Alaska from comparatively shallower waters (1,550–4,260 m) (Kudinova-Pasternak 1973). Finally, *P. rectus* and *M. setosa* have been reported from the abyssal plain of Central Pacific at 6,770–6,890 m depth (Kudinova-Pasternak 1966, 1976).

Family *incertae sedis*

Two species *Exspina typica* and *Robustochelia robusta*, which that have not been assigned so far to any of the existing tanaidacean families have been recorded in deep NW Pacific: (Kudinova-Pasternak 1970, 1978b). *Exspina typica*, was found in the Kuril-Kamchatka Trench at 4,895 m



Map 10. Spatial distribution of Pseudotanaidae species in the NW Pacific (*Mystriocentrus* sp. 1, *P. nipponicus, P. vitjazi, Pseudotanais sp.* 7, *Pseudotanais* sp. 8, *Pseudotanais* sp. 9, *Pseudotanais* sp. 10, *Pseudotanais* sp. 11, *Pseudotanais* sp.)



Map 11. Spatial distribution of Typhlotanaidae species in the NW Pacific (*Larsenotanais kamchatikus, M. setosa, Meromonakantha cf., Paratyphlotanais japonicus, Peraeospinosus brachyurus, P. magnificus, P. rectus, Torquella angularis, T. grandis, Torquella* sp., *Typhlamia mucronata, Typhlamia* sp., *Typhlotanais compactus, T. longicephala, Typhlotanais* sp.)

depth (Kudinova-Pasternak 1970) and *R. robusta* in the Izu-Bonin Trench, between 6,770–6,890 m depth (Kudinova-Pasternak 1978a). Furthermore, another three undescribed species have been found in the Sea of Okhotsk (Stępień et al. 2019b).

4.2. Biogeographic patterns

Almost one quarter of the NW Pacific species were originally described by Kudinova-Pasternak from the deep-sea material obtained during the

RV *Vityaz* expeditions (Kudinova-Pasternak 1970, 1976). Recent deep sea exploration programs conducted since 2007 (e.g. Japanese exploration of Japanese Trench, SoJaBio, SokhoBio, KuramBio, etc) have resulted in such a large amount of new taxa that many of them are still undescribed (Figure 1; see List above). From 14 families present in the NW Pacific deep-sea, only Typhlotanaidae was present in all the regions. Another five families show wide distributions, such as Pseudotanaidae, Neotanaidae, Leptognathiidae, Apseudidae and Akanthophoreidae, all recorded in most regions comprised here. Agathotanaidae, Anarthruridae, Colletteidae and Cryptocopidae were present in two or three areas and other families, like Tanaidae, are known from only one species.

The Marine Ecoregions Of the World (MEOW) classification system defines areas characterized by the presence of distinct biotas that might have arisen as a result of distinctive abiotic features (Spalding et al. 2007). Taking into account the biogeography of the NW Pacific, the records compiled in this review span four biogeographic ecoregions: the Sea of Okhotsk, the Oyashio Current, NE Honshu and the Sea of Japan. The number of records and sampling intensity was clearly biased towards the Sea of Okhotsk (41.9%) and the Oyashio Current (37.4%) ecoregions, but some overall patterns can be highlighted from the data at hand. For example, the Oyashio Current ecoregion presents the largest number of species reported, despite being the second in sampling effort (e.g. number of records). Most importantly, the Tanaidacea fauna of the Sea of Japan is clearly distinct from that found in the Sea of Okhotsk, NE Honshiu or the Oyashio Current ecoregion, with Jaccard distances going from 0.926 to 0.905. The fact that the Sea of Japan deep sea waters include a very low (only two families and three genera occur below 2,000 m) and unique (endemic) diversity (Błażewicz-Paszkowycz et al. 2013) makes it the most distinct NW Pacific ecoregion. The isolation from the Pacific Ocean due to the Sakhalin and Japanese Islands together with its relatively young geological age, are considered to be the main factors shaping the diversity of the Sea of Japan and causing its significant distinctiveness. Furthermore, the Sea of Japan suffered oxygen depletion during the Pleistocene glacial periods, which must have played an important role in the impoverished species diversity observed (Golovan et al. 2013).

Situated just north from the Sea of Japan, and more open towards the Pacific Ocean, the Sea of Okhotsk presents a much more diverse Tanaidacea fauna that holds 44 species, 23 genera and 13 families. Jaccard distances between the Sea of Okhotsk and either NE Honshiu or the Oyashio Current tanaidacean fauna were comparatively lower, and ranged between 0.580 and 0.611. Nevertheless, the set of species present in the Sea of Okhotsk is rather unique and only one taxon out of the 44 species (i.e. *Leptognathia* sp.) is shared with the Oyashio Current. The Sea of Okhotsk is generally shallower than the other two regions, and the Pacific Kruzenshtern Strait (max. depth of 1,920 m) and Bussol Strait (2,318 m), clearly limit the species exchange. Sampling biases could also be at play here, because the fauna was collected at different depths in both regions. The Sea of Okhotsk samples were generally taken in waters shallower than 3,300 m (Malyutina et al. 2015), much shallower than the 4,900–5,400 m for the Oyashio Current region (Jakiel et al. 2020). Finally, the most similar areas were NE Honshiu and the Oyashio Current, with the lowest Jaccard

distance value (0.467). As many as 15 species are shared between the NW Honshiu and Oyashio Current ecoregions, which represents 47% and 28% of the species known in each area, respectively. The species common for both regions are *Peraeospinosus rectus*, *Typhlotanais compactus*, *Parakanthophoreus gracilis*, A. *undulates*, *Leptognathia aneristus*, L. *rotundicauda*, *Leptognathiopsis langi Paranarthrura vitjazi*, *Protanais birsteini*, *Pseudotanais sp* 7–11, and S. *tenebrosus*.

Population connectivity between distant locations in the deep-sea seems to be a common fact (Brandt et al. 2012, Havermans et al. 2013, Jakiel et al. 2019) occurring in every ocean with a depth range covering the bathyal, abyssal and hadal zones. Previous studies; however, indicated the existence of several genetically and morphologically divergent lineages, questioning the assumption of its cosmopolitan and eurybathic distribution. For the first time, its genetic diversity was explored at the global scale (Arctic, Atlantic, Pacific and Southern oceans and, for several *Pseudotanais* species, specimens from both the NW Honshiu and Oyashio Current have been confirmed to be genetically identical. Although the idea of large distributions for the small deep sea tanaidaceans is widely accepted, some records should be treated with caution. For example, *P. gracilis* was originally described from the North Atlantic, and the specimens identified as such in NW Pacific waters might be with a high probability a different (congeneric) species with. *Typhlotanais compactus* recorded from an extremely large depth range (1,550–6,090 m) or S. *tenebrosus* (3,146–7,433 m) might also represent complexes of closely related species.

5. Discussion

Current knowledge about diversity and zoogeography of tanaidaceans in NW Pacific deep sea waters has significantly expanded during the last few decades (Figure 8). Tanaidacea records in NW Pacific begin with the *Challenger* expedition, when *Peraeospinosus brachyurus* was first reported (Beddard 1886). Eight decades separate that first historical record from the next significant scientific approach towards the NW Pacific tanaidacean diversity. Although some North Atlantic taxa described by Hansen (1913) will be later reported in the NW Pacific (Figure 8). It is in 1966 that Kudinova-Pasternak reported nine genera and eleven tanaidacean species from five stations located at abyssal depths (6,051–6,680 m) (Kudinova-Pasternak 1966). Her following contributions will include up to 75 nominal species, mainly from abyssal depths (Kudinova-Pasternak 1970, 1978a, 1978b, 1984).

The special volume dedicated to the Tanaidacea diversity of the Kuril-Kamchatka and Japanese Trench (Larsen & Shimomura 2007) further expanded the studies initiated by Kudinova-Pasternak. From twenty-six species recorded from those two trenches sixteen were new for science (Figure 8), six species were know from previous studies (Kudinova-Pasternak 1984, Błażewicz-Paszkowycz & Bamber 2007), and four species considered as valid taxa were not formally described due to scarcity of material (Bamber 2007a, Bird 2007b, 2007c, Błażewicz-Paszkowycz 2007, Larsen 2007, Larsen & Shimomura 2007, McLelland 2007, Błażewicz-Paszkowycz et al. 2013). Those 26 species still did not comprehend the total Tanaidacea fauna that occupies those two trenches (Jóźwiak

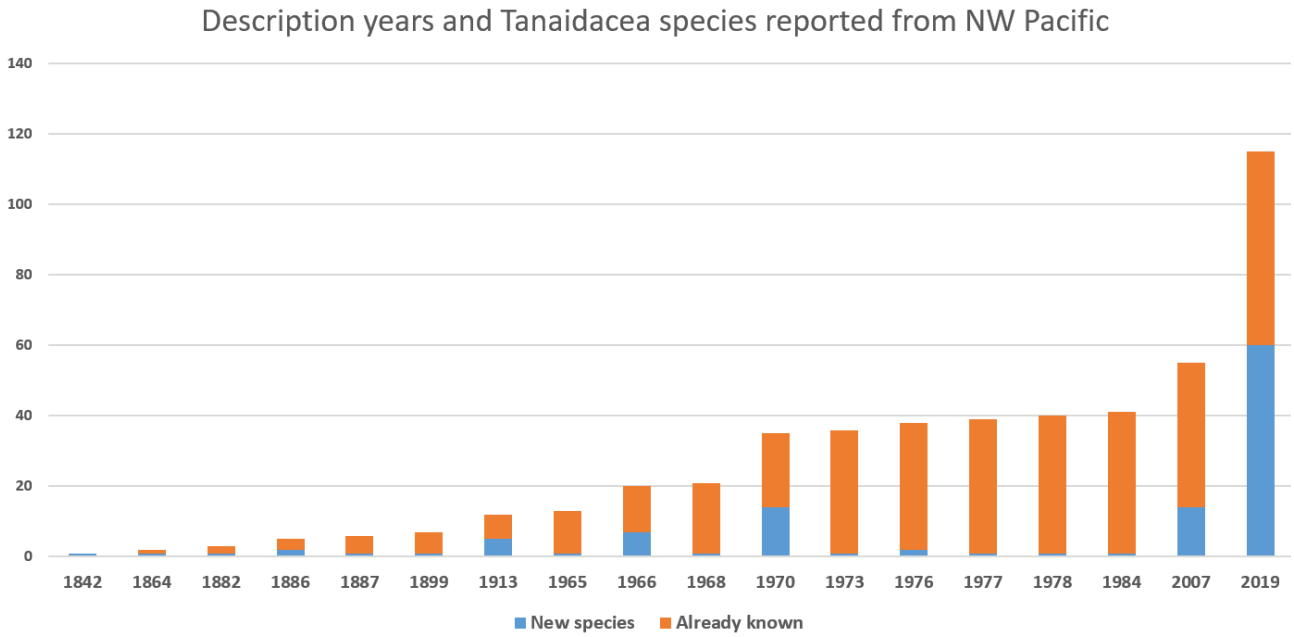


Figure 8. Cumulative bar chart showing the number of Tanaidacea species present deep NW Pacific waters (below 2,000 m) and sorted by the year of description. For each particular year, both the number of new species described or reported (marked in blue), and the number of species already known (orange) are shown.

2016). Extensive sampling with specialized gear (epibenthic sledge, recommended for collecting small peracarids) and sieving abyssal samples with 300 µm mesh size (Hessler & Sanders 1967) proved that the abyssal NW Pacific is highly diverse (Golovan et al. 2013, Brandt et al. 2019). Furthermore, the application of new genetic methods to help with the identification of the deep sea fauna has revealed that species numbers have been severely underestimated in the NW Pacific, and elsewhere (Pabis et al. 2014, Jakiel et al. 2018, Kaiser et al. 2018, Jakiel et al. 2019).

Several studies have demonstrated that diversity-depth patterns may vary in different geographical areas (Rex et al. 2005) and a complex of different environmental factors may operate at various temporal and spatial scales (Levin & Dayton 2009). The homogeneity of environmental factors like temperature, conductivity or salinity (Alalykina 2015, Elsner et al. 2015) suggests that biodiversity patterns at the KKT may depend on ecological features at a regional scale (Danovaro et al. 2014). Sediment particle heterogeneity may influence diversity because it results in a greater habitat complexity or food availability, which is particularly important in deep-sea trenches, accumulating particles from the surface layers and the ocean bottom near the trench (Zeppilli et al. 2016). Heterogeneous grain size and input of relatively fresh, surface-derived organic matter have been suggested to explain high diversity of nematodes and asellote isopods (Schmidt & Martínez Arbizu 2015, Jennings et al. 2018), and they probably have an impact on tanaidaceans diversity. Some tanaidaceans are selective in their choice of tube-building materials and sediment structure may determine survival (Hassack & Holdich 1987). For example, the abundance of

Tanais dulongii was strongly associated with the relative abundance of the sediment fraction (250–500 μm) used to build its tube (Prathep et al. 2003). Further studies are still needed to improve our current knowledge and to better describe the relative importance of ecological and environmental conditions on the distribution of deep-sea biodiversity.

5.1. Underestimated diversity

Tanaidaceans are one of the marine groups most profoundly underestimated with only less than 2% of all existing species known to science (Appeltans et al. 2012, Błażewicz-Paszkowycz et al. 2012, Poore et al. 2015). The analysis of the NW Pacific tanaidaceans collected during the recent expeditions confirms that only a small fraction of the total diversity of the tanaidacean is currently recognized (Błażewicz-Paszkowycz et al. 2013, Golovan et al. 2013, Brandt et al. 2019). Results from explorations in different parts of the world, from the Ross Sea (Pabis et al. 2015), Scotia Sea and Amundsen Sea (Pabis et al. 2014), off west Australian coast (McCallum et al. 2015), and Great Barrier Reef (Stępień et al. 2019b), reveal that the number of tanaidacean species new to science may me more than 70% or even 100% of those previously known in each area (Poore et al. 2015). Indeed, the number of species new to science collected in recent years doubled the number of species known previously form the NW Pacific area (Figure 19). Up to twelve species recorded below 2,000 m in the NW Pacific had been originally described and recorded from North Atlantic waters (see above). Records of benthic species separated by thousands of kilometers or by distinct physical barriers are often questioned, particularly due to the modern genetic species concept and our understanding of the important role of physical barriers in allopatric speciation. NW Pacific Tanaidacea records were already questioned by previous studies. For example, Bird (2007a) suggested that *Parakanthophoreus gracilis* from Japan and Kuril-Kamchatka Trenches (Kudinova-Pasternak 1970) might be *A. undulatus*, and *Collettea cylindrata* (Sars, 1882) from the Kuril-Kamchatka Trench (Kudinova-Pasternak 1970) could be the Aleutian species *C. larviformis* (Bird 2007b). Similarly, Larsen (2007) pointed out that Pacific records of *Agathotanais ingolfi* (Kudinova-Pasternak 1970) originally described from Davis Strait, may refer to *A. hadalis*, and McLelland (2007) stated that at least some Pacific records of *Cryptocopoides arcticus* (Kudinova-Pasternak 1970) may represent *C. pacificus* McLelland, 2007.

5.2. Future perspectives

The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services panel, backed by the United Nations, recently announced in a comprehensive report that the Earth is facing enormous biodiversity crisis associated with various kinds of human activities (Tollefson 2019). Millions of species face the risk of extinction even before they have been studied. At the same time, even basic information about taxonomy and biodiversity of many marine and terrestrial taxonomic groups is lacking (Appeltans et al. 2012, Grosberg et al. 2012). Despite the increase in knowledge on the diversity of marine ecosystems triggered by the Census of Marine Life initiative (2000–2010), the small tanaidaceans are certainly among the least studied marine organisms. Despite

substantial changes in the methodological approach to the study of benthic organisms, the deep-sea still belongs to the most scarcely studied ecosystems on Earth (Danovaro et al. 2017). Many important groups are known from a small number of described species and available datasets impede comprehensive zoogeographic and ecological studies (McClain & Mincks 2010, Danovaro et al. 2017). An intensive taxonomic effort is required in the case of tanaidaceans recently collected from the NW Pacific. Only the combination of molecular and morphological approaches, together with more extensive samplings, will allow us to properly understand the main factors determining the zoogeography, spatial and bathymetric distributions of deep sea tanaidaceans.

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CHAPTER 21

ECHINOIDEA AND ASTEROIDEA

TAXONOMY AND BIOGEOGRAPHY OF DEEP-SEA ECHINOIDEA AND ASTEROIDEA ALONG THE NW PACIFIC

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1. Introduction

Echinoids (Echinodermata: Echinoidea) and asteroids (Echinodermata: Asteroidea), commonly known as sea urchins and sea stars, are diverse groups of benthic animals found at a wide range of ocean depths from intertidal to hadal. The deepest occurring species is *Hymenaster* sp., 9,990 m (Belyaev and Mironov 1977). Although not as speciose as other key deep-sea taxa (e.g. peracarid crustaceans, polychaetes and holothurians), asteroids and echinoids are well represented in the deep NW Pacific, where they utilize a variety of life strategies. The majority of them are epifaunal and infaunal deposit-feeders with the most specialized burrowers found within the families Pourtalesiidae and Porcellanasteridae (Mironov et al., 2015). Some taxa, recorded from this region, are known as sessile suspension-feeders (Brisingidae and Freyellidae), scavengers (Ctenocidaridae, Echinothurioida) and predators (some Pterasteridae) (Jangoux and Lawrence 1982; Sokolova 1998). Of particular interest is the bizarre family Caymanostellidae, which comprises flattened asteroids, associated with waterlogged wood (Belyaev 1974; Dilman et al. 2020).

The NW Pacific is characterized by a complex bottom topography with the presence of abyssal depressions in the marginal seas and sharp depth gradients in the open-oceanic areas. In the marginal seas of the NW Pacific, the degree of geomorphological isolation decreases from south to north. The most isolated Sea of Japan is connected to the open-oceanic abyssal plain at the depths of ca. 140 m (Tsugaru and Korea straits), the semi-enclosed Sea of Okhotsk – at the depths of 2,318 m (Bussol Strait), and the least isolated Bering Sea – at the depths of 4,420 m (Kamchatka Strait). Among three NW Pacific hadal trenches – Aleutian, Japan and Kuril-Kamchatka – the latter is the deepest and largest (in terms of area). At depths below 6,500 m, the Kuril-Kamchatka Trench covers the area of 91 692 km^2 (Jamieson 2015) with a maximum depth of 9,717 m (Mikhailov 1970). Jamieson (2015) gives even greater depth of 10,542 m. This sets, therefore, the deepest point for the NW Pacific.

The first deep-sea investigations of the NW Pacific echinoids and asteroids (along with other echinoderms) were carried out in 1875 by HMS *Challenger*. However, the northernmost deep-sea (>2,000 m) sample was taken by HMS *Challenger* only at 36°10'N. North of 40°N deep-sea echinoderms were first sampled in 1906 during the expedition of USFC *Albatross* (Agassiz and Clark, 1907; Ohshima, 1915). This effort was followed by numerous Russian expeditions on board of the RV *Rossinante* and RV *Gagara* in 1932, RV *Vityaz*, from 1949 to 1976, RV *Dmitry Mendeleev* in 1985, RV *Akademik Mstislav Keldysh* in 1990, and RV *Professor Khromov* in 2005. Single abyssal stations were also taken by RV *Severny Polyus* in 1946 (Djakonov 1952), RV *Toporok* in 1948 (Djakonov 1958), RV *Spencer F. Bair* in 1953, RV *Sea Scope* in 1972 (Luke 1982), and by RV *Professor Shirshov* in 1981 (Sagaydachny and Chistikov 1987). As a result of these expeditions, numerous species were described and a basic knowledge of echinoid and asteroid biodiversity in the deep NW Pacific was established (Mironov 1973, 1976, 1995, 1997a, 1997b; Korovchinsky 1976; Belyaev 1985, 1989; Belyaev and Moskalev 1986a, b, c; Korovchinsky and Galkin 1984). After these early expeditions, 48 echinoid and asteroid species belonging to 34 genera were known from the NW Pacific below 2,000 m. More

recently, these benthic studies were continued in expeditions on board of the RV *Akademik M. A. Lavrentyev* (2010–2018) and RV *Sonne* (2012 and 2016). Publications from these expeditions has increased our knowledge of echinoid and asteroid diversity in deep NW Pacific, and added in 13 new species (Mironov et al. 2015, 2018, 2019a; Dilman et al. 2019).

Menzies et al. (1973) distinguished the separate NW Pacific province in the abyssal World Ocean. Other biogeographical schemes (Vinogradova 1959, 1997; Kussakin 1979; Belyaev 1989; Mironov 2014; Watling et al. 2013) group western and eastern North Pacific abyssal sectors under the name of the North Pacific abyssal province. Mironov (2014) includes this province into the NE Pacific region. Markedly high numbers of hadal (unknown from depths <6,000 m) endemics in the Aleutian, Kuril-Kamchatka, Japan and Izu-Bonin trenches led Belyaev (1989) and Vinogradova (1997) to distinguish a separate Aleutian-Japan hadal province. In each of these trenches, hadal endemics account for 42 to 53%, and in the fauna of all four trenches they make 51% (Belyaev 1989).

2. Objectives

The objectives of this chapter were (1) to present the most recent account on taxonomic diversity and occurrence record of Echinoidea and Asteroidea in the deep NW Pacific, (2) to detect spatial (both vertical and horizontal) patterns in their distribution, and (3) to update the knowledge on the biogeographic patterns and processes in the NW Pacific in the light of this new data.

3. Material and Methods

3.1. Coverage area

This chapter considers the part of the Pacific Ocean extending from 40° to 60°N and from 120° to 180°E (NW Pacific). Within the NW Pacific, only depths exceeding 2,000 m are considered. The NW Pacific encompasses seven distinct deep-sea areas: open-oceanic abyssal plain, abyssal basins of three marginal seas (Sea of Japan, northern part; Sea of Okhotsk; Bering Sea, western part) and three hadal trenches (Japan Trench, northernmost part; Kuril-Kamchatka Trench; Aleutian Trench, western part).

3.2. Occurrence data

The core occurrence dataset was compiled from all available published records of the NW Pacific echinoids and asteroids (Table 1), and then expanded by adding the records that had not been published at the time of the preparation of this chapter (Mironov et al. 2019a, 2019b; Dilman et al. 2019). It was further augmented by adding unpublished records from the collections, housed at the P. P. Shirshov Institute of Oceanology and Zoological Institute, Russian Academy of Sciences. The resulting working dataset holds a total of 370 records, 155 for Echinoidea and 215 for Asteroidea.

Echinoid and asteroid diversity is known from uneven sampling across the deep NW Pacific. The majority of abyssal (2,000–6,000 m) records come from the areas surrounding the Kuril Islands, whereas open-oceanic abyssal plain east of 160°E remains clearly under-sampled. The hadal (>6,000 m) fauna is most fully studied in the Kuril-Kamchatka trench.

Table 1. Published records of the Echinoidea and Asteroidea from the NW Pacific (40°–60°N, 120°–180°E) below 2,000 m.

Echinoidea	Asteroidea
Agassiz and Clark 1907	Baranova 1957
Baranova 1955	Belyaev 1966
Baranova 1957	Belyaev 1969
Belyaev 1989	Belyaev 1985
Djakonov 1952	Belyaev 1989
Djakonov 1958	Belyaev and Mironov 1993
Mironov et al. 2015	Belyaev and Moskalev 1986a
Mironov et al. 2018	Belyaev and Moskalev 1986b
Mironov 1971	Belyaev and Moskalev 1986c
Mironov 1973	Djakonov 1950
Mironov 1976	Djakonov 1952
Mironov 1995	Djakonov 1958
Mironov 1997a	Fisher 1911
Mironov 1997b	Fisher 1928
Saeedi et al. 2018	Golotsvan 1998
	Gruzov 1964
	Korovchincky 1976
	Korovchinsky and Galkin 1984
	Luke 1982
	Saeedi et al. 2018

A set of maps was created to show the occurrence records of ten key species: echinoids *Kamptosoma abyssale* Mironov, 1971, *Aeropsis fulva* (A. Agassiz, 1898), *Cystechinus loveni* A. Agassiz, 1898, *Ceratophysa ceratopyga* (A. Agassiz, 1879), 1879 and *Echinosigra* (*Echinogutta*) *amphora* Mironov, 1974; asteroids *Abyssaster tara* (Wood-Mason & Alcock, 1891), *Eremicaster crassus* (Sladen, 1883), *Styracaster longispinus* Belyaev et Moskalev, 1986, *Vitjazaster djakonovi* Belyaev, 1969 and *Astrocles actinodetus* Fisher, 1917. These species are widespread in the deep (>2,000 m) NW Pacific and best documented in terms of distribution data.

To assess global distribution patterns of deep NW Pacific echinoid and asteroid genera, data on their records from other regions were compiled from various published and unpublished sources.

3.3. Depth gradient

Vertical distribution ranges were calculated based on NW Pacific records only. For each individual species, distribution range was treated as continuous from the shallowest to the deepest occurrence. When species had the shallowest occurrence at depths <2,000 m, its upper distribution limit was set as 2,000 m. Based on these

ranges, number of species and genera was calculated for each 500 m depth interval, and then depth gradients were traced.

3.4. Latitudinal gradient

Latitudinal distribution ranges were calculated only for the species recorded from the depths ≥2,000 m. Ranges were treated as continuous throughout the NW Pacific, extending from the northernmost occurrence to the southernmost one. If the species had additional deep-sea (≥2,000 m) records in the western Pacific at latitudes ca. 30°–40°N or >60°N, its southern or northern distribution limit was set as 40°N or 60°N respectively. This was done to minimize the effect caused by under-sampling of certain areas. Based on these ranges, numbers of species and genera per each 2° latitudinal band were calculated to detect possible gradients.

3.5. Regional richness patterns

For assessing regional richness patterns in the NW Pacific, number of species was calculated for seven deep-sea areas: Sea of Japan, Sea of Okhotsk, Bering Sea, open-oceanic abyssal plain (below 2,000 m), Japan Trench, Kuril-Kamchatka Trench and Aleutian Trench. A 6,000 m isobath was used to outline the trench areas. The deep-sea areas of the Sea of Japan, Bering Sea, Japan and Aleutian trenches extend beyond the limits of the NW Pacific outlined in this study. Additional occurrence data, comprising species distribution records made in this areas south of 40°N (Sea of Japan and Japan Trench) and east of 180°E (Bering Sea, Aleutian Trench), was considered in order to get full species lists for these distinct geomorphological entities (see Figure 1). However, these additional records are not considered in Tables 2 and 3.

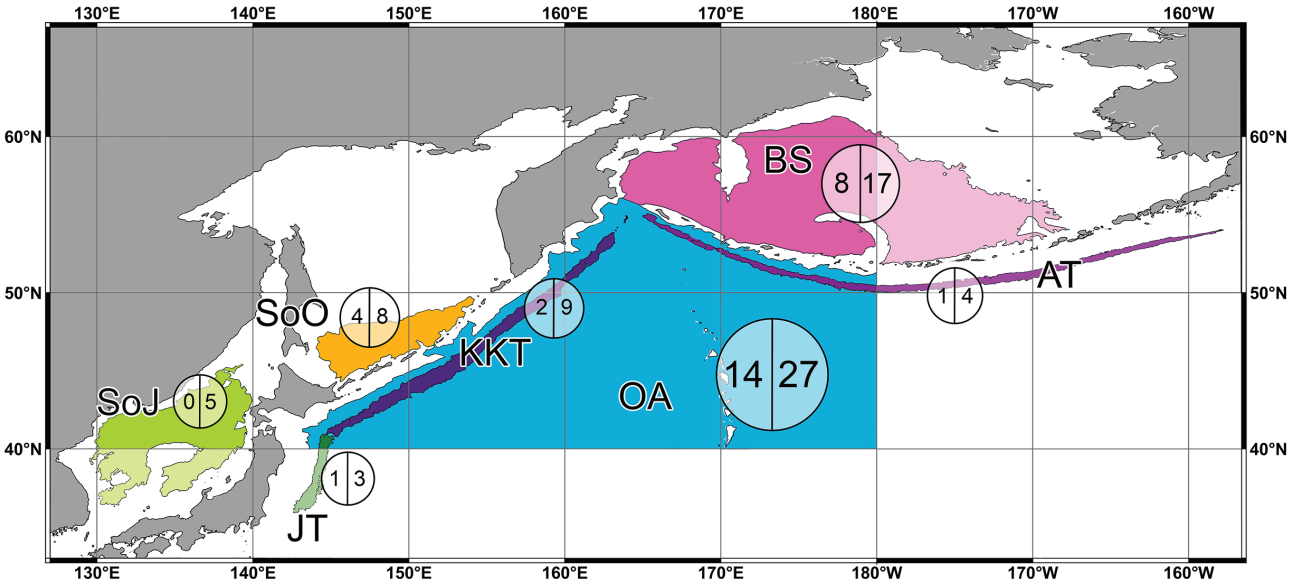


Figure 1. Echinoid and asteroid species richness in different NW Pacific deep-sea areas. SoJ – Sea of Japan, SoO – Sea of Okhotsk, BS – Bering Sea, OA – open-oceanic abyssal, JT – Japan Trench, KKT – Kuril-Kamchatka Trench, AT – Aleutian Trench. SoJ, SoO, BS are outlined by 2000 m isobath; OA is outlined by 2,000 m isobath, 40°N latitude in the south and 180°E longitude in the east. JT, KKT and AT are outlined by 6,000 m isobaths. Species number for each region is given in circle: left half – Echinoidea, right half - Asteroidea.

3.6. Biogeographic patterns

The term "pseudoabyssal species" is used here for eurybathic species that have penetrated the upper abyssal zone of one area (or two adjacent areas) but do not occur in the abyssal zone of other areas of the World Ocean.

For the analysis of the large-scale distribution patterns, the Pacific Ocean was subdivided into four regions. The NW Pacific is bordered by latitude 40°N in the south and separated by longitude 180°E from the NE Pacific extending northwards from 30°N. The West Pacific extends from 40°N to the Sub-Antarctic and separated by longitude 180°E from the East Pacific that extends from 30°N to the Sub-Antarctic. The Sub-Antarctic is outlined here as a region encircling the Antarctic and roughly corresponding to the latitudinal band 46°–60°S.

Table 2. Echinoidea and Asteroidea from the NW Pacific (40°–60°N, 120°–180°E), below 2,000 m. Jap – Sea of Japan, Okh – Sea of Okhotsk, Ber – Bering Sea, OA – open oceanic areas (outlined by isobath 2,000 m), HT – hadal trenches (outlined by isobath 6,000 m).
Other – outside NW Pacific, including areas with depths less than 2,000 m; NEP – North-East Pacific, EP – East Pacific, WP – West Pacific, Ind – Indian Ocean, ASA – Antarctic and Sub-Antarctic, Atl – Atlantic Ocean, Arc – Arctic Ocean. Endemics of the NW Pacific are marked with an asterisk (*). Species, identified only to generic level are marked with a dagger (†).

Species	Jap	Okh	Ber	OA	HT	Others
Echinoidea (16 species)						
Aeropsis fulva	–	+	+	+	–	NEP, EP, WP
Aporocidaris fragilis	–	–	+	–	–	NEP
Brisaster latifrons	–	–	–	+	–	NEP, EP
Ceratophysa ceratopyga	–	–	–	+	–	NEP, EP, ASA
Cystechinus loveni	–	+	+	+	–	NEP, EP
Echinocrepis rostrata	–	–	–	+	–	NEP, EP
Echinosigra amphora	–	–	–	+	+	WP, Ind.
**Echinosigra mortenseni*	–	–	–	+	–	–
Kamptosoma abyssale	–	–	–	+	+	NEP, WP, Ind.
Pilematechinus vesica	–	–	+	+	–	ASA
Pourtalesia beringiana	–	–	+	–	–	NEP
Pourtalesia heptneri	–	–	–	+	–	WP
Pourtalesia thomsoni	–	+	+	+	–	NEP, EP
Rodocystis rosea	–	–	–	+	–	NEP, EP, Ind, Atl
Urechinus naresianus	–	+	+	+	–	NEP, EP, Atl, ASA
Urechinus perfidus	–	–	–	+	–	NEP
Asteroidea (45 species)						
Abyssaster tara	–	–	–	+	–	NEP, EP, WP, Ind
**Amembranaster dimitatus*	–	–	–	–	+	–

Species	Jap	Okh	Ber	OA	HT	Others
Astrocles actinodetus	–	+	+	+	–	NEP
**Astrocles djakonovi*	–	+	–	–	–	–
**Astrocles japonicus*	–	–	–	+	–	–
†*Caymanostella* sp.	–	–	–	+	–	–
Crossaster japonicus	+	–	–	–	–	WP
Crossaster papposus	–	+	+	–	–	EP, Atl, Arc
Ctenodiscus crispatus	+	–	+	–	–	NEP, EP, Atl, Arc
Dipsacaster anoplus	–	–	+	+	–	NEP
†*Dytaster cf. grandis*	–	–	–	+	–	–
Dytaster gilberti	–	–	–	+	–	EP
Eremicaster crassus	–	–	+	+	–	NEP, EP, Ind, ASA, Atl
Eremicaster pacificus	–	+	+	+	–	NEP, EP, Ind, ASA
Eremicaster vicinus	–	–	–	+	+	NEP, EP, WP, Atl, ASA, Ind
**Freyella hexactis*	–	–	+	–	–	–
Freyella kurilokamchatica	–	–	–	+	+	WP
Freyella loricata	–	–	–	+	–	WP
Freyella oligobrachia	–	–	–	+	–	NEP, EP, WP
Gaussaster antarcticus	–	–	–	+	–	ASA
†*Henricia* sp	–	+	–	–	–	–
†*Hydrasterias* sp.	–	–	–	+	+	–
Hymenaster crucifer	–	–	–	+	–	WP, Atl, ASA
Hymenaster latebrosus	–	–	–	+	–	Atl, ASA
Hymenaster pellucidus	–	–	+	–	–	Atl, Arc?, ASA
Hymenaster quadrispinosus	–	+	+	–	–	NEP, Atl
†*Hymenaster* aff. *blegvadi*	–	–	–	–	+	–
†*Hymenaster* sp. A	–	–	–	–	+	–
†*Hymenaster* sp. B	–	–	–	–	+	–
†*Hymenaster* sp. C[a]	–	–	–	+	–	–
**Hymenodiscus beringiana*	–	–	+	–	–	–
**Hyphalaster multispinus*	–	–	–	+	–	–
Leptychaster anomalus	+	–	–	–	–	EP
Lophaster furcilliger	–	+	+	+	–	NEP, EP, Arc?
Nearchaster variabilis	–	–	–	+	–	–
Paralophaster lorioli	–	–	–	+	–	ASA
**Pedicellaster orientalis*	+	–	–	–	–	–
Pseudarchaster parelli	+	–	–	–	–	Atl
Psilaster pectinatus	–	+	+	–	–	NEP, EP
**Pteraster ifurus*	–	–	–	–	+	–
**Pteraster texius* + *P. cf. texius*	–	–	–	+	+	–

Species	Jap	Okh	Ber	OA	HT	Others
Styracaster longispinus	–	–	–	+	–	NEP
Styracaster paucispinus	–	–	–	+	–	NEP
Thoracaster cylindratus	–	–	–	+	–	NEP, EP, WP, Ind, Atl
Vitjazaster djakonovi	–	–	–	+	–	NEP
Total (61)	5	12	19	41	11	

[a] – Mentioned as *Hymenaster* sp. in Mironov et al. (2015)

Table 3. Distribution of echinoid and asteroid genera occurring in the NW Pacific (40°–60°N, 120°–180°E) below 2,000 m.
Abbreviations as in Table 2. Endemics of the Pacific Ocean are marked with an asterisk (*). Genera, occurring only in the Pacific, Antarctic and Sub-Antarctic, are marked with a dagger (†).

Genus	NEP	EP	WP	Ind	ASA	Atl	Arc
Echinoidea: 12							
Aeropsis	+	+	+	+	–	+	–
†*Aporocidaris*	+	+	–	–	+	–	–
Brisaster	+	+	+	–	+	+	–
†*Ceratophysa*	+	+	–	–	+	–	–
†*Cystechinus*	+	+	–	–	+	–	–
†*Echinocrepis*	+	+	–	–	+	–	–
Echinosigra	+	+	+	+	+	+	–
Kamptosoma	+	+	+	+	+	–	–
Pilematechinus	+	+	–	–	+	+	–
Pourtalesia	+	+	+	+	+	+	+
Rodocystis	+	+	+	+	–	+	–
Urechinus	+	+	–	–	+	+	–
Asteroidea: 27							
Abyssaster	+	+	+	+	+	–	–
**Amembranaster*	–	–	–	–	–	–	–
**Astrocles*	+	–	–	–	–	–	–
Caymanostella	–	–	+	+	–	+	–
Crossaster	+	+	+	–	–	+	+
Ctenodiscus	+	+	+	–	+	+	+
Dipsacaster	+	–	+	+	–	+	–
Dytaster	+	+	+	–	+	+	–
Eremicaster	+	+	+	+	+	+	–
Freyella	+	+	+	+	+	+	–
†*Gaussaster*	–	–	–	–	+	–	–

Genus	NEP	EP	WP	Ind	ASA	Atl	Arc
Henricia	+	+	+	+	+	+	+
Hydrasterias	–	+	+	–	–	+	–
Hymenaster	+	+	+	+	+	+	+
Hymenodiscus	+	+	+	–	+	+	+
Hyphalaster	+	+	+	+	+	+	–
Leptychaster	+	+	–	–	+	+	+
Lophaster	+	+	+	+	+	+	+
**Nearchaster*	+	+	+	–	–	–	–
†*Paralophaster*	–	–	–	–	+	–	–
Pedicellaster	+	+	+	+	+	+	+
Pseudarchaster	+	+	+	+	+	+	+
Psilaster	+	+	+	+	+	+	+
Pteraster	+	+	+	+	+	+	+
Styracaster	+	+	+	+	+	+	–
Thoracaster	–	+	–	+	–	+	–
**Vitjazaster*	+	–	–	–	–	–	–
In total: 39 genera (100%)	33 (85%)	32 (82%)	26 (67%)	20 (51%)	28 (72%)	27 (69%)	12 (31%)

4. Results

4.1. Taxonomic diversity

According to the most recent data, including species records and descriptions yet unpublished at the time of chapter preparation (Mironov et al 2019a; Dilman et al. 2019), deep-sea echinoid and asteroid fauna of the NW Pacific comprises 61 species belonging to 39 genera. Echinoid fauna (16 species and 12 genera) is poor compared to asteroids, represented by 45 species and 27 genera (Tables 2 and 3). The most speciose families in the North Pacific abyss are Freyellidae (seven species), Porcellanasteridae (nine species), Pterasteridae (11 species), and Pourtalesiidae (seven species). The most speciose genus is Hymenaster (eight species) from the family Pterasteridae.

4.2. Distribution of key NW Pacific species.

Class Echinoidea Leske, 1778

Order Echinothurioida Claus, 1880
Family Kamptosomatidae Mortensen, 1934
Genus Kamptosoma Mortensen, 1903
***Kamptosoma abyssale* Mironov, 1971**
(Figure 2, Map 1)
Distribution in the NW Pacific is shown in Map 1. Global distribution: From Aleutian Islands south to Tasman Sea and from Madagascar east to Hawaii; 4,374–6,235 m.

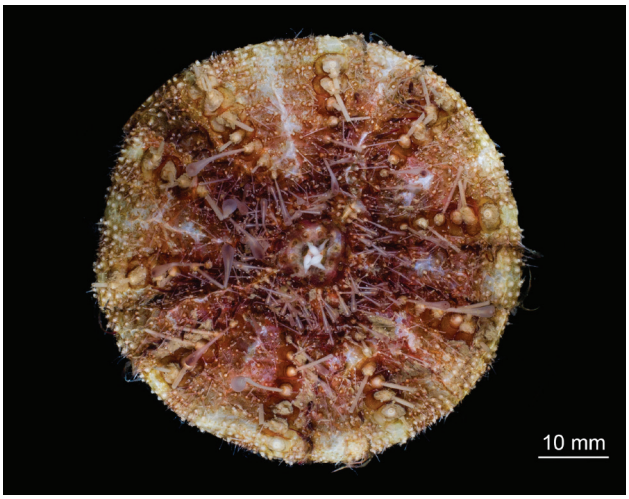
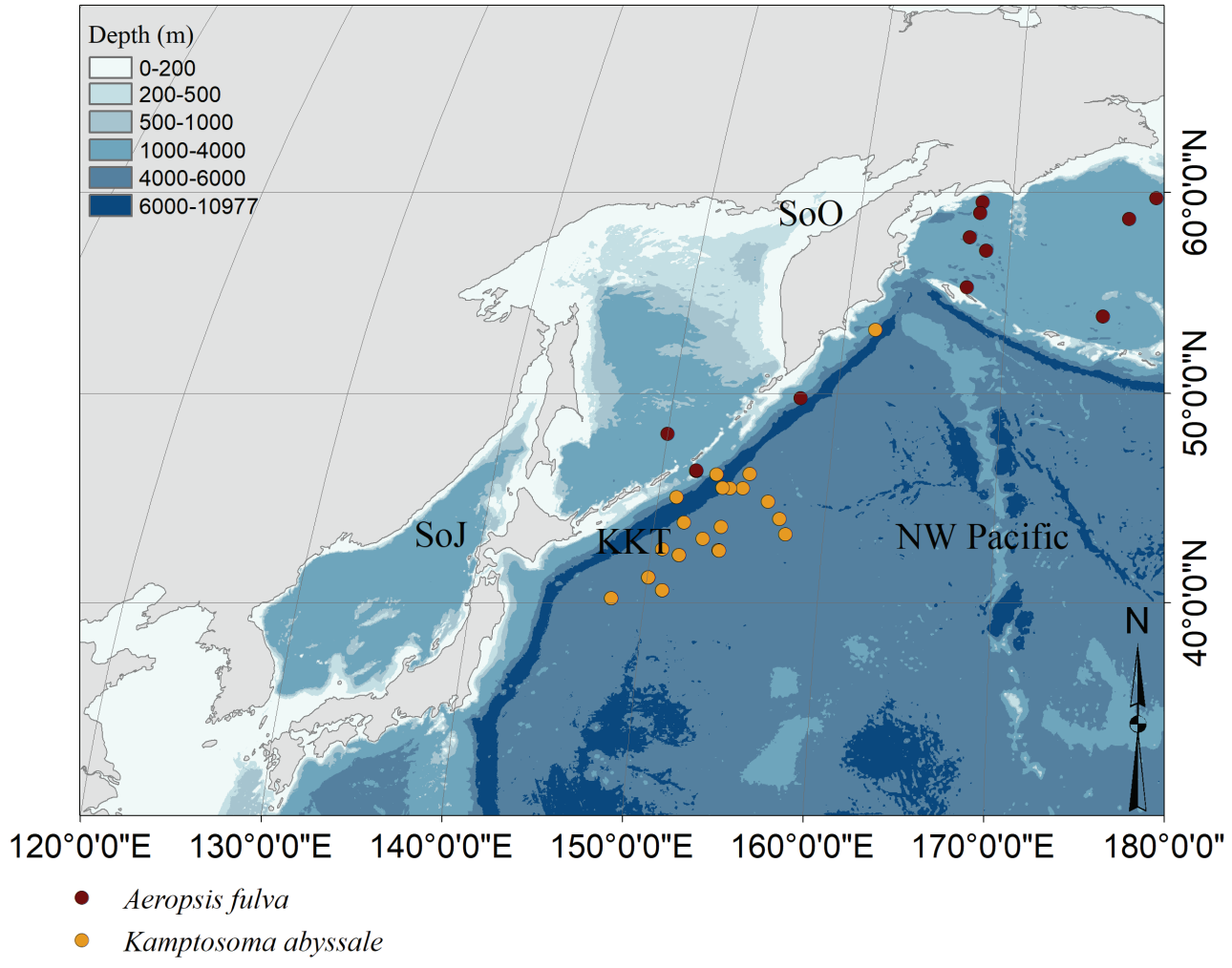


Figure 2. *Kamptosoma abyssale* viewed from below. Specimen photographed before ethanol fixation. Image: Anastassya Maiorova, NSCMB FEB RAS

Order Holasteroida Durham & Melville, 1957
Family Urechinidae Duncan, 1889
***Cystechinus loveni* A. Agassiz, 1898**
***Cystechinus loveni* (Agassiz, 1898)**
(Figure 3, Map 2)
Distribution in the NW Pacific is shown in Map 2. Global distribution: northern Pacific Ocean – Bering Sea, Okhotsk Sea, off Kuril Isl., southern California coast, Baja California, Acapulco, Mexico; 2,600–4,800 m.



Map 1. Distribution of *Kamptosoma abyssale* and *Aeropsis fulva* (Echinoidea) in the NW Pacific.

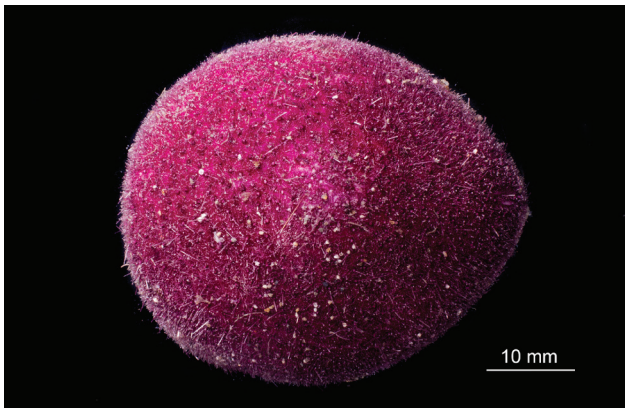


Figure 3. *Cystechinus loveni* viewed from above. Specimen photographed before ethanol fixation. Reprinted from: Deep Sea Research Part II: Topical Studies in Oceanography, Vol. 154, Mironov A.N., Minin K.V., Dilman A.B., Smirnov I.S., Deep-sea echinoderms of the Sea of Okhotsk, Pages 342–357, Copyright (2017), with permission from Elsevier.

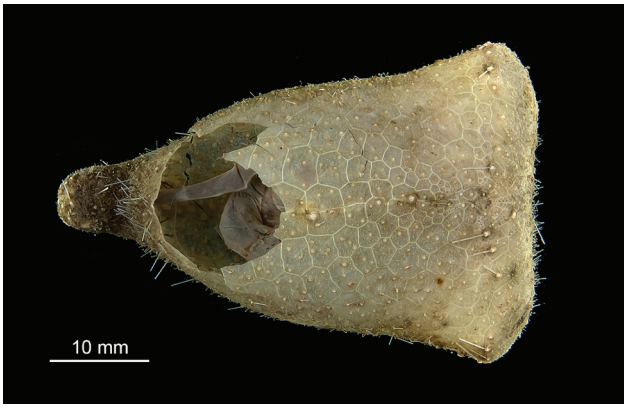


Figure 4. *Ceratophysa ceratopyga valvaecristata* young specimen viewed from above. Specimen photographed after ethanol fixation. Reprinted from: Deep Sea Research Part II: Topical Studies in Oceanography, Vol. 111, Mironov A.N., Minin K.V., Dilman A.B., Abyssal echinoid and asteroid fauna of the North Pacific, Pages 357–375, Copyright (2014), with permission from Elsevier. 2014.

Family Pourtalesiidae A. Agassiz, 1881

Genus *Ceratophysa* Pomel, 1883

***Ceratophysa ceratopyga* (A. Agassiz, 1879)**

(Figure 6, Map 3)

This species is represented in the NW Pacific by subspecies *Ceratophysa ceratopyga valvaecristata* Mironov, 1976 (see Map 3 for distribution records). Global distribution of *C. ceratopyga valvaecristata*: from Japan to Alaska, and off California, 4,200–6,320 m. The subspecies *C. ceratopyga ceratopyga* (A. Agassiz, 1879) is known from Antarctic and off Chile; 3,165–4,600 m. *C. ceratopyga* sub/spp. was recorded off Peru: RV *Dmitry Mendeleev*, St. 1636, 07°56' S, 81°10' W, 5,770–5,800 m.

Genus *Echinosigra* Mortensen, 1907

Subgenus *Echinosigra (Echinogutta)* Mironov, 1997

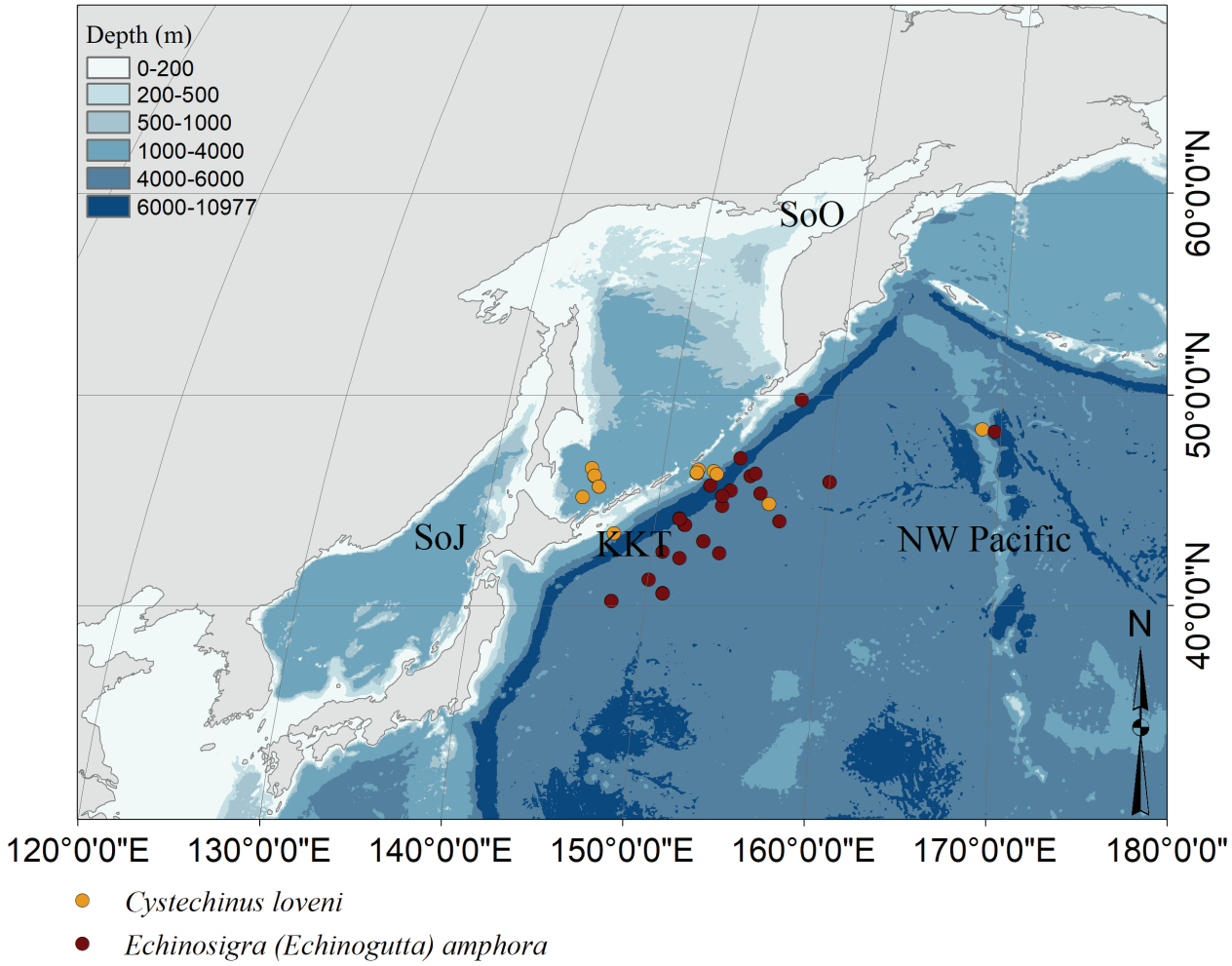
***Echinosigra (Echinogutta) amphora* Mironov, 1974**

(Figure 5, Map 2)

This species is represented in the NW Pacific by subspecies *Echinosigra (Echinogutta) amphora amphora* Mironov, 1974 (see Map 2 for distribution records). Global distribution of *E. (Echinogutta) amphora amphora*: NW Pacific – Kuril-Kamchatka Trench and adjacent abyssal plain; 4,650–7,119 m. The subspecies *E. (E.) am-*



Figure 5. *Echinosigra (Echinogutta) amphora amphora* viewed from the side. Specimen photographed after ethanol fixation. Reprinted from: Deep Sea Research Part II: Topical Studies in Oceanography, Vol. 111, Mironov A.N., Minin K.V., Dilman A.B., Abyssal echinoid and asteroid fauna of the North Pacific, Pages 357–375, Copyright (2014), with permission from Elsevier. 2014.



Map 2. Distribution of *Cystechinus loveni* and *Echinosigra* (Echinogutta) *amphora* (Echinoidea) in the NW Pacific.

phora indica Mironov, 1974 is known from the Java Trench, 6,433–6,850 m. Fragments of E. (E.) *amphora* sub/spp. were collected in the Palau Trench, 7,000–7,170m.

Order Spatangoida L. Agassiz, 1840
Family Aeropsidae Lambert, 1896
Genus *Aeropsis* Mortensen, 1907
***Aeropsis fulva* (A. Agassiz, 1898)**
(Figure 6, Map 1)
Distribution in the NW Pacific is shown in Map 1. Global distribution: Pacific Ocean from Bering Sea to Indo-Malayan Archipelago and from Aleutian Islands to Peru; 1,463–5,390 m.



Figure 6. *Aeropsis fulva* viewed from the side. Specimen photographed before ethanol fixation.

Class Asteroidea de Blainville, 1830

Order Paxillosida Perrier, 1884

Family Porcellanasteridae Sladen, 1883

Genus *Abyssaster* Madsen, 1961

Abyssaster tara (Wood-Mason & Alcock, 1891)

(Figure 7, Map 4)

Distribution in the NW Pacific is shown in Map 4. Global distribution: North Pacific from Kuril-Kamchatka Trench to Gulf of Alaska; north of New Guinea; Indian Ocean from the southern and eastern Africa to Sumatra and the western Australia; 2,550–6,282 m.

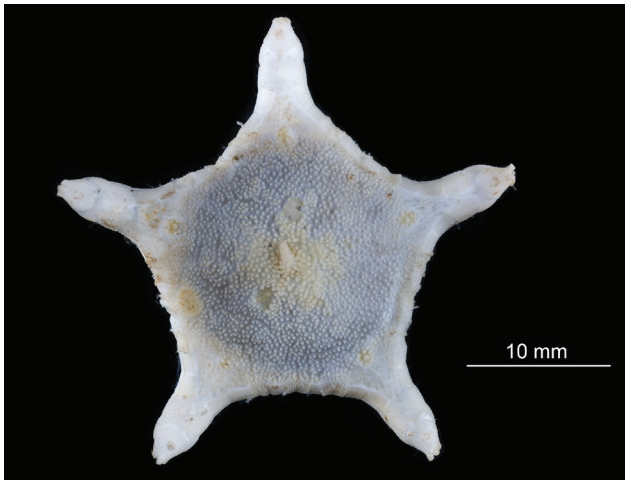
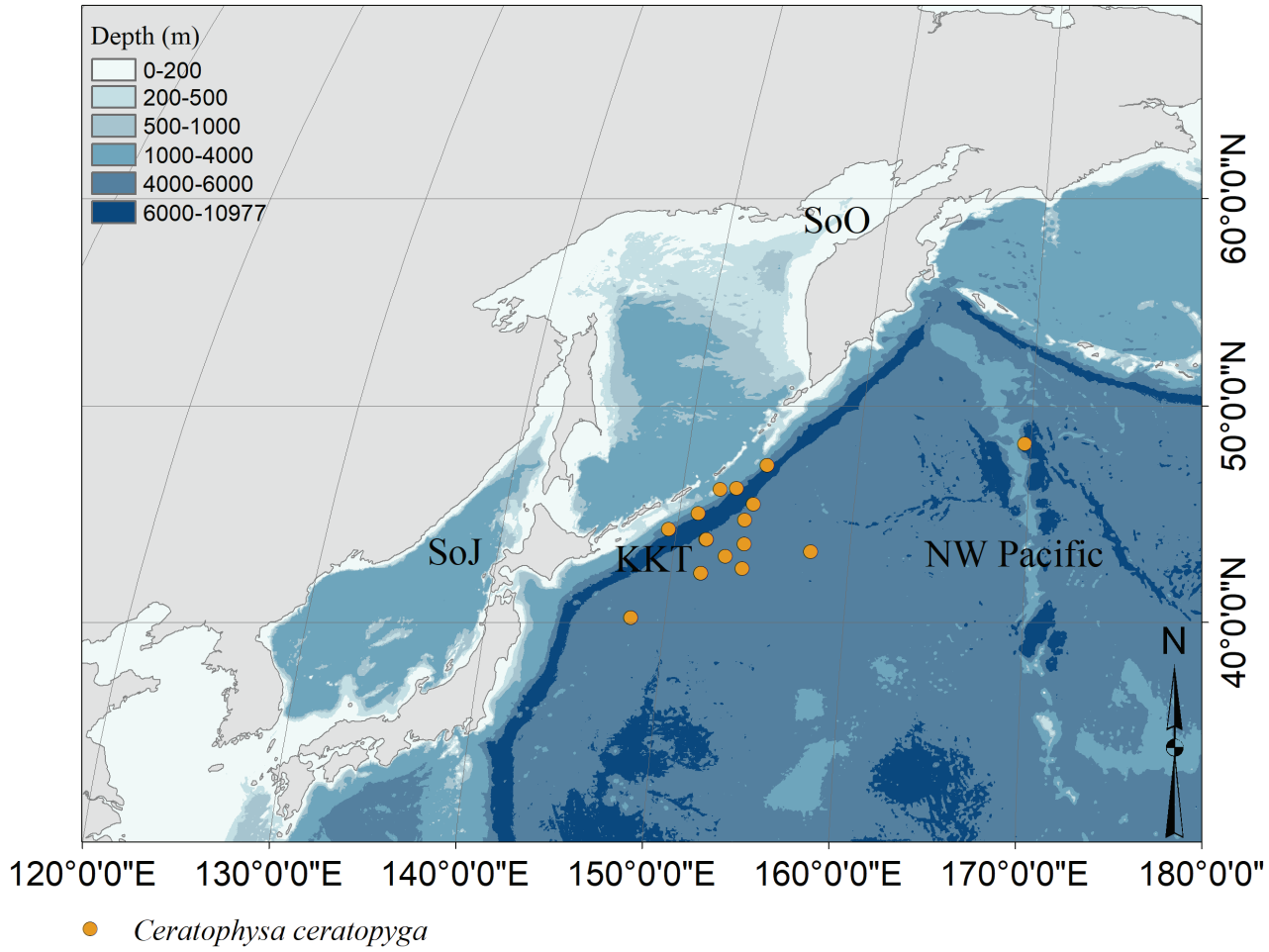


Figure 7. *Abyssaster tara* viewed from above. Specimen photographed after ethanol fixation.



Map 3. Distribution of *Ceratophysa ceratopyga* (Echinoidea) in the NW Pacific.

Genus *Eremicaster* Fisher, 1905

***Eremicaster crassus* (Sladen, 1883)**

(Figure 8, Map 5)

Distribution in the NW Pacific is shown in Map 5. Global distribution: Pacific Ocean, Indian Ocean, Antarctic, off Uruguay in the Atlantic; 2,418 to 6,328 m.

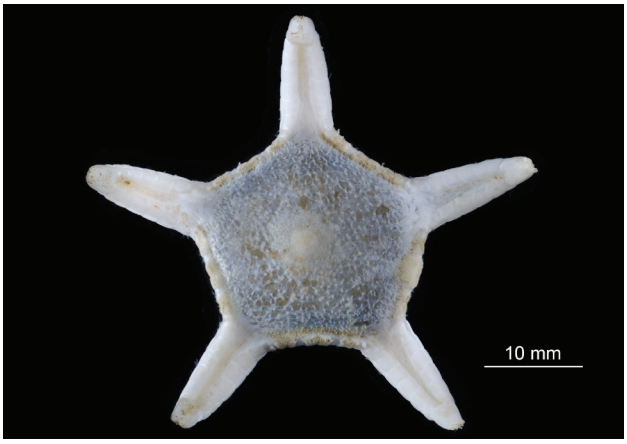
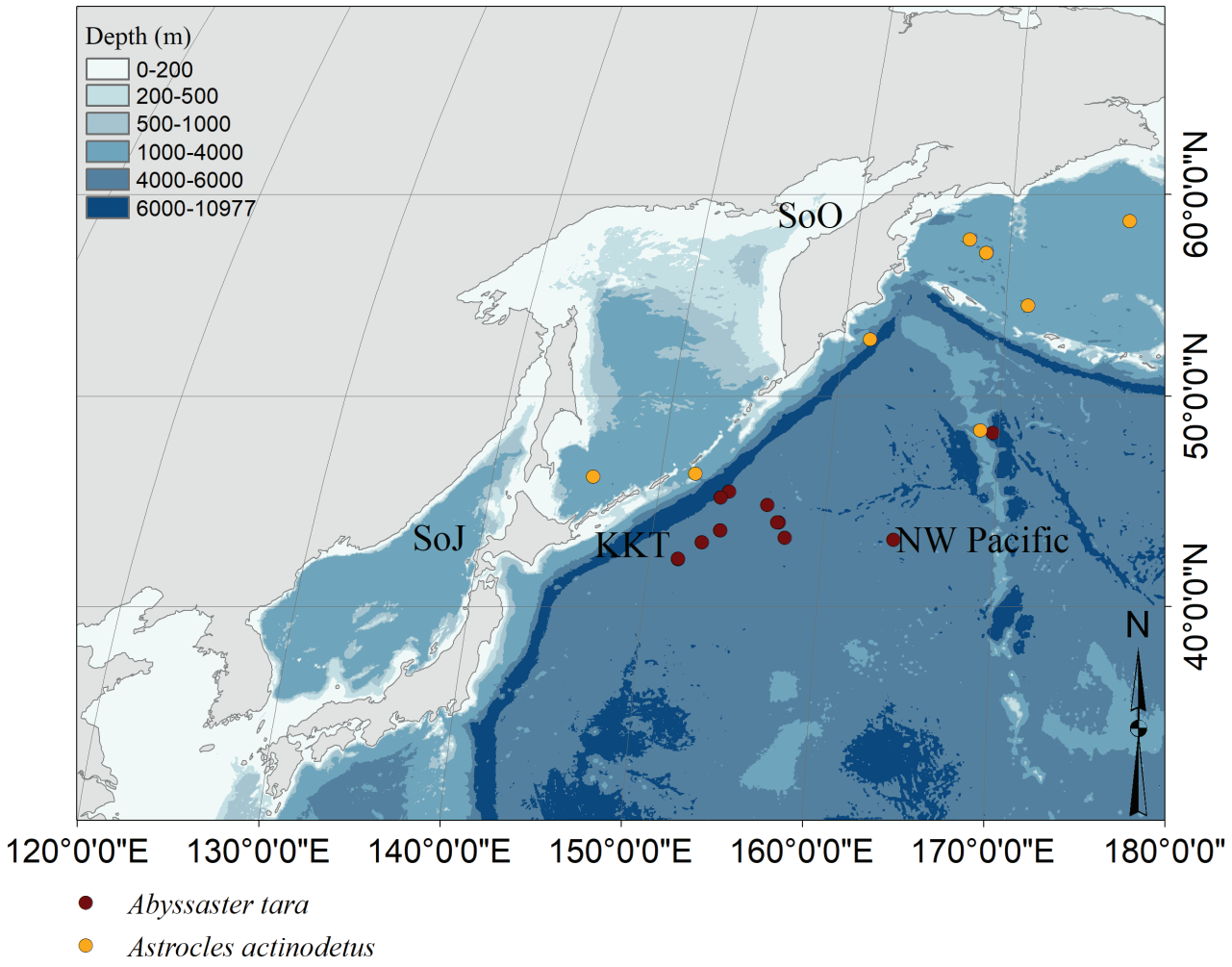


Figure 8. *Eremicaster crassus* viewed from above. Specimen photographed after ethanol fixation.



Map 4. Distribution of *Abyssaster tara* and *Astrocles actinodetus* (Asteroidea) in the NW Pacific.

Genus *Styracaster* Sladen, 1883

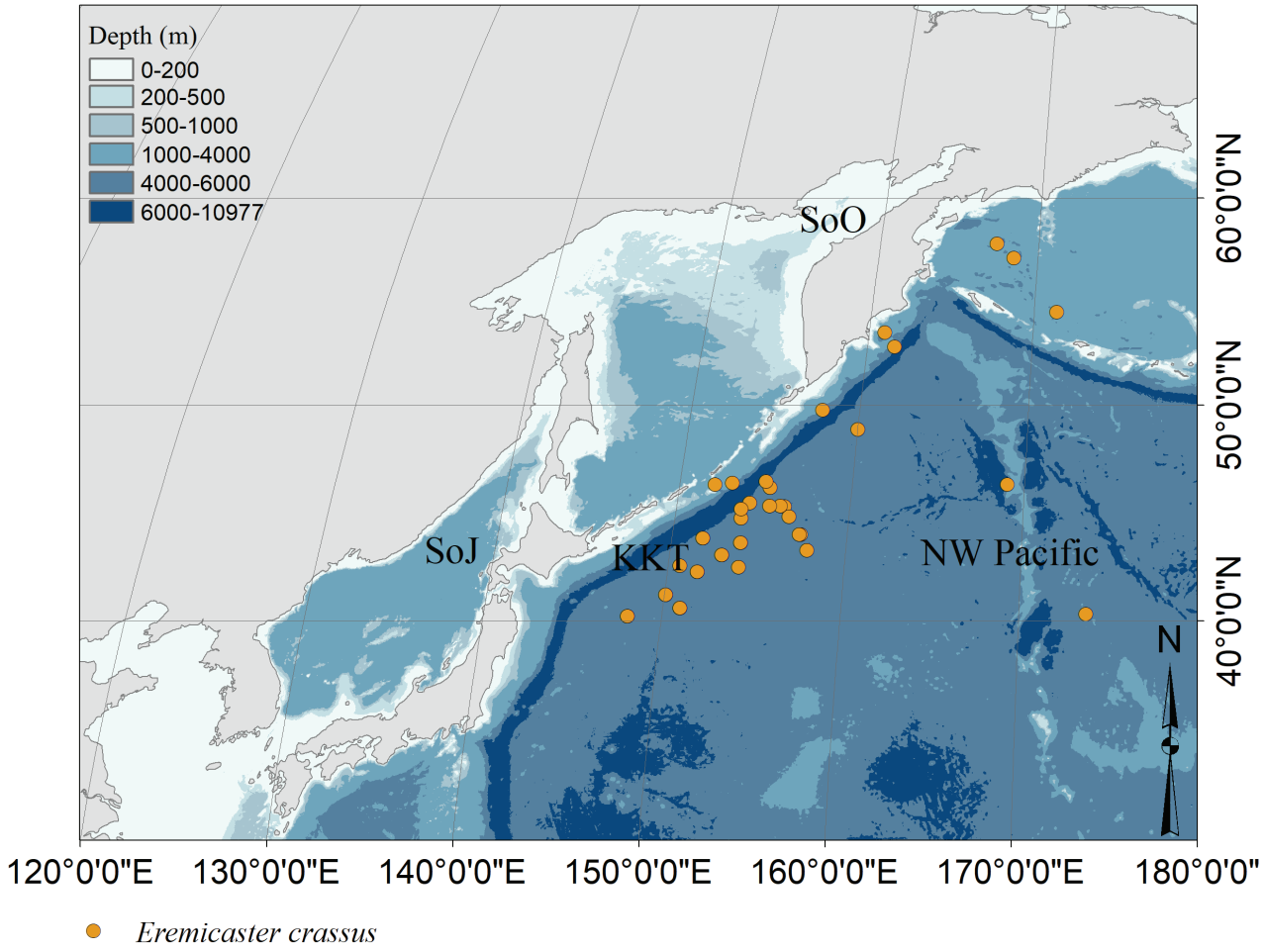
***Styracaster longispinus* Belyaev & Moskalev, 1986**

(Figure 9, Map 6)

Distribution in the NW Pacific is shown in Map 6. Global distribution: North Pacific from 38°N to 47°N and from 151° E to 159° W, 4,995–6,328 m.



Figure 9. *Styracaster longispinus* viewed from above. Specimen photographed before ethanol fixation. Image: Anna Lavrentyeva, NSCMB FEB RAS.



Map 5. Distribution of *Eremicaster crassus* (Asteroidea) in the NW Pacific.

Genus *Vitjazaster* Belyaev, 1969

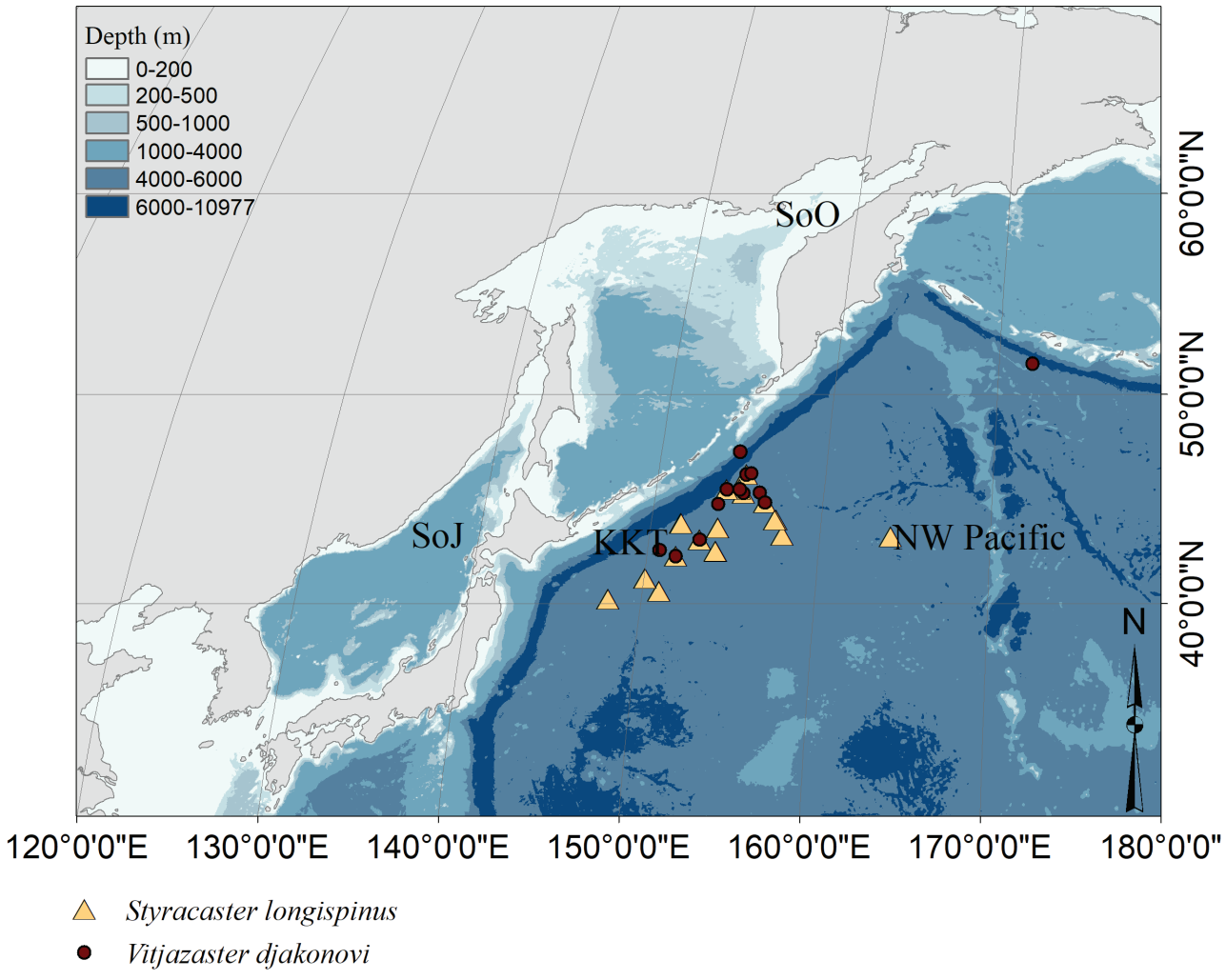
***Vitjazaster djakonovi* Belyaev, 1969**

(Figure 10, Map 6)

Distribution in the NW Pacific is shown in Map 6. Global distribution: North Pacific from 42°N to 52°N and from 150° E to 144° W, 4,550–5,222 m.



Figure 10. *Vitjazaster djakonovi* viewed from above. Specimen photographed after ethanol fixation.



Map 6. Distribution of *Styracaster longispinus* and *Vitjazaster djakonovi* (Asteroidea) in the NW Pacific.

Order Brisingida Fisher, 1928

Family Freyellidae Downey, 1986

Genus *Astrocles* Fisher, 1917

***Astrocles actinodetus* Fisher, 1917**

(Figure 11, Map 4)

Distribution in the NW Pacific is shown in Map 4. Global distribution: North Pacific from Kamchatka off Avacha Bay to Sea of Okhotsk and Pacific slope of the Kuril Islands, and from southwestern Bering Sea to British Columbia and Oregon; 2,870–4,200 m.



Figure 11. *Astrocles actinodetus* viewed from above. Specimen photographed after ethanol fixation. Reprinted from: Deep Sea Research Part II: Topical Studies in Oceanography, Vol. 154, Mironov A.N., Minin K.V., Dilman A.B., Smirnov I.S., Deep-sea echinoderms of the Sea of Okhotsk, Pages 342–357, Copyright (2017), with permission from Elsevier.

4.3. Richness patterns

4.3.1. Depth gradient

In the NW Pacific, the combined echinoid and asteroid species richness slightly decreases from 2,000 to 3,500 m, more rapidly decreases at the depths 3,500-4,500 m, and then abruptly increases until it reaches its maximum at the depths 5,000–5,500 m. Below 5,500 m, the number of echinoid and asteroid species again decreases with depth (Figure 12). The deepest-occurring species, sea star *Hymenaster* sp. B (Mironov et al. in 2019a), is recorded from the depths of 8,185–8,400 m. Unlike crinoids or holothurians, no echinoids or asteroids are known to occur in the NW Pacific below 8,500 m. Gradients in genus richness are similar to those observed at the species level.

The observed trends are similar when only asteroid richness is considered. Echinoids are incongruent with the general trend in having an increase in species richness from 2,000 m to 3,000 m. Depth-related changes in species richness are significantly less pronounced in echinoids (Figure 1).

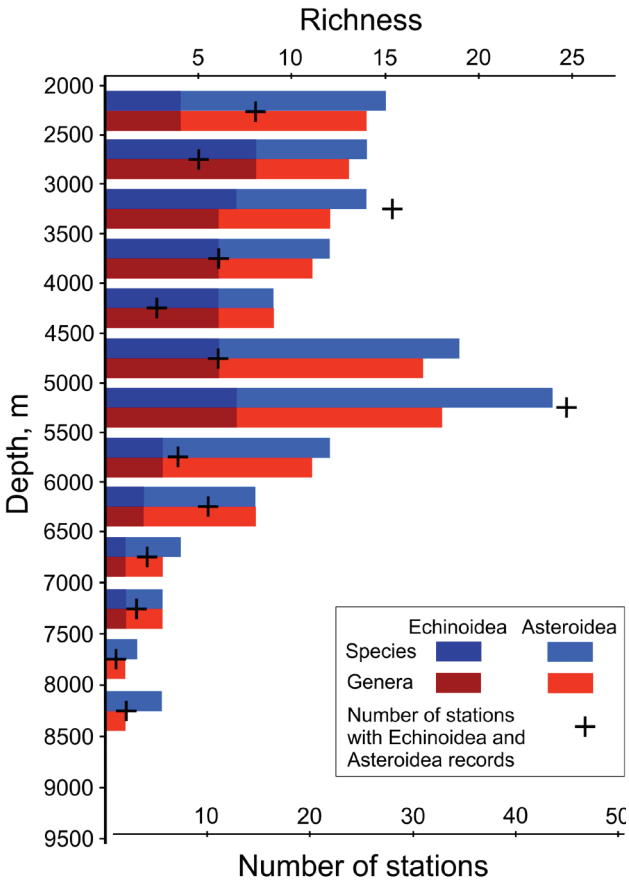


Figure 12. Depth gradient in echinoid and asteroid richness.

4.3.2. Latitudinal gradient

The number of echinoid and asteroid species increases in the NW Pacific from 40°N to 48°N and then steadily decreases northwards to 60°N. When analyzed separately, asteroid species diversity expresses the same trend, whereas echinoids have a peak of species richness in lower latitudes, 42°N to 44°N (Figure 13). Latitudinal richness gradients for genera repeat those observed for the species.

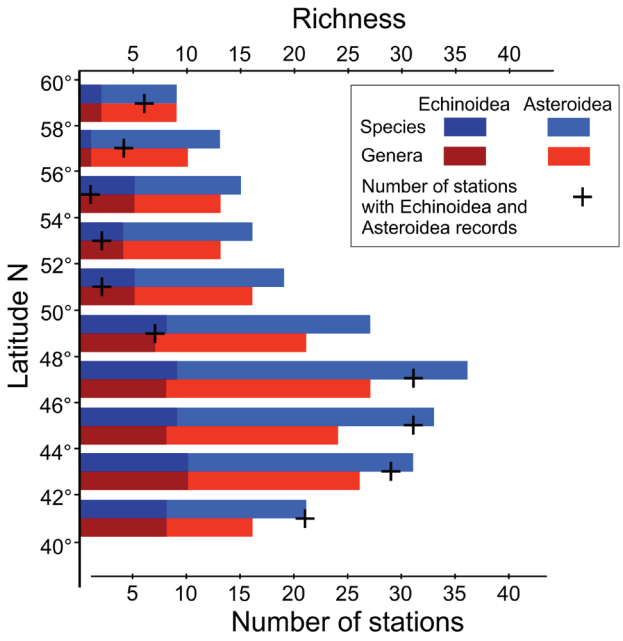


Figure 13. Latitudinal gradient in echinoid and asteroid richness.

4.3.3 Regional richness patterns

Echinoid and asteroid species richness varies among different NW Pacific deep-sea areas. In the marginal seas of the NW Pacific, species richness of the abyssal echinoderm fauna increases along with decrease in level of their geomorphological isolation – from south to north. The number of echinoid and asteroid species in the abyssal zone is five in the most isolated Sea of Japan, 12 species in the semi-enclosed Sea of Okhotsk, and 19 species are found in the less enclosed Bering Sea. Forty-one species are recorded from the open NW Pacific abyssal plain. The Kuril-Kamchatka Trench (11 species) is characterized by the richest fauna compared to other trenches. Four species are recorded from the Japan Trench, and five are known from the Aleutian Trench (Figure 1).

These patterns in species richness distribution correspond perfectly to the patterns observed for distribution of all five echinoderm classes analyzed together (Mironov et al. 2018, Mironov et al. 2019a).

4.4 Biogeographic patterns

4.4.1. Endemism

The endemics of the NW Pacific (10 species) constitute 16% of the deep-sea echinoid and asteroid diversity of the region. Six more species, identified only to the generic level, are also not known outside the NW Pacific (Table 2). Endemism is much less pronounced at higher taxonomic levels: only one genus (the hadal monotypic *Amembranaster* from the family Pterasteridae) is endemic to the NW Pacific. Among the endemic species, *Echinosigra mortenseni* Mironov, 1974, *Amembranaster dimidatius* Golotsvan, 1998, *Astrocles djakonovi* Gruzov, 1964, *Astrocles japonicus* Korovchinsky, 1976, *Freyella hexactis* Baranova, 1957, *Hymenodiscus beringiana* (Korovchinsky, 1976) and *Hyphalaster multispinus* Belyaev & Mironov, 1993 are each known by a single occurrence. Two of the remaining three species, namely *Pteraster texius* Golotsvan, 1998 and *Pteraster ifurus* Goltsvan, 1998, are characterized by very narrow distribution ranges

coinciding with the most sampled areas. This indicates that at least some species might have broader distributions, than is currently known. It is likely that the degree of endemism in the NW Pacific echinoid and asteroid fauna will decrease after further sampling is conducted in adjacent abyssal areas.

4.4.2. Pseudoabyssal species

The Sea of Japan abyssal (depths >2,000 m) fauna is characterized by the absence of echinoids and presence of only five asteroid species. Three of them (*Crossaster japonicus* (Fisher, 1911), *Leptychaster anomalus* Fisher, 1906, *Pedicellaster orientalis* Fisher, 1928) can be classified as pseudoabyssal. These species are known from other NW Pacific areas exclusively from shallower depths. Two pseudoabyssal species (both asteroids) are known from the Sea of Okhotsk: *Crossaster papposus* and *Henricia* sp. Although the latter is not identified to the species level, it is recognized here as pseudoabyssal because none of the numerous Pacific *Henricia* species are known to occur below 2,000 m. Only one pseudoabyssal species, echinoid *Pourtalesia beringiana* (Baranova, 1955), is known from the Bering Sea.

4.4.3. Global distribution patterns of the genera

NW Pacific deep-sea echinoid and asteroid fauna is characterized by the high percentages of genera common with the NE Pacific, East Pacific and Antarctic–Sub-Antarctic (72–85%). It also shows close affinities with the faunas of West Pacific and Atlantic Ocean (67–69% of shared genera). Percentages of genera shared with the Indian Ocean and Arctic are the lowest, 51% and 31% respectively (Table 3). Four genera are not found outside the Pacific Ocean, six genera are known only from the Pacific and Antarctic, one genus (*Hydrasterias*) was reported only from the Pacific and Atlantic oceans and the remaining 26 genera are cosmopolitan.

Compared to asteroids, echinoid fauna shows closer affinities with those of the East Pacific (100% of shared genera) and Antarctic–Sub-Antarctic (83% of shared genera). Among ten echinoid genera shared with the Antarctic–Sub-Antarctic, six (*Aporocidaris*, *Ceratophysa*, *Cystecinus*, *Echinocrepis*, *Pilematechinus* and *Urechinus*) are characterized by a specific distribution pattern in the eastern Pacific: their ranges are limited to a narrow zone extending meridionally along the base of the American western continental slope (Figure 14).

5. Discussion

5.1. Spatial richness gradients

Despite the limited number of species (61) and occurrence records (370) available for the analysis, echinoid and asteroid fauna of the deep NW Pacific displays clear spatial richness gradients – both vertical (depth) and horizontal (latitudinal). These gradients can be linked to an array of various factors, such as seafloor trophic conditions, area, geomorphologic peculiarities and sampling heterogenity.

Vinogradova (1969) separately analyzed the depth gradients in species richness of the

Pacific Echinoidea and Asteroidea. The number of echinoid species decreased with depth, more abruptly between 2,000 and 5,500 m. Although asteroid species richness also showed a general decrease below 2,000 m, it had three clear peaks at the depths ca. 3,200 m, ca. 4,700 m and ca. 6,300 m. The more recent study (Saeedi et al., 2019) considered distribution of all taxa and showed that the species richness in the NW Pacific is highest at the shallow (0–500 m) depths and sharply decreases with depth below 2,000 m. Our data shows that depth-related changes of the echinoid and asteroid species richness display in the NW Pacific a complex pattern that differs from the results obtained in both previous studies. High species richness observed at the depths 2,000–3,500 m is likely underpinned by the existence of the marginal seas with their own abyssal fauna. In our dataset, 13 of 61 species (ca. 21%) are not known from the open NW Pacific abyssal plain and recorded below 2,000 m exclusively from the deep basins of the marginal seas (Table 2). The depth of these basins rarely exceeds 3,500 m. As a result, echinoid and asteroid fauna remains species enriched throughout the depths 2,000–3,500 m. There is even a slight increase in the number of echinoid species below 2,000 m. Species number at these depths shows no correlation with the number of samples (Figure 12); therefore, this enrichment is unlikely to reflect the sampling discrepancies.

Remarkable increase in richness below 4,500 m can be explained by the existence of a vast, mostly eutrophic area of the open-oceanic abyssal plain, capable of accommodating more species compared to the relatively smaller surface of shallower areas. However, the exact position of the richness peak between 5,000 and 5,500 m quite likely reflects the extensive sampling effort undertaken within this depth range (Figure 12).

The presence of the mid-latitude species richness peak with a subsequent poleward decrease matches in general the global gradient in marine taxonomic diversity (Chaudhari et al. 2016). However, in most global-scale studies considering all-depth marine taxa distribution this peak was observed at much lower latitudes (10°–35°N; Crame 2004; Chaudhari et al. 2016). Woolley et al. (2016) pointed at the peculiarity of distribution patterns observed in the deep-sea. According to their data, in the lower bathyal and abyssal zones (2,000–6,500 m), ophiuroid species richness is highest in the temperate latitudes. Particularly the northern richness peak occurs at latitudes 40°–50°N (Woolley et al. 2016).

It can be noted that the latitudes 42°–48°N, where high echinoid and asteroid richness was observed (Figure 13), roughly correspond to the part of the NW Pacific characterized by highly eutrophic seafloor conditions (Sokolova 1977; Lutz et al. 2007). According to Watling et al. (2013), the highest POC (particulate organic carbon) flux to the seafloor in the deep (>3,500 m) NW Pacific is observed between ca. 35°N and ca. 45°N. Wolley et al. (2016) also linked deep-sea ophiuroid richness peaks to the eutrophic seafloor conditions in temperate latitudes.

High echinoid and asteroid richness, recorded at 42–48°N, can also be explained by an extensive sampling effort undertaken within this latitudinal range (Figure 13). In our dataset more than half (11 of 17) of the species, known from the NW Pacific by a single record, were

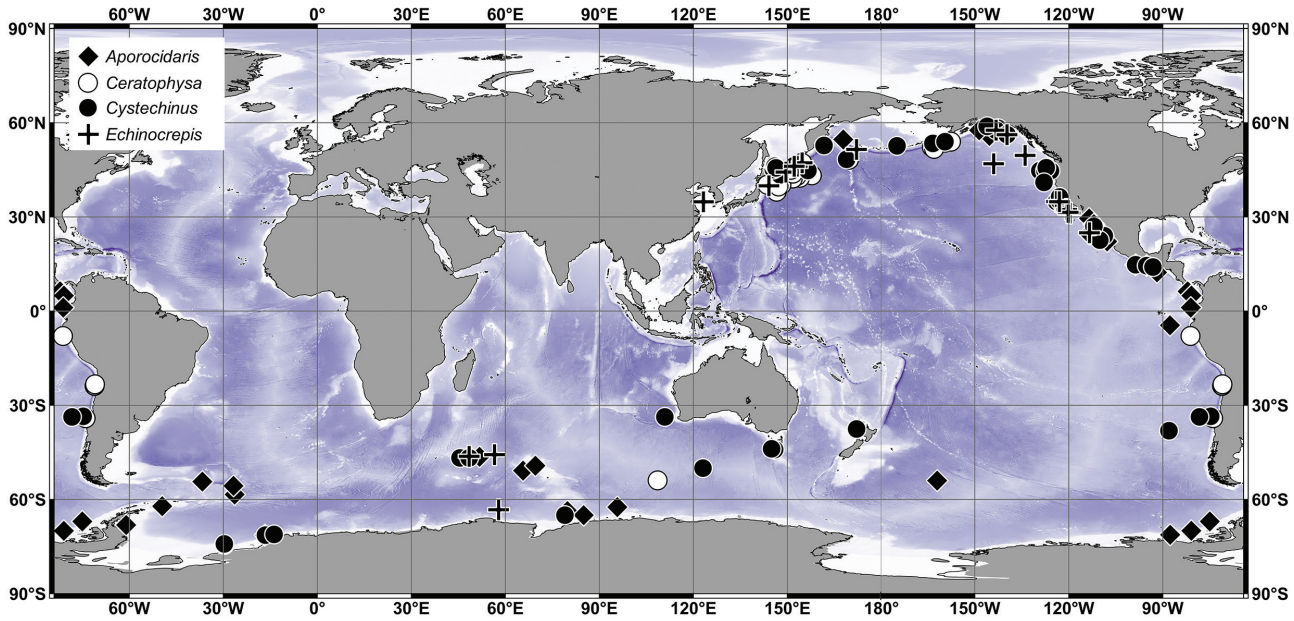


Figure 14. Distribution of echinoid genera with North Pacific–East Pacific–Antarctic ranges.

sampled within these latitudes. Deep-sea echinoid and asteroid fauna of the North Pacific appears to still be insufficiently known and further exploration is needed to understand whether these gradients reflect a true diversity patterns or just a result of a sampling bias.

5.2. Biogeographic patterns and processes in the NW Pacific deep-sea

According to Mironov et al. (2015, 2018), Antarctic and West Pacific centers of deep-sea fauna redistribution served as the donors for the abyssal fauna of the NW Pacific. High percentage of echinoid and asteroid genera, shared by the deep-sea fauna of the NW Pacific with those of the West Pacific (67%) and Antarctic–Sub-Antarctic (72%), likely reflects the influence of these two centers. The influence of the Antarctic center is more prominent in the NW Pacific echinoid fauna (83%, or 10 shared genera). Six of the shared genera are also distributed along the western American continental slope (Figure 14). These genera are thought to be adapted to highly eutrophic conditions (Mironov et al. 2015). Most probably, their current distribution reflects an earlier dispersal via the eutrophic near-continental zone of the East Pacific (Mironov 1982; Mironov et al. 2015). Two more of the remaining four genera (*Pourtalesia* and *Echinosigra*) are specialized burrowers, less sensible to the trophic conditions of the seafloor. They are not known from the East Pacific and likely dispersed from the Antarctic via the West Pacific.

The open-oceanic abyss of the NW Pacific is characterized by the most diverse fauna in the region and likely served as a species donor for other abyssal and hadal regions of the NW Pacific, except for the Sea of Japan abyss. The percentage of echinoid and asteroid species, common with the open abyssal NW Pacific or having there a close congener, ranges from 52% in the Bering Sea to 80% in the Aleutian Trench. Higher species richness of the Bering

Sea abyssal fauna, compared to the one of the more isolated Sea of Okhotsk, indicates that the former has a better established connection with the fauna of open-oceanic abyss.

The share of the pseudoabyssal species is significantly higher in the Sea of Japan compared to the less isolated Sea of Okhotsk and Bering Sea (60%, 17% and 4% respectively). Mironov et al. (in 2019b) showed that the similarly large share of pseudoabyssal species (62%) is characteristic for the Sea of Japan macro- and megafauna in general. This is more than in any other abyssal region of the World Ocean. The high proportion of the pseudoabyssal species was repeatedly discussed to be a result of local submergence of the sublittoral-bathyal fauna to the abyssal zone (Zenkevitch 1963; Tyler 2002; Mironov et al. 2019b). In the Sea of Japan, this process was likely driven by the geomorphological isolation of the abyssal basin. Similar submergence, although much less pronounced, might have also occurred in the two other NW Pacific marginal seas.

Therefore, the composition of the abyssal faunas of the NW Pacific marginal seas is likely shaped by two contrasting processes. The dispersal from the open-oceanic abyssal plain plays major role in the less isolated seas. On the contrary, local submergence of the sublittoral-bathyal fauna prevails in the more isolated seas.

There are several possible explanations for the high species richness of the Kuril-Kamchatka Trench fauna. The southern part of this trench is located in the part of the NW Pacific with the highest POC flux to the deep seafloor (Watling et al. 2013). The Kuril-Kamchatka Trench is significantly larger (in terms of area) than two other trenches and, therefore, can accommodate more species. Differences in species richness can also be explained by uneven sampling effort: number of trawl/sledge stations taken in the Kuril-Kamchatka Trench is more than three times higher than in either of the two other trenches (Mironov et al. in press a).

5.3. Biogeographic regionalization

Although data on echinoid and asteroid distribution is insufficient to provide a basis for biogeographic regionalization of the NW Pacific, it can be used for the evaluation of the existing schemes. Distribution ranges of the genera *Aporocidaris*, *Ceratophysa*, *Cystechinus*, *Echinocrepis*, *Pilematechinus* and *Urechinus* in the Pacific Ocean correspond to the NE Pacific region in the regionalization scheme proposed by Mironov (Mironov 2014; Mironov et al. 2015) for the abyssal zone. In the NW Pacific, the southern boundary of the NE Pacific biogeographic region (ca. 33°N) coincides with the southern distribution limits of these genera. In the East Pacific, the genera distribution ranges and biogeographic region are both limited to a narrow near-continental zone.

Information on vertical and horizontal distribution of echinoid and asteroid species is insufficient to confirm the Aleutian-Japan hadal province proposed by Belyaev (1989). Although this might be caused by limited and unequal sampling, the distribution of other echinoderm taxa makes it too controversial to currently include the Izu-Bonin Trench into this province. The distribution patterns of some crinoid and holothurian genera suggest that congeneric species in the Kuril-Kamchatka and Izu-Bonin trenches emerged

as a result of trench populations being isolated owing to the topographic barrier (Belyaev 1989; Mironov 2019).

Although treated here as the part of the abyssal fauna, all five asteroid species occurring in the Sea of Japan deeper than 2,000 m are known from bathyal depths and limited in their vertical distribution to 2,300 m. No echinoids are known from the Sea of Japan below 2,000 m. These distribution patterns corroborate the existence of a transitional zone between the Sea of Japan bathyal and abyssal fauna, located at the depths 1,800–2,300 m (Derjugin 1939; Mironov et al. in 2019b). This zone corresponds to a crowding of lower bathymetrical distribution limits of sublittoral-bathyal species. The Sea of Japan abyssal fauna, comprising 85 mega- and macrofaunal species, is mostly formed by the sublittoral-bathyal species occurring below this zone (79 species or 94%; Mironov et al. 2019b). As a result, it differs greatly from faunas of adjacent abyssal areas. In accordance with the biotic approach, it was classified by Mironov et al. (2019b) as the Deep Seas of Japan province belonging to the North Pacific Sublittoral-Bathyal biogeographic region erected by Kafanov (1991).

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