

**Biodiversity and distribution of the deep-sea fauna
in the Sea of Japan and in the Kuril-Kamchatka Trench area
with focus on Isopoda as a model organism**

Dissertation

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Nikolaus Oskar Elsner

aus Frankfurt am Main

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Professor Dr. C. Lohr
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Fach-Promotionsausschusses Biologie

“The ocean is a desert with its life underground

And a perfect disguise above”

America, (1972). A Horse with No Name

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Abstract

The aim of this dissertation is to analyze the diversity and distribution of the deep-sea fauna of the Northwest Pacific, more specifically the Sea of Japan and the abyssal plain adjacent to the Kuril-Kamchatka Trench. Deep-sea benthic structure of both areas is analyzed at higher taxonomic level and in greater detail exemplarily for isopods at species and population level. The main focus herein lies on the diversity recorded for each of the areas and the comparison between both.

Two deep-sea expeditions were conducted in order to obtain samples from the Sea of Japan and the Kuril-Kamchatka Trench with the Russian research vessel *Akademik M. A. Lavrentyev* in 2010 (Sea of Japan Biodiversity Studies; SoJaBio) and the German research vessel *Sonne* in 2012 (Kuril-Kamchatka Biodiversity Studies; KuramBio), respectively. Additionally, samples from the Kuril-Kamchatka Trench area, conducted with the Russian research vessel *Vityaz* in the 1950s, were used for further comparisons.

After a general introduction is given in Chapter 1, Chapter 2 therefore initially gives a faunistic overview over the phyla, classes and orders collected on the northern continental slope of the Sea of Japan. Chapter 3 subsequently provides an overview over the phyla, classes and orders collected on the abyssal plain of the North Pacific Basin adjacent to the Kuril-Kamchatka Trench. In the Sea of Japan, Malacostraca (and therein Peracarida), Polychaeta and Ophiuroidea were most abundant, whereas Polychaeta, Copepoda and Malacostraca (therein Peracarida) were most abundant in the Kuril-Kamchatka Trench area.

Chapter 4 analyzes in detail the diversity of the superorder Peracarida of the Sea of Japan at species level, because Peracarida was the most abundant taxon in the samples. A general decrease in diversity with increasing depth was determined for this taxon in this area. The abundance of three peracarid species increases notably below a depth of about 2,500 m, while the abundance of all other species notably decreases. These three species presumably are eurybathic, opportunistic species migrating downslope.

In Chapter 5 diversity patterns of Isopoda in the Sea of Japan are examined and compared to *Vityaz* samples from adjacent areas in the same depth range. Chapter 6 examines diversity patterns of isopods of the Kuril-Kamchatka Trench area. Both studies reveal an impoverished fauna in the deep Sea of Japan due to geologically recent anoxia (~8,000 years ago) and the absence of recolonization of true deep-sea faunal elements mainly attributed to the lack of

deep-water straits into this marginal sea. In contrast, a high regional and local biodiversity could be recorded in the Kuril-Kamchatka Trench area.

In Chapter 7 the population structure and reproductive mode of a single, highly abundant and, within the Sea of Japan, widely distributed munnopsid isopod, *Eurycope spinifrons* Gurjanova, 1933 are analyzed. For this species, no seasonality in breeding could be recognized, but instead repeated reproduction throughout the year can be assumed. This is in contrast to the results of the population structure analysis of two species of *Pleurogonium* Sars, 1864 (Paramunnidae) from the Sea of Japan (Chapter 8). For these two species, seasonal reproduction could be observed, but also an unusually high percentage of brooding females (marsupium present) ever recorded to this extent and at this time of year (August) for any isopod species.

Chapter 9 gives a description of a new munnopsid species as well as the redescription of the highly abundant species *E. spinifrons*. Such detailed species descriptions are the basis of unambiguous species identification and enable diversity studies and comparisons which otherwise would not be possible.

Appendix I shows a work in progress of a manuscript on the biogeography of both areas. This manuscript compares the data of the SoJaBio and KuramBio expeditions with the Global Open Oceans and Deep Seabed (GOODS) biogeographic classification and distribution of certain species.

In conclusion, the studies conducted in the framework of this thesis improved our knowledge and understanding of the deep-sea fauna of the Northwest Pacific, namely the Sea of Japan and the abyssal plain southeast of the Kuril-Kamchatka Trench. The former is impoverished due to its geological history and characteristics, the latter exhibits high diversity, which can mainly be explained by the old age of the Pacific, the connectivity of the area with adjacent basins and the Oyashio current bringing nutrient-rich waters into the area. Furthermore, the populations of three species of isopods in part co-occurring in the Sea of Japan do not share the same population structure and reproductive mode, which might suggest avoidance of direct competition and occupation of different ecological niches. This could lead to differences in distributional patterns and may help to explain the distributional limits and possibilities of individual species, both bathymetrically and geographically.

Zusammenfassung

Das Ziel dieser Dissertation ist die Analyse der Diversität und Verteilung der Tiefseefauna des Nordwest Pazifiks, im Speziellen des Japanischen Meeres und der Abyssalfläche, die an den Kurilengraben angrenzt. Die Analyse der Struktur des Tiefseebenthos beider Gebiete wurde auf höherer Taxonebene und detaillierter am Beispiel der Isopoda (Asseln) auf Art- und Populationsebene durchgeführt. Dabei liegt der Hauptfokus auf der erfassten Diversität beider einzelner Gebiete und dem Vergleich zwischen beiden.

Zwei Tiefseeexpeditionen wurden durchgeführt, um Proben aus dem Japanischen Meer mit dem russischen Forschungsschiff *Akademik M. A. Lavrentjev* im Jahr 2010 (Sea of Japan Biodiversity Studies; SoJaBio) und aus dem Gebiet des Kurilengrabens mit dem deutschen Forschungsschiff *Sonne* im Jahr 2012 (Kuril-Kamchatka Biodiversity Studies; KuramBio) zu erhalten. Zusätzlich wurden Proben aus dem Gebiet des Kurilengrabens, die in den Fünfzigerjahren des letzten Jahrhunderts mit dem russischen Forschungsschiff *Vitjaz* genommen wurden, für einen Vergleich herangezogen.

Nach einer generellen Einführung in Kapitel 1 gibt Kapitel 2 deshalb zunächst einen faunistischen Überblick über die Stämme, Klassen und Ordnungen, die auf dem nördlichen Kontinentalhang des Japanischen Meeres gesammelt wurden. Anschließend gibt Kapitel 3 einen Überblick über die Stämme, Klassen und Ordnungen, die auf der Abyssalfläche des Nordpazifischen Beckens, welches an den Kurilengraben angrenzt, gesammelt wurden. Im Japanischen Meer waren Malacostraca (höhere Krebse; darin Peracarida (Ranzenkrebse)), Polychaeta (Meeresborstenwürmer) und Ophiuroidea (Schlangensterne) am abundantesten, während Polychaeta, Copepoda (Ruderfußkrebse) und Malacostraca (darin Peracarida) die abundantesten Gruppen im Gebiet des Kurilengrabens waren.

Kapitel 4 analysiert im Detail die Diversität der Superordnung Peracarida im Japanischen Meer auf Artebene, weil Peracarida das häufigste Taxon in den Proben war. Für dieses Taxon wurde in diesem Gebiet eine generelle Abnahme der Diversität mit zunehmender Tiefe festgestellt. Die Abundanz dreier Arten von Peracarida nahm unterhalb einer Tiefe von 2.500 m merklich zu, während die Abundanz aller anderen Arten merklich abnahm. Diese drei Arten sind vermutlich eurybathe, opportunistische Arten die hangabwärts migrieren.

In Kapitel 5 werden die Diversitätsmuster der Isopoda im Japanischen Meer untersucht und mit denjenigen Proben der *Vitjaz* verglichen, die im angrenzenden Gebiet und im selben Tiefenbereich genommen wurden. Kapitel 6 untersucht die Diversitätsmuster der Isopoda des Gebiets des Kurilengrabens. Beide Untersuchungen zeigen eine Verarmung der Fauna in der Tiefsee des Japanischen Meeres, die auf die geologisch kürzlich vergangene Anoxie (bis vor etwa 8.000 Jahren) und die fehlende Wiederbesiedlung mit echter Tiefseefauna zurückzuführen ist. Die fehlende Wiederbesiedlung selbst ist auf das Fehlen von tiefen Meeresstraßen in dieses Randmeer hinein

zurückzuführen. Im Gegensatz dazu konnte eine hohe regionale und lokale Biodiversität für das Gebiet des Kurilengrabs festgestellt werden.

In Kapitel 7 wird die Populationsstruktur und die Art der Fortpflanzung einer einzelnen, höchst abundanten und, innerhalb des Japanischen Meeres, weitverbreiteten munnopsiden Isopodenart, *Eurycope spinifrons* Gurjanova, 1933 analysiert. Für diese Art konnte keine Saisonalität im Brutverhalten festgestellt werden, deshalb wird eine wiederholte Reproduktion das ganze Jahr über angenommen. Dieses Ergebnis steht im Gegensatz zu den Ergebnissen der Populationsstrukturanalyse zweier Arten der Gattung *Pleurogonium* Sars, 1864 (Paramunnidae) aus dem Japanischen Meer (Kapitel 8). Für diese zwei Arten konnte saisonale Reproduktion festgestellt werden und zusätzlich ein ungewöhnlich hoher Prozentsatz von eiertragenden Weibchen mit ausgebildetem Marsupium (Brutbeutel), der in diesem Ausmaß und dieser Jahreszeit (August) bislang für Isopoden noch nicht bekannt war.

Kapitel 9 enthält die Beschreibung einer neuen Isopoden-Art (Familie Munnopsidae) sowie die Wiederbeschreibung der höchst abundanten Art *E. spinifrons*. Solche detaillierten Artbeschreibungen sind die Grundlage für zweifelsfreie Artbestimmungen und ermöglichen Diversitätsstudien und Vergleiche, die andernfalls nicht möglich wären.

Anhang I (Appendix I) zeigt die laufende Arbeit an einem Manuskript über die Biogeographie beider Gebiete. Dieses Manuskript vergleicht die Daten der Expeditionen SoJaBio und KuramBio mit der biogeographischen Klassifizierung GOODS (Global Open Oceans and Deep Seabed) und die Verbreitung gewisser Arten.

Als Fazit tragen die Studien, die im Rahmen dieser Dissertation durchgeführt worden sind, zur verbesserten Kenntnis und zum verbesserten Verständnis der Tiefseefauna des Nordwest Pazifiks bei, und zwar des Japanischen Meeres und der Abyssalfläche südöstlich des Kurilengrabs. Erstere ist durch die geologische Geschichte und Gegebenheiten verarmt, letztere zeigt eine hohe Diversität, die hauptsächlich durch das hohe Alter des Pazifiks, die Verbundenheit mit angrenzenden Gebieten und den Oyashio-Strom erklärt werden kann, der nährstoffreiches Wasser in das Gebiet bringt. Des Weiteren teilen drei Isopoden-Arten, die teilweise in denselben Gebieten im Japanischen Meer vorkommen, nicht dieselbe Populationsstruktur und Art der Fortpflanzung, welches auf die Vermeidung direkter Konkurrenz und Besetzung unterschiedlicher ökologischer Nischen hindeuten könnte. Dieses könnte auch zu einem unterschiedlichen Verbreitungsmuster führen und könnte generell helfen, die Grenzen und Möglichkeiten der Verbreitung einzelner Arten zu verstehen, sowohl bathymetrisch als auch geographisch.

Резюме

Целью данной диссертации является анализ разнообразия и распределения глубоководной фауны северо-западной части Тихого океана, в частности Японского моря и абиссальной равнины, прилегающей к Курило-Камчатскому желобу. Структура глубоководного бентоса в обеих областях анализируется на высоком таксономическом уровне и значительно более детально на видовом и популяционном уровне исследуются изоподы. Основное внимание в работе уделено биоразнообразию и сравнению исследованных областей.

Сборы бентоса выполнялись в ходе двух глубоководных экспедиций: на российском научно-исследовательском судне Академик М.А. Лаврентьев в 2010 году в Японском море (Исследование биоразнообразия Японского моря - SoJaBio) и в районе Курило-Камчатского желоба на немецком НИС Sonne в 2012 (Исследования биоразнообразия Курило-Камчатского района - KuramBio). Кроме того, для сравнительных анализов были использованы данные сборов российского НИС Витязь в 1950-х годах в районе Курило-Камчатского желоба.

После основного введения в главе 1, в главе 2 дается фаунистический обзор типов, классов и отрядов, собранных на северном материковом склоне и котловине Японского моря. Далее в главе 3 представлен обзор типов, классов и отрядов, собранных на абиссальной равнине Северной Тихоокеанской котловины, прилегающей к Курило-Камчатскому желобу. В Японском море наиболее многочисленными и распространенными оказались Malacostraca (в основном Peracarida), Polychaeta и Ophiuroidea, в то время как в районе Курило-Камчатского желоба это были Polychaeta, Copepoda и Malacostraca (в основном Peracarida)

Глава 4 подробно анализирует разнообразие на видовом уровне надотряда Peracarida в Японском море, поскольку Peracarida были преобладающим таксоном в сборах. Для этого таксона в целом отмечено уменьшение разнообразия с увеличением глубины в районе исследования. Выяснено, что численность трех видов Peracarida увеличивается глубже 2500 м, в то время как обилие всех других видов уменьшается. Эти три вида предположительно являются эврибатными, оппортунистическими видами, мигрирующими вниз по склону.

В главе 5 исследуется разнообразие Isopoda в Японском море в сравнении с данными Витязя из соседних областей в том же диапазоне глубин. Глава 6 рассматривает разнообразие изопод района Курило-Камчатского желоба. Оба исследования выявили что фауна в глубоководной котловине Японского моря обеднена в связи с явлением аноксии в недавнем геологическом прошлом (~8000 лет назад) и отсутствие элементов настоящей глубоководной фауны в основном связано с отсутствием глубоководных проливов в это окраинное море. В

противоположность этому, в районе Курило-Камчатского желоба был отмечен высокий уровень регионального и локального биоразнообразия.

В главе 7 анализируются популяционная структура и репродуктивная модель одного, самого многочисленного и широко распространенного на больших глубинах Японского моря вида изоподы, *Eurycope spinifrons* Gurjanova, 1933. Для этого вида сезонность в размножении не выявлена, вместо этого предполагается непрерывное размножение в течение всего года. Это отличается от результатов анализа популяционной структуры двух видов *Pleurogonium* Sars, 1864 (Paramunnidae) из Японского моря (глава 8). Для этих двух видов наблюдалась сезонность размножения, но также был отмечен и высокий процент яйценосных самок с выводковыми сумками в это время года (август) для всех видов изопод.

Глава 9 представляет собой описание нового вида Munnopsidae, а также переописание самого массового вида *E. spinifrons*. Такие детальные описания видов являются основой правильных определений видов при исследованиях биоразнообразия и сравнений, которые в противном случае были бы невозможны.

Приложение I показывает продолжающуюся работу над рукописью по биогеографии обеих областях. Эта рукопись сравнивает данные экспедиций SoJaBio и KuramBio с биогеографическими данными по распространению отдельных видов в системе Global Open Oceans and Deep Seabed (GOODS)

В заключении диссертации говорится, что проведенные исследования расширили наши знания и понимание глубоководной фауны Северо-Западной Пацифики, а именно Японского моря и абиссальной равнины к юго-востоку от Курило-Камчатского желоба. Первый район обеднен из-за его геологических особенностей и истории, второй район демонстрирует высокую степень разнообразия, которую в основном можно объяснить древностью Тихого океана, открытыми связями района с соседними областями и влиянием течения Ойясио, приносящего сюда богатые питательными веществами воды. Кроме того, популяции трех видов изопод, населяющих Японское море, имеют различную популяционную структуру и репродуктивную модель, что предполагает отсутствие прямой конкуренции и использование различных экологических ниш. Это объясняет различия в картине распределения и может помочь выявить как батиметрические так и географические пределы расселительных возможностей отдельных видов.

Translated by Dr. M. Malyutina

Introduction

“From water does all life begin.”

Frank Herbert, *Dune* (1965)

Chapter 1: Introduction

The Ocean and the deep sea

Oceans have always covered more than half of the earth's surface. They played a vital role in the origin of life, which is hypothesized to have originated in the vicinity of deep-sea hydrothermal vents (Miller and Bada, 1988; Miller and Lazcano, 1995; Pace, 1991). In any case, the oceans have always represented an important habitat for both extinct and recent species. Today, the ocean floor (and surface) covers about 71% of the earth's surface (Tardent, 2005). With an average depth of 2,400–2,500 m, the oceans cover an area of 361 million km² and a volume of 1.4 billion km³ (Tardent, 2005), and thus exhibit the largest living space on earth.

About 90% of the oceans' surface lie beneath a depth of 200 m and hence are ecologically attributed to the deep sea (Hempel et al., 2006). The deep sea is divided into three depth regions: bathyal (200–3,000 m depth), abyssal (3,000–6,000 m) and hadal (deeper than 6,000 m). Abyssal plains cover an area of over 50% of the earth's surface (Smith et al., 2008). Despite and because of its immense size, very little is known about the biodiversity and distribution of fauna inhabiting this region. Only about 0.0001% of the sea floor has been studied in detail so far (Tyler et al., 2002).

For example with regard to deep-sea fisheries (Roberts, 2002) and deep-sea mining (Ahnert and Schriever, 2001; Veillette et al., 2007), it is important to understand this environment characterized by, for example, low abundance levels (away from chemosynthetic systems), slow growth and recovery (Grassle, 1977).

The Pacific Ocean

The Pacific is the largest, deepest and oldest ocean on earth. It covers an area of 174.9 km² with an average depth of 4,028 m (Tardent, 2005). Within the Pacific Ocean, as a result of subduction zones of the Pacific Plate with adjacent tectonic plates, there are regions of high volcanic activity and formation of deep ocean trenches in the north, east, south and west, referred to as the circum-Pacific belt or "Ring of Fire" (Duda, 1965; Embley et al., 2007). Thus, such tectonic and seismic active regions can be found throughout the Pacific Ocean.

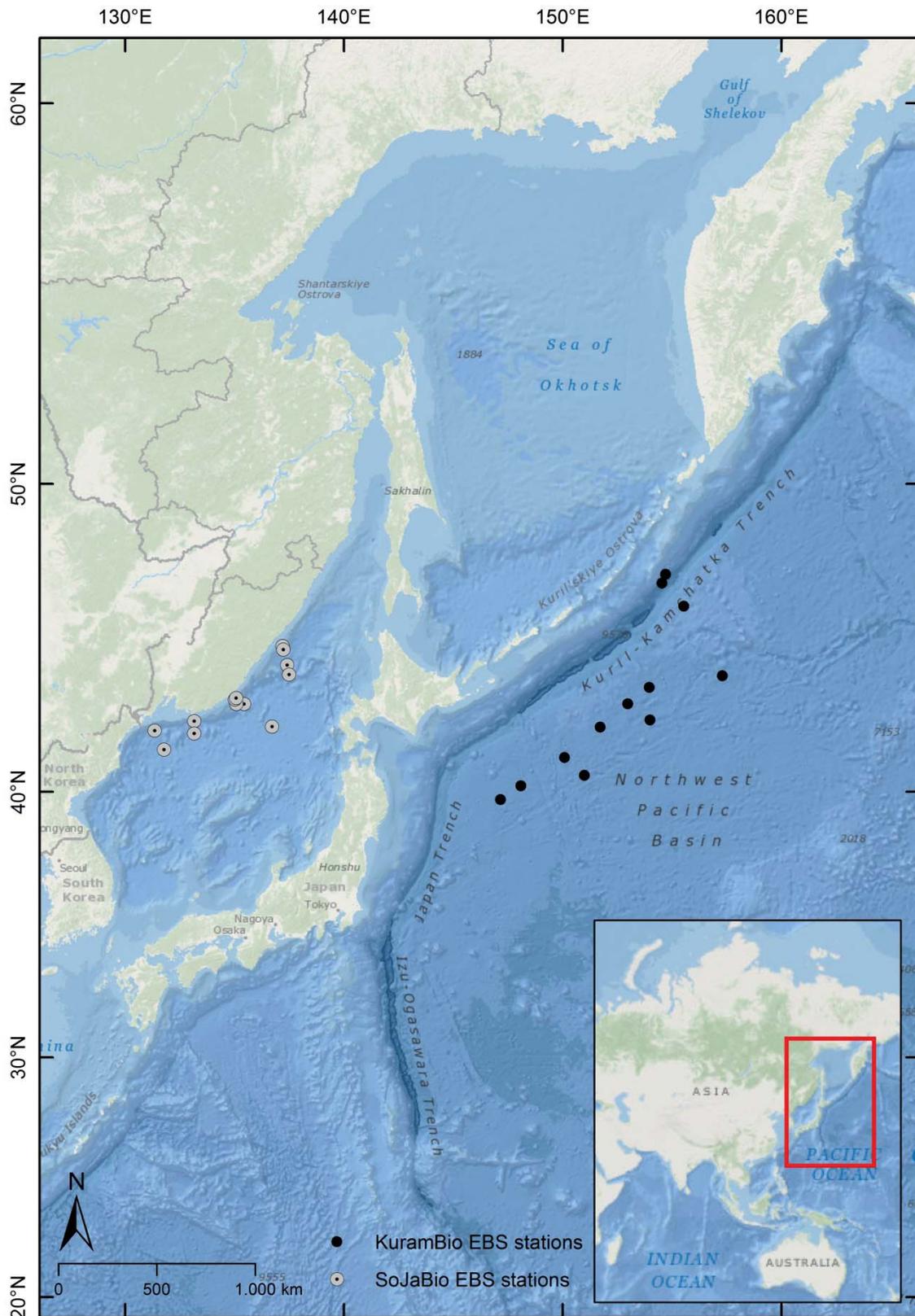


Fig. 1.1: Map of the Northwestern Pacific showing the stations of the two expeditions discussed in this dissertation: Sea of Japan Biodiversity Studies (SoJaBio) and Kuril-Kamchatka Biodiversity Studies (KuramBio). The map was created using Esri ArcGIS 10.2 by T. Springer.

The Northwest Pacific is characterized by a topographically rather homogeneous abyssal plain at about 5,000 m depth with generally just a change of several hundred meters in depth (Zenkevitch, 1963). In regions where the Pacific plate subducts under the North American plate, deep-sea trenches form. The Japan Trench and the Kuril-Kamchatka Trench run along the Japanese Islands and the Kurile Islands (Fig. 1.1). Northwest of these trenches, the Sea of Japan and the Okhotsk Sea, respectively, formed as back-arc basins (Tatsumi et al., 1989). The area southeast of the Kurile Islands is mainly influenced by the Oyashio, a cold ocean surface, originating in the Bering Sea and consisting of upwelling and nutrient-rich waters. The Oyashio flows along the Kamchatka Peninsula and the Kurile Islands and meets the Kuroshio east of Honshu. The Kuroshio is a warm and, in contrast to the Oyashio, oligotrophic water ocean current originating east of the Philippines (Qiu, 2001). Consequently, at least the surface waters of the abyssal area southeast of the Kuril-Kamchatka Trench are eutrophic.

Sea of Japan

The Sea of Japan is a marginal sea in the Northwest Pacific, adjacent to the Sea of Okhotsk to the northeast and to the East China Sea to the southwest (Fig. 1.1). To the west and northwest it is bordered by the mainland of Russia, North Korea and South Korea (north to south). To the east and southeast, the Sea of Japan is framed by the Russian island Sakhalin and the islands of Japan, mainly Hokkaido and Honshu (north to south). The Sea of Japan has four shallow-water straits connecting it to adjacent marginal seas and the Pacific Ocean: In the North and in the East, it is connected with the Sea of Okhotsk through the narrow and shallow Tatarskiy Strait (15 m depth) and through the Soya Strait (53 m depth), respectively. To the East, it is also connected to the open Pacific through the Tsugaru Strait (130 m depth). To the southwest, it is connected to the East China Sea through the broadest strait, the Tsushima Strait (130 m depth; Tyler, 2002). The Sea of Japan is characterized by a steep slope off the mainland and three deep-sea basins located within (north to south): the Japan basin west of Hokkaido, the Yamato basin west of Honshu and the Tsushima basin east of South Korea.

The Sea of Japan covers an area of about 978,000 km² and its deepest point extends to 4,036 m (Zenkevitch, 1963). The Sea of Japan is a rather unique area, as it represents a semi-enclosed basin with only shallow-water linkage to adjacent marine areas. The Sulu Sea southwest of the Philippines and northeast of Borneo exhibits similar characteristics. Through

the Tsushima Strait in the South, the warm Tsushima Current (originating from the Kuroshio current) flows into the Sea of Japan and splits into three branches: one along the Korean mainland, one along Honshu and one offshore branch (Ito et al., 2014; Kawabe, 1982). In the Sea of Japan, 84% of the water volume and the bottom layer below 2,000 m are very homogenous with regard to temperature, salinity and dissolved oxygen. Downwelling and vertical convection in the winter lead to an anomalously high concentration of dissolved oxygen especially for the deep sea (Chen et al., 1999). The subpolar front of the Arctic divides the Sea of Japan at around 40°N and causes subarctic circulation in the northern and subtropical circulation in the southern half of the Sea of Japan (Senju, 1999).

The geological history of the Sea of Japan is characterized by several changes directly influencing the diversity of the benthos. In the Miocene, the Sea of Japan supposedly was a freshwater lake (Burckle and Akiba, 1978). In the Pleistocene, almost all of the deep-water benthos underwent extinction due to low-salinity surface waters and anoxic deep waters (Amano, 2004). About 20,000 to 15,000 years ago, the Sea of Japan again experienced severe anoxic conditions due to a significant amount of freshwater input, probably from the Yellow River in China, which resulted in a stratification of the water column (Kojima et al., 2001; Oba et al., 1991). During the Last Glacial Maximum, a eustatic sea level decline of 120-135 m (compared to today's sea level) was the result of massive glacier forming, resulting in a complete isolation of the Sea of Japan as the shallow-water straits fell dry (Clark and Mix, 2002; Fairbanks, 1989). Oba et al. (1991) date the emergence of the present conditions to about 8,000 years ago. The lower sublittoral and upper bathyal waters (~100–400 m) were presumably of normal salinity and oxic during glacial lowstands (Amano, 2004), but this depth range most likely is far too shallow to provide a proper refuge for true deep-sea fauna during anoxia. The combination of this geological history, the resulting mass extinction and the lack of deep-water straits which prevent recolonization from adjacent deep-sea basins leads to the assumption that the deep fauna today is impoverished and composed of cold-adapted eurybathic species rather than true deep-sea species (Tyler, 2002; Zenkevitch, 1963).

Kuril-Kamchatka Trench area

The Kuril-Kamchatka Trench is originated and formed by the Pacific plate being subducted beneath the North American plate. Thus, the Trench and the surrounding area are characterized by high volcanic activity. As a result of the subduction of the tectonic plates, the

Sea of Okhotsk was formed as a back-arc basin (Tyler, 2002) and the Kurile Island as an island arc. The Trench itself reaches down to a maximum depth of 10,542 m, is 2,200 km long and 120 km wide (Angel, 1982). To the North, the Kuril-Kamchatka Trench becomes the Aleutian Trench, to the South the Japan Trench. On the other side of the trench lies the vast and generally rather homogeneously formed Northwest Pacific Basin with a depth of about 5,000 m (Zenkevitch, 1963).

The Oyashio, a cold surface current originating in the Bering Sea and flowing southward along the Kamchatka Peninsula and the Kurile Islands, brings nutrient-rich waters into the Kuril-Kamchatka Trench area which is characterized as a eutrophic region (Angel, 1982; Belyaev, 1972). About half-way along the Sea of Japan and south of the Western Subarctic Gyre, it turns east. From the South, the Kuroshio, a warm surface current, flows northward along Honshu and turns east as well, forming a body of mixed water together with the Oyashio east of Honshu (Qiu, 2001).

Isopoda

The order Isopoda Latreille, 1817 belongs to the subphylum Crustacea, the class Malacostraca and the superorder Peracarida (Brusca and Brusca, 2003). The Peracarida, such as isopods, are characterized by a marsupium, a brooding pouch formed by the oostegites on the coxae of the anterior thoracopods (Kästner, 1993). Thus, all peracarid crustaceans perform brood care and tend their young in the ventilated marsupium. This, amongst other things, classifies them as predominantly K-strategists, limiting their range to reach new areas because of the lack of larval dispersal and thus making them a valuable group for examining biodiversity and distribution patterns across different spatial scales.

Isopods can be found in marine, freshwater and even terrestrial habitats. One species, *Hemilepistus reaumuri* (Audouin, 1826), even lives in the dry North of Africa in underground burrows (Linsenmair, 1979). Isopods range from a few millimeters in length (most species) to as much as 400 mm in the deep-sea species *Bathynomus giganteus* Milne Edwards, 1879 (Briones-Fourzán and Lozano-Alvarez, 1991; Kästner, 1993). Thus, isopods are morphologically highly variable and have adapted to a wide variety of different environmental conditions, such as deep-sea and polar environments.

Isopods are generally an abundant and diverse taxon of the marine benthos (Brandt et al., 2009; Hessler and Sanders, 1967; Sanders, 1968). In the deep sea, the asellotan superfamily

Janiroidea is particularly successful, often representing the majority of total isopod species and individuals (Birstein, 1963; Brandt et al., 2007a; Hessler and Sanders, 1967; Wilson, 1987). Janiroideans have been reported to occur on the abyssal plains and the deep-sea basins of many oceans, including the Southern Ocean (Brandt et al., 2004; Brandt et al., 2007b; Brandt et al., 2007c; Brökeland et al., 2007; Kaiser et al., 2009; Malyutina and Brandt, 2007), the Atlantic (Brandt et al., 2005; Brenke et al., 2005; Brix, 2007; Brix et al., 2014; Schnurr et al., 2014) and the Pacific Ocean (Birstein, 1963; Kussakin, 1971, 1972a, b, c, 2004; Malyutina, 2013; Malyutina, 2011; Malyutina et al., 2013; Zenkevitch, 1963).

The remarkable predominance and diversity of janiroideans in the deep sea has been partly attributed to their highly specialized and sexually dimorphic pleopods: gonopodia in males and opercula in females (Wägele, 1989). Within the Janiroidea, the family Munnopsidae is particularly species-rich and highly abundant in deep-sea samples with most species and individuals (>50%) belonging to this family (Malyutina and Brandt, 2007; Malyutina, 2011). This family has been described as being fully natatory (Wilson, 1989) which at least potentially makes them part of the suprabenthos in addition to being part of the epibenthos and expands their distribution ability (Schnurr et al., 2014).

Some families, like Paramunnidae (Shimomura, 2009) and Munnidae (Kussakin, 1972b; Wilson, 1980), are known as shallow-water families, while others, like Munnopsidae (Kussakin, 2003), Desmosomatidae or Macrostylidae (Kussakin, 1999) are known as ‘true’ deep-sea families and hypothetically have their origin there (Hessler and Thistle, 1975).

Isopoda have been reported to occur on the abyssal plains and the deep-sea basins of many oceans, including the Southern Ocean (Brandt et al., 2004; Brandt et al., 2007b; Brandt et al., 2007c; Brökeland et al., 2007; Kaiser et al., 2009; Malyutina and Brandt, 2007), the Atlantic (Brandt et al., 2005; Brenke et al., 2005; Brix, 2007; Brix et al., 2014; Schnurr et al., 2014) and the Pacific Ocean (Birstein, 1963; Kussakin, 1971, 1972a, b, c, 2004; Malyutina, 2013; Malyutina, 2011; Malyutina et al., 2013; Zenkevitch, 1963). Isopods are known to generally be an abundant taxon in the benthos (Brandt et al., 2009; Hessler and Sanders, 1967; Sanders, 1968). Isopoda have been chosen in this thesis as a model taxon due to their ubiquity, relative high abundances, their diversity and distribution in the deep sea. Their wide distribution and high abundance allow reliable comparisons between different areas (cp. Chapters 5 and 6).

Deep-sea biodiversity, distribution and biogeography

The term biodiversity refers to the variety of different life including genetic, species and ecosystem diversity. It can be assessed across a wide range of spatial and temporal scales, e.g. ranging from small areas in the Southern Ocean (Brandt et al., 2007a; Brökeland et al., 2007; Kaiser et al., 2009; Lörz and Brandt, 2003) to regional and global scales (Heywood, 1995; McCann, 2000; Menot et al., 2010; Rex et al., 1997; Tittensor et al., 2010). Sirenko (2013) provided a thorough overview of the fauna of the area from the Bering Sea in the North to the Sea of Japan in the South.

Taxonomic species descriptions are vital, as they provide the basic unit for both biodiversity and biogeographic studies. However, many deep-sea species are new to science and still need to be formally described (Brandt et al., 2005; Brandt et al., 2007a; Mora et al., 2011). It could be shown that these high rates of novelty greatly affect the evaluation biodiversity and distributions in the deep sea (for the Southern Ocean see Kaiser et al., 2013).

Originally, the deep sea had been hypothesized to be a hostile environment not capable of sustaining any organisms (Mills, 1983). However, the deep sea has been proven to be, on the contrary, very species-rich both locally and at larger spatial scales (Brandt et al., 2007b; Grassle and Maciolek, 1992; Hessler and Sanders, 1967; Ramirez-Llodra et al., 2010). Areas covered by soft sediment are generally species-rich but have a low abundance of individuals, while the opposite is the case for hard substrate like whale falls (Amon et al., 2013; Baco and Smith, 2003; Smith, 2006) or hot vent communities (Jollivet, 1996; Ramirez-Llodra et al., 2007). Both provide energy which otherwise is scarce in the deep sea. Following the diversity-stability hypothesis, a higher regional diversity results in a greater stability of food webs and community responses to changes in environmental factors and perturbations (Ives and Carpenter, 2007; McCann, 2000). Why are there so many species with arguably similar functions locally? Factors shaping diversity at local scales, e.g. isolation by distance, neutral processes, micro-habitat heterogeneity (whale falls, sediment differences, drop stones, bioturbation etc.) most likely positively influence the increase of diversity.

For abyssal depths, the source-sink hypothesis has been postulated (Rex and Etter, 2010; Rex et al., 2005). According to this hypothesis, abyssal depths may be suitable for adult individuals, but not for reproduction and are therefore only populated by constant dispersal and/or migration. For isopods, as an obligate brooding taxon, this scenario seems unlikely though; Breeding is known from deep-sea species (Elsner et al., 2013; Eustace et al., 2013;

Wilson, 1983). Kussakin (1973) considered, in retrospect in accordance with this hypothesis, the deep-sea isopods to be the younger group compared to shelf fauna. On the contrary, it has been argued that deep-sea isopods have developed *in situ* in the deep sea and thereafter emerged onto the shelf (Hessler and Wilson, 1983; Hessler et al., 1979). Another approach seems more complex and includes different scenarios for different taxa and widespread anoxia in different deep-sea areas (Wilson, 1999).

Biogeographic studies, in general, help to expand our knowledge and understanding of origin and evolution of deep-sea faunal assemblages and connectivity or lack thereof between different areas and regions (McClain and Hardy, 2010). With regard to conservational purposes so called biodiversity hotspots are of special interest. These are regions with a high amount of species endemic to a specific area (Myers et al., 2000; Nakajima et al., 2014). Politically, a classification of biodiversity hotspots and regions with fauna distinctly different from the fauna of other regions are important to ensure the possibility for an appropriate conservation management. Scientifically, such a classification is important in order to test hypotheses regarding, for example, the origin and evolution of deep-sea faunal assemblages and connectivity between and within deep-sea basins. In order to establish a consistent, reliable classification of biogeographic regions, the Global Open Oceans and Deep Seabed (GOODS) biogeographic classification was introduced (O'Boyle, 2010; Vierros et al., 2008).

Aims of the Study

The aim of this dissertation is to assess the biodiversity, distribution and biogeography of the fauna of the Sea of Japan and the abyssal area of the Kuril-Kamchatka Trench and the comparison of both areas.

Therefore, faunal assemblages were examined from the complementary Russian-German Sojabio and German-Russian KuramBio expeditions at different organizational levels, from phylum through class and order to species and population level, across different spatial scales (local to regional) and depth using taxonomic, ecological and biogeographical methods.

First of all, an overview on abundance and distribution patterns of macrobenthos at higher taxonomic level (phylum to class level) are given for the Sea of Japan (**Chapter 2**) and for the Kuril-Kamchatka Trench area (**Chapter 3**), providing important insights into the general community structure of the benthos composition. Subsequently, the taxonomic resolution increases and a detailed analysis of the peracarid community in the Sea of Japan is presented

in **Chapter 4**. In **Chapters 5** and **6**, species diversity of Isopoda of the Sea of Japan compared to the Kuril-Kamchatka Trench area is analyzed to further decipher variation in diversity and related historical factors and processes. **Chapter 7** and **8** focus on the population structure of three isopod species from the slope (**Chapter 8**) and abyss (**Chapter 7**) of the Sea of Japan, respectively, which greatly extends our knowledge and understanding of reproduction in the deep sea and which, in turn, are important as a baseline to evaluate biodiversity and distributional patterns. While in **Chapter 7** the endemic and highly abundant munnopsid species *Eurycope spinifrons* Gurjanova, 1933 is investigated; **Chapter 8** analyzes the population structure of two species of the genus *Pleurogonium* Sars, 1864 (Paramunnidae). **Chapter 9** represents the highest taxonomic resolution and contains one description and one redescription of Munnopsidae species from the Sea of Japan. The dissertation itself is concluded by a final comparison and conclusion (**Chapter 10**) of all previous chapters **Appendix I** presents a biogeographical study (work in progress) containing both areas.

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Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems

Chapter 2: Epifauna of the Sea of Japan collected via a new epibenthic sledge equipped with camera and environmental sensor systems

Angelika Brandt^a, **Nikolaus O. Elsner^a**, Nils Brenke^b, Olga A. Golovan^c, Marina V. Malyutina^c, Torben Riehl^a, Enrico Schwabe^d, Laura Würzberg^a

^a*Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany*

^b*German Centre for Marine Biodiversity Research, Südstrand 44, D-26382 Wilhelmshaven, Germany*

^c*A.V. Zhirmunsky Institute of Marine Biology, FEB RAS, Palchevskogo 17, 690041 Vladivostok, Russia*

^d*Zoological State Collection Munich, Münchhausenstr. 21, D-81247 Munich, Germany*

Abstract

Faunistic data from a newly designed camera-epibenthic sledge (C-EBS) are presented. These were collected during the joint Russian-German expedition SoJaBio (Sea of Japan Biodiversity Studies) on board the R.V. *Akademik M. A. Lavrentyev* from four transects (A–D) between 460 and 3660 m depth. In total, 244,531 macro- and megafaunal individuals were sampled with the classes Malacostraca (80,851 individuals), Polychaeta (36,253 ind.) and Ophiuroidea (34,004 ind.) being most abundant. Within the Malacostraca, Peracarida (75,716 ind.) were most abundant and within these, the Isopoda were the dominant taxon (27,931 ind.), followed by Amphipoda (21,403 ind.), Cumacea (13,971 ind.) and Tanaidacea (10,830 ind.). Mysida (1581 ind.) were least frequent. Bivalvia, Amphipoda, Cumacea and Mysida as well as inbenthic meiofaunal Nematoda occurred in higher numbers at the shallower stations and their numbers decreased with increasing depth. Polychaeta, Isopoda, and Tanaidacea, on the contrary, increased in abundance with increasing depth. Only one isopod species was sampled at abyssal depths in the Sea of Japan but at very high abundance: *Eurycope spinifrons* Gurjanova, 1933 (Asellota: Munnopsidae). Echinoderms occurred frequently at the shallower slope stations. Ophiuroids were dominating, followed by holothurians, and echinoids and asteroids which occurred in lower numbers and primarily at the shallower stations of transects A and B. Only 2163 individual anthozoans were recorded and these were

mostly confined to the lower slope. The technical design of a new C-EBS is described. Next to temperature-insulated epi- and suprabenthic samplers, it is equipped with still and video cameras, which deliver information on seabed topography and megafaunal occurrence. Furthermore, Aanderaa CTD and SEAGUARD RCM allow for collection of physical parameters, such as near bottom oxygen composition, temperature and conductivity.

Keywords: Sea of Japan, deep sea, biodiversity, epibenthic sledge, macrofaunal abundance

Introduction

The joint Russian/German expedition SoJaBio (Sea of Japan Biodiversity Studies) on board R.V. *Akademik M. A. Lavrentyev* was successfully carried out from 11 August to 5 September 2010. The project aimed to study the abundance, composition, biodiversity and ecology of the benthic organisms of all size classes. Collections were made along two transects of four stations from 500 m to a maximum depth of 3660 m (transects A and B) and two additional transects of only two stations at bathyal and abyssal depths from 2619 to 3435 m depth (areas C and D) in Russian territory of the Sea of Japan.

In the past, few expeditions to the Sea of Japan were performed and about 30 species of organisms were known from depths > 2000 m in this area (Derjugin, 1933, 1939; Golovan, 2007; Golovan and Maljutina, 2010; Gurjanova, 1936; Levenstein and Pasternak, 1976; Ushakov, 1952; Zenkevitch, 1963). The low degree (21%) of endemism of the deep-sea benthic organisms compared to other deep-sea basins (Brandt et al., 2005; Brandt et al., 2007a; Brandt et al., 2007b; Brandt et al., 2007c; Ramirez-Llodra et al., 2010) was explained by the relatively young age of the basin (Vinogradova and Filatova, 1983) which was formed in the Cenozoic and was anoxic in the last glacial period until around 8000 years ago. At present, the Sea of Japan is semi-isolated from the adjacent deep-sea areas of the Pacific Ocean by the archipelago of Japan. The Soja Strait connecting with the Okhotsk Sea in the north has a depth of only 53 m and the Tartarskiy Strait only 15 m. In the south, towards the East China Sea, the Tsushima Strait is 130 m, and towards the Pacific, the Tsugaru Strait is 130 m deep. The deepest basin is the Japan Basin, with depths of 3700 m (Talley et al., 2004). Surface waters are influenced by the Tsushima Current bringing warm water from the south. In the north, the water masses are significantly influenced by cold water inflow from the north (Liman Current), through the Tartarskiy Strait into the deep basin of the Sea of Japan. These

water masses are characterized by very low temperatures of $< 1^{\circ}\text{C}$, and accordingly, oxygen values from the surface down to the bottom are very high (saturation 80-100%) (Talley et al., 2006). This is the only place in the world to have such oceanographic features.

The Japan Sea is a unique marginal sea which can reproduce a “world ocean in miniature”. Such an effect is achieved due to the system of cold and warm currents (Talley et al., 2006) and its subtropical and subarctic areas which are separated by the subpolar front. All of these peculiarities allow researchers to observe climatic changes in the Japan Sea basin which are also applicable to the World Ocean but which occur over a more rapid time scale (Kapulenko, pers. comm.).

Tyler (2002) compiled characteristics of the Sea of Japan deep-sea fauna in a review of the ecology of deep-sea eukaryotes in the semi-isolated basins off Japan and also provides physical and geological background information of the area. Moreover, the Sea of Japan is characterized by high productivity and influence by anthropogenic impacts, especially in the vicinity of the Peter the Great Bay, the biggest bay in the sea. In order to obtain a high number of benthic macrofaunal animals, we deployed a C-EBS manufactured by Co. OKTOPUS (Kiel, Germany). This is 3.5 m long, 1.2 m high, and 1.8 m wide. The whole frame is constructed of stainless steel (DIN 1.4462). The nominal diving depth is 6000 m (600 b), weight 750 kg in air, serial no: 05/15-SN 001. The main purpose of the C-EBS is to collect macrofauna. Therefore, the present paper focusses on the description of the faunal composition and the newly designed sledge rather than a detailed analysis of the photographs or the environmental parameters.

As detailed sample sorting and species level identification is still ongoing. We focus on the abundance and higher taxon composition in order to document general macrofaunal patterns. We further describe the technical design and use of this upgraded C-EBS in the present paper.

Material and methods

Study area

The area is briefly described in the introduction of this paper. A more detailed description is presented in the introduction of (Malyutina and Brandt, 2013). Stations were sampled along four transects. Transect A is furthest away from Vladivostok (Fig. 2.1) and consists of four

stations covering 455–3357 m. Transect B consists of five stations between 470 and 3666 m. Transect C contains two stations between 2670 and 3435 m and transect D also consists of two stations between 2619 and 3357m. Georeferenced C-EBS stations are presented in Tab. 2.1 and Fig. 2.1.

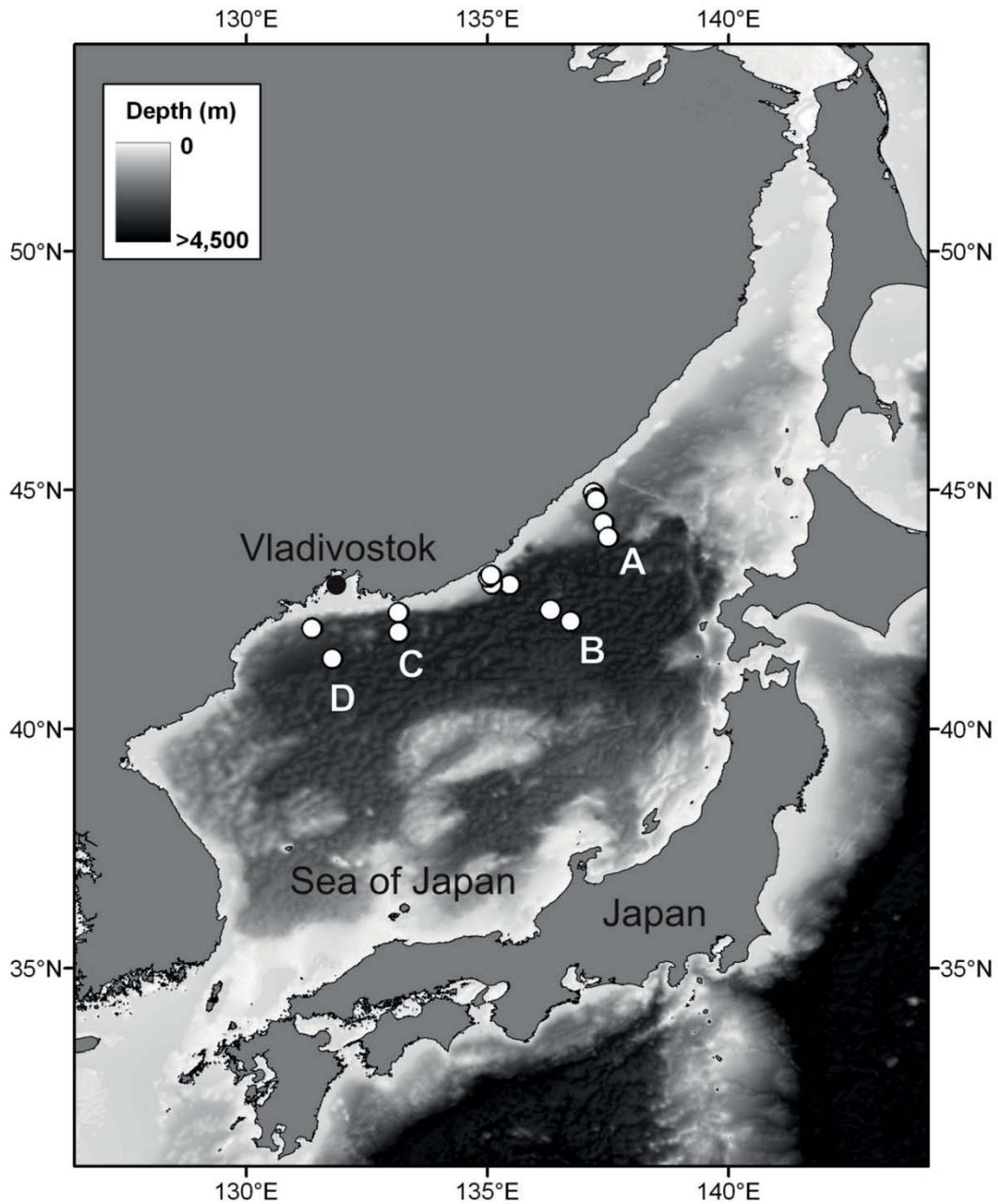


Fig. 2.1: C-EBS stations of transects A, B, C and D sampled in the Sea of Japan from board of the RV *Akademik M. A. Lavrentyev*.

Tab. 2.1: Station and environmental data from epibenthic sledge deployments. Abbreviations: 1C¹/temperature measured in Celsius; cm/s¹/centimeter per second; (kPa)¹/kilopascals; m¹/meter; (mS/cm)¹/milli-Siemens per cm; O₂ conc. dissolved oxygen concentration in mM/l—at standard barometric pressure (100 kPa). Abiotic parameters measured show the mean value and standard deviation of all measurements over the trawling period.

Station	Start–end of trawling	Depth (m)	O ₂ (μM)	Cond. (mS/cm)	Bottom current (cm/s)	Temp. (°C)
A2-10	44°56.9197N 137°11.8947E 44°57.0193N 137°11.9896E	455–465	259.4 ± 0.8	29.3 ± < 0.1	8.1 ± 2.8	0.8 ± < 0.1
A3-10	44°49.8620N 137°13.9974E 44°50.2803N 137°14.2177 E	1354–1356	226.4 ± 0.8	29.2 ± 0.1	4.2 ± 1.8	0.2 ± < 0.1
A3-11	44°47.6338N 137°15.3182E 44°48.1762N 137°15.3039 E	1494–1525	223.7 ± 1.0	29.3 ± 0.1	2.5 ± 0.9	0.2 ± < 0.1
A6-7	44°19.4270N 137°24.1964E 44°18.7422N 137°24.0524E	2511–2534	225.5 ± 0.6	29.7 ± 0.1	6.0 ± 2.5	0.2 ± < 0.1
A6-8	44°18.6270 N 137°24.4079E 44°18.3034N 137°24.0370E	2545–2555	225.0 ± 1.1	29.7 ± 0.1	3.6 ± 1.9	0.2 ± < 0.1
A7-8	44°00.8871N 137°29.7822E 44°00.7933N 137°30.2780E	3345–3357	223.9 ± 0.3	30.1 ± < 0.1	5.7 ± 0.7	0.3 ± < 0.1
A7-9	44°00.8871N 137°29.7822E 43°59.9124N 137°31.7745E	3340–3347	223.5 ± 0.4	30.1 ± 0.1	4.1 ± 0.9	0.3 ± < 0.1
B1-7	42°15.5533N 136°43.2772E 42°15.9748N 136°42.8880E	3665–3666	222.6 ± 0.2	30.2 ± < 0.1	8.4 ± 1.2	0.3 ± < 0.1
B4-7	43°01.5063N 135°26.4484E 43°00.9932N 135°26.1730E	3298–3353	225.0 ± 0.6	30.1 ± < 0.1	2.7 ± 0.8	0.3 ± < 0.1
B4-8	43°01.3440N 135°28.0092E 43°00.7508N 135°28.5344E	3312–3334	224.6 ± 1.1	30.1 ± < 0.1	2.2 ± 0.9	0.3 ± < 0.1
B5-7	43°01.6964N 135°05.2859E 43°01.7389N 135°05.9690E	2661–2688	226.1 ± 1.0	29.8 ± < 0.1	4.8 ± 1.5	0.2 ± < 0.1
B5-8	43°01.3064N 135°05.9562E 43°00.9363N 135°06.5366E	2609–2655	226.0 ± 1.3	29.8 ± 0.1	2.0 ± 1.0	0.2 ± < 0.1
B6-6	43°10.6362N 135°00.8476E 43°10.2744N 135°00.7990E	970–994	240.1 ± 0.3	29.2 ± < 0.1	4.6 ± 2.0	0.4 ± < 0.1
B6-7	43°10.3999N 135°00.9751E 43°10.1336N 135°00.8996E	1001–1011	239.0 ± 0.4	29.3 ± < 0.1	5.4 ± 1.2	0.4 ± < 0.1
B7-6	43°13.4229N 135°04.2286E 43°13.6089N 135°04.3934E	517–521	264.5 ± 2.2	29.3 ± < 0.1	n/a	0.7 ± < 0.1
B7-7	43°13.4578N 135°04.3295E 43°13.6318N 135°04.1490E	470–528	263.5 ± 1.2	29.3 ± < 0.1	n/a	0.7 ± < 0.1
C1-8	42°26.5832N 133°09.1471E 42°26.7298N 133°09.7430E	2670–2681	227.2 ± 1.3	29.8 ± < 0.1	2.6 ± 1.2	0.2 ± < 0.1
C1-9	42°26.4275N 133°08.6525E 42°26.5707N 133°E09.4842	2693–2725	227.2 ± 0.7	29.8 ± 0.1	2.0 ± 1.2	0.2 ± < 0.1
C3-3	42°01.3458N 133°09.7454E 42°01.0547N 133°09.9003E	3431–3435	223.5 ± 0.5	30.1 ± 0.1	1.7 ± 0.9	0.3 ± < 0.1
C3-4	42°01.5613N 133°09.5741E 42°01.4637EN 133°09.8288	3427–3431	223.6 ± 0.4	30.1 ± < 0.1	2.4 ± 1.6	0.3 ± < 0.1

D1-3	41°28.3497N 131°46.6929E 41°27.9058N 131°46.2575E	3355–3357	224.2 ± 0.9	30.1 ± < 0.1	2.4 ± 1.1	0.3 ± < 0.1
D1-4	41°28.7198N 131°46.7702E 41°28.3427N 131°46.5050E	3356	224.3 ± 1.1	30.1 ± < 0.1	3.1 ± 1.2	0.3 ± < 0.1
D2-7	42°07.1711N 131°21.1091E 42°06.8608N 131°20.9826E	2619–2637	227.9 ± 0.7	29.8 ± < 0.1	1.8 ± 0.9	0.2 ± < 0.1
D2-8	42°06.6051N 131°21.0149E 42°06.1140N 131°20.7726E	2653–2683	227.5 ± 0.7	29.8 ± 0.1	2.2 ± 1.1	0.2 ± < 0.1

Deployment of the C-EBS

A camera equipped epibenthic sledge (C-EBS) has been deployed successfully 24 times along four transects from 500 m to the abyssal depths in the north-western part of the Sea of Japan. The C-EBS was deployed similarly to the former EBS model (e.g. Brenke 2005) using 1.5 times the cable length to water depth. While the EBS is lowered with 0.5 m/s the vessel has to compensate the speed of the wire (for example, 0.5 m/s lowering = 1 knots ship speed over ground). When the cable length reaches 1.5 times the length of the water depth, hauling is done for 10 min. After 10 min the ship must stop at end of hauling and the winch starts to hoist the C-EBS at 0.5 m/s while the vessel remains on position until the C-EBS is back on deck of the research vessel. The haul distances would usually be calculated for the comparative abundance analysis on standardized 1000 m length hauls. However, in the present paper we could not standardize the data because ship-board data (especially of the winch but also the ship's speed) to calculate haul length were not reliable on R.V. *Akademik M. A. Lavrentyev*. The main purpose of the C-EBS is to collect macrofauna. The environmental parameters obtained will help to analyze faunistic composition on the background of abiotic factors. The video images shall help to understand how the C-EBS samples and moves on the ground, and the still camera provides information on bottom topography and megafaunal densities.

Sample treatment

On deck, the complete samples (except freshly picked material for biochemical analyses) were immediately transferred into precooled 96% ethanol and kept for at least 48 h in a -20°C freezer for DNA studies.

Technical description of C-EBS

Mechanic construction

The mechanic construction of the C-EBS (constructed in the framework of the Clisap (Integrated Climate Analysis and Prediction) excellence cluster in Hamburg in 2010) is based on the sledge frame originally designed by Rothlisberg and Percy (1976) (RP 77-EBS), modified by Brattegard and Fosså (1991) (BF91-EBS), extended by Brandt and Barthel (1995) and later rebuilt by Brenke (2005). For all these sledges it is common that the frame is the carrier for the catching device: the opening-closing mechanism and one net (RP77-EBS; BF91-EBS) or two nets (Brandt and Barthel 95-EBS, Brenke 05-EBS).

The C-EBS is containing cameras and environmental sensors. It was manufactured by Co. OKTOPUS (Kiel, Germany) and its frame is 3.5 m long, 1.2 m high and 1.8 m wide. It is equipped with supra- and epibenthic samplers possessing two plankton nets (500 mm) on top of each other leading to two cod ends (300 mm) in temperature-isolated thermo boxes. The height and length dimensions of the frame, the samplers and technical specifications of this central section are identical to the Brenke 05-EBS (Brenke, 2005). The C-EBS is characterized by a widened frame with lateral extensions carrying the holders for underwater photo- and video devices, auxiliary equipment, Recorder Doppler Meter (RDM) and CTD. Consequently, the C-EBS is 0.7 m broader than the preceding models. All electronic parts, digital underwater video camcorder, two spotlights, still camera, flashlight, control unit, rechargeable battery pack, RDM and CTD, were installed in the frame on both sides of the sledge (Figs. 2.2 and 2.3). The entire system has a nominal diving depth of 6000 m (600 bar).

C-EBS camera systems

For visual observation of the seafloor in front of the C-EBS, the sledge is equipped with a video camcorder and a digital still-camera (Figs. 2.2–2.4).

The underwater HD video camcorder (Sony HDR SR11E/SR12E) is installed in stainless steel (DIN 1.4462) pressure housing (30 kg i.a.) on the left side of the sledge, 0.6–0.8 m above the sediment surface (Figs. 2.2A and 2.3). The observed area is trapezoidal, approximately 2 m wide and in front of the sledge. The camcorder and the two spotlights (left and right side in

the frame: OKTOPUS HID 50; 60W/2.6A; housing DIN 1.4462; 16 kg i.a.) are connected to the control unit via SUBCONN plugs (BH 2 and 4 FTI/BH 8 MTI). For the HD-video footage, the camcorder features a 120 GB internal hard drive. This allows an operating time of approx. 14 h. Simultaneously, the camcorder records pictures (10 megapixels) at 20 s intervals on a memory card to be downloaded.

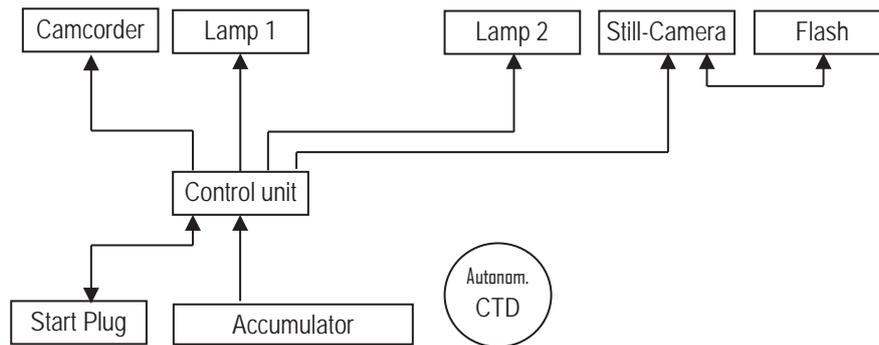


Fig. 2.2: Overview diagram of the electronic connections of the photo- and video devices and the auxiliary equipment in the C-EBS.

The underwater digital stills camera (KONGSBERG oe14-208/ Canon G5) is installed in a titanium (6AL/4V ASTM 834G) pressure housing (11 kg i.a.) on the right side of the sledge 0.6–0.8 m above the sediment surface (Figs. 2.2–2.4). The still camera is connected to a flashlight mounted below the camera (KONGSBERG oe11-242; 80W/max 1.5A; housing titanium; 4 kg i.a.) via BURTON plugs (8pin 5506-1508/1608) and to the control unit via BURTONSUBCONN plugs (BH 8 FTI). The observed area is trapezoidal, approximately 2 m x 10 m. In the current configuration, the camera is able to record 1560 pictures (2592 x 1944 pix) on an internal memory card, with a minimum time interval of 20 s. This allows an operating time of approximately 8.6 h.

The control unit is located on the left-hand side in the frame behind the camcorder, protected by titanium (grade 5) pressure housing (11 kg i.a.; supply voltage: 2 x 24 DCV). It is connected to the video camcorder, two spotlights, stills camera and the accumulator via nine SUBCONN plugs (BH 2 and 4 FTI/BH 6 MTI/BH 8 MTI) (Fig. 2.3). The camcorder and the digital stills camera are triggered by the control unit. Shortly before the deployment of the C-EBS, the prepared and assembled camcorder, camera and flashlight need to be mounted and connected. Afterwards, the delay time (e.g. the time the sledge needs to reach the ground/start), the time frame length (trawl time/stop, end of trawl), the time intervals for the

digital stills camera and the camcorder stills pictures have to be programmed. The control unit of the C-EBS is in standby until triggered by a start-plug.

The entire system is powered by an oil-embedded deep-sea battery (EA-BC 500, 600 bar) which provides 2 x 24 V with 28 Ah (or 2 x 14 Ah). This allows an operating time of approx. 10 h. After each deployment, both cameras have to be removed from the C-EBS and partially disassembled in order to download the digital material.

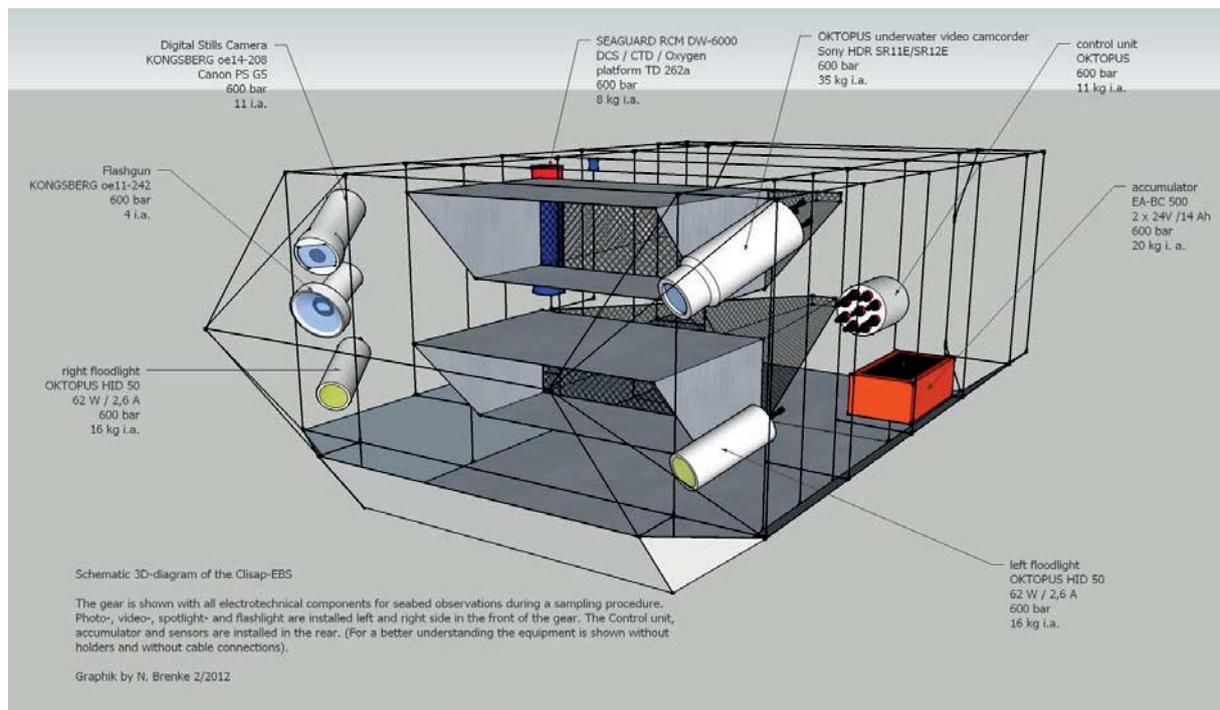


Fig. 2.3: Technical design of C-EBS. Illustration of the camera and sensor systems positioning on C-EBS frame.

Environmental sensors

In addition to the visual observation of the seafloor, the C-EBS is equipped with an autonomous multi-sensor (SEAGUARD RCM DW SN 102; 13 kg i.a.). The SEAGUARD RCM (Recording Current Meter) is equipped with a standard multi-frequency Doppler Current Sensor (DCS; AADI 4420/4520) for measurements of current speed and direction. Optionally, this SEAGUARD RCM is equipped with an Aanderaa CTD which consists of a conductivity cell (AADI4319A), temperature sensor (AADI 4060B) and a pressure sensor (AADI 4117F). Furthermore, this SEAGUARD RCM includes an oxygen optode (AADI

4330) for measurements of dissolved oxygen. The SEAGUARD RCM handles all data on an internal computer platform (TD262a) and saves the data on an internal SD memory card (512 MB). After each deployment, the SEAGUARD RCM has to be removed from the C-EBS and the oceanographic data must be downloaded in the laboratory. The SD card has to be removed from the device and the data imported into the PC using the provided program SEAGUARD Studio.

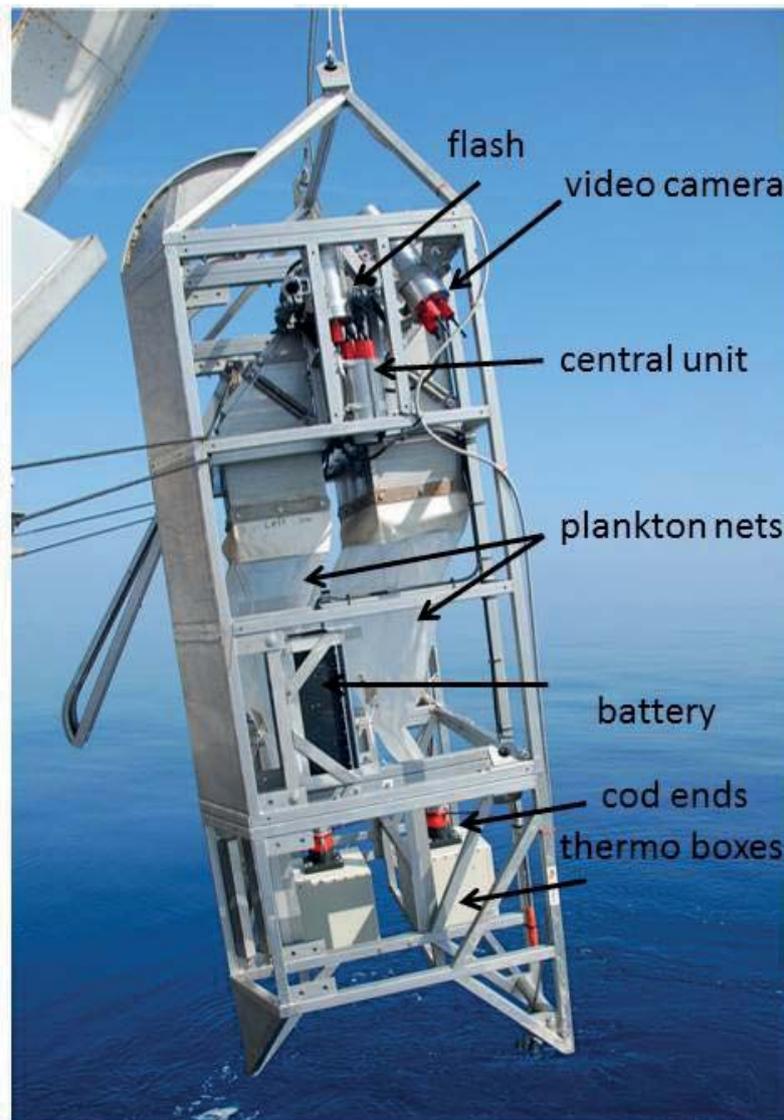


Fig. 2.4: Photograph of C-EBS.

Results

C-EBS

The georeferenced locations of the sampling stations and their physical parameters measured by SEAGUARD RCM and CTD at seafloor depths are presented in Tab. 2.1. Fig. 2.5 illustrates bottom topography and megafaunal taxa through underwater images of transects A and B and the abyssal stations of C and D. Megafauna was not observed at bathyal and abyssal depths (Fig. 2.5), but occurs in almost all images around 500 m depth at transects A and B. Between 1,000 and 1,500 m many images showed little mounds, while lower bathyal and abyssal stations were characterized by a more even bottom topography, and several images of the deepest stations of all four transects documented sea grass (Fig. 2.5). The CTD and camera collected data and images flawlessly during every deployment; only the video camera had some problems with recording. However, it filmed 45.8% of the time, and due to the sampling of two replicates per station (with the exception of two stations) we obtained footage from 84.6% of the stations. Thus, we received valuable information on the seafloor and the behavior of the sledge at the bottom. For example, we could see that the sledge always reached the ground upside-up and never upside-down, probably due to the heavy weights fixed to the frame at the bottom. The sledge once reached the ground standing on the back frame. However, as soon as hauling started, it was pulled straight down on its bottom side and started trawling properly. The still and video cameras also documented that the sledge remained still on the ground for some time before trawling, due to the fact that the wire, which was laid out in front of the sledge, had to be pulled straight before the sledge started to move. A cloud of sediment, caused by the landing of the C-EBS, was frequently visible on photo and video footage. The SEAGUARD RCM helped to derive the exact time the sledge was trawled on the sea floor (pressure values, time and speed at the bottom). Oxygen concentration was highest at the shallowest stations (259–265 μM) and relatively similar at the deepest stations (223 μM). Temperature was highest at the shallowest stations (0.8° C at station A2 - 10) and ranged between 0.2–0.3 °C at abyssal depths. Current speed was highest at the shallow sites (e.g. 8 cm/s at station A2-10, ranging between 2–3 cm/s at the deepest stations, except for station B1-7 in 3666 m, where a higher current velocity was measured (8.4 cm/s) (Tab. 2.1).

Faunistic composition

The number of individuals per taxon sampled as well as the mean depth (depth ranges of stations is provided in Tab. 2.1) and the number of taxa (richness) of the different stations respectively is documented in Tab. 2.2. In total, 244,531 macro- and megafaunal individuals were sampled, sorted and distributed to specialists for further identification. In the samples the classes Malacostraca (80,851 individuals), Polychaeta (36,253 ind.) and Ophiuroidea (34,004 ind.) occurred most frequently. Malacostraca were almost completely represented by the superorder Peracarida (75,716 ind.). Within the Peracarida, Isopoda were dominant in terms of abundance (27,931 ind.), followed by Amphipoda (21,403 ind.), Cumacea (13,971 ind.) and Tanaidacea (10,830 ind.), as well as Mysidacea (1,581 ind.). Stations A2-10 (460 m) and B7-7 (500 m) are characterized by the highest abundance of macro- and megafaunal taxa followed by stations B7-6 (520 m), C3-3 (3,430 m) and D2-7 (2,630 m) (Fig. 2.6 B). Bivalvia, Amphipoda, Cumacea and Mysidacea as well as inbenthic meiofaunal Nematoda occurred in higher numbers at the shallower stations of the transects A and B and their numbers decreased with increasing depth. Polychaeta, Isopoda, and Tanaidacea increased in abundance with increasing depth (Tab. 2.2 and Fig. 2.6) at transects A and B but also occurred in high numbers at stations of the deep transects C and especially D. At the deepest stations of all transects, polychaetes and isopods were dominant. Amphipods were more abundant at the shallower slope stations and their abundance decreased with increasing depth. Echinoderms also occurred more frequently at the shallower slope stations. Among them ophiuroids were dominant, followed by holothurians, echinoids and asteroids which occurred in lower numbers. Anthozoa were in low abundance with 2,163 individuals and were mostly confined to the lower slope around 2,500 m depth. Within the Mollusca, where 11,827 individuals were sampled, Bivalvia (8,769) dominated over Gastropoda (2,618). With regard to the bathymetric distribution, Mollusca were most abundant at the shallowest stations, with the exception of gastropods which also occurred in high numbers at station C3 (3,430 m depth). Euphausiacean crustaceans totalled 4,974 individuals and were most abundant at the shallowest stations: A2 (460 m), B7 (520 m) and B7 (500 m) (Tab. 2.2; Figs. 2.6 A, B). A correlation between faunistic abundance or composition and abiotic factors was not found.

The most abundant higher taxon, Peracarida, was analyzed in more detail (Golovan et al., 2013) (Chapter 4). Peracarid taxon composition varied between the different transects (Figs. 2.7 A, B). Amphipoda were most frequent at transects A and B, comprising 34 and 30% of the

peracarid fauna. At transect D they represented about 21% of all peracarids, at transect C they were rare with only 5%. Cumacea were most dominant in transect A (31% of all peracarids in that transect), followed by transect B (12%) and D (3%); in transect C they were almost absent. Isopoda occurred in all transects A-D (23%, 40%, 84%, 37%), but dominated lower bathyal and abyssal depths where *Eurycope spinifrons* Gurjanova, 1933 (Munnopsidae) occurred in high numbers. Most of the Isopoda belonged to the Asellota, and the families Munnopsidae and Desmosomatidae were most frequent. However Munnidae, Paramunnidae, and the flabelliferan family Bopyridae also occurred in these samples. Tanaids dominated transect D (39%), especially station D2-7 at 2,569 m with 2,262 individuals, and also occurred in transects A-C (11%, 14%, 11%). Mysids were most frequent in transect B with 4% of the fauna. In transect A they only occurred at 1% and in C and D they were rare or absent (Figs. 2.7 A, B).

Tab. 2.2: Abundances and taxon richness of benthic fauna in Sea of Japan.

Phylum/ Class/Order	A2-10	A3-10	A3-11	A6-7	A6-8	A7-8	A7-9	B1-7	B4-7	B4-8	B5-7	B5-8	B6-6	B6-7	B7-6	B7-7	C1-8	C1-9	C3-3	C3-4	D1-4	D1-7	D2-7	D2-8	Total
Cnidaria																									
Hydrozoa	11	91	0	2	2	0	0	0	1	0	0	0	3	0	3	10	2	0	0	0	0	0	7	3	135
Anthozoa	2	6	1	85	210	197	42	0	63	177	10	521	0	0	1	2	50	459	12	17	0	5	41	262	2163
Ctenophora	25	1	0	0	0	0	0	0	0	0	0	0	7	6	357	417	0	0	0	0	0	0	0	0	813
Plathelminthes	0	36	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	261	0	297
Nemertea	13	1	5	0	1	0	0	0	0	0	0	11	0	0	0	38	54	87	0	0	0	0	32	0	242
Nematoda	997	616	28	9	6	3	0	5	42	0	134	37	132	2	2064	4208	55	34	231	0	16	0	626	39	9284
Priapulida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	59	0	0	0	0	0	0	0	0	59
Mollusca																									
Aplacophora	6	5	0	0	0	0	0	0	0	0	1	0	1	2	19	45	63	0	0	0	200	0	0	0	342
Bivalvia	820	230	518	37	16	18	5	0	23	9	54	134	617	1709	1198	898	770	642	12	10	0	0	970	79	8769
Gastropoda	488	81	189	125	28	14	1	3	10	0	8	6	180	461	317	454	11	0	282	0	0	0	9	0	2667
Scaphopoda	14	19	0	0	0	8	0	0	0	0	0	0	0	0	29	28	0	0	0	0	0	0	0	0	98
Cephalopoda	1	0	0	0	0	0	0	0	0	0	0	0	1	2	0	1	0	0	0	0	0	0	0	0	5
Annelida																									
Polychaeta	1683	1119	654	285	289	1628	969	880	2706	621	486	1024	178	244	1895	7040	1354	1238	6397	841	1265	36	2820	601	36,253
Oligochaeta	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	3
Hirudinea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	0	0	0	0	0	0	0	0	10
Sipuncula	193	15	0	5	0	45	0	0	0	0	0	3	8	1	86	19	34	0	69	0	0	0	588	0	1066
Arthropoda																									
Ostracoda	4319	58	11	0	1	3	3	0	1	0	3	0	599	284	799	1805	7	1	1	0	0	4	66	2	7967
Maxillopoda																									
s/cl Copepoda	20,427	971	37	3	16	25	8	11	18	2	36	0	800	266	3872	24,973	21	0	26	8	80	2	483	2	52,087
Malacostraca																									
Leptostraca	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Amphipoda	10,474	439	447	177	205	10	3	12	5	3	259	407	766	478	1828	4085	235	138	12	0	0	0	1259	161	21,403

<i>Isopoda</i>	4170	140	51	69	399	2409	829	1903	2757	2789	202	881	163	103	183	1598	1118	725	3214	1754	1034	4	1334	102	27,931	
<i>Tanaidacea</i>	3204	104	46	2	18	301	33	0	155	290	36	16	237	100	704	2099	235	241	265	160	52	2	2262	268	10,830	
<i>Gamacea</i>	10,178	232	96	60	116	0	0	0	0	0	21	32	239	169	416	2152	18	12	1	0	0	0	0	219	10	13,971
<i>Mysidacea</i>	371	5	9	9	16	0	0	0	0	1	0	1	87	100	430	546	3	0	0	0	0	0	3	0	1581	
<i>Euphausiacea</i>	1614	27	20	0	0	0	0	0	0	0	1	0	3	2	2028	1278	0	0	0	0	0	0	1	0	4974	
<i>Decapoda</i>	78	6	0	0	0	0	0	0	0	0	0	0	33	19	5	20	0	0	0	0	0	0	0	0	161	
Pycnogonida	6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	
Arachnida																										
s/cl Acari	3	0	0	0	0	0	0	0	0	0	0	0	0	0	16	26	0	0	0	0	0	0	0	0	45	
Bryozoa	4	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	7	
Echinodermata																										
Crinoidea	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	20	
Asteroidea	31	3	39	0	0	0	0	0	0	0	0	0	1	76	5	41	0	0	0	0	0	0	0	0	196	
Echinoidea	16	114	20	0	0	0	0	0	4	0	0	0	81	0	25	49	0	0	0	0	0	0	0	0	309	
Holothuroidea	0	41	7	187	220	0	0	0	166	0	311	0	27	0	4	1	258	0	0	0	114	0	1223	0	2559	
Ophiuroidea	9644	1209	1046	774	1415	18	6	0	12	3	57	143	2697	1062	1945	12,916	491	166	1	0	0	0	367	32	34,004	
Chaetognathia	620	4	0	1	0	27	0	0	0	0	0	0	5	1	567	579	0	0	0	0	0	0	7	0	1811	
Chordata																										
Ascidiacea	0	6	0	2	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	12	
Appendicularia	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	21	0	0	0	0	0	0	0	0	21	
Unidentified	141	30	46	21	175	15	121	231	603	42	0	0	168	152	55	235	54	234	9	33	0	3	0	54	2422	
N individuals	69,560	5610	3270	1853	3136	4721	2020	3045	6566	3937	1619	3217	7033	5239	18,853	65,670	4833	3977	1055	2823	2762	56	1265	1615	244,525	
N taxa	31	28	18	17	17	14	10	6	14	9	15	14	23	20	26	32	18	11	13	6	8	6	20	12	37	
Mean	depth	460	1350	1510	2520	2550	3350	3340	3660	3330	3320	2670	2630	980	1000	520	500	2670	2710	3430	3430	3350	3350	2630	2670	

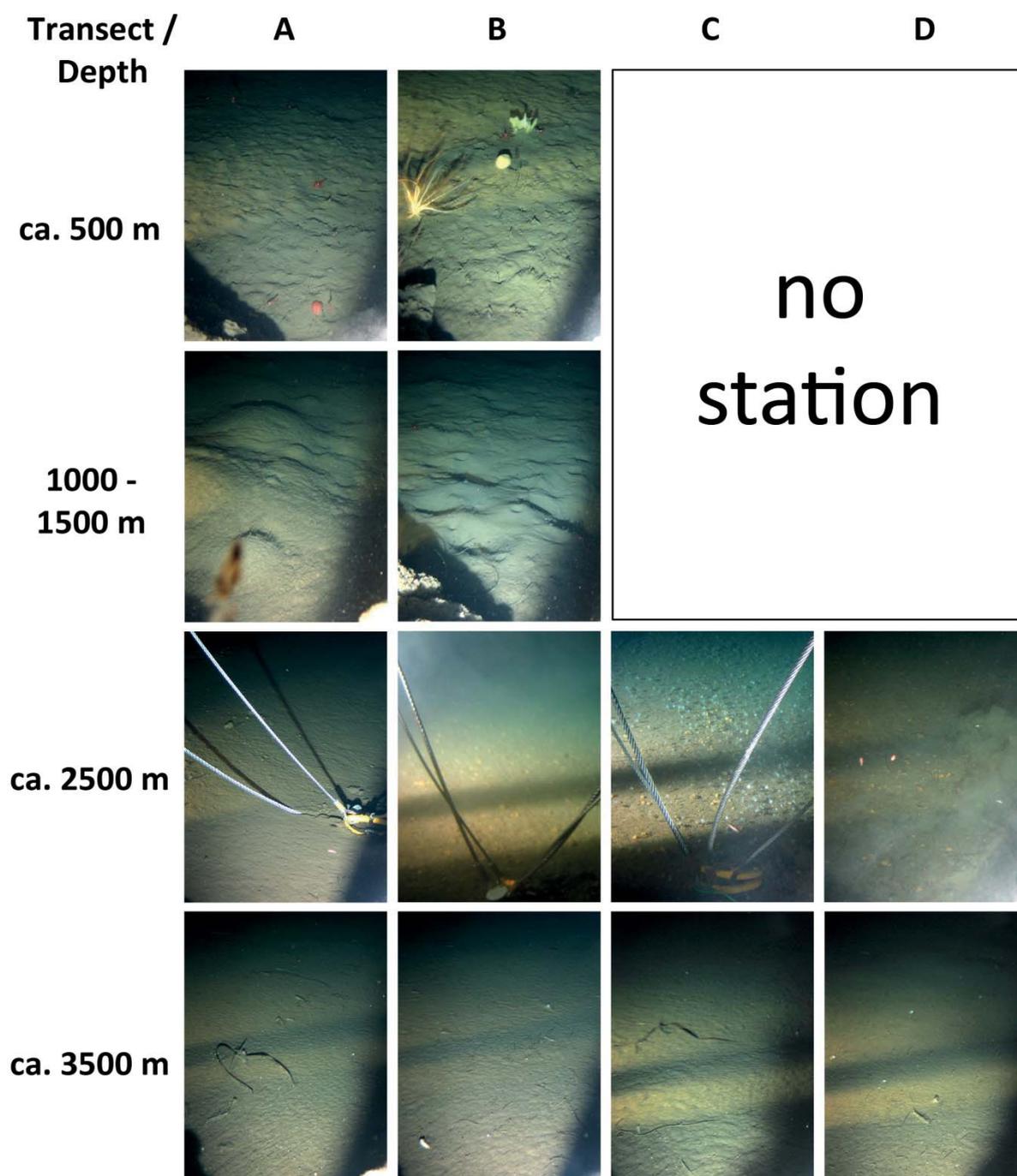


Fig. 2.5: Seafloor images per depth level at transects A–D in the Sea of Japan.

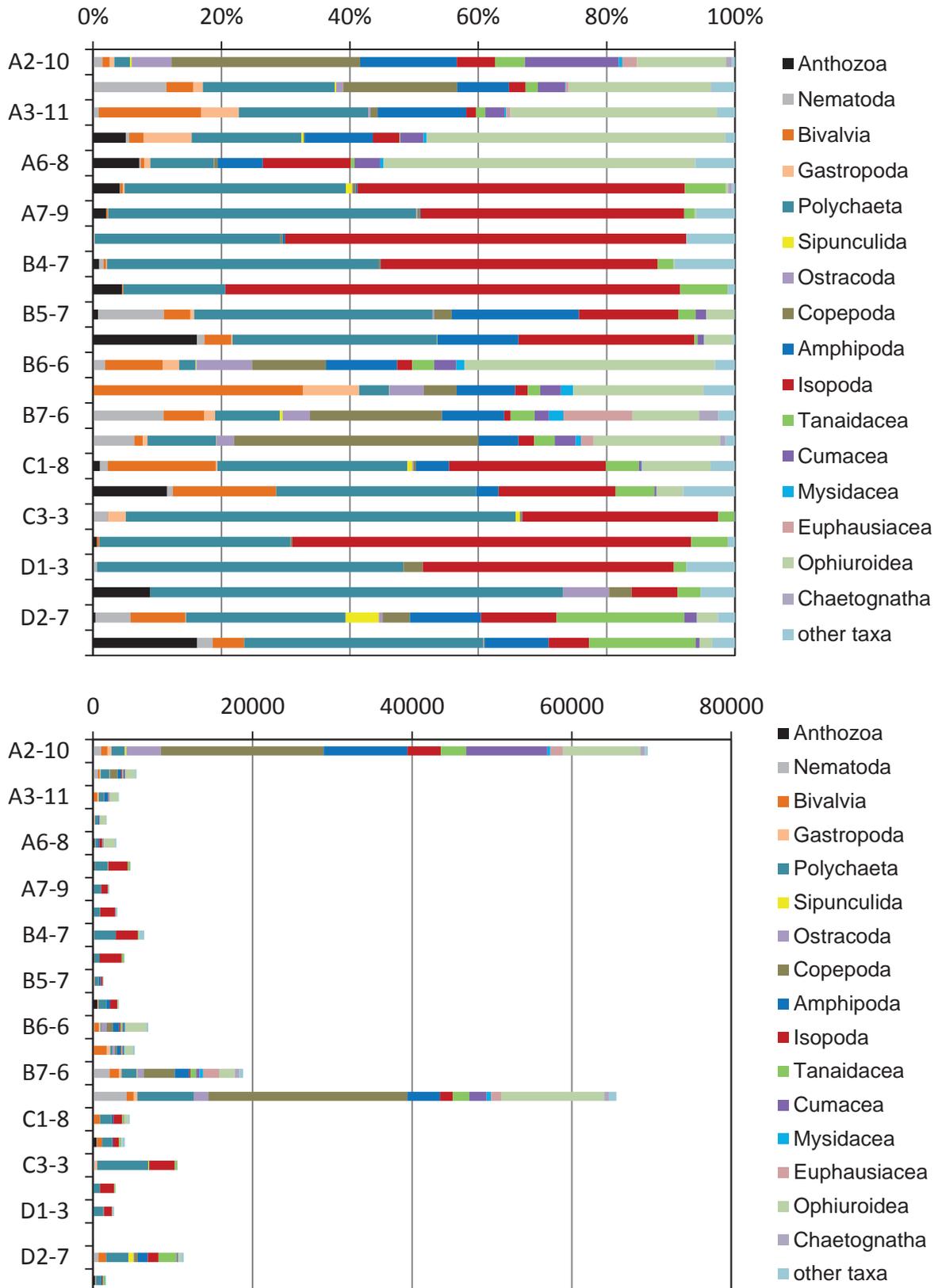


Fig. 2.6: Assemblage composition of higher taxa in Sea of Japan C-EBS samples sorted by transects and depth. Only those taxa are included which occur with more than 500 specimens in all samples. All others were pooled in “other taxa”. Stations are sorted by transects and within transects by depth from shallower to deeper stations: (A) relative numbers of taxa; (B) absolute numbers of taxa per C-EBS haul.

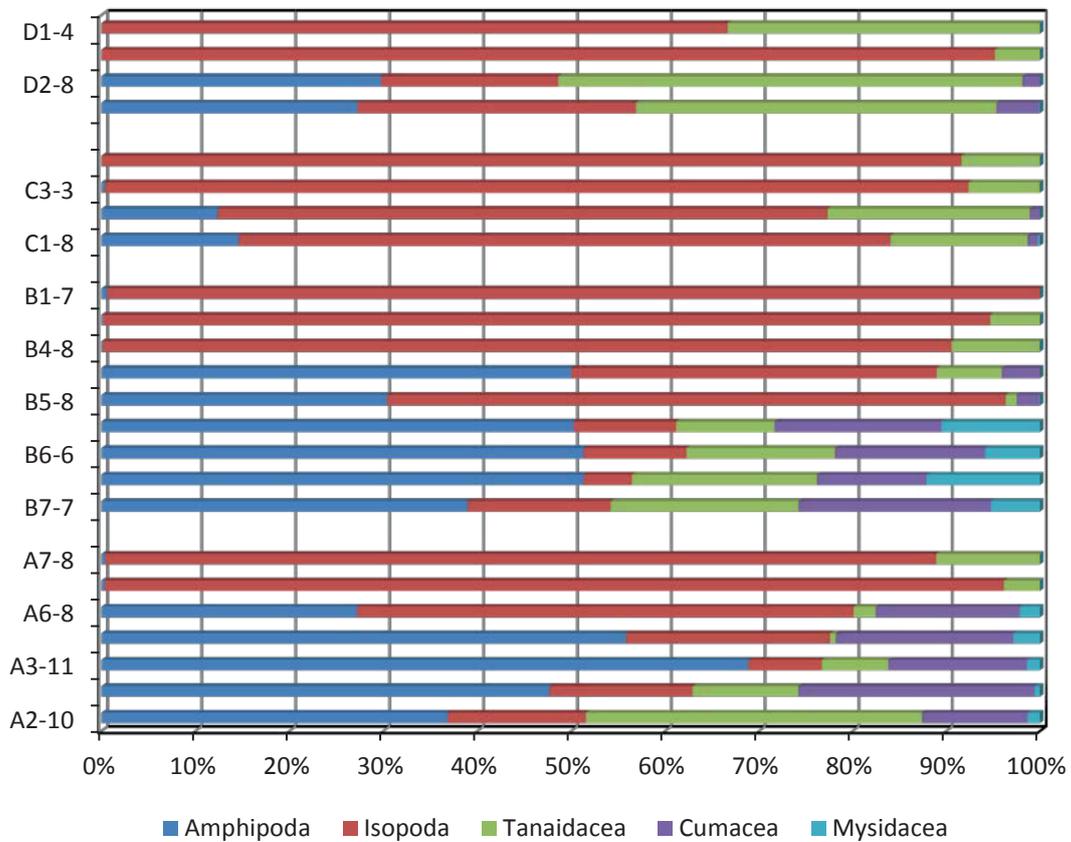
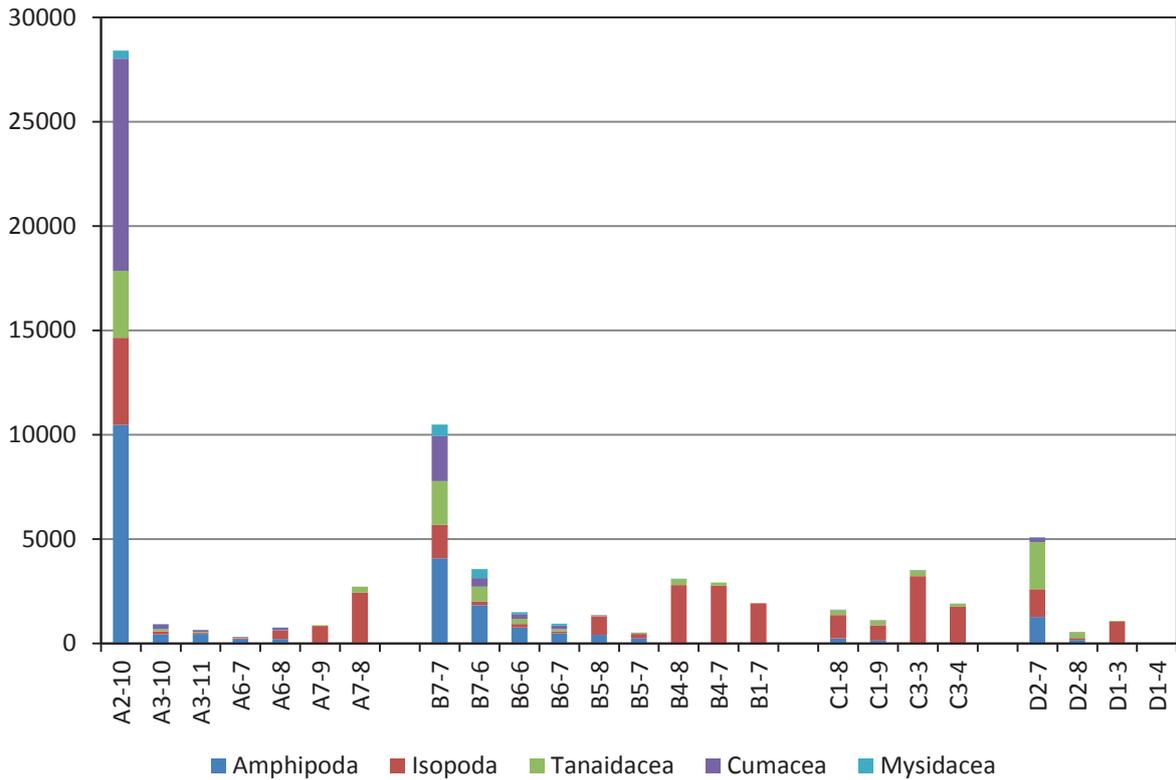


Fig. 2.7: Assemblage composition of peracarid taxa in Sea of Japan C-EBS samples sorted by transects and depth: (A) absolute numbers of taxa and (B) relative numbers of taxa per C-EBS haul.

In general, within Peracarida, Cumacea and Amphipoda were most abundant at the shallower stations, whereas Isopoda were more numerous at deeper abyssal sites. Polychaeta are more evenly distributed with depth and occurred at all depths. Bivalvia dominated over Gastropoda and occurred in high numbers especially at the shallower deep-sea stations. Ophiuroidea were the dominant echinoderm taxon followed by Holothuroidea and Echinoidea.

Discussion

C-EBS

Since 1995 the epibenthic sledge design with an epi- and suprabenthic sampler has successfully collected macro- and megafauna from the shallow shelf (200 m) to the hadal deep sea (6,300 m) (e.g. Brandt and Barthel, 1995, Brenke, 2005, Brandt et al., 2007a). The idea behind the newly designed, upgraded C-EBS was to obtain additional oceanographic data as well as visual data during the sampling process. These supplementary data enable analysis of the sampling process. It provides a better understanding of life at the seafloor by showing the organisms in their natural conditions. The main purpose of this type of EBS is to catch animals dwelling on the seafloor and in the near-bottom nepheloid layer just above. It is one of the most effective gears for sampling macrofauna in high numbers and qualitatively well-preserved for any systematic, phylogenetic or ecological investigation (Brenke, 2005). The camera systems on the C-EBS help to improve our understanding of the behaviour and sampling efficiency of the EBS on the ground, and to analyze the seafloor morphology and sedimentology at the same time while trawling and catching animals. This new C-EBS now enables us to obtain additional data on current speed and direction, temperature, pressure, conductivity and oxygen concentration as well as the time spent on the ground.

In terms of relative sampling efficiency, the C-EBS is comparable to the former EBS types and constructions. It has the same frame construction, measurements of the sampler openings, height above the ground, and net characteristics as the epibenthic sledges described by Brandt and Barthel (1995) and Brenke (2005). The frame, however, that Brenke (2005) constructed and described was more solid than that of Brandt and Barthel (1995) and allowed better protection for the nets and cod ends, in case the sledge went to the bottom upside down. The new construction described in the present paper also contains this solid frame around the sampling nets, but additionally, this frame is laterally extended in order to provide space for

the electronic systems (Fig. 2.2). The consequences of the lateral extensions and camera equipment for dynamic pressures developing in front of the net openings are currently unknown but may slightly influence the performance. The light of the EBS attracts vagile fauna such as amphipods, decapods or euphausiids, as can be seen when the sledge sits on the ground waiting for trawling. However, due to the trawling speed of 1 knot, we regard a systematic bias caused by the light attraction unlikely. Given the great numbers of individuals and the general composition of taxa collected, we think that the material collected with the new C-EBS is comparable to that of previous studies which applied the Brandt and Barthel 95-EBS or Brenke 05-EBS (Brandt and Barthel, 1995; Brandt et al., 2005; Brandt et al., 2007a; Brandt et al., 2007b; Brandt et al., 2007c).

In a comparison of the SEAGUARD RCM data with data from a CTD-profiler SBE-911 (Sea Bird Electronics) (Kaplunenko, personal communication), a slight deviation became apparent in the conductivity data. This was probably caused by the steel frame of the epibenthic sledge. SBE-911 data are presented in Tab. 2.1 of this volume only. The deviation of the conductivity data from Kapulenko et al. (2013) is 0.2 mS/cm.

Faunistic composition

The C-EBS collected a quarter of a million marine organisms during the SoJaBio expedition. Although the sledge is constructed to sample macrofauna, it always contained additional elements of the meiofauna (e.g. foraminiferans, copepods, nematodes) as well as the megafauna (e.g. anthozoans and echinoderms). No correlation of abiotic factors with the presence or absence of organisms could be observed.

Megafauna was only visible on photographs of the shallowest stations of transects A and B, but at the deepest stations sea-grass debris occurred on several images. With regard to the general composition and bathymetric distribution of the fauna, it is interesting to note that the anthozoans were sampled more frequently at the lower slope stations than at shallower slope sites where we would have expected them due to a generally higher food availability (sedimentation of organic matter) (e.g. Rodriguez et al., 2007). A potential reason for this could be the high competition of anthozoans with bivalves and especially ophiuroids for food at the shallower stations, but more detailed studies are needed to address this topic.

Although the taxonomic work with the SoJaBio collections is not finished yet, some interesting conclusions can already be made. Thus, at the generic level some similarities with the faunas of the adjacent open, non-isolated deep-sea areas were observed. Species composition, abundance and diversity of epi- and endofaunal macrobenthos will be compared in future with the biodiversity of an open, non-isolated deep-sea area of the Pacific (close to the Kurile Kamchatka Trench) and with other existing deep-sea data from the Atlantic and Pacific Oceans obtained in the framework of the Census of the Diversity of Abyssal Marine Life (CeDAMar) project (www.cedamar.org). The fauna found in the adjacent Kurile-Kamchatka Trench has been described in many publications, for example data on 660 species covering foraminiferans (Saidova, 1970), poriferans (Koltun, 1970), siphonophores (Stepanjants, 1970), pennatularians (Pasternak, 1970), polychaetes (Ushakov, 1972, 1982), molluscs (Filatova, 1971; Lus, 1971), pantopods (Turpaeva, 1971), cirripeds (Zevina, 1970), isopods (Birstein, 1963, 1970, 1971; Kussakin, 1971), amphipods (Birstein and Vinogradov, 1970; Vinogradov, 1970), tanaids (Kudinova-Pasternak, 1970), mysids (Birstein and Tchindonova, 1970), decapods (Birstein and Zarenkov, 1970), ophiuroids (Litvinova, 1971), holothurians (Belyaev, 1970, 1983, 1989), ascidians (Vinogradov, 1970) were published by P.P. Shirshov Institute of Oceanology. However, only common deep-sea genera, not species, have been reported from the Sea of Japan. For Isopoda further extensive publications were published from the Kurile Kamchatka area (Kussakin, 1972a, b, c, 1978, 1979, 1988, 1999, 2004; Kussakin and Mezhov, 1979; Kussakin and Vasina, 1990). However, few isopod species have also been reported from the Sea of Japan, namely *Bopyroides hippolytes* (Krøyer, 1838), *Ilyarachna zachsi* Gurjanova, 1933 (Golovan and Malyutina, 2010). Ophiuroids of the genus *Amphiophiura* include several ultraabyssal species from the Kurile-Kamchatka Trench. Two species previously known from the northwestern Pacific off the Kurile Islands are recorded from the Sea of Japan; the shallow-water species *Amphiophiura oedioplax* (H.L. Clark, 1911) and the upper bathyal species *A. megapoma* (H.L. Clark, 1911) (Litvinova, 1971). Polychaetes (Alalykina, 2013) of the genus *Lacydonia* are found for the first time in the Sea of Japan at depths ~500-1,500 m. *Lacydonia papillata* Ushakov, 1958 previously was reported from the Kurile-Kamchatka Trench at a depth of 5,070 m (Ushakov, 1972). The widespread arctic-boreal species *Macellicephalo violacea* (Levinsen, 1887) is known from depths between 46 to 8,400 m and reported from the Kuril-Kamchatka and Aleutian Trenches (Ushakov, 1982). It is recorded for the first time in the Sea of Japan at a depth of ~500 m. The genus *Sosane*, known from the northwestern Pacific (Jirkov, 1994) is also reported for the Sea of Japan for the first time. *Eulalia sigeiformis* Annenkova, 1937,

sampled at 445 m depth of the Sea of Japan, was previously known from the abyss of the Aleutian Trench (Ushakov, 1972). Within the molluscs, bivalves occurred in the sample with more individuals than gastropods, possibly due to enhanced food availability for filter feeders. The frequent heterobranch gastropod *Diaphana hiemalis* (Couthouy, 1839) from the western Pacific has been recorded from the north Kurile Islands from 130 m depth, near the Pacific coast of northern Honshu Island from depths between 200–350 m and in the northwestern part of the Sea of Japan from depths 190–2,681 m, where it occurs at the deepest known record for the species (Chaban and Chernyshev, 2013). Echinoderms are generally widely distributed in the deep sea and usually dominate abyssal megabenthic communities (especially ophiuroids) (Piepenburg et al., 1997). They are more rare in the abyssal stations in the Sea of Japan than on the shallower stations.

Cumacea also show an unexpected bathymetric distribution. They occurred more frequently at the shallower stations than in the deep, although it is reported from many deep-sea expeditions that isopods and cumaceans increase in diversity and abundance with increasing depth (Brandt et al., 2007a; Brandt et al., 2007b; Brandt et al., 2007c; Dahl, 1954; Ebbe et al., 2010; Gage and Tyler, 1991; Hessler and Thistle, 1975; Hessler and Wilson, 1983; Hessler and Strömberg, 1989; Rex et al., 1997; Rex et al., 2006). Cumaceans, which burrow in the upper sediment layer, occur most frequently at transect A (31% of all peracarids, Fig. 2.5), which is furthest away from Vladivostok and possible anthropogenic impact. Euphausiids and amphipods occurred in high numbers at the shallowest stations of all transects and only 12 specimens occurred at the deepest station. These taxa are both highly vagile and it might be possible that they were attracted by the light of the C-EBS. However, mysids are also vagile and also occurred at bathyal stations down to 1,000 m, deeper than amphipods and euphausiids. Moreover, the sledge is hauled at 1 knot over the ground. It is therefore not likely that these taxa are not swimming fast enough to escape the C-EBS and get caught by the sledge due to the speed of the gear on the ground. Amphipods usually occur on sediment which is coarser and therefore are usually more frequent at shallower sites than at deeper, soft-sedimented ones, where isopods and cumaceans generally dominate (Brandt et al., 1997; Brandt and Piepenburg, 1994; Lörz and Brandt, 2003; Mühlenhardt-Siegel, 2011; Piepenburg et al., 1997). Higher current velocities mean coarser sediment (Brandt and Piepenburg, 1994). That is a possible explanation why amphipods occur in higher numbers at stations A2-10 and B7-7. Tyler (2002: 317) reviewed the faunal composition of the Sea of Japan as follows: “Zenkevitch (1963) and Nishimura (1966, 1968, 1969; 1983) have suggested that the fauna of the deep Sea of Japan is composed of cold-adapted eurybathic species with affinities to Arctic

species rather than true deep-sea fauna.” Further, Tyler (2002: 317) summarized that “Zenkevitch (1963) records only 25 species between 2,000 and 3,000 m and five macrofaunal species from below 3,000 m (Terazaki, 1999). Down to 2,000 m the fauna is dominated by the cnidarians *Primnoea resdaeformis pacifica*, *Caryophyllia clavus*, *Lafoeina maxima*, the echinoderms *Thaumatomera tenuis*, *Ctenodiscus crispatus* and *Luidiaster tuberculatus*, the polychaetes *Nephtys longisetosa*, *Harmothoe impar* and *Jasmineria pacifica*, as well as decapods and molluscs, particularly the Buccinidae.” Interestingly, numbers of gastropods were low in our samples. This could be due to the sampling; previous data were obtained primarily using grab samplers rather than the C-EBS used in this study. Bivalves thrive in the deep Sea of Japan, though more at the upper bathyal stations than the lower.

In general, species richness of Isopoda was low in the Sea of Japan compared to other recently studied deep-sea areas (Brandt et al., 2007c). Most of the Isopoda belonged to the Asellota, and the families Munnopsidae and Desmosomatidae were most frequent, as also reported for other deep-sea basins (Brandt et al., 2005; Brandt et al., 2007c); however Munnidae, Paramunnidae, and the flabelliferan family Bopyridae also occurred in the samples (Golovan et al., 2013) (**Chapter 4**). Only one species was sampled in the deep sea of the Sea of Japan but at very high abundances: *Eurycope spinifrons* (Asellota: Munnopsidae). It might be possible that they feed on sea grass, as they frequently occurred at those lower bathyal and abyssal stations where sea grass was visible on the digital images. The sex and stage composition of *Eurycope spinifrons* as well as a redescription of this species are provided by Elsner et al. (2013) (**Chapter 7**) and Maljutina et al. (2013) (**Chapter 9**). Contrastingly, the shallow stations offered a higher diversity at the family and species level.

The determination of the fauna to species level is still in progress. The distribution of the species will be biogeographically compared with the occurrence of these species in the Pacific and other world oceans, and in particular the adjacent Kurile-Kamchatka Trench and abyssal plain will be sampled by the German RV *Sonne* between July and September 2012.

More detailed analyses of the species composition of selected taxa are presented in subsequent publications in this issue.

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Author's contribution:

I supervised the sample sorting process, conducted the data input and created the graphs for this publication from the resulting matrix.

Abyssal macrofauna of the Kuril-Kamchatka Trench area (Northwest Pacific) collected by means of a camera-epibenthic sledge

Deep Sea Research II (In Press, Accepted Manuscript)

Chapter 3: Abyssal macrofauna of the Kuril-Kamchatka Trench area (Northwest Pacific) collected by means of a camera-epibenthic sledge

Angelika Brandt^a, **Nikolaus O. Elsner^a**, Nils Brenke^b, Olga A. Golovan^c, Anna V. Lavrenteva^c, Marina V. Malyutina^c, Torben Riehl^a

^a*Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany.*

^b*German Centre for Marine Biodiversity Research, Südstrand 44, D-26382 Wilhelmshaven, Germany*

^c*A.V. Zhirmunsky Institute of Marine Biology, FEB RAS, Palchevskogo 17, 690041, Vladivostok, Russia*

Abstract

Abyssal macrofaunal composition of 21 epibenthic sledge hauls from twelve stations taken in the Kuril-Kamchatka Trench (KKT) and at the adjacent abyssal plain, Northwest Pacific, is presented. Sampling with the fine meshed epibenthic sledge yielded higher abundances and species richness than was reported from previous expeditions from board of RV *Vityaz*. In total 84,651 invertebrates were sampled with RV *Sonne* between July and September of 2012 (31,854 invertebrates if standardized for 1000 m² trawled distances) from 41 taxa of different taxonomic ranks (15 phyla, 28 classes, 7 orders) were sampled from a trawled area of 53,708 m² and have been analyzed. Few taxa were frequent and most taxa were rare in the samples, twelve taxa occurred with more than 1% frequency. Of these, the Polychaeta were most abundant followed by the benthic Copepoda and Isopoda. Total numbers of individuals varied between stations and were highest with 4,238 individuals at station 2-10 close to the KKT in 4,865 m depth and lowest with 374 individuals at station 6-11 in 5,305 m depth. At this station also the lowest number of taxa occurred (18 taxa) while the highest number occurred with 31 taxa at station 3-9 in 4,991 m depth. Numbers of individuals decreased with increasing depth between 4,830 and 5,780 m. Crustaceans of the superorder Peracarida were one of the dominating taxa with four orders occurring frequently in most samples. In total, Isopoda were most important and occurred with 59% of all peracarid orders sampled,

followed by Amphipoda with 21%, Tanaidacea with 11%, Cumacea with 9%, and Mysidacea with <1%. The communities of the stations (and hauls) of the KKT abyssal area differ in terms of taxon composition from each other. A cluster analysis (nMDS) performed for all sampled stations revealed no clear pattern of community similarity between stations or hauls. All hauls close to the trench (2-9 and 2-10 close to the eastern slope of the KKT; and 3-9 and 4-3 at the western slope) were most different to the other hauls. Hauls 8-9 and 8-12 as well as 5-10 and 7-10 in the approximate centre of the overall research area were most similar (88% similarity). The non-isolated KKT area is characterized by higher abundances and higher benthic species richness than the geographically isolated and young deep-sea basin of the Sea of Japan.

Keywords: Deep sea, benthos, macrofauna composition, similarity, cluster analysis, nMDS, camera-epibenthic sledge

Introduction

The hydrography of the Kuril-Kamchatka Trench (KKT) is complex (Arseniev and Leontieva, 1970). Oceanographic properties differ in the western and the eastern part of the KKT and are mainly influenced by the Oyashio (Kurile Current) and the Kuroshio (Kurile Countercurrent) (Qiu, 2001; Zenkevitch, 1963). The cold Subarctic Oyashio current with its high nutrient content originates in the Arctic and flows southwards into the Pacific. The Kuroshio transports warm tropical waters northwards and originates at the east coast of Taiwan (Qiu, 2001). Moreover, water masses from the Sea of Okhotsk influence the Oyashio in the study area through the Bussol and the Krusenstern straits (Tyler, 2002; Yasuda, 2003; Zenkevitch, 1963). Rabinovich et al. (2002) found evidence for anticyclonic eddies near Bussol' Strait which are located over the KKT. In general terms, eddy movements might facilitate migrations of the benthic fauna or the transport deep-sea products (Adams et al., 2011). Uehara and Miyake (1999) showed that deep flows (>3000 m) on the slope inshore of the KKT southeast of Hokkaido are controlled by the local bottom topography and form in part a southward deep western boundary current.

The abyssal area of the Northwest Pacific Ocean is ancient, open (not isolated from other basins by ridges and the like), as well as rather homogenous in depth and topography (Bogorov, 1973; Mikhailov, 1972) in comparison to the young, semi-enclosed deep-sea basin

of the Sea of Japan which have been investigated faunistically during the SoJaBio (Sea of Japan Biodiversity Studies) expedition in 2010 (Malyutina and Brandt, 2013a, b). The SoJaBio expedition has extended our knowledge on the deep-sea fauna deeper than 455 m significantly. More than 600 species were sampled in the Sea of Japan and about one third of these are new to science and within the macrofaunal organisms, Malacostraca, Polychaeta and Ophiuroidea were most abundant (Brandt et al., 2013).

The deep Northwest part of the Pacific Ocean was amongst the first globally to be thoroughly studied. Pioneering biological expeditions to this region were performed onboard the RV *Vityaz* in 1949, 1953-1955, 1957 and 1966 (Belyaev, 1970, 1983, 1989; Belyaev and Vilenkin, 1983; Ushakov, 1952; Zenkevich et al., 1955; Zenkevitch, 1963). The fauna found in the KKT and on the adjacent abyssal plain has been described in many publications (e.g. in two volumes of the transactions of the P.P. Shirshov Institute of Oceanology 1970, 1971; Bogorov, 1972 [translation of the first volume]). In this volume first data on hydrology, topography, chemical characteristics and organic matter of the bottom water and sediments of the KKT area are presented. Some information about the KKT fauna is presented in a list of "Animals and Plants, previously unknown to science, described from the RV "Vityaz" collections" in a book entitled "Research vessel *Vityaz* and her expeditions 1949–1979", 1983 and in a recently published a check list of free-living invertebrates of the Russian Far Eastern Seas (Sirenko, 2013). Birstein, who described about 100 species of Isopoda collected during nine RV *Vityaz* expeditions from the deep sea of the Northwest Pacific (Birstein, 1957, 1960, 1961, 1963, 1970, 1971), noticed that in the collections of the 39th *Vityaz* cruise in 1966 (the last biological expedition in the KKT area) only 42% of all collected species have been resampled (known for this area after eight previous expeditions). Most of the species collected during the 39th cruise were thus new to science (Birstein, 1971). Therefore, any subsequent sampling in the same area is likely to discover additional species.

On this background, we aimed to test the following hypotheses: 1.) Sampling with a fine-meshed epibenthic sledge has to be more effective than previously employed apparatus and increase the number of species for the abyssal area of the Kuril-Kamchatka Trench. 2.) The communities of the stations (and transects) of the of the studied abyssal area differ in terms of taxon composition from each other. 3.) The non-isolated abyssal plain of the Kuril-Kamchatka Trench area comprises higher benthic biodiversity in comparison to the geographically isolated and young deep-sea basin of the Sea of Japan.

Material and methods

The joint German-Russian expedition KuramBio (Kurile Kamchatka Biodiversity Studies) on board of the RV *Sonne* (cruise SO 223) to the Kuril-Kamchatka Trench and adjacent abyssal plain started in Busan, South Korea on July 21st and terminated in Busan on September 7th, 2012. The KuramBio project follows up on the joint Russian-German project SoJaBio (Sea of Japan Biodiversity Studies) from board of the RV *Akademik M. A. Lavrentyev* (11.8. – 5.9.2010). First results from the SoJaBio expedition are published in a special volume in Deep-Sea Research II (Malyutina and Brandt, 2013b).

Study area

The Northwest Pacific KKT is a northward extension of the Mariana and Japan Trenches and extends down to 9,717 m depth. The trench and the adjacent abyssal plain are situated in an area of high surface productivity; especially during the summer period (Bogorov, 1973; Zenkevitch, 1963). This area has been investigated in the last century during ten expeditions with the RV *Vityaz* in 1949, 1953–1955, 1957 and 1966. The deep-sea fauna of this area was described as unusually rich (Zenkevitch, 1963), however, it is supposed that major fractions of the fauna were not sampled due to inappropriate sampling gear and methods used for sieving (Birstein, 1971). Since the *Vityaz* expeditions, the KuramBio expedition was the first biological survey in the area, and modern equipment and sampling methods were applied for the first time. The area is briefly described in the introduction of this volume (Brandt and Malyutina, submitted). Samples from 21 C-EBS hauls at twelve stations at abyssal depths between 4,830 and 5,780 m were analyzed. Geo-referenced C-EBS stations are presented in Tab. 3.1 and Fig. 3.1.

Deployment of C-EBS

A camera-epibenthic sledge (C-EBS) especially designed for sampling small epi-benthic and supra-benthic fauna of roughly a few millimeter to one centimeter of size at any depth and on any substrate was used (Brandt et al., 2013). The C-EBS is equipped with supra- and epibenthic samplers possessing plankton nets of 500 μm and a cod end of 300 μm as

described by Brandt and Barthel (1995) and Brenke (2005). However, at station 4-3 only the supranet was filled with sediment and macrofauna. An entangled fisher net probably tore the epinet off from the cod end during trawling, therefore the sample got lost. An opening-closing device prevents that pelagic fauna is caught during heaving. The haul distances were calculated using the time and the speed (ships speed with 1 knot, and then winch speed with - 0.5 m/sec. (equals one knot)) until the C-EBS left the ground, which was indicated by the tension meter. As the haul lengths varied, the data were standardized to 1,000 m² hauls for the comparative analysis.

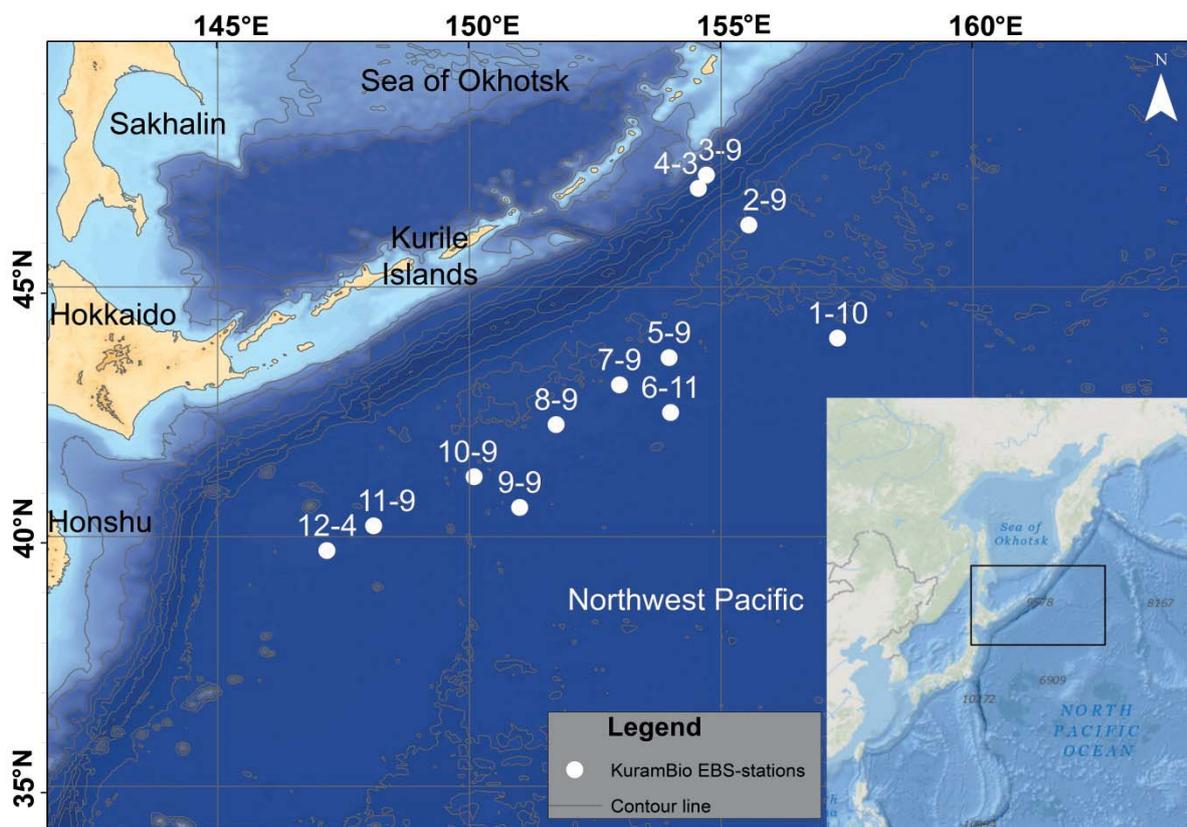


Fig. 3.1: Station locations of the KuramBio expedition with RV *Sonne* in 2012.

Additionally, the C-EBS was the carrier for an autonomous digital underwater video camcorder and a still camera and the required energy and control units. The cameras were installed in an additional frame on both sides of the sledge. The C-EBS is also equipped with sensors (Seaguard RCM DW) for measuring data on temperature, pressure, conductivity, and oxygen concentration (Brandt et al., 2013) (Fig. 3.13). Camera and CTD data are summarized in Tab. 3.1.

Stations were subsequently numbered (1–12) and if two different C-EBS hauls were taken these are numbered as indicated after the hyphen (e.g. 1-10, means station 1 haul 10). As trawled gear never hits the same spot when repeating a station (Brattegard and Fosså, 1991), the different hauls are as different as stations in most cases (Figs. 3.8, 3.9).

Tab. 3.1: Station and environmental data from epibenthic sledge deployments. Abbreviations: °C = temperature measured in Celsius; cm/s = centimeter per second; O₂ conc. µM = Oxygen concentration in µM per liter. Abiotic parameters measured show the mean value and standard deviation of all measurements over the trawling period.

Station No.	Date 2012	Position start	Position end	Area [m ²]	Depth [m]	Temperature [°C]	O ₂ [µM/l]	Bottom current [cm/s]
01-10	30.07.	43.9710°N 157.3278°E	43.9722°N 157.2995°E	2222	5418 - 5429	1.6 ± 0.001	155.3 ± 0.3	7.4 ± 1.8
01-11	30.07.	43.9725°N 157.3290°E	43.9768°N 157.3022°E	2161	5412 - 5418	1.6 ± 0.001	154.7 ± 0.2	4.3 ± 1.6
02-09	02.-03.08.	46.2268°N 155.5567°E	46.2487°N 155.5428°E	3117	4830 - 4864	1.5 ± 0.001	156.7 ± 0.3	5.9 ± 2.6
02-10	03.08.	46.2260°N 155.5595°E	46.2499°N 155.5438°E	2932	4859 - 4863	1.5 ± 0.001	156.7 ± 0.3	8 ± 4.8
03-09	05.08.	47.2307°N 154.6982°E	47.2477°N 154.7197°E	2840	4859 - 4863	1.5 ± 0.001	160.1 ± 0.2	2.1 ± 1.2
04-03	06.-07.08.	46.9640°N 154.5398°E	46.9747°N 154.5565°E	1574	5681 - 5780	1.6 ± 0.001	156.4 ± 0.2	3.5 ± 1.7
05-09	11.08.	43.5913°N 153.9647°E	43.5717°N 153.9693°E	2469	5376 - 5379	1.6 ± 0.001	155.5 ± 0.3	3.1 ± 0.8
05-10	11.08.	43.5912°N 153.9635°E	43.5699°N 153.9691°E	2624	5375 - 5379	1.6 ± 0.001	155.4 ± 0.3	3.8 ± 1.7
06-11	15.08.	42.4927°N 154.0005°E	42.4745°N 153.9943°E	2624	5291 - 5305	1.6 ± 0.001	155.8 ± 0.3	6.2 ± 6.5
06-12	15.08.	42.4915°N 153.9989°E	42.4704°N 153.9953°E	2562	5291 - 5307	1.5 ± 0.001	155.7 ± 0.3	4.4 ± 3.2
07-09	17.08.	43.0473°N 152.9905°E	43.0248°N 152.9727°E	2994	5216 - 5223	1.5 ± 0.001	157.8 ± 0.3	2.3 ± 1.2
07-10	17.08.	43.0463°N 152.9882°E	43.0276°N 152.9743°E	2624	5218 - 5221	1.5 ± 0.001	157.8 ± 0.3	4 ± 2.5
08-09	20.08.	42.2447°N 151.7351°E	42.2378°N 151.7082°E	2840	5125 - 5140	1.5 ± 0.002	157.5 ± 0.2	3.3 ± 1.3
08-12	21.08.	42.2453°N 151.7391°E	42.2387°N 151.7157°E	2408	5115 - 5124	1.5 ± 0.002	157.6 ± 0.3	2.6 ± 2
09-09	23.08.	40.5913°N 150.9987°E	40.5708°N 150.9985°E	2315	5399 - 5408	1.6 ± 0.001	158.3 ± 0.3	3.3 ± 3.2
09-12	24.08.	40.5918°N 150.9976°E	40.5713°N 150.9864°E	2377	5392 - 5397	1.6 ± 0.001	158 ± 0.3	2.3 ± 1.7
10-09	26.08.	41.2077°N 150.0940°E	41.1862°N 150.0933°E	2778	5248 - 5265	1.5 ± 0.001	156.2 ± 0.4	5.5 ± 2.6
10-12	27.08.	41.1939°N 150.0928°E	41.2169°N 150.0942°E	2778	5249 - 5262	1.5 ± 0.001	156.4 ± 0.5	3.7 ± 2
11-09	29.08.	40.2210°N 148.1038°E	40.2062°N 148.0905°E	2408	5362 - 5362	1.5 ± 0	157.6 ± 0.6	12.4 ± 18.8
11-12	31.08.	40.2184°N 148.1088°E	40.2018°N 148.0923°E	2346	5348 - 5351	1.5 ± 0.001	158.1 ± 0.8	11.2 ± 9.9
12-04	31.08.	39.7300°N 147.1813°E	39.7082°N 147.1562°E	2716	5215 - 5228	1.5 ± 0.002	160.3 ± 0.6	5 ± 2.8

Sample treatment

On deck, the complete samples (except freshly picked material for biochemical analyses) were immediately transferred into chilled (-20°C) 96% ethanol and kept in a -20°C freezer for at least 48 h for subsequent DNA studies. In the laboratories of the ship and in the home institutes, sorting of the macrofauna was done on ice in order to avoid DNA decomposition (Riehl et al., 2014). For macrofaunal analysis, the supra- and epinet samples were pooled for every haul. The material was sorted and identified using stereomicroscopes. Additionally, after every deployment, all sensor, picture and video data were downloaded from the internal hard drives and memory cards.

Statistical analysis

For the analysis of the similarity of stations all macrofauna was considered. A similarity matrix was constructed using square-root transformed standardized abundance data and the Bray-Curtis coefficient (Bray and Curtis, 1957). Classification (cluster) employing group-average linking (e.g. Clifford and Stephenson, 1975) and ordination by nonmetric multidimensional scaling (MDS) based on the Bray-Curtis similarity matrix (e.g. Kruskal and Wish, 1978; Clarke and Green, 1988; Clarke and Ainsworth, 1993) were used to provide a graphical presentation faunal similarity in the area. These univariate and multivariate measurements are implemented in the PRIMER (6.0) package, described in Clarke and Warwick (2001; 1994).

Terminology

The term “rare” refers to singletons or doubletons (a very low number of individuals) at stations. On the contrary, common is used to refer to a higher number of individuals per station (~100). The term “taxa” is used, as we compare the main sorted groups of invertebrates of the different taxonomic ranks: the phylum, the class or the order within the most-abundant phyla (Tab. 3.2). The term abundance is used for the number of individuals occurring in the hauls standardized to 1000 m² trawled distance.

Results

C-EBS deployment

The 21 C-EBS hauls at the seafloor of the KKT covered an area that varied between 1,574 and 3,117 m², however, most hauls ranged between approximately 2,200 and 2,700 m². A total of 53,708 m² were sampled with the C-EBS and numbers of higher taxa varied between 18 at station 6-11 in 5,305 m depth and 31 at station 3-9 in 4,991 m depth (Tab. 3.1; Fig. 3.3).

The camera systems were deployed 18 times. Only at six stations the camcorder as well as the still camera worked faultlessly. The C-EBS produced 5,538 informative pictures and approximately eight hours of useful video feature. For a documentation of the seafloor, six pictures (stations #1-10, #2-9, #5-9, #8-9, #10-9, #11-9) are also shown in Fig. 3.11.

The data from the Seaguard system show that the bottom water temperature varied between 1.5-1.6°C (± 0.001) and O₂ concentration between 154.7 and 160.3 $\mu\text{M/l}$ (± 0.2 –0.8). Bottom currents ranged from 2.1 (± 1.2) to 12.4 (± 18.8) cm/s. For an overview of all stations see Tab. 3.1.

Faunistic composition

From the trawled area of 53,708 m², a total of 84,651 invertebrates (31,854 invertebrates if standardised for 1000 m²) from 15 phyla were sampled. Seven of the collected phyla were allocated to 25 classes, and only the class Malacostraca of the most numerous phylum Arthropoda was sorted to seven orders. Therefore, for the analysis we used the following 41 taxa: nine low-abundance phyla by themselves, 25 classes and seven orders of the macrobenthic invertebrates. 98% of all collected invertebrates belong to five phyla: Arthropoda (42%; 13,531 individuals), Annelida (27%; 8,602 individuals), Mollusca (16%; 5,124 individuals), Echinodermata (8%; 2,470 individuals), and Nematoda (5%; 1603 individuals), ten other phyla are presented by low numbers of individuals (Cnidaria by 202 individuals and the remaining nine phyla by 450 individuals in total; Tab. 3.2).

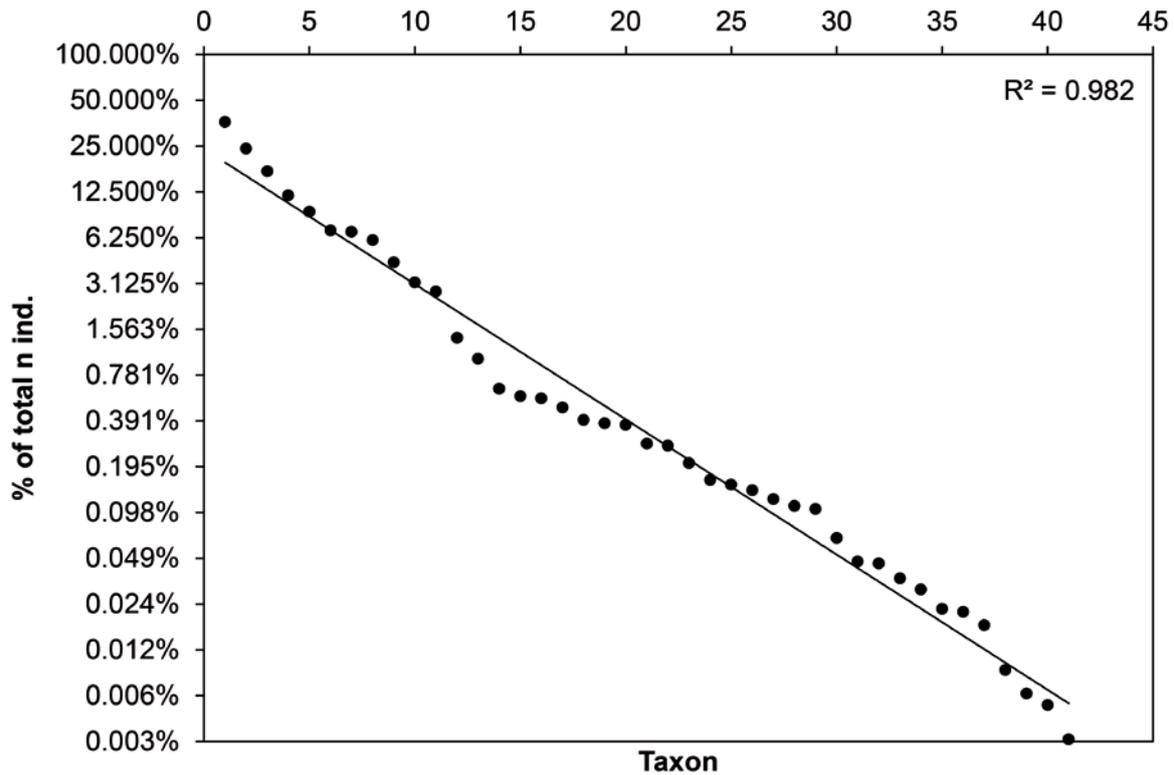


Fig. 3.2: Percentage of individuals per ranked taxon (from most abundant to least abundant) pooled from all stations on a semi logarithmic scale.

Ten taxa occurred at all stations and in all hauls (Polychaeta, Copepoda, Isopoda, Amphipoda, Cumacea, Tanaidacea, Ostracoda, Nematoda, Bivalvia, Gastropoda) (Tab. 3.2).

Twelve taxa occurred with more than 1% frequency, but most taxa were rare or occurred patchily in the samples. Relative abundance of the most abundant taxa occurring with 2% and more in the samples is illustrated in Fig. 3.6. These taxa are compared between stations in Figs. 3.6 and 3.7.

Polychaeta were the most frequent taxon with 8,423 individuals, second most frequent were benthic Copepoda with 5,649 individuals, third most frequent were Isopoda with 4,006 individuals. Also amongst the dominant taxa were Bivalvia (2,782 individuals), Holothuroidea (2,170 individuals), Gastropoda (1,631 individuals), Nematoda (1,603 individuals), Amphipoda (1,413 individuals), Ostracoda (1,008 individuals), Tanaidacea (743 individuals), Cumacea (648 individuals) and Scaphopoda (322 individuals). Total numbers of individuals varied between stations. They were highest at station 2-10 close to the Kuril-Kamchatka Trench in 4,865 m depth where 4,238 individuals were sampled and lowest at

station 6-11 in the abyssal plain with 374 individuals in 5,305 m depth (Tab. 3.2, Figs. 3.3, 3.7 B).

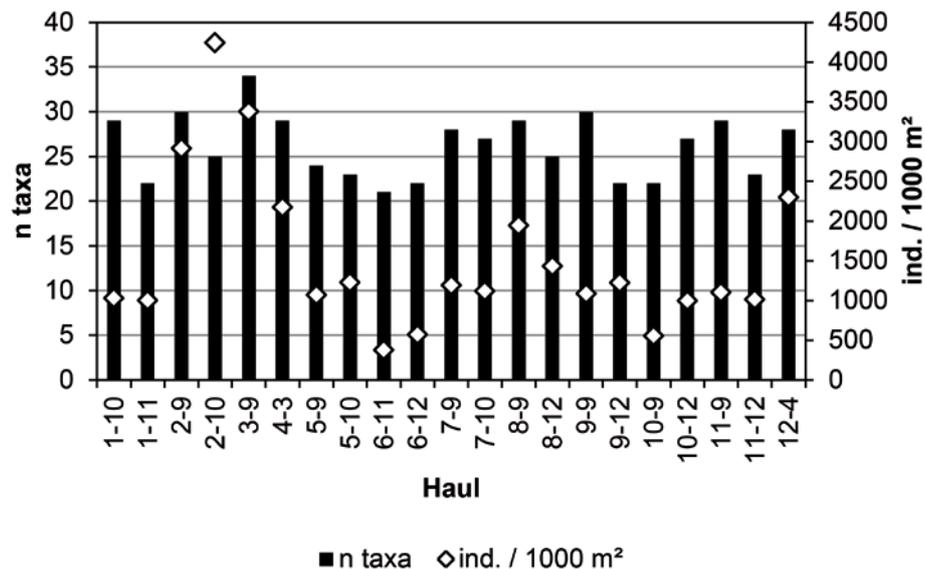


Fig. 3.3: Total number of individuals (1000 m²; black bars) and number of taxa (white diamonds) of the KuramBio expedition with RV *Sonne* in 2012.

Of the macrofaunal taxa only few show a high abundance, while most taxa occur with low abundance. In the rank abundance diagram (Fig. 3.2), we noticed an exponential decline from the abundant taxa to the less abundant taxa. The correlation analysis yielded a R^2 -value of 0.982 on taxon level for our data.

Numbers of individuals decreased with increasing depth between 4,830 and 5,780 m, though insignificantly ($R^2 = 0.4107$; Fig. 3.4). The lowest number of individuals was found at station 6-11 in 5,305 m depth. No trend between depth and number of taxa could be observed in samples ($R^2 = 0.0874$; Fig. 3.5).

Of the five most frequent taxa (Fig. 2.7), Polychaeta occurred at station 3-9 with 1,520 individuals. Copepoda were most frequent at station 4-3 with 804 individuals, most Isopoda were found at station 3-9 with 695 individuals, most Bivalvia at station 2-10 with 666 individuals and most Holothuroidea at station 2-10 with 1,053 individuals (Tab. 3.2, Fig. 3.7).

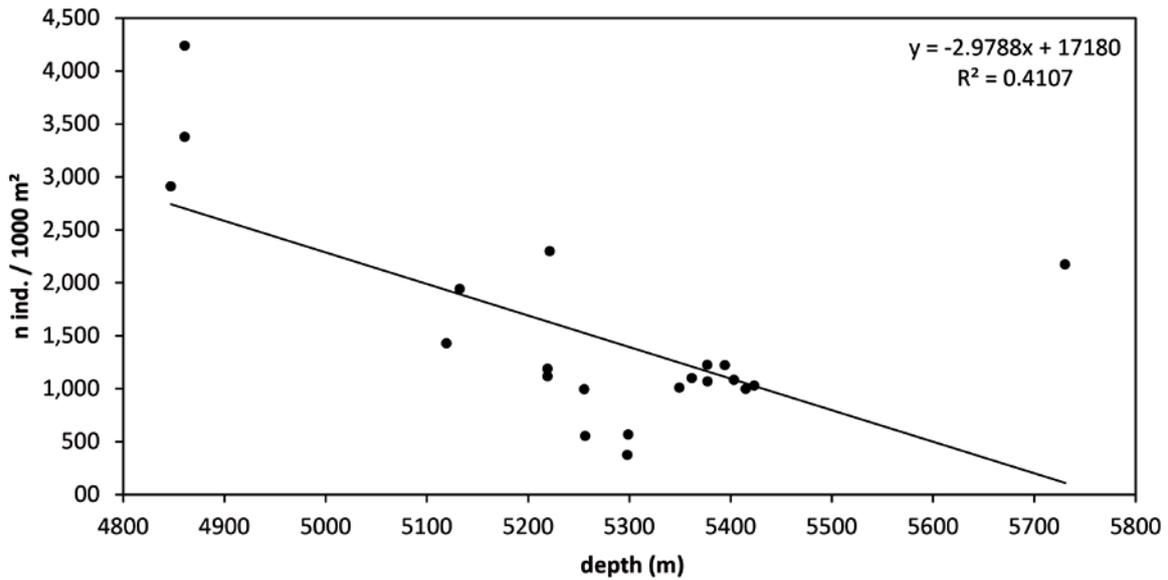


Fig. 3.4: Depth correlation with number of individuals (1000 m²) from the KuramBio expedition with RV *Sonne* in 2012.

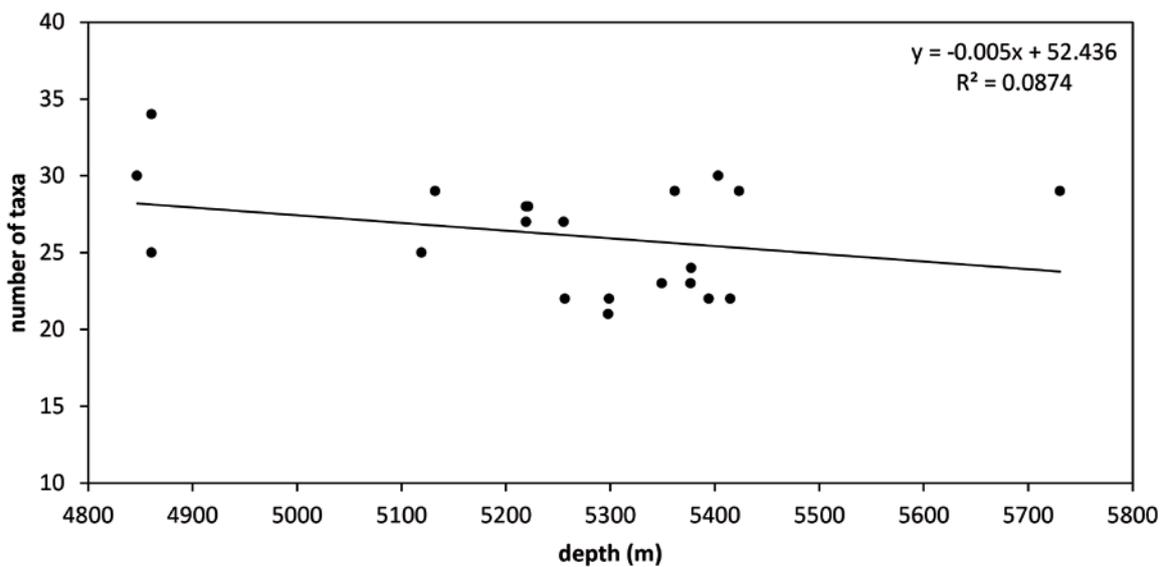


Fig. 3.5: Depth correlation with number of taxa from the KuramBio expedition with RV *Sonne* in 2012.

Overall, Polychaeta were the dominating taxon in the C-EBS samples (Alalykina, submitted). Within Crustacea, benthic Copepoda occur with 42% of the individuals, Decapoda, Euphausiacea and Mysidacea (Peracarida) with less than 1% and the other Peracarida (Amphipoda, Isopoda, Cumacea, Tanaidacea) with 57%. Crustacea Peracarida is the second most dominant macrofaunal taxon with 6,842 individuals and occurred frequently in most samples (Tab. 3.2, Figs. 3.6–3.8). In total, Isopoda comprised 59% of all peracarid taxa

sampled followed by Amphipoda with 21%, Tanaidacea with 11%, Cumacea with 9% and Mysidacea with <1% (Tab. 3.2, Fig. 3.8). Percentage of isopod occurrence was highest at stations 6-11 and 6-12 in 5,305–5,307 m depth, percentage of amphipod and cumacean occurrence was highest at station 4-3 in 5,780 m depth (Fig. 3.9). Mysidacea occurred at 11 stations but were rare, highest number of mysids (8 individuals) was found at station 3-9 in 4,991 m depth (Tab. 3.2), where the number of all Peracarida per station was highest (Fig. 3.7). Second most abundant occurrence of Peracarida was found at station 12-4, followed by stations 2-10 and 2-9 (Fig. 3.7).

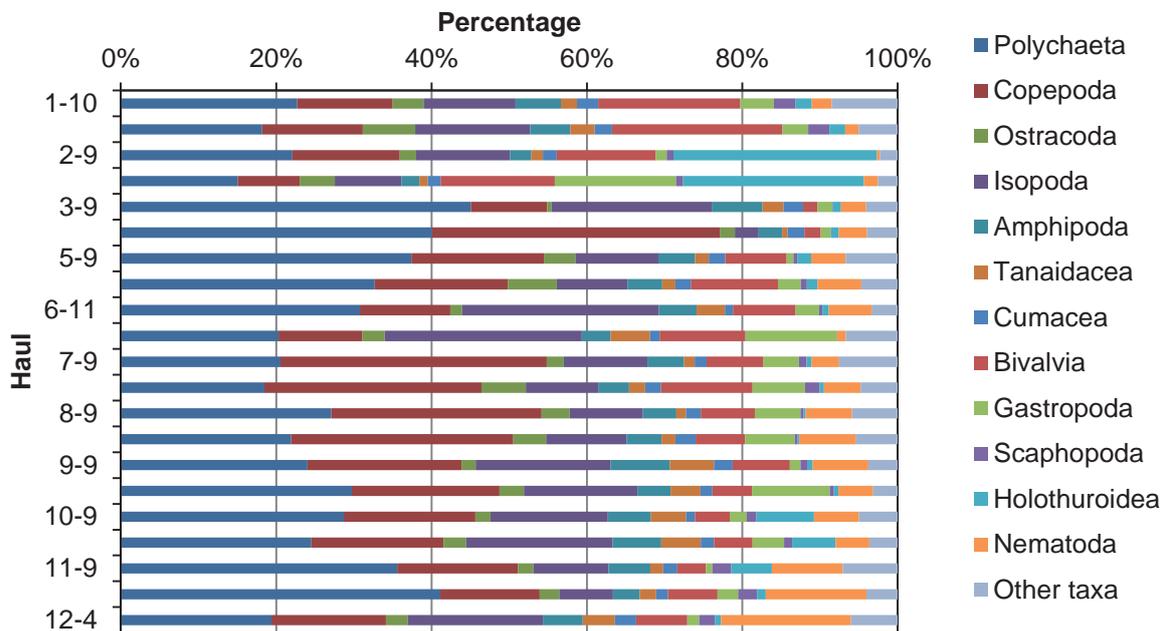


Fig. 3.6: Relative percentage of macrofauna of 1000 m² of the KuramBio stations (only taxa occurring with > 1 % of the total taxon composition per station).

At station 4-3, which is located at the upper north-western slope of the KKT, numbers of Isopoda were lowest, but were only retrieved from the supranet (see material and methods, 2.2.). Composition of Isopoda is described in detail by Elsner et al. (submitted) (**Chapter 6**).

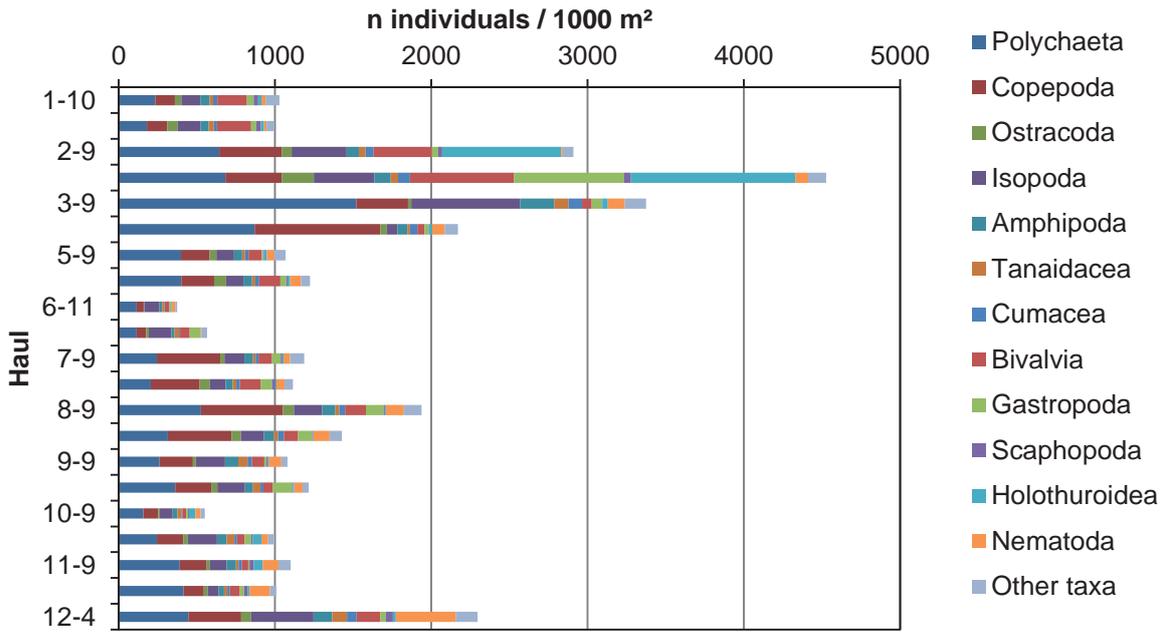


Fig. 3.7: Abundance of taxa (1000 m²) of the KuramBio stations (only taxa occurring with > 1 % of the total taxon composition per station).

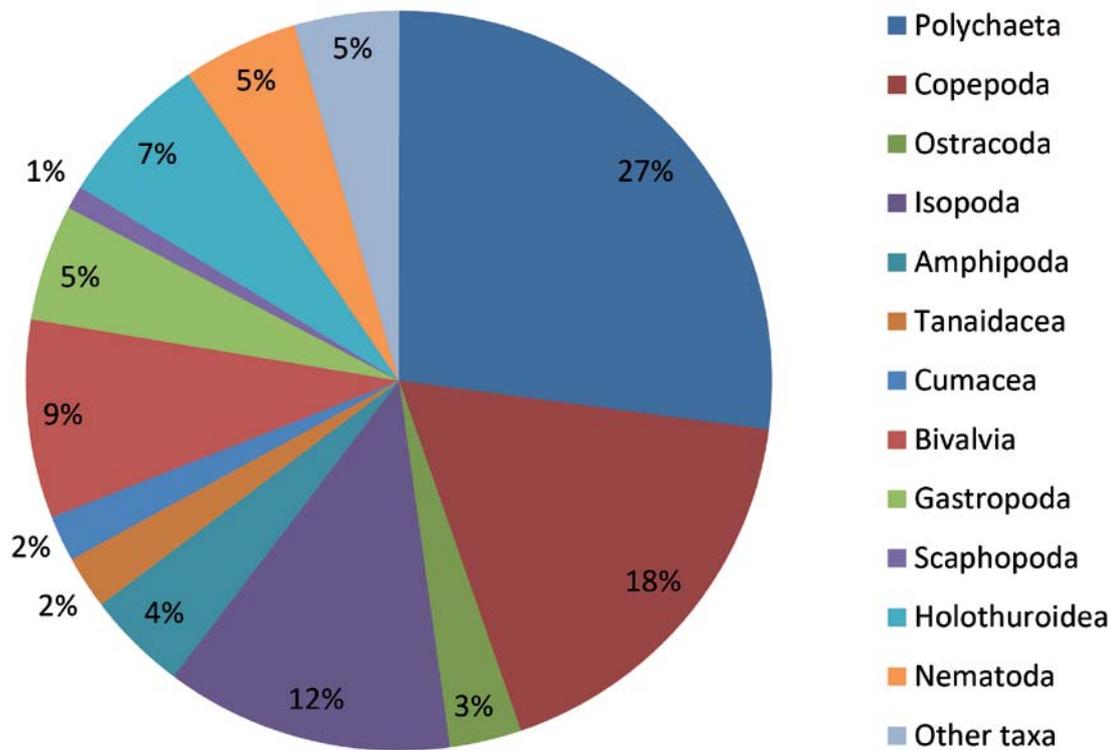


Fig. 3.8: Total percentage of the most abundant taxa across all KuramBio stations.

A cluster analysis (nMDS) revealed no clear pattern (Fig. 3.9) of similarity of stations. Stations 2-9 and 2-10 are most different from the other stations, but stations 3-9, and 4-3 are also standing out in general taxa composition. Some of the stations in close proximity (e.g. 2-9 and 2-10 or 6-11 and 6-12) were found more different than for example stations 5-9, 9-9, 7-9 or stations 5-10, 7-10, 8-12, 9-12, 10-12. Stations 3-9 and 4-3 at the western margin of the KKT are different (especially in abundance (see above) to the other abyssal stations. The classification (cluster) analysis, employing group-average linking, shows that similarity (Bray-Curtis similarity) of stations 3-9 and 4-3 is about 75% (Fig. 3.10). Stations 8-9 and 8-12 as well as 5-10 and 7-10 are most similar (88%) (Fig. 3.10).

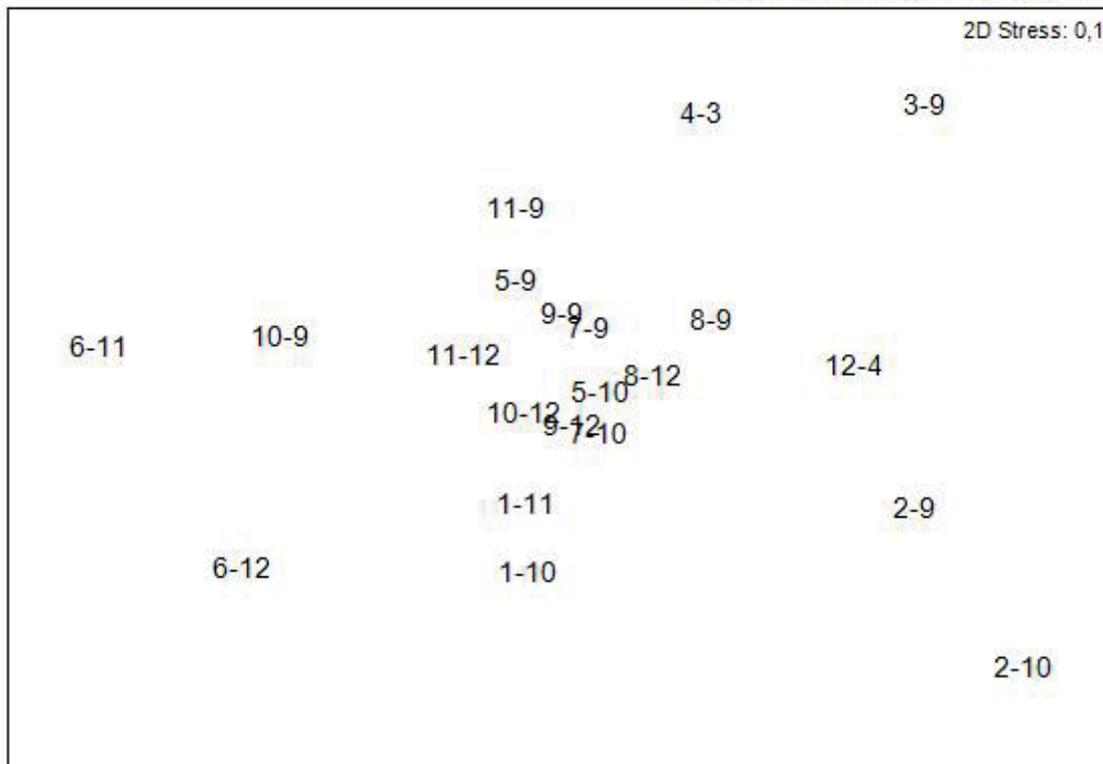


Fig. 3.9: Non-metric multidimensional scaling (nMDS) of the abyssal stations based on numbers of individuals (1000 m²) using Bray-Curtis-Similarity, square-root-transformation and standardization of data.

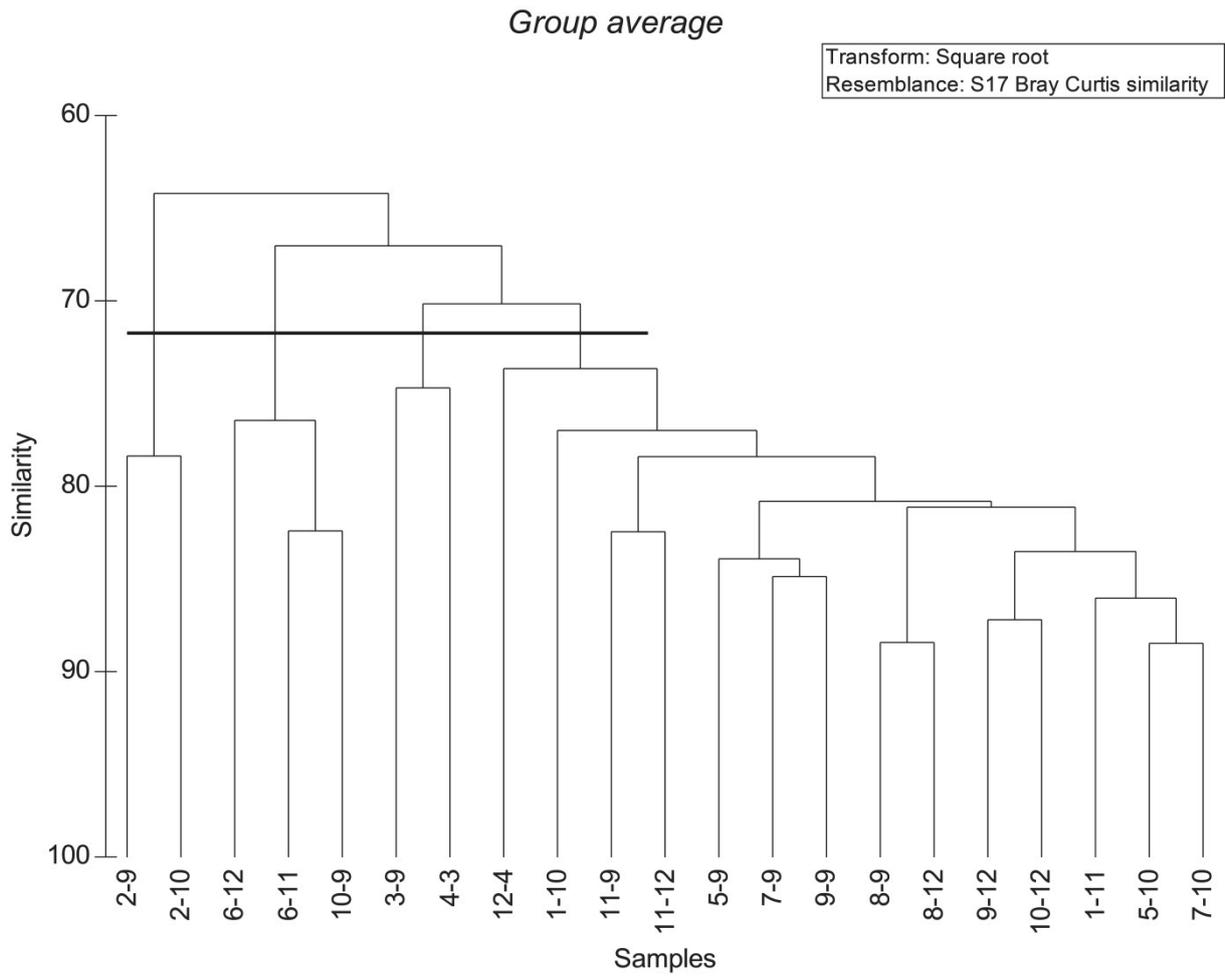


Fig. 3.10: Classification (cluster) employing group-average linking of 21 abyssal stations from KuramBio using all taxa, Bray-Curtis-Similarity, square-root-transformation and standardization of data.

Tab. 3.2: Taxon richness of benthic fauna from 12 stations (21 C-EBS hauls) sampled in the KKT and adjacent abyssal plain (standardised for 1000 m²).

Haul #	1-10	1-11	2-9	2-10	3-9	4-3	5-9	5-10	5-11	6-11	6-12	7-9	7-10	8-9	8-12	9-9	9-12	10-9	10-12	11-9	11-12	12-4	N	% N	Tax/stat
Median depth (m)	5424	5415	4847	4861	4861	5731	5378	5377	5298	5299	5220	5220	5220	5133	5120	5404	5395	5257	5256	5362	5350	5222			
<i>Phylum/Class/Order</i>																									
Porifera	6.3	0.9	1.0	2.7	2.8	0.0	0.4	0.8	1.1	1.2	5.7	1.5	1.1	1.1	0.0	0.4	3.8	0.4	5.0	0.0	1.3	1.1	37.5	0.1%	18
Cnidaria	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Anthozoa	1.3	1.4	1.6	0.3	6.0	2.5	1.6	0.8	0.8	1.2	3.0	0.8	4.9	5.0	1.3	0.0	0.0	4.7	0.4	7.1	2.1	65.5	112.3	0.4%	20
Coronata	1.3	13.4	0.0	3.1	2.8	2.5	0.0	3.8	0.0	5.1	0.3	3.4	9.2	9.6	0.0	5.9	0.0	1.8	0.4	1.7	0.0	0.0	64.8	0.2%	15
Hydrozoa	0.9	0.0	2.2	0.0	11.6	4.4	0.0	0.0	0.0	0.0	1.3	0.4	0.7	0.0	0.9	0.4	0.0	0.4	0.4	1.7	0.0	0.4	25.3	0.1%	12
Ctenophora	0.0	0.0	0.0	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	0.0	3.3	7.1	0.0%	3
Nematoda	26.5	17.1	10.6	82.5	108.8	78.8	47.4	69.0	20.6	6.2	42.4	52.6	116.2	103.0	77.8	54.3	32.0	42.8	42.8	99.7	130.9	383.6	1602.8	5.0%	21
Nemertea	14.4	0.0	0.3	1.0	18.0	10.2	9.3	0.0	1.1	0.0	3.7	0.0	8.8	0.0	4.3	0.0	4.7	0.0	0.0	14.5	0.0	2.6	92.9	0.3%	13
Priapulida	0.4	0.0	0.3	0.3	0.7	0.0	0.0	0.0	0.0	5.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	1.7	0.0	6.3	15.6	0.0%	8
Mollusca	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Aplacophora	7.6	0.0	7.4	0.0	0.4	1.3	0.0	0.0	4.6	9.4	4.3	0.0	17.6	1.2	8.2	0.0	5.4	0.0	0.0	14.5	4.3	0.0	86.2	0.3%	13
Bivalvia	188.1	218.4	371.5	666.0	63.0	45.7	84.6	137.2	30.1	62.5	86.8	131.5	134.9	91.4	79.5	61.9	24.5	49.0	40.3	40.3	64.4	150.9	2782.1	8.7%	21
Caudofoveata	0.0	20.4	5.8	31.7	0.0	0.0	2.0	25.2	0.0	8.6	5.3	19.1	9.5	28.2	2.6	13.0	4.3	15.1	0.0	0.0	14.9	28.0	233.7	0.7%	16
Gastropoda	44.1	32.9	40.7	706.3	64.4	27.3	9.3	35.8	11.4	66.7	53.8	75.1	113.4	90.5	14.7	122.0	12.2	40.3	9.1	26.4	34.6	1631.3	5.1%	21	
Nudibranchia	3.6	0.0	0.0	0.0	1.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.1	0.0%	3
Monoplacophora	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.7	0.0%	1
Scaphopoda	28.8	27.3	25.3	43.0	2.1	1.3	5.3	9.5	1.5	0.0	12.0	20.6	7.4	5.4	10.4	6.3	6.8	10.4	27.0	24.7	47.1	322.3	1.0%	20	
Solenogastres	6.7	0.0	3.5	0.0	0.7	4.4	28.3	0.0	0.0	0.8	11.7	0.0	3.2	0.0	2.6	0.0	0.0	0.4	0.4	0.0	0.4	0.0	62.8	0.2%	11
Annelida	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Echiuridea	0.0	0.0	0.0	0.0	18.3	0.6	1.2	0.0	0.0	0.0	1.7	0.0	1.1	0.0	0.4	0.0	0.0	0.0	0.0	0.8	0.0	0.0	24.1	0.1%	7
Oligochaeta	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.0	1.5	8.1	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	10.9	0.0%	5
Polychaeta	233.1	181.0	642.8	387.4	1520.1	869.0	398.9	399.8	115.1	114.8	243.8	205.8	525.0	313.2	259.6	361.4	158.0	243.3	390.8	414.8	445.1	8423.0	26.4%	21	
Pogonophora	0.0	0.0	0.0	0.0	4.9	2.5	0.0	1.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.4	0.4	0.4	0.7	10.6	0.0%	6
Sipunculida	0.4	1.4	9.3	11.6	29.6	11.4	6.1	10.3	1.5	2.3	5.3	2.7	10.6	8.7	5.2	0.0	2.2	2.2	5.0	1.3	6.3	133.3	0.4%	20	
Arthropoda	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

Discussion

The KuramBio expedition with RV *Sonne* was the first extensive biological expedition in the abyssal plain of the Northwest Pacific since the RV *Vityaz* expeditions in the mid twentieth century (Bogorov, 1973). After more than 40 years of investigations, about 660 species were recorded in the collections of the *Vityaz* expeditions from the extensive area of the Northwest Pacific where the sampling depth ranged from bathyal to hadal. During the KuramBio expedition, we sampled a more restricted area with a depth range between 4,830 to 5,780 m by means of an epibenthic sledge and collected 84,651 invertebrates (31,854 invertebrates standardised for 1000 m²) which represent more than 700 species.

C-EBS deployment

The C-EBS was deployed 18 times with the optical system. For different reasons and many technical problems the still camera only worked during 11 hauls and during during 13 hauls the video system recorded data. Additionally, the flashlight and the spotlights did not work properly at several stations. Thus, from the overall 11,330 pictures and 18 hours of video footage, 5,538 pictures and approximately eight hours of videos are useful. The documentation of the sediment surface in parallel to sampling the macrofauna is a time saving method to get high quality impressions of the undisturbed living environment of the abyssal area of investigation. These seafloor-surface observations are very useful for the identification of sediments and geomorphologic structures, Lebensspuren and the densities of large organisms in their natural habitat Fig. 3.11). A comparable type of an EBS (without sensory and camera systems) has been deployed in a standardised manner in different basins (Brandt and Barthel, 1995; Brenke, 2005), mainly in the Atlantic at bathyal and abyssal depths for more than 20 years and thus results of the different areas are comparable and due to its opening and closing device no pelagic fauna is collected.

Bottom-water temperatures were very similar at all stations, as typical for deep-sea bottom water. We therefore have to assume that the strong oceanographic gradients in surface temperatures as described for the KKT (Arseniev and Leontieva, 1970) as well the existence of eddies (Rabinovich et al., 2002) are not affecting the benthos in the area investigated. Even though it has been reported that transport of deep-sea material via eddies might occur (Adams et al., 2011), we conclude that eddies observed in the KKT area are not reaching abyssal

depths and are thus not influencing faunal composition at our stations in the KKT and abyssal plain.

Highest oxygen concentration was measured at stations 3 and 12, (haul 3-9 at the entrance of the KKT as well as haul 12-4, closest to the Japan Trench). In both of these hauls numbers of macrofaunal individuals was high (highest in haul 3-9). It is, however, not possible to deduce that high oxygen levels have led to high abundances as it is difficult to distinguish the relative effects of oxygen or other sediment measure, like organic matter (e.g. Huges et al., 2009; Levin and Gage, 1998) on community composition or abundances. Content of sand (% compared to Silt/clay and gravel) was highest at stations 3, 4 and 6-8 (though medium grain sizes at all station varied only between 7 and 9 median phi (Schmidt and Martinez Arbizu, submitted), however, abundances and macrofaunal composition varied strongly between these stations, therefore the sediment parameters also unlikely explain the differences found between stations and hauls. Sattarova and Artemova (submitted), found highest sediment concentrations of diatoms at station 2, followed by stations 12 and 1 in values. At station 2 (especially in haul 2-10) we found the highest abundance. However, abundance was much lower at station 1, whereas it was second high at station 3 where diatom values are much lower in the sediment. At this stage it is therefore impossible to attribute differences in abundance to content of diatoms either. In the northern hemisphere, north of Iceland, as well as east of Greenland, Amphipoda were the dominant peracarid taxon at stations sampled on the shelf of the continental slope (Brandt, 1993, 1995, 1997a, c; Brandt and Piepenburg, 1994; Brandt et al., 1996; Piepenburg et al., 1997; Piepenburg et al., 2001). In this area, Amphipoda were prevalent at the shallower stations down to 500 m and preferred coarse sediment, while Isopoda and Cumacea increased in abundance with depth and with the occurrence of fine and silty sediment.

Bottom currents varied tremendously between stations and we have no explanation for the high values at station 11 (haul 11-9), as during all hauls the values were recorded and were lower (including the standard deviation) during the period when the C-EBS stayed on the ground and did not move.

Faunistic composition

The C-EBS collected a high number of macrofaunal marine organisms during the KuramBio expedition, and it also included elements of the meiofauna (e.g. foraminiferans, benthic copepods, nematodes) as well as the megafauna (e.g. anthozoans and echinoderms). Meiofaunal composition is referred to by Schmidt (2013) and Schmidt et al. (submitted). Many of the taxa collected occurred in the samples with very low densities. This could be due to patchiness, as it is known that many deep-sea species occur highly patchily, as singletons in the samples (Brandt et al., 2007a; Brandt et al., 2007b; Brandt et al., 2007c; Kaiser et al., 2007; Kaiser et al., 2009). The KuramBio expedition extended the number of known species in the abyssal depth sampled (Brandt and Maljutina, submitted). Macrofaunal taxa sorted from the C-EBS samples show highest numbers of individuals in hauls 2-9, 2-10 and 3-9 close to the KKT and in haul 12-4 closest to the Japan Trench. At all other stations the numbers of individuals are lower and there are fewer differences between stations. Therefore it cannot be excluded that the high abundances could be due to higher levels of oxygen (Tab. 3.1, but see Huges et al., 2009; Levin and Gage, 1998). In these hauls (2-9, 2-10, 3-9) polychaetes are the dominant taxon (Alalykina, 2013) besides peracarid crustaceans (especially Amphipoda and Isopoda). Dominance of Isopoda and increase in diversity and abundance with increasing depth has already been reported in the past (Brandt et al., 2011; Brandt et al., 2007a; Brandt et al., 2007b; Brandt et al., 2007c; Dahl, 1954; Ebbe et al., 2010; Gage and Tyler, 1991; Golovan et al., 2013; Hessler and Thistle, 1975; Hessler and Wilson, 1983; Hessler and Strömberg, 1989; Rex et al., 1997; Rex et al., 2005a; Rex et al., 2005b), in the Atlantic Ocean in the Angola Basin (Brandt et al., 2005) and in the Southern Ocean (Brandt et al., 2007a; Brandt et al., 2007b; Brandt et al., 2007c) as well as in the Pacific Sea of Japan (except for the lower bathyal and abyssal stations) (Brandt et al., 2013). Peracarid composition was described from the Sea of Japan (Golovan et al., 2013) (**Chapter 4**) where Amphipoda and Cumacea were dominant at the bathyal sites, whereas Isopoda clearly dominated in abundance (but not diversity) at low bathyal and abyssal stations. Cumacea, however, are usually more frequently occurring and more speciose in the deep sea than on the shelf, as they prefer soft sediment (Brandt, 1997a; Brandt and Piepenburg, 1994; Lörz and Brandt, 2003; Mühlenhardt-Siegel, 2011; Piepenburg et al., 1997). Echinodermata usually dominate abyssal benthic communities at least within the megafauna, especially Ophiuroidea (Piepenburg et al., 1997; Piepenburg et al., 2001). At Ross Sea shelf stations echinoderms were by far the most abundant taxon, followed by Arthropoda (24%), Polychaeta (14%), and

Mollusca (12%) (Rehm et al., 2012) in the KuramBio material, however, Holothuroidea are more important than any other echinoderm taxon (Minin et al., 2013; Mironov et al., submitted).

Similarities between stations (Fig. 3.11) shows that most stations differ from each other, even if these are taken almost at the same spot (e.g. 6-11, 6-12 or 10-9, 10-12, and 2-9, 2-10. On the contrary, stations 9-12 and 10-12 as well as 5-10 and 7-10, and even 1-11 are more similar in terms of general taxon composition. Due to the fact that the bottom water temperature and also the oxygen content of these station are similar (Tab. 3.1) cannot explain these differences or similarities, we have to anticipate that differences in taxon compositions can only be explained by random sampling, explanations or interpretations at this stage would probably be mere speculations.

The rank abundance diagram of taxa sampled at all stations (Fig. 3.2) coincides with the species abundance model (Fisher et al., 1943) and shows a logarithmic series (Whittaker, 1972).

During the KuramBio expedition on board of the RV *Sonne* we already identified roughly 700 species from the material sorted, in the meantime many taxa have been worked up in detail and numbers of species will be corrected and may be higher than estimated. For example only two species of Cumacea were known from the KKT area, whereas in the C-EBS samples, 72 species were found (Lavrenteva and Mühlenhardt-Siegel, submitted; Lavrenteva, 2013). About 50 species of Isopoda (Crustacea, Malacostraca) were known from abyssal depths of the Kuril-Kamchatka area (Birstein, 1963, 1970, 1971; Kussakin, 1971, 1972a, b, c, 1978, 1979, 1988, 1999, 2003; Kussakin and Vasina, 1990) and from the KuramBio material composition of the 207 species of Isopoda from these samples is analyzed by Elsner et al. (submitted) (**Chapter 6**) documenting that the KKT isopod fauna is a typical deep-sea fauna consisting mainly of Asellota (97%), of which Munnopsidae (47.4%), and Desmosomatidae (20%) are the dominant families. Only three species of the Desmosomatidae, were described based on few specimens collected by RV *Vityaz* (Birstein, 1963; Kussakin, 1999). In the C-EBS samples, however, 28 species were identified from 922 specimens. 54 specimens of 11 species of Munnopsidae have been sampled by four *Vityaz* expeditions (Birstein, 1963, 1970, 1971; Kussakin, 2003) and from KuramBio samples we already identified 80 species from 4,787 collected munnopsids (for details see Elsner et al., submitted; Malyutina and Brandt, submitted; Golovan, submitted; Brandt et al., submitted). In the Sea of Japan, only one isopod species, *Eurycope spinifrons*, has been found to occur in high abundances at lower bathyal

and abyssal depths (Brandt et al., 2013; Elsner et al., 2013; Golovan et al., 2013; Malyutina et al., 2013).

In the Southern Ocean peracarid crustaceans, polychaetes and bivalve molluscs belonged to the most dominant groups (e.g. Brandt et al., 2007; Brandt et al., 2011). In the Ross Sea (sampled by means of a Rauschert dredge), Amphipoda have been found to dominate within peracarids (Brökeland et al., 2007; Rehm et al., 2012), followed by Isopoda. The high abundances of Amphipoda in the Southern Ocean might be explained by their evolutionary and ecological success on the Antarctic continental shelf (e.g. Arntz et al., 1994; De Broyer and Jazdzewski, 1996; De Broyer et al., 2003), the almost isothermal water column and the deep shelf, favoring species submergence (Brandt, 1991). This could explain the high abundances at Southern Ocean abyssal stations (> 4,000 m) compared to much lower abundances in the Angola basin (Brandt et al., 2005). In the Angola basin, (> 5,000 m), Isopoda were most abundant (1,326 ind./1,000 m²), followed by Cumacea (479 ind./1,000 m²), Tanaidacea (194 ind./1,000 m²), Amphipoda (150 ind./1,000 m²) and Mysidacea (34 ind./1,000 m²) (Brandt et al., 2005). Peracarid abundance data from abyssal samples in the abyssal Weddell Sea were magnitudes higher than those reported from the South Polar Front where only 476 specimens/1000 m² of Isopoda have been sampled at seven stations (Brandt et al., 2007a; Brandt et al., 2007b; Brandt et al., 2007c). In the abyssal Weddell Sea, on the contrary, 13,046 isopod individuals were sampled / 1,000 m² (Brandt et al., 2007a; Brandt et al., 2007b; Brandt et al., 2007c). During these expeditions, in the Powell Basin 10,735 peracarids were collected with a single EBS haul (Brökeland et al., 2007), and over 4,000 polychaetes we sampled in the abyssal Weddell Sea within one EBS cast (Schüller et al., 2009). In the Beagle Channel (shelf - 665 m) abundances of Mollusca, occurred with 107,223 individuals/1,000 m². Within these samples Bivalvia were most abundant (78,615 individuals) followed by Gastropoda (17,289), Aplacophora (4,745), Polyplacophora (4,665) and Scaphopoda (1,909) (Brandt, 1997b, 1999; Linse and Brandt, 1998). In the deep sea in 665 m, we found an abundance of 21,244 molluscs of which bivalves comprised 17,605 individuals (Linse and Brandt, 1998). 55,633 individuals/1,000 m² peracarids were collected in the Beagle Channel at stations between 25–663 m, comprising 15,025 Amphipoda, 28,650 Isopoda, 7,868 Cumacea, 1,636 Mysidacea and 2,454 Tanaidacea (Brandt, 1997b, 1998). Until now, lowest macrofaunal abundances in the abyssal Atlantic were documented in the South Polar Front (Brandt et al., in press), followed by the Angola basin (Brandt et al., 2005), though, stations sampled in the Angola basin were much deeper than those of the South Polar Front.

In the North Atlantic, abundance values of macrofaunal peracarid crustaceans published from north of Iceland and east of Greenland are highest, however, these stations were shallower and mostly sampled on the continental shelf or at the slope (e.g. Brandt, 1993, Brandt et al., 1996; Piepenburg et al., 1997). Peracarids sampled off Greenland (79°N) showed considerably higher abundances. Cumacea occurred with 32,123 ind./1,000 m², followed by Isopoda with 26,914 ind./1,000 m² and Amphipoda with 20,900 ind./1,000 m² in these samples (Brandt and Schnack, 1999). It could be possible that besides depth of the samples age has an importance for abundances and species richness, as the North Atlantic is much younger than the South Atlantic and higher abundances with lower species richness were reported from the European Northern Seas (e.g. Brandt, 1993, 2001, Brandt et al., 1996). General macrofaunal composition of the Sea of Japan compared to that of the open Kuril-Kamchatka abyssal plain shows that Malacostraca (Crustacea) dominate over Polychaeta in this young and semi-enclosed sea, but total numbers of individuals cannot be compared because the data from the Sea of Japan could not be standardized for 1,000 m² trawled distance due to logistic constraints (Brandt et al., 2013). Within the Malacostraca, however, Isopoda also dominated over Amphipoda, Cumacea, Tanaidacea and Mysidacea in the Sea of Japan. In the Pacific Ocean data on macrofaunal abundances from EBS hauls are otherwise not available until now. Therefore, further analyses of the faunal composition of the deep-sea benthos in the Northwest Pacific, including the Sea of Okhotsk, will be necessary for our understanding of macrofaunal abundance and diversity as well as biogeographic ranges and origins of species inhabiting the area.

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I supervised the sample sorting process, conducted the data input and created the graphs for this publication from the resulting matrix.

**Diversity and distribution of peracarid crustaceans (Malacostraca) from
the continental slope and the deep-sea basin of the Sea of Japan**

Chapter 4: Diversity and distribution of peracarid crustaceans (Malacostraca) from the continental slope and the deep-sea basin of the Sea of Japan

Olga A. Golovan^a, Magdalena Błażewicz-Paszkowycz^b, Angelika Brandt^c, Liudmila L. Budnikova^d, **Nikolaus O. Elsner**^c, Victor V. Ivin^a, Anna V. Lavrenteva^{a,f}, Marina V. Malyutina^a, Victor V. Petryashov^e, Ludmila A. Tzareva^a

^a*A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, 17 Palchevsky St, Vladivostok 690041, Russia*

^b*University of Łódź, Laboratory of Polar Biology and Oceanobiology, Banacha 12/16, 90-237 Łódź, Poland*

^c*Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany*

^d*Pacific Research Fisheries Centre (TINRO-Centre), Shevchenko Alley 4, Vladivostok 690950, Russia*

^e*Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St.-Petersburg 199034, Russia*

^f*Far Eastern Federal University, School of Natural Sciences, 29 Oktiabrskaya St, Vladivostok 690091, Russia*

Abstract

During the expedition SoJaBio (Sea of Japan Biodiversity studies) a rich collection of peracarid crustaceans from the slope and the deep-sea basin of the Sea of Japan (at depth range from 450 to 3660 m) was made. The superorder Peracarida was recognized as the most abundant taxon of the macrobenthos in the investigated area and comprised 146 species, 85 genera, 42 families and five orders. From these taxa 93 species, 18 genera and 10 families are reported for the first time in the Sea of Japan below 500 m. Among them, 42 species and two genera were apparently new to science. The diversity and species richness as well as abundance of most of the peracarid species were highest at the shallowest slope stations (~450–550 m) and decreased with depth. Conversely, the abundance of three species, *Eurycope spinifrons* Gurjanova, 1933 (Isopoda), *Chauliopleona hansknechti* Larsen & Shimomura, 2007 and *Paratyphlotanais japonicus* Kudinova-Pasternak, 1984 (Tanaidacea) increased distinctly below the slope (~2600–3300 m). It is assumed that these species are

opportunistic taxa which have recently colonized the geologically young pseudo-abyssal habitats of the Sea of Japan. On the basis of faunistic similarity between 24 stations, three distinct faunal assemblages were identified, distributed on the slope (~450-1500 m), lower slope (~2500-2700 m) and at the pseudoabyssal stations. The key peracarid species for each of them were determined.

Keywords: Crustacea; Malacostraca; Peracarida; diversity; distribution; Sea of Japan; deep sea

Introduction

The Sea of Japan is a relatively young deep-sea basin. It is supposed to have been formed in the Cenozoic as a result of subsidence of the mainland, and connected with the Pacific Ocean by shallow straits (within shelf depth). During Pleistocene glacial periods (from 85–27 kya to 10–8 kya), the Sea of Japan was isolated from the Pacific Ocean owing to the lowering of the sea level; its deep sea became anoxic and reached a state of stagnation (Oba et al., 1991; Tyler, 2002). The circulation resumed in the Holocene. Currently, the deep-sea basin of the Sea of Japan deeper than 500 m is a single homogenous water-mass of the same origin, which derives in winter from the surface water layer mainly in the north-western part of the Sea of Japan. This water mass consists of oxygen-enriched water (up to 70% saturation), colder (0.03–0.4°C) and less salty (34.04–34.13‰) than masses of water at the same depth in the adjacent regions of the Pacific Ocean and the Sea of Okhotsk (Derjugin, 1939; Leonov, 1960; Luchin and Manko, 2003; Tyler, 2002; Zenkevitch, 1963). The Sea of Japan is characterized by a narrow shelf that covers only 24% of the bottom area and a steep continental slope which plunges abruptly (with the ledge of 10-12°, sometimes of 25-30°) into the deep central basin. The sea floor of the deep-sea basin is almost completely flat (Dobrovolsky and Zalogin, 1982; Larina, 1968). The relief contributes to the deposition of sediments when organic material, including the debris of plants, is washed down the slope and accumulates at the sea floor of the deep-sea basin, providing an organic input to the pseudo-abyssal plain. Another feature of the Sea of Japan is its position at the intersection of the boreal and subtropical zone: a boundary between the faunas of different origins and directions of dispersal can be observed at least for the shelf and the upper bathyal (Kafanov, 1991; Kafanov and Kudryashov, 2000; Petryashov, 2005). Thus, owing to its geologically young age, isolation, and geographical

location, the Sea of Japan can be considered a natural model of geological scale to study the processes of colonization of deep-sea areas, dispersal of species and the development of a semi-isolated deep-sea ecosystem that we can observe in its initial stages of succession.

Deep-sea investigations of the Sea of Japan started with the expedition of the Pacific Institute of Fisheries and the State Hydrological Institute in 1932 and then continued with the expeditions on board the RV *Vityaz* in 1972 and 1976. During those investigations, benthic material was collected with Sigsbee trawl and bottom grab samplers (such as the “Ocean” grab sampler). The fauna was described as poor, deprived of true deep-sea elements owing to its isolation and consisted of eurybathic cold-water species present also on the shelf of the adjacent high-boreal regions (Derjugin, 1933, 1939; Nishimura, 1966, 1968, 1969; Zenkevitch, 1963). In addition a low degree of endemism was emphasized and explained by the evolutionary youth of the basin (Zenkevitch, 1963). The relatively low temperature and salinity were identified as potential factors limiting the colonization of the deep-sea basin by the Pacific fauna (Nishimura, 1966; Zenkevitch, 1963).

Until now only some tens of invertebrate species had been recorded from bathyal and abyssal depths of the Sea of Japan (Derjugin, 1939; Nishimura, 1966; Zenkevitch, 1963). However, regarding the small fast-moving epi- and nectobenthic animals, such as the peracarid crustaceans, it is not possible to be sure whether the fauna is actually impoverished or just underreported. For example, the results of the recent CeDAMar (Census of the Diversity of Abyssal Marine Life) expeditions in the Atlantic and the Antarctic have shown that the use of an epibenthic sledge, specially designed for the sampling of the mobile epibenthic macrofauna, revealed that the number of the species was underestimated severalfold, even from previously-studied areas (Brandt et al., 2007a; Brandt et al., 2007b; Malyutina and Brandt, 2007). Furthermore, it has been demonstrated that the Peracarida, together with the Polychaeta, constitute the most abundant and diverse element of macrozoobenthos communities on the slope (Poore et al., unpublished) and in the abyss (Brandt et al., 2005; Brandt et al., 2007a; Brandt et al., 2007b).

In 2010, during the Russian-German deep-sea expedition SoJaBio (Sea of Japan Biodiversity Studies), rich peracarid material was collected at depths between ~450 to 3,660 m (i.e. below the upper limits of the deep-water mass of the sea). It gave an opportunity to reassess the species richness of this group in the deep-sea basin of the Sea of Japan. In addition, an overview of the taxonomic composition and the distribution of the peracarid fauna from the SoJaBio data are presented.

Material and methods

The material for this study was collected in August–September 2010 from the continental slope and in the deep-sea basin of the Sea of Japan, during the Russian-German expedition SoJaBio (Sea of Japan Biodiversity studies) on board the RV *Akademik M. A. Lavrentyev* (Cruise 51) (see Malyutina and Brandt, 2013). Macrofauna was sampled using a newly-modified camera-epibenthic sledge (C-EBS). For detailed description of this gear and the sampling process see Brandt et al. (2013) (**Chapter 2**).

During the expedition, 13 C-EBS stations were sampled with 24 deployments (two deployments at each station apart from A2 and B1) along four transects in the northwestern part of the Sea of Japan and at depths ranging from 455 to 3,666 m (Tab. 4.1). At the two shallowest stations (A2-10, B7-7), the closing mechanism of the C-EBS was blocked by pebbles jamming the mechanism and the nets remained open throughout the water column. In consequence numerous pelagic organisms (Cephalopoda, Copepoda, Euphausiacea and Chaetognatha) were caught in addition to the benthic sample, which has been taken into consideration during the analyses.

All the samples were washed onboard with ice-cold water immediately after hauling, through sieves of 300 µm mesh size. The material from the first deployment at each station was fixed in pre-cooled 96% ethanol for genetic studies, while the sample from the second deployment was initially preserved in 4% formaldehyde for morphological studies, and then washed and re-fixed in 96% ethanol 48 hours later. The material was sorted into the major taxonomic groups using stereomicroscopes, initially on board the vessel, and later in the laboratories at the Institute of Marine Biology (Vladivostok) and in the Zoological Museum of the University of Hamburg. In the case of the “ethanol” samples, iced platens for keeping specimens at low temperature were used. All the “ethanol” samples have been kept in the freezer. The samples from the epi- and supra- C-EBS nets were sorted separately, but for the analysis the data from the epi- and supra- macrofaunal fractions of the same sample were combined.

Peracarida were found in all samples. In total, 57,797 peracarid individuals were studied and identified to the species or genus level, or in a few cases to the family level.

As it was impossible to measure precisely the speed of the ship or the winch, or the tension of the wire, only approximate trawling distances could be estimated. For this reason we refrained from standardization of the hauls to 1,000 m trawling distance and the samples were not regarded as quantitative. Nevertheless even the raw data might be used for estimation of the

character and dominance structure of the communities, as well as for comparison of the assemblages (based on presence or absence of the species) and of approximate abundance of the macrobenthos between the stations.

Tab. 4.1: SoJaBio C-EBS station list.

Assemblage	Station	Date (2010)	Depth (m)	Haul	start	Haul	end	S	N	ES[50]
I	A2-10	14.08.	455–465	44°56.9197'N	137°11.8947'E	44°57.0966'N	137°12.0732'E	93	27,012	22.8
	A3-10	14.08.	1354–1356	44°49.8620'N	137°13.9974'E	44°50.0210'N	137°14.0932'E	35	245	17.2
	A3-11	14–15.08.	1494–1525	44°47.6338'N	137°15.3182'E	44°47.8110'N	137°15.3922'E	24	541	10.6
	B6-6	25.08.	970–994	43°10.6362'N	135°00.8476'E	43°10.4546'N	135°00.8247'E	26	417	9.6
	B6-7	25.08.	1001–1011	43°10.3999'N	135°00.9751'E	43°10.2513'N	135°00.9239'E	25	247	13.5
	B7-6	25.08.	517–521	43°13.4229'N	135°04.2286'E	43°13.5581'N	135°04.3569'E	46	949	13.9
	B7-7	25.08.	470–528	43°13.4578'N	135°04.3295'E	43°13.5809'N	135°04.1939'E	78	3558	22.9
II	A6-7	16.08.	2511–2534	44°19.4270'N	137°24.1964'E	44°19.2650'N	137°24.1206'E	11	274	7.5
	A6-8	16.08.	2545–2555	44°18.6270'N	137°24.4079'E	44°18.4712'N	137°24.3985'E	16	716	7.4
	B5-8	23.08.	2609–2655	43°01.3064'N	135°05.9562'E	43°00.9363'N	135°06.5366'E	8	936	2.9
	C1-8	27.08.	2670–2681	42°26.5832'N	133°09.1471'E	42°26.6230'N	133°09.3740'E	14	1293	4.4
	C1-9	27.08.	2693–2725	42°26.4275'N	133°08.6525'E	42°26.4636'N	133°08.8737'E	9	794	3.8
	D2-8	01.09.	2653–2683	42°06.6051'N	131°21.0149'E	42°06.4555'N	131°20.9308'E	11	239	8.5
III	A7-8	17.08.	3345–3357	44°00.8871'N	137°29.7822'E	44°00.7933'N	137°29.8060'E	4	2511	2.2
	A7-9	18.08.	3340–3347	44°00.8871'N	137°29.7822'E	44°00.1668'N	137°31.3496'E	4	845	1.7
	B1-7	19.08.	3665–3666	42°15.5533'N	136°43.2772'E	42°15.7357'N	136°43.3044'E	2	1904	1.0
	B4-7	21.08.	3298–3353	43°01.5063'N	135°26.4484'E	43°01.3831'N	135°26.3669'E	5	2830	1.8
	B4-8	21–22.08.	3312–3334	43°01.3440'N	135°28.0092'E	43°01.2126'N	135°28.1308'E	2	2790	1.0
	B5-7	23.08.	2661–2688	43°01.6964'N	135°05.2859'E	43°01.7360'N	135°05.4958'E	2	228	2.0
	C3-3	28.08.	3431–3435	42°01.3458'N	133°09.7454'E	42°01.2359'N	133°09.8746'E	3	3131	2.0
	C3-4	28.08.	3427–3431	42°01.5613'N	133°09.5741'E	42°01.4637'N	133°09.7381'E	1	1754	1.0
	D1-3	30.08.	3355–3357	41°28.3497'N	131°46.6929'E	41°28.1326'N	131°46.4722'E	3	1082	1.9
	D1-4	30.08.	3356	41°28.7198'N	131°46.7702'E	41°28.6028'N	131°46.6796'E	1	4	1.0
D2-7	01.09.	2619–2637	42°07.1711'N	131°21.1091'E	42°07.0405'N	131°21.0345'E	8	2494	3.2	

Multivariate analyses were performed using the Plymouth Routines in the Multivariate Ecological Research (PRIMER) package, version 6.0 (Clarke and Gorley, 2006). The raw data were initially transformed to presence/absence data, which provided information about the species composition of the community. A triangular similarity matrix between every pair of stations was constructed using the Bray-Curtis similarity index (Bray and Curtis, 1957). This matrix was then subjected to hierarchical clustering methods using group-average linking (CLUSTER) and ordination using non-metric multidimensional scaling (nMDS) (Clarke, 1993). Formal significance tests for differences between the groups of samples, as determined

via CLUSTER and nMDS, were performed using the ANOSIM permutation test (Clarke and Ainsworth, 1993). ANOSIM's statistic R estimates the difference between average rank similarity among samples within each of the groups and the average rank similarity between groups. The taxa contributing to dissimilarities between groups of samples were investigated using the similarities percentages procedure SIMPER (Clarke and Ainsworth, 1993; Clarke and Warwick, 2001). In order to select the dominant species of each of the complexes, the relative "contribution" of the species to the average intra-complex affinity was estimated. Peracarid diversity was calculated using the Hurlbert rarefaction index ES[50] (Magurran, 1995).

Results

Taxonomic composition

Crustaceans were predominant in the communities of macrobenthos of the sampled area, constituting 57.3% of all specimens in the C-EBS samples. The superorder Peracarida was the dominant taxon, exceeding even the class Polychaeta (31.4%) in abundance (see also Brandt et al., 2013). The proportion of the Peracarida was even higher (40.9%) when the mostly planktonic groups (pelagic Cephalopoda, Copepoda, Euphausiacea and Chaetognatha) were excluded from the analysis.

The peracarids were represented by five main orders. Isopoda was the most abundant order, comprising 15.2% of all specimens of the macrobenthos and 37% of all peracarids. Amphipoda ranked second in abundance (11.8% and 28.7%, respectively), followed by Cumacea (7.7% and 18.8% respectively) and Tanaidacea (5.5% and 13.4%). Mysida was the least abundant group of peracarids (0.9%, 2.1%) (Fig. 4.1).

The Peracarida included 146 species, 85 genera and 42 families (Tab. 4.2). Ninety-three species (63.7% of the species list), 18 genera and 10 families were recorded for the first time from the deep-sea basin of the Sea of Japan below 450–500 m. Among these, 17 species of Amphipoda, nine species of Isopoda, seven species of Cumacea, eight species and two genera of Tanaidacea and one species of Mysida were apparently new to science. It is assumed, that intensive taxonomic studies will increase the present number of species, as some of the identified morphospecies (e.g. *Eudorella* spp. 2 (Cumacea), *Westwoodilla* spp. and *Bathymedon* spp. (Amphipoda)) are probably complexes of species.

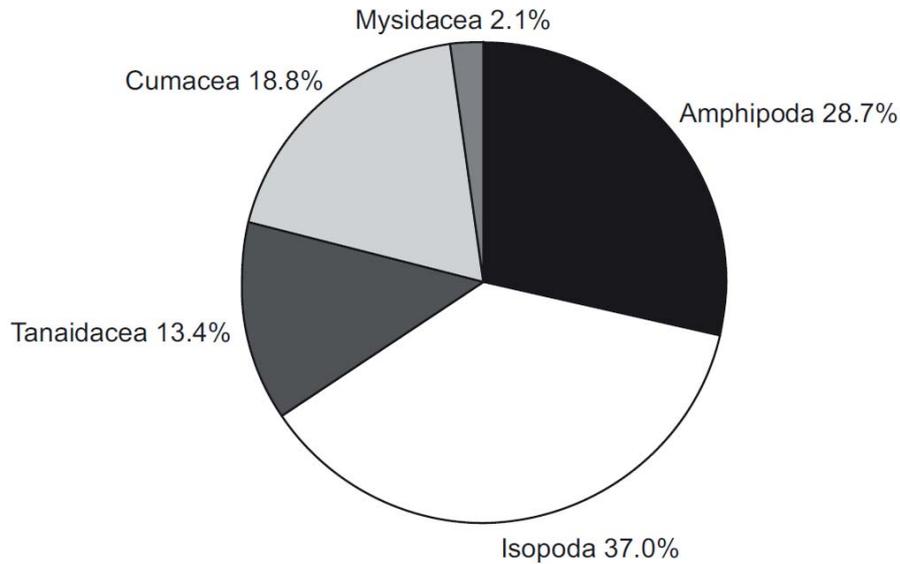


Fig. 4.1: Proportions of the number of specimens by the orders of Peracarida in SoJaBio C-EBS samples.

Despite being less abundant than the Isopoda, the Amphipoda was the most diverse peracarid order, being represented by 65 species, 41 genera, 21 families and three suborders. Two species belonged to the pelagic suborder Hyperiidea, one to the climbing Caprellidea and 62 species were members of 18 families of the Gammaridea. The most diverse gammarid families were the Oedicerotidae (15 species) and Stenothoidae (11), with a predominance of the genera *Monoculodes* (7) and *Metopa* (8) respectively. The remaining families were represented by less than four species. Hitherto 27 (41%) of amphipod taxa were identified to the species level while for the others only the genus was ascertained. Seventeen species were found in the deep-sea basin of the Sea of Japan at depths ≥ 450 m for the first time; two genera *Bruzelia* (?) and *Pardaliscella* (?) were new for the Sea of Japan. It is assumed that most of the amphipod species identified to genus level might be new species to science, while some of the species belonging to the genera *Monoculodes*, *Westwoodilla*, *Bathymedon*, or *Aceroides* will eventually be attributed to already-known species, although at the moment reliable identification is impossible owing to incomplete and poorly-illustrated original descriptions.

Tab. 4.2: List of Peracarida of the continental slope and the deep-sea basin of the Sea of Japan according to the expedition SoJaBio.

Order	Suborder	Family	Species	SoJaBio stations	
Amphipoda	Caprellidea	Caprellidae	Caprellidae gen sp.	A2-10	
	Gammaridea	Ampeliscidae	<i>Ampelisca furcigera</i> Bulycheva, 1936	A2-10	
			<i>A. macrocephala</i> Liljeborg, 1852	A2-10	
			<i>Byblis</i> sp.	A2-10	
			<i>Haploops sibirica</i> Gurjanova, 1929 (here this species is considered as valid)	A2-10	
			Argissidae	<i>Argissa hamatipes</i> (Norman, 1869) (?)	A2-10
				Dexaminidae	<i>Guernea</i> sp.
			Dogielinotidae	Dogielinotidae (?) gen. sp.	A6-8, B7-6, B7-7
			Eusiridae	<i>Eusirus cuspidatus</i> Krøyer, 1845	A2-10, B7-7
				<i>Leptamphopus longimanus</i> (Boeck, 1871)	A6-8, B7-6
				<i>Rhachotropis oculata</i> (Hansen, 1888)	A2-10
		<i>Rhachotropis</i> sp. 1		A2-10, A3-10, A3-11, B6-6, B7-6, B7-7	
		Lysianassidae	<i>Lepidepcreum comatum</i> Gurjanova, 1962 (?)	B7-7	
			<i>Orchomenella</i> sp.	A2-10, A3-10, A3-11	
		Melphidippidae	<i>Melphidippa macruroides</i> Gurjanova, 1946	A2-10	
			<i>Melphidippa</i> sp.	A2-10, B7-6, B7-7	
		Oedicerotidae	<i>Aceroides</i> (?) sp.	A3-10, A3-11, B7-6, B7-7	
			<i>Arrhis lüthkei</i> Gurjanova, 1936 (?)	B7-6, B7-7	
			<i>Bathymedon</i> sp.	A2-10, A3-10, A3-11, A6-7, A6-8, B6-6, B7-6, B7-7, C1-8	
			<i>Monoculodes semenovi</i> Gurjanova, 1938 (?)	A2-10	
			<i>M. synophthalmus</i> Bulytscheva, 1952 (?)	A3-10	
			<i>Monoculodes</i> sp. 1	A2-10, A3-10, A3-11, A6-7, A6-8, B5-8, B6-6, B7-6, B7-7, C1-8, C1-9, D2-8	
			<i>Monoculodes</i> sp. 2	A2-10, A3-11, A6-8, B4-7, B7-6, B7-7, C1-8, D2-8	
			<i>Monoculodes</i> sp. 3	A2-10, A6-8, B4-7, B7-7	
			<i>Monoculodes</i> sp. 4	A2-10	
			<i>Monoculodes</i> sp. 5	A3-11, A6-8, B6-6, B7-6, B7-7, D2-8	
			<i>Paroedicerus lynceus</i> (Sars, 1858)	A2-10, B7-7	
			<i>Paroedicerus</i> sp.	A2-10	
			<i>Perioculodes</i> (?) sp.	A2-10, B7-7	
			<i>Synchelidium gurjanovae</i> Kudrjaschov et Tzvetkova, 1975 (?)	A2-10, B7-7	
			<i>Westwoodilla</i> sp.	A2-10, A3-10, A3-11, A6-8, B5-8, B6-6, B7-6, B7-7, C1-8, C1-9, D2-8	
			Pardaliscidae	<i>Nicippe tumida</i> Bruzelius, 1859	A2-10, B6-6
		<i>Pardaliscella</i> (?) sp.		A6-8	
		Photidae	<i>Gammaropsis</i> (?) sp.	A2-10, C1-8, C1-9, D2-8	
			<i>Protomedeia</i> (?) sp.	A2-10	
		Phoxocephalidae	<i>Harpiniopsis orientalis</i> (Bulycheva, 1936)	A6-7, B7-6	
			<i>H. pacifica</i> (Bulycheva, 1936) (?)	A6-7, A6-8, B5-8, D2-8	
			<i>H. tarasovi</i> (Bulycheva, 1936)	A2-10, B7-6, B7-7	
			<i>Harpiniopsis</i> sp.	B7-7	
		Pleustidae	<i>Parapleustes</i> (?) sp.	B7-7	
	Podoceridae	<i>Dulichia</i> sp.	B6-6, B7-7		

	Stegocephalidae	<i>Andaniopsis</i> (?) sp.	C1-8, C1-9, D2-8
		<i>Phippsiella</i> (?) sp. or <i>Stegocephalus</i> (?) sp.	A6-8, C1-8
		<i>Stegocephalopsis</i> (?)	B6-6
	Stenothoidae	<i>Metopa clypeata</i> (Krøyer, 1842) (?)	A2-10
		<i>Metopa</i> (?) sp. 1	A2-10, A3-10
		<i>Metopa</i> (?) sp. 2	A2-10, B7-7
		<i>Metopa</i> (?) sp. 3	A2-10, B7-7
		<i>Metopa</i> (?) sp. 4	A2-10, B7-7
		<i>Metopa</i> (?) sp. 5	A2-10
		<i>Metopa</i> (?) sp. 6	A2-10
		<i>Metopa</i> (?) sp. 7	A2-10, B7-7
		<i>Metopelloides</i> (?) sp.	A2-10, B7-7
		<i>Parametopella stelleri</i> Gurjanova, 1948 (?)	A2-10
		<i>Stenothoides</i> (?) <i>Metopa</i> (?) sp.	A2-10
	Synopiidae	<i>Bruzelia</i> (?) sp.	A2-10
		<i>Syrrhoe</i> sp.	A2-10, A3-10, B7-6, B7-7
		<i>Tiron spiniferus</i> (Stimpson, 1853)	A2-10
	Uristidae	<i>Anonyx derjugini</i> Gurjanova, 1962	A6-7, A6-8, B5-8, C1-8, C1-9, D2-8
		<i>A. liljeborgii</i> Boeck, 1870	A2-10
		<i>A. ochoticus</i> Gurjanova, 1962 (?)	A3-11
		<i>Anonyx</i> sp.	A6-8
	Urothoidae	<i>Urothoe denticulata</i> Gurjanova, 1951	A2-10
Hyperiidea	Hyperiidae	<i>Themisto japonica</i> (Bovallius, 1887)	A2-10, A3-10, A3-11, A6-7, A7-9, B6-6, B7-6, B7-7, C1-8
	Phrosinidae	<i>Primno macropa</i> Guerin-Meneville, 1836 (?)	A2-10, A3-10, B7-6, B7-7
Cumacea	Diastylidae	<i>Brachydiastylis hexaceros</i> Lomakina, 1952	A2-10
		<i>Diastylis bidentata</i> Calman, 1912	A2-10
		<i>D. loricata</i> Lomakina, 1955 (?)	B6-7, B7-7
		<i>D. ornata</i> Lomakina, 1952 (?)	A2-10, A3-10, B7-6, B7-7
		<i>D. paraspinus</i> Zimmer, 1926	A2-10, A3-10, A3-11, B6-7, B7-6, B7-7
		<i>Leptostylis villosa</i> Sars, 1869	B7-7
		<i>Leptostylis</i> sp. 1	A2-10, A3-10
		<i>Makrokyllindrus</i> (<i>Adiastylis</i>) <i>hirsuta</i> (Lomakina 1955)	A2-10, A3-11, B6-7, B7-6, B7-7
		<i>Paraleptostylis viryazi</i> Vassilenko et Tzareva, 2004 (?)	B7-7
		Diastylidae (?) gen. sp. 1	B7-7
	Lampropidae	<i>Hemilamprops pectinatus</i> Lomakina, 1955	A2-10, A3-10, B6-7, B7-6, B7-7
		<i>Hemilamprops</i> (?) sp. 1	B7-7
		<i>Lamprops fuscatus</i> Sars, 1865 (?)	A2-10, B7-7
	Leuconidae	<i>Eudorella emarginata</i> (Krøyer, 1846)	B6-7
		<i>E. pacifica</i> Hart, 1930	B6-7
		<i>Eudorella</i> sp. 1	A3-11, C1-9
		<i>Eudorella</i> spp. 2	A2-10, A3-10, A3-11, A7-8, B5-8, B6-6, B6-7, B7-6, B7-7
		<i>Eudorellopsis uschakovi</i> Lomakina, 1955	A2-10, B7-6, B7-7
		<i>Leucon acutirostris</i> G.O. Sars, 1865 (?)	A2-10, B7-7
		<i>L. fulvus</i> G.O. Sars, 1865 (?)	A2-10, A3-10, A3-11, A6-7, A6-8, A7-8, B5-8, B6-6, B6-7, B7-6, B7-7, C1-8, C1-9, D2-8

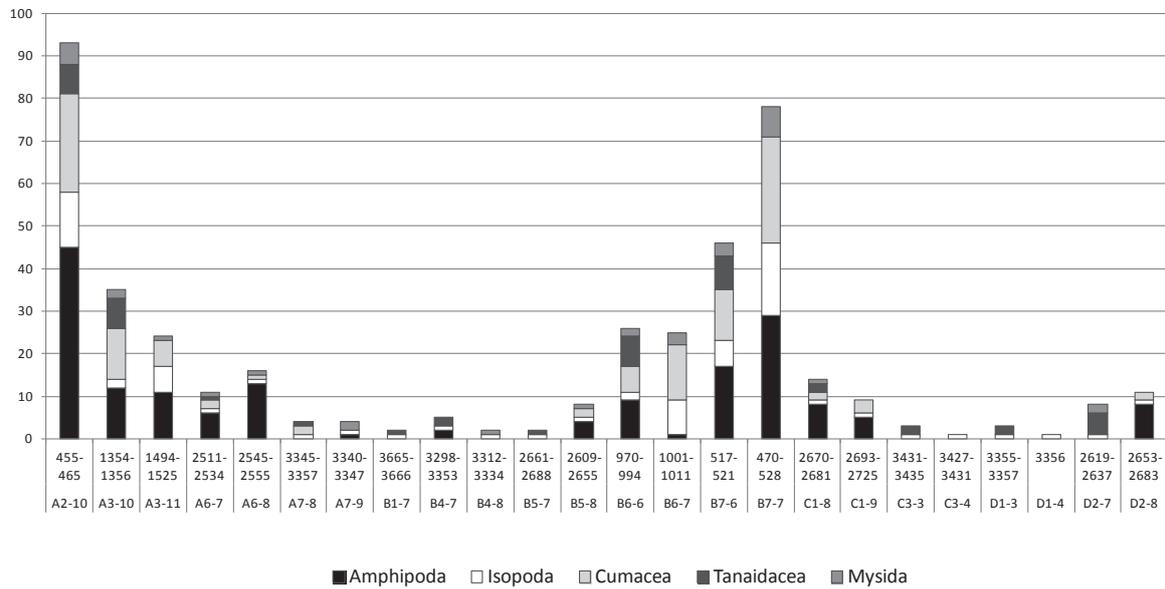
			<i>L. kobjakovae</i> Lomakina, 1955	A2-10, A3-10, B6-6, B6-7, B7-7
			<i>L. minor</i> Lomakina, 1955 (?)	A2-10, A6-7, B6-7, B7-7
			<i>Leucon</i> sp. 1	C1-9
			<i>Leucon</i> sp. 2	A2-10, A3-11, B7-6, B7-7
			Leuconidae (?) gen. sp. 1	A2-10
			Leuconidae (?) gen. sp. 2	B7-7
		Nannastacidae	<i>Campylaspis clavata</i> Lomakina, 1952	A2-10, B7-6
			<i>C. crisper</i> Lomakina, 1955	A2-10, B6-6, B7-7
			<i>C. papillata</i> Lomakina, 1952	A2-10, A3-10, B7-7
			<i>C. rubicunda</i> (Liljeborg, 1855)	A2-10, B6-7, B7-6, B7-7
			<i>Campylaspis</i> sp. 1	A2-10, A3-10, B6-6, B6-7, B7-6, B7-7
			<i>Campylaspis</i> sp. 3	B7-7
			<i>Cumella</i> (?) sp. 1	A3-10
			<i>Cumella</i> sp. 2	A2-10
			<i>Pavlovskeola</i> (?) sp. 1	B7-7, B6-6, B6-7,
		Pseudocumidae	<i>Petalosarsia declivis</i> (Sars, 1865)	A2-10, A3-10, B7-6, B7-7
Isopoda	Asellota	Desmosomatidae	<i>Desmosoma lobipes</i> Kussakin, 1965	A3-11, B7-7
			<i>Desmosoma</i> sp. 1	A2-10, B7-7
			<i>Desmosoma</i> sp. 2	A2-10, B7-7
			<i>Eugerdia fragilis</i> (Kussakin, 1965)	A2-10, A3-10, A3-11, B6-7, B7-7
			<i>Eugerdia</i> (?) sp. 1	A2-10, B7-7
			<i>Eugerdia</i> (?) sp. 2	B7-7
			<i>Mirabilicoxa kussakini</i> Golovan, 2007	A2-10, B6-7, B7-7
			<i>Mirabilicoxa</i> sp.	A3-11, B6-7, B7-7
			<i>Prochelator</i> sp.	B7-7
			Desmosomatidae gen. sp. 8	A2-10, B7-7
			Desmosomatidae gen. sp. 18	B7-7
		Munnidae	<i>Munna</i> sp. A2-10	
		Munnopsidae	<i>Baeonectes brandtae</i> Malyutina et al., 2013	A2-10, A3-10, A3-11, B6-6, B6-7, B7-6, B7-7
			<i>Eurycope spinifrons</i> Gurjanova, 1933	A2-10, A3-11, A6-7, A6-8, A7-8, A7-9, B1-7, B4-7, B4-8, B5-7, B5-8, B6-7, B7-7, C1-8, C1-9, C3-3, C3-4, D1-3, D2-7, D2-8
			<i>Ilyarachna zachsi</i> Gurjanova, 1933	A2-10, B7-6, B7-7
			<i>Munnopsurus minutus</i> Gurjanova, 1933	B7-7
		Paramunnidae	<i>Pleurogonium</i> aff. <i>kyusuense</i> Shimomura, 2009	A2-10, B6-7, B7-6, B7-7
	Epicaridea	Bopyridae	<i>Bopyroides hippolytes</i> (Krøyer, 1838)	A2-10
			<i>Hemiarthrus abdominalis</i> (Krøyer, 1840)	B7-6
			Bopyridae gen.sp. (cryptoniscium)	B6-7
		Dajidae	Dajidae gen.sp.	B7-6
	Gnathiidea	Gnathiidae	<i>Caecognathia elongata</i> (Krøyer, 1849)	A2-10, A3-11, B6-6, B7-6, B7-7
Mysida	Mysida	Mysidae	<i>Holmesiella anomala</i> Ortmann, 1908	A2-10, B7-6, B7-7
			<i>Meterythrops microphthalma</i> W.M. Tattersall, 1951	A2-10, A7-9, B6-6, B6-7, B7-6, B7-7
			<i>Meterythrops</i> sp. aff. Murano, 1977	A2-10, B6-7, B7-7
			<i>Mysidella orientalis</i> Murano, 2002	B7-7
			<i>Pseudomma izuensis</i> Murano, 1966	B7-7

			<i>P. okiyamai</i> Murano, 1974	A3-10, A3-11, A6-7, A6-8, A7-9, B4-8, B5-8, B6-6, B6-7, B7-6, B7-7, C1-8, D2-7
			<i>P. truncatum</i> Smith, 1879	A2-10
			<i>Pseudomma</i> sp.	A2-10, A3-10
			<i>Stilomysis major</i> W.M. Tattersall, 1951	B7-7
Tanaidacea	Apseudomorpha	Sphyrapodidae	<i>Pseudosphyrapus malyuinae</i> sp. n.	A2-10, A3-10, B6-6
	Tanaidomorpha	Akanthophoreidae	<i>Akanthophoreus lispopygmos</i> sp. n.	A2-10, B6-6, B7-6
			<i>Akanthophoreus verutus</i> sp. n.	B6-6, B7-6, D2-7
			<i>Chauliopteona hansknechti</i> Larsen et Shimomura, 2007	A2-10, A3-10, D2-7
		Anarthruridae	<i>Keska sei</i> sp. n.	A3-10, B6-6, B7-6
			indet. manca	C1-8, D2-8
		Colletteidaesensu lato	<i>Nippognathiopsis petila</i> sp. n.	A3-10, B7-6
		Pseudotanaidae	<i>Pseudotanais abathagastor</i> sp. n.	A2-10, B7-6
			<i>Pseudotanais intortus</i> sp. n.	B7-6, B6-6
			<i>Pseudotanais soja</i> sp. n.	A3-10, B7-6
			<i>Pseudotanais</i> sp. A	A2-10
		Tanaellidae	<i>Tanaella kommitza</i> Larsen et Shimomura, 2007	B6-6
		Tanaopsidae	<i>Tanaopsis rugaris</i> sp. n.	A2-10
		Typhlotanaidae	<i>Paratyphlotanais japonicus</i> Kudinova-Pasternak, 1984	A6-7, A7-8, B4-7, B5-7, C1-8, C3-3, D1-3, D2-7
			<i>Torquella</i> sp.	D2-7
			<i>Typhlotanais simplex</i> Kudinova-Pasternak, 1984	A2-10, A3-10, B4-7, B6-6, B7-6, C3-3, D1-3, D2-7

Tab. 4.3: Results of ANOSIM test comparing within group and between group similarities of peracarid crustaceans assemblages I-III.

	R	P
Global test	0.929	0.001
Pair wise contrasts:		
I-II	0.905	0.060
I-III	0.999	0.003
II-III	0.008	0.891

A



B

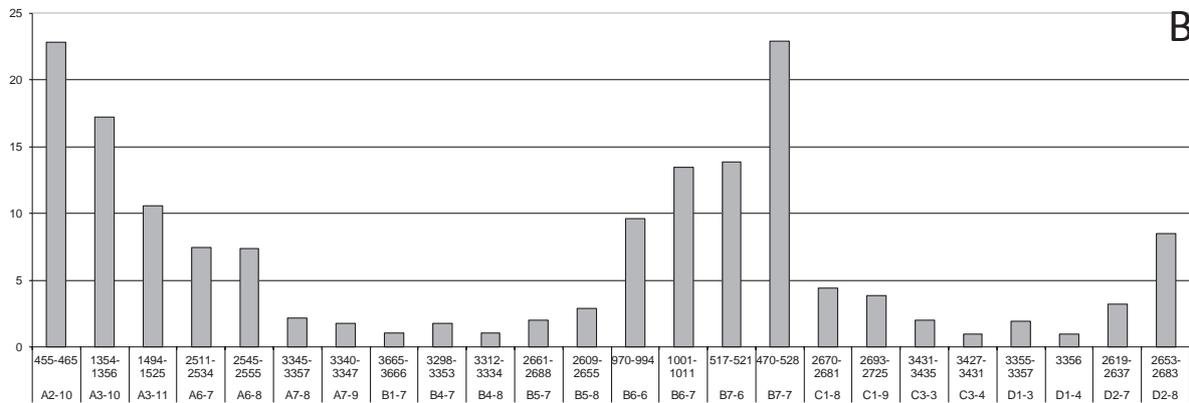


Fig. 4.2. The number of peracarid species per SoJaBio C-EBS stations (A) and Hurlbert rarefaction index ES[50] (B).

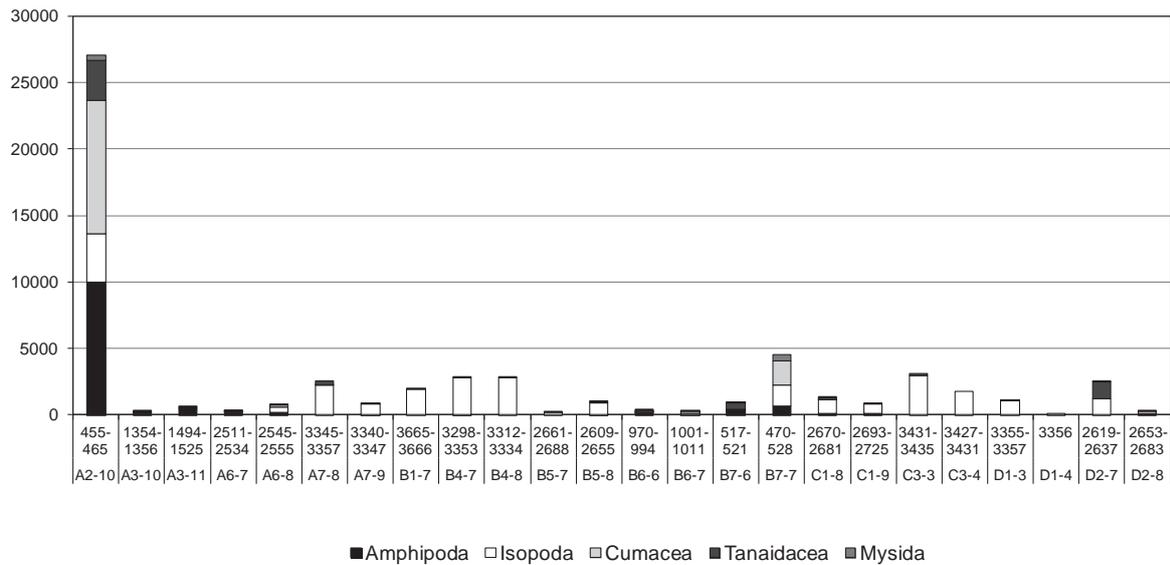


Fig. 4.3: The number of peracarid specimens per SoJaBio C-EBS stations.

Cumacea ranked second of the peracarid orders in term of richness, represented by 36 species, 14 genera and five families. The predominant families were the Leuconidae (13 species) with the richest genera *Eudorella* (4 species, probably in complexes) and *Leucon* (6). They are followed by the Diastylidae (10) with the genus *Diastylis* (4), and the Nannastacidae (9) with the genus *Campylaspis* (6). Twenty-two of the taxa were identified to species level. The undefined species of the genera *Leucon*, *Campylaspis* and *Eudorella* are apparently new to science. The following taxa have been recorded below 500 m for the first time: the genera *Lamprops* (at ~500 m), *Pavlovskeola* (up to 1,000 m depth), *Cumella* and the family Pseudocumidae (the genus *Petalosarsia*, up to 1,356 m depth in SoJaBio material).

Isopoda was represented by 22 species, 14 genera, seven families and three suborders. The members of the suborder Asellota prevailed, mainly represented by the primarily deep-sea families Munnopsidae (four species) and Desmosomatidae (at least 11 species). It is possible that the desmosomatid species list will be extended, as it includes at present only those morphospecies (most likely new species) for which mature males were found. The exception is one species of the genus *Prochelator*, collected as a few specimens, for which identification is possible from the female. Three other undefined desmosomatid morphospecies were represented in the material by females only and they have not been included in the list.

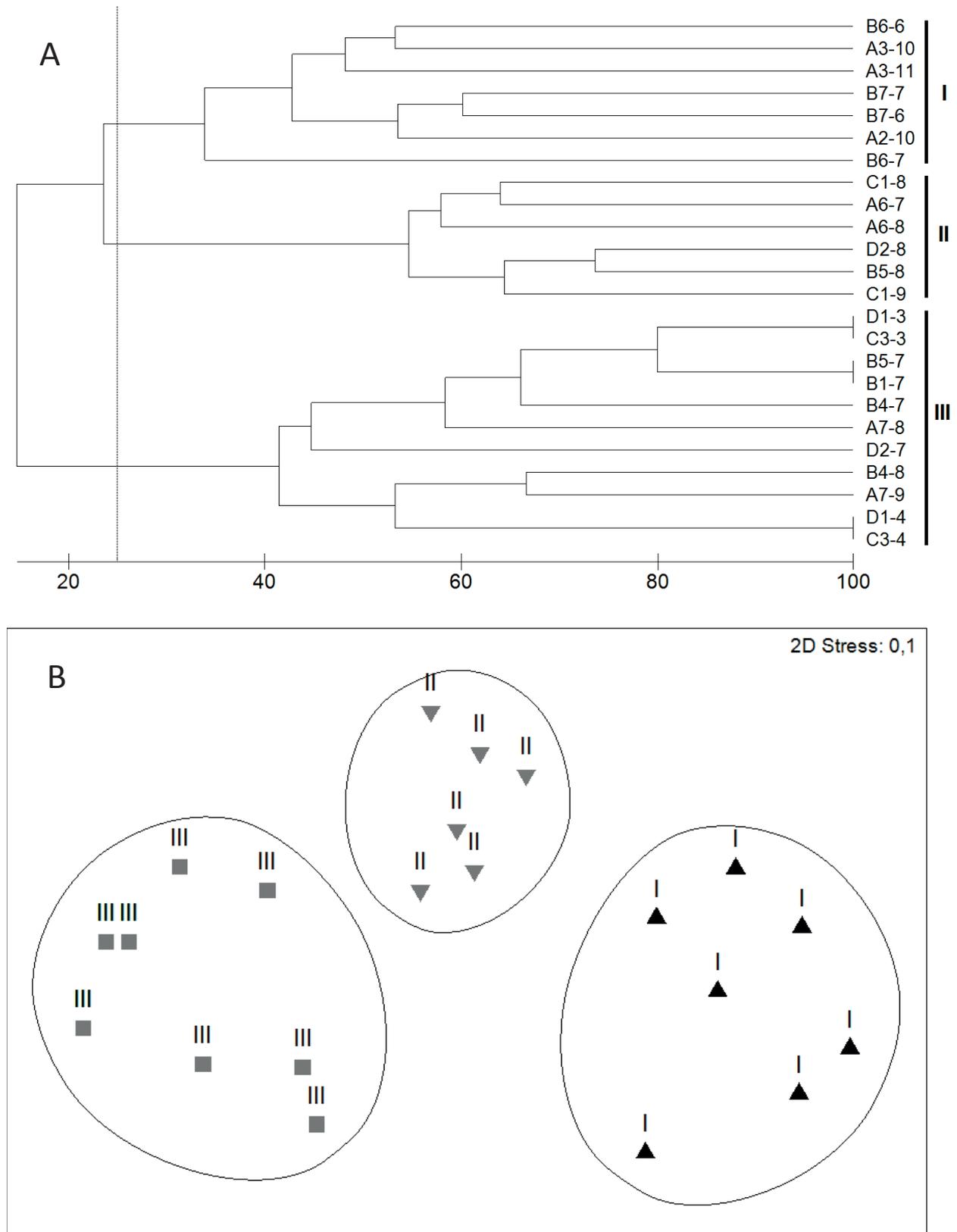


Fig. 4.4: Dendrogram (A) and nMDS ordination plots (B) of peracarid assemblages on the continental slope and the deep-sea basin of the Sea of Japan.

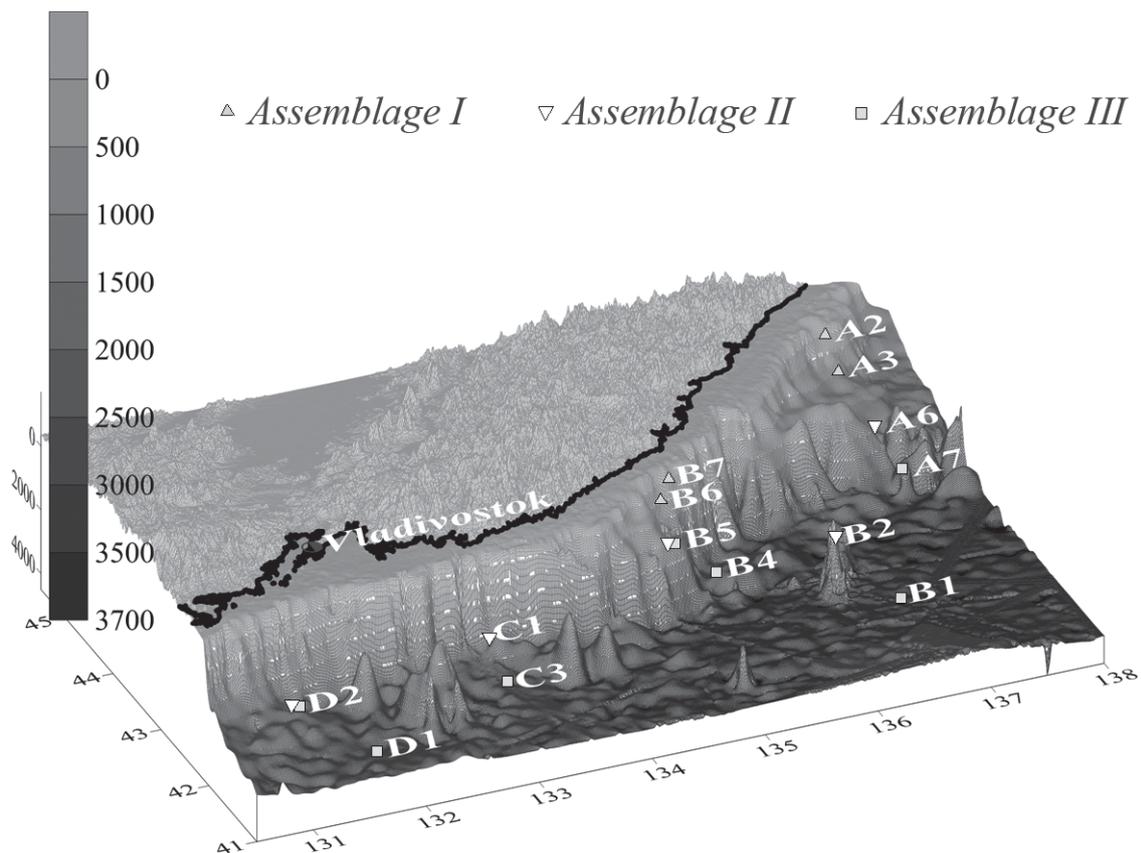


Fig. 4.5: Map of the SoJaBio C-EBS stations with the distribution of three peracarid species assemblages.

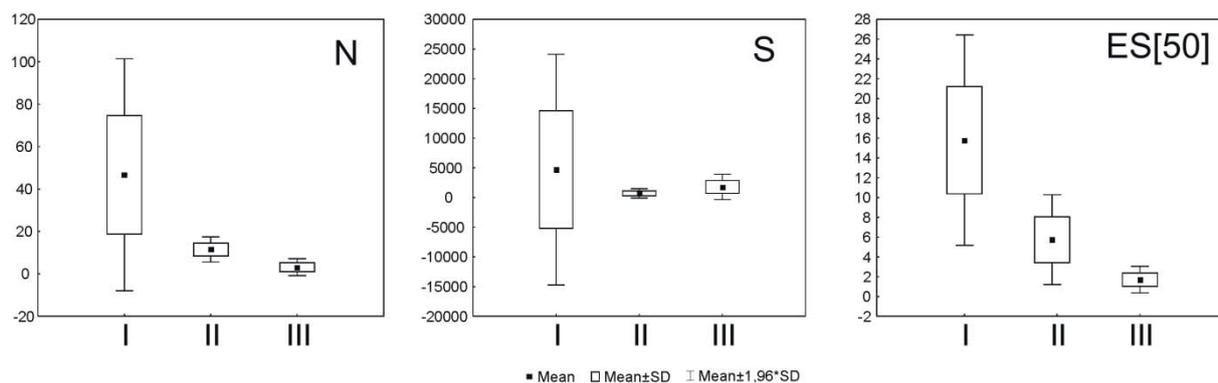


Fig. 4.6: The mean value of species richness (S), Hurlbert rarefaction index ES[50] and number of specimens (N) for three peracarid species assemblages (I-III).

Tab. 4.4: Results from SIMPER analysis of the Peracarida (data presence/absence transformed), listing the most characteristic species within each assemblage (to a total of 50% contribution).

Assemblage		Average frequency	Average similarity	Contribution (%)	Cumulative (%)	Average similarity (%)
I	<i>Baeonectes brandtae</i>	1	2.46	5.86	5.86	42.01
	<i>Eudorella</i> spp. 2	2	1	2.46	5.86	11.72
	<i>Leucon fulvus</i> (?)	1	2.46	5.86	17.58	
	<i>Pseudomma okiyamai</i>	0.86	2.02	4.81	22.39	
	<i>Diastylis paraspinus</i>	0.86	1.62	3.86	26.24	
	<i>Themisto japonica</i>	0.86	1.6	3.81	30.05	
	<i>Primno macropa</i> (?)	0.86	1.6	3.81	33.86	
	<i>Rhachotropis</i> sp. 1	0.86	1.6	3.81	37.67	
	<i>Westwoodilla</i> spp.	0.86	1.6	3.81	41.48	
	<i>Monoculodes</i> sp. 1	0.86	1.6	3.81	45.29	
	<i>Bathymedon</i> spp.	0.86	1.6	3.81	49.1	
	<i>Campylaspis</i> sp. 1	0.86	1.6	3.81	52.91	
II	<i>Anonyx derjugini</i>	1	8.9	15.45	15.45	57.62
	<i>Monoculodes</i> sp.	1	8.9	15.45	30.89	
	<i>Eurycope spinifrons</i>	1	8.9	15.45	46.34	
	<i>Leucon fulvus</i> (?)	1	8.9	15.45	61.78	
III	<i>Eurycope spinifrons</i>	1	37.44	71.35	71.35	52.47
	<i>Paratyphlotanais japonicus</i>	0.64	11	20.96	92.32	

Two species of the mostly shallow-water asellote families Munnidae and Paramunnidae were found at the slope stations (at ~450 m and 450–1,000 m respectively), as well as the parasitic suborders Epicaridea (four species) and Gnathiidea (one species). Only nine taxa were identified to species level and those identified to genus level are apparently new to science. The description of one new species, *Baeonectes brandtae* Malyutina *et al.*, is published in (2013). Twelve other species, five genera and three families (Munnidae, Paramunnidae and Dajidae) were found in the Sea of Japan at bathyal depths ≥ 500 m for the first time also. The Family Dajidae has never been recorded in the Sea of Japan before. For two other families the species occurring on the shelf of the Sea of Japan are known (Golovan and Malyutina, 2010).

The order Tanaidacea was represented by 15 species, 11 genera, eight families and two suborders (Błażewicz-Paszkwycz *et al.*, 2013). Other than *Pseudosphyrapus malyutinae* (Apseudomorpha), all the species belong to the suborder Tanaidomorpha. Four tanaidomorph species appeared to be previously-described taxa, while the other ten species and two genera were apparently new. Two of the previously described species were new for the Sea of Japan.

The order Mysida was represented by eight species, five genera and one family. One species, *Meterythropus* sp. aff. *Murano*, 1977, seems to be new to science.

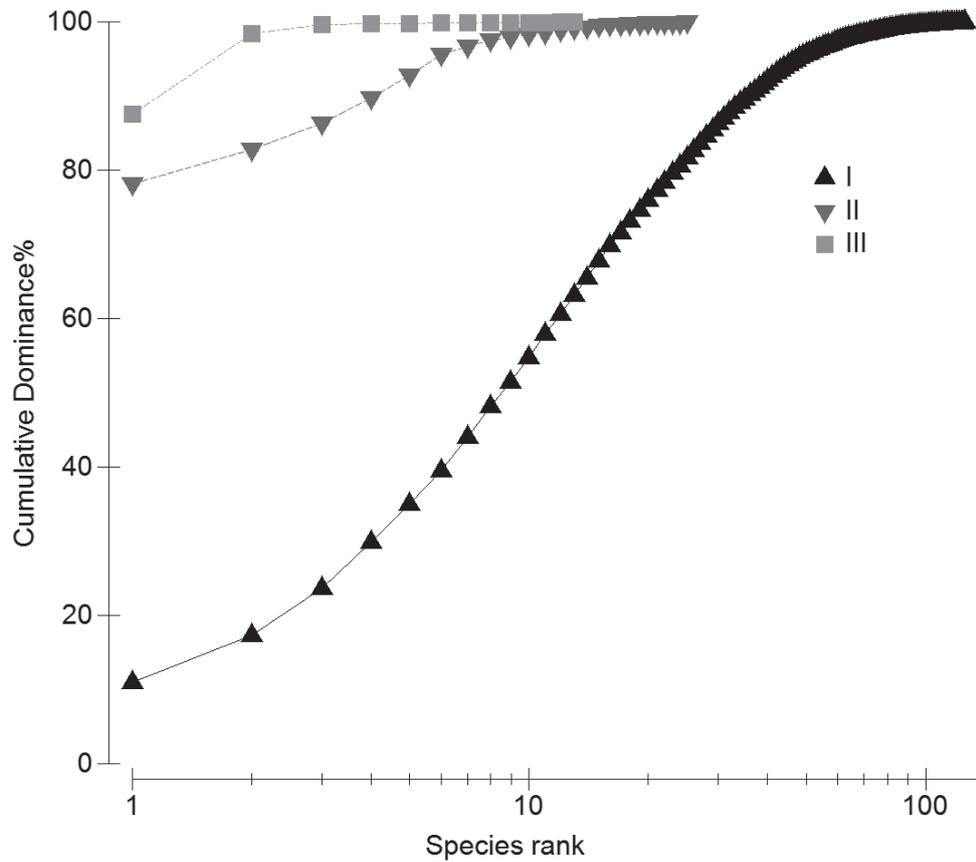


Fig. 4.7: The cumulative dominance curve for three peracarid species assemblages I-III of SoJaBio C-EBS stations.

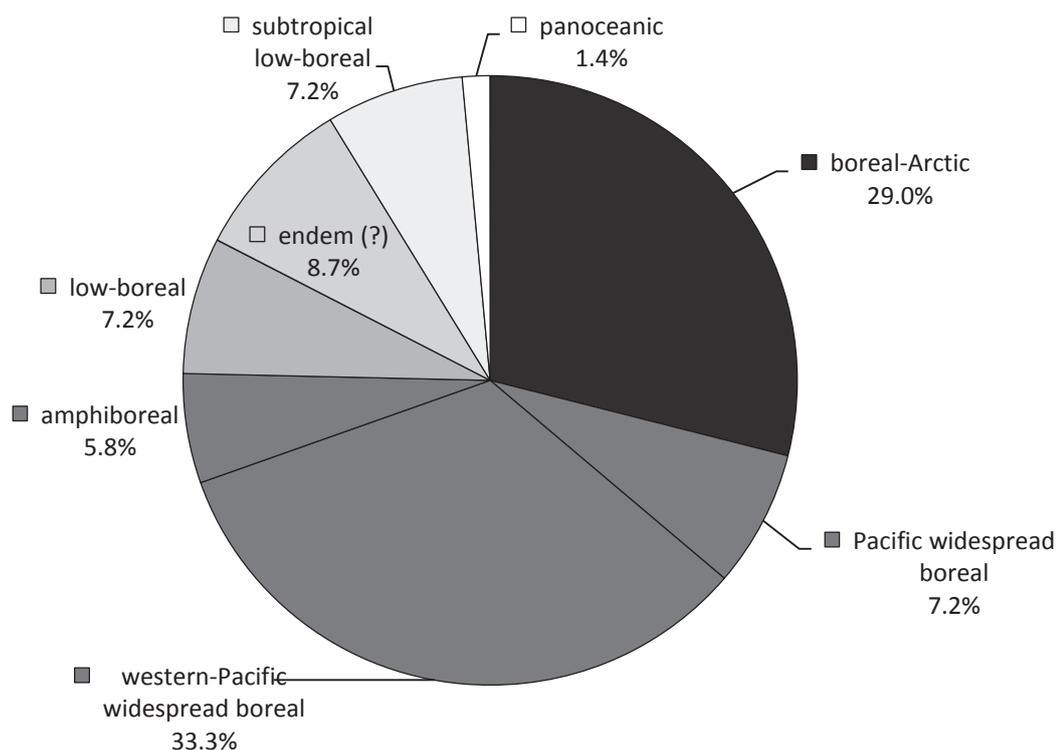


Fig. 4.8: Zoogeographical composition of the peracarid fauna of the Sea of Japan deep-sea basin (based on the identified species).

Distribution

The diversity and species richness of all Peracarida were highest at the shallow stations and consistently decreased with depth (Tab. 4.1, Fig. 4.2): 124 species were found in the depth range ~450–550 m, 44 species in the depth range ~1,300–1,500 m, 30 species in the depth range ~2,500–2,700 m and 10 species below 3,300 m. Similarly, the diversity of peracarids per 50 individuals (ES[50]) decreased from 23 (at ~450–550 m) to 1–2 ($\geq 3,300$ m).

The values of abundance showed no such clear relationship with depth as species composition. In general, two maxima of abundance were observed (Fig. 4.3). The first coincides with the shallowest slope stations, at ~500 m depth (A2-10, B7-7), where up to 27,012 specimens were recorded (A2-10). The other maximum occurred at the pseudo-abyssal stations along the base of the slope (D2-7 at ~2,600 m; C3, B4 and A7-8 between ~3,300–3,400 m), where up to 2,498 specimens were recorded (D2-7). At the intermediate depths (~1,000–2,700 m), where the bottom has a steep gradient (A3-11, A6, B5, B6), the peracarid abundance was relatively low, ranging from 228 to 936 specimens. Intermediate values of

abundance of ~1082–1904 specimens were observed at the pseudo-abyssal plain stations distant from the slope base (D1-3 and B1-7, ~3,550–3,660 m).

The changes in abundance with depth differed between the various orders of the Peracarida. The abundance of Amphipoda, Cumacea, Mysida and of most species of Isopoda and Tanaidacea decreased sharply with increasing depth. At the shallowest slope stations (~450–500 m) Amphipoda and Cumacea were especially abundant (each order with up to ~10,000 specimens at A2-10) and together contributed the significant portion of the peracarid abundance (up to 74 and 54% at transects A and B, respectively). Isopoda and Tanaidacea were generally less abundant at the same depths, but there they also had their maximal abundance (up to 3,647 individuals of Isopoda and 3,037 of Tanaidacea at A2-10). Even at the depth of ~1,000 m, the abundance of each peracarid order usually did not exceed ~150 individuals (except for the A3-11 at ~1,500 m depth where 404 amphipod specimens were sampled). At most of deeper stations Amphipoda, Cumacea, and Mysida were represented by few specimens. Indeed, excluding the 15 rarest species, most peracarid species were either found at the shallowest stations only (73 species) or they were most abundant at the shallow stations while also present at deeper stations: up to ~1,000 m (10 species), ~1,350–1,500 m (28 species), ~2,500–2,700 m (12 species) or $\geq 3,300$ m (5 species).

The amphipods *Harpiniopsis pacifica* (?) and *Anonyx derjugini* were found only at depths between ~2,600–2,700 m, where they were recorded as a few tens of individuals at almost every station.

Three peracarid species showed a direct correlation between abundance and depth. The first, *Chaulioleona hansknechti* (Tanaidacea), occurred occasionally at the slope stations A2-10 and A3-10 (~450 and 1,300 m), but it was relatively abundant (165 ind.) at the deep-sea station D2-7 (~2,600 m). Another tanaidacean species, *Paratyphlotanais japonicus*, was found only at depths between ~2,500–3,400 m with the highest abundance (1,087 specimens) at D2-7. The third species, *Eurycope spinifrons* (Isopoda) was sampled at almost all stations from ~450 m to the maximum sampling depth ~3,660 m, but on the slope its abundance was low (single to tens of specimens), and very high (~2,800–2,900 ind.) at the pseudo-abyssal plain – up to at ~3,300 m depth (B4, C3). At depths $\geq 3,300$ m *E. spinifrons* was dominant in the macrobenthos, representing from 30 to 70% of all macrobenthic individuals.

The species assemblages of Peracarida

Multivariate data analysis revealed low similarity between the stations (minimum 16.3%). Such low similarity might be expected owing to the known bathymetrical and environmental conditions along the study region, and it is consistent with the results of other deep-sea studies and with the occurrence of many rare and few abundant species (Brandt et al., 2007a; Brandt et al., 2007b). The dendrogram from the hierarchical agglomerative clustering indicated three distinct biological assemblages (at 25% similarity) (Figs. 4.4, 4.5). ANOSIM *R* statistics confirmed that these assemblages (I–III) are significantly different (at 0.001% significance; Tab. 4.3). The number of species, abundance and diversity were different for each of these faunal assemblages.

Assemblage I was comprised seven samples which represented the slope stations at depths from ~450 to ~1,500 m (A2, A3, B6, B7) with an average similarity within the cluster of 42.0%. The assemblage included 136 taxa. Mean values of the species richness *S* (47), number of specimens *N* (4710) and diversity *ES*[50] (15.8) were the highest in the sampled area (Fig. 4.6). SIMPER analyses revealed that 12 species accounted for 52.9% of the cumulative similarity in the assemblage (Tab. 4.4). These comprised one isopod, four cumacean, six amphipod and one mysid species, which occurred in 86–100% samples. The assemblage showed a relatively high diversity without strongly dominant species (the dominance did not exceed 10%) (Tab. 4.4; Fig. 4.7), although *Baeonectes brandtae*, *Eudorella* spp. 2 and *Leucon fulvus* were taxa discriminating this assemblage, and were present in all samples of the assemblage.

Assemblage II included six samples from the lower slope stations (A6, B5–8, C1, and D2–8) at depths ~2,500–2,700 m and was represented by 25 taxa. The average similarity within the assemblage was 57.6%. Mean values of *S* (15) and *ES*[50] (5.7) were three times lower than those for assemblage I, and *N* (709) more than six times lower, in fact lowest for the whole sampled area. Four species, the amphipods *Anonyx derjugini* and *Monoculodes* sp. 1, the cumacean *Leucon fulvus* and the isopod *Eurycope spinifrons* with equal contribution accounted for 61.8% of the cumulative similarity. The cumulative dominance curve (Fig. 4.7) showed that the assemblage II is dominated by only one species *E. spinifrons* (dominance ~78%), but contributions of a few others also can be detected. The fauna had an intermediate character between those from the slope and from the pseudo-abyssal plain. Thus, for example,

two samples at the stations B5 and D2 grouped with assemblage II, while two others from the same stations were included in assemblage III.

Assemblage III combined the pseudo-abyssal deep-sea stations, represented by 11 samples. The assemblage was represented by 13 taxa. The average similarity within the assemblage was 52.5%. Mean values of S (3) and ES[50] (1.7) were extremely low, but the number of specimens N (1779) was intermediate. Only two species, *E. spinifrons* and the tanaidacean *Paratyphlotanais japonicas* accounted for 92.3% of the cumulative similarity in the assemblage, and of these the contribution of *E. spinifrons* was 71.3%. The dominance of the single species *E. spinifrons* was almost 90% and the cumulative dominance of both main species was almost 100%.

Discussion

Taxonomic and zoogeographic composition

Previously, 76 peracarid species (41 Amphipoda, 13 Isopoda, 13 Cumacea, three Tanaidacea and six Mysida) had been found in the Sea of Japan below 500 m (Bulycheva, 1952; Fukuoka and Murano, 2006; Gamo, 1999; Golovan, 2007; Golovan and Malyutina, 2010; Gurjanova, 1933, 1936, 1951, 1962; Kudinova-Pasternak, 1970; Kussakin, 1979, 1982, 1988, 1999, 2003; Lomakina, 1958; Murano, 1974, 1977; Petryashov, 2005; Petryashov, 2004; Richardson, 1909; Saito et al., 2000; Vassilenko and Tzareva, 2004; Vassilenko et al., submitted). Among the 146 species from the SoJaBio collections, only 53 (36.3%) have been recorded previously, 93 (63.7%) species were new to the fauna and 42 (28.8%) were new to science. However, at least 35 (about half) of the previously-recorded species which had been sampled at comparable depths (31 Amphipoda, three Isopoda, four Cumacea and one Tanaidacea) were not found again during the SoJaBio. This indicates that the real number of peracarid species in the deep-sea basin of the Sea of Japan is apparently higher than was found.

Two amphipod genera, *Bruzelia* (?) and *Pardaliscella* (?) were found in the Sea of Japan for the first time at about 450–1,350 m and 2,500 m, respectively. Both genera consist of few species, inhabiting cold waters and the deep sea from the low shelf to abyssal depths, from 121 to 3,716 m and from 27 to 3,015 m, respectively (Barnard and Karaman, 1991). *Melphidippa macruroides* Gurjanova, 1946 is an arctic-boreal species that was previously known from the shelf of the eastern Arctic and the Chukchi Sea and now is recorded from the

bathyal of the Sea of Japan for the first time. Only 10 amphipod species from the material studied have been previously reported at depths ≥ 450 m: *Themisto japonica* (Bovallius, 1887), *Anonyx lilljeborgi* Boeck, 1870, *A. derjugini* Gurjanova, 1962, *Paroedicerus lynceus* (Sars, 1858), *Nicippe tumida* Bruzelius, 1859, *Eusirus cuspidatus* Krøyer, 1845, *Argissa hamatipes* (Norman, 1869), *Harpiniopsis pacifica* (Bulycheva, 1936), *H. orientalis* (Bulycheva, 1936), *Leptamphopus longimanus* (Boeck, 1871). Other identified species were known from the shelf of the Sea of Japan (Budnikova and Bezrukov, 2008; Bulycheva, 1952; Gurjanova, 1951, 1962; Pavlyuchkov, 1975). Most of the identified species (12) have a Pacific boreal distribution, with a predominance of widespread boreal species (10). Almost all of them (9) occur only along the Asian coast and have not been collected along the American coast. Two species seem to be low-boreal taxa. The other large group was made up by 10 arctic-boreal species. The other zoogeographical complexes were represented with fewer species: only four amphiboreal and one panoceanic species were found in our samples.

Among the identified cumacean species, as in the Amphipoda, widespread boreal species prevailed (12 species from three families: Leuconidae, Diastylidae and Lampropidae) while nine of these species have a western-Pacific distribution. This group was followed by the boreal-Arctic species (6 species from the families Diastylidae, Nannastacidae and Pseudocumidae). In addition, three low-boreal species (Nannastacidae) were found.

Among the isopods the munnopsid species *Ilyarachna zachsi* Gurjanova, 1933 and *Munnopsurus minutus* Gurjanova, 1933 as well as the desmosomatids *Eugerda fragilis* (Kussakin, 1965) and *Desmosoma lobipes* Kussakin, 1965 have also been recorded before from the shelf and the upper bathyal of the Sea of Okhotsk. The munnopsid species *Baeonectes brandtae* is presently known only from the bathyal of the Sea of Japan, but two other species of this genus were earlier recorded from the shelf of the Sea of Japan and from the Sea of Okhotsk respectively (Golovan and Malyutina, 2010). All the defined species of Epicaridea and Gnathiidea (three species) are widespread eurybathic boreal-arctic species. But the asellote species *Eurycope spinifrons* Gurjanova, 1933 and *Mirabilicoxa kussakini* Golovan, 2007 seem to be endemic to the bathyal and (*E. spinifrons*) pseudo-abyssal of the Sea of Japan. Moreover, the deep-sea genera *Eurycope* and *Mirabilicoxa* have never been found in the Sea of Okhotsk but occur in the closest non-isolated area – the Kuril-Kamchatka Trench (Birstein, 1963; Kussakin, 1999, 2003).

The tanaidacean species *Typhlotanais simplex* and *Paratyphlotanais japonicus* were recorded before in the Sea of Japan from the depth ranges 525–1,130 m and 2,790–3,650, respectively

(Kudinova-Pasternak, 1970). In addition, two species found in the SoJaBio collection, *Tanaella kormritza* and *Chaulipleona hansknehti* were recorded previously in the West Pacific Ocean (off Honshu) from the upper bathyal (169–574 m and 260–278 m, respectively: Larsen and Shimomura, 2007). Additionally *T. kormritza* was recorded on the slope of the East China Sea in a depth range from 444–574 m (Larsen and Shimomura, 2007). In our material, the species was found at only one station (~970 m), its first record for the Sea of Japan (Błazewicz-Paszkowycz et al., 2013).

Three mysid species are widely distributed on the shelf in the upper epi-bathyal and bathypelagial of the North Pacific boreal region. These are the widespread boreal-Arctic species *Pseudomma truncatum* Smith, 1879, the Pacific widespread boreal species *Holmesiella anomala* Ortmann, 1908, and the western-Pacific widespread boreal species *Meterythropus microphthalmus* W.M. Tattersall, 1951. Other three subtropical low-boreal species, *Pseudomma okiyamai* Murano, 1974, *P. izuensis* Murano, 1966 and *Mysidella orientalis* Murano, 2002, were previously known from the bathyal depths of the Sea of Japan, the East China Sea and the Pacific coast of southern Japan. Two probably subtropical low-boreal species, *Meterythropus* sp. aff. Murano, 1977 and *Stilomysis major* W.M. Tattersall, 1951, are currently known only from the bathyal of the Sea of Japan (Fukuoka and Murano, 2006; Murano, 1974, 1977, 2002; Petryashov, 2005; Petryashov, 2004; Tattersall, 1951).

Thus, excluding species with uncertain distribution, two main zoogeographic groups of species prevailed (Fig. 4.8): the widespread boreal species (46.4%), most of which are western-Pacific species (33.3%), and the widespread boreal-Arctic species (33.3%). The contributions of other zoogeographical complexes (low-boreal, supposedly endemic, subtropical low-boreal species) were lower (7.2-8.7%).

Peracarida in isolated and non-isolated deep-sea areas

Peracarida were recorded as the dominant taxon in the macrobenthos on the continental slope and in the deep-sea basin of the Sea of Japan, at least in term of abundance. Since the taxonomic work with most groups of macrobenthos has not been completed yet, it is not possible to estimate their contribution to the total species richness of the investigated area, but preliminary studies have revealed that peracarids made up a quarter of all SoJaBio macrobenthic species. Such results are consistent with those reported for non- or less-isolated deep-sea areas of comparable depths. For example in the abyssal of the Atlantic, bathyal and

abyssal of the Antarctic and bathyal of the western Australia peracarids predominated together with such taxa as Polychaeta and Bivalvia, although their contributions were different (Brandt et al., 2005, Brandt et al., 2007a, Brandt et al., 2007b; Poore et al., unpublished).

The proportion of the particular peracarids varied noticeably in the deep-sea areas studied and these differences depended on the sampled depths and on the geographical location. Despite this, general distributional patterns can be revealed. Isopoda and Amphipoda in the bathyal of the Antarctic, off Western Australia and in the Kuril-Kamchatka Trench are usually reported as the most abundant and diverse peracarid taxa (Zenkevich, 1977; Brandt et al., 2005, Brandt et al., 2007a, Brandt et al., 2007b; Brökeland et al., 2007; Poore et al., unpublished). The exception here was Western Australia, where Tanaidacea was clearly the most diverse taxon, exceeding all other peracarids in both abundance and species richness (the material was collected mainly by a Smith-McIntyre grab) (Poore et al., unpublished). Cumacea are usually reported as an important element of benthic communities, but never as the dominant taxon, constituting about 13-22% of the peracarid specimens and species (Brandt et al. 2005; Brökeland et al., 2007; Poore et al., unpublished). Mysida are the rarest peracarids in the deep-sea of the mentioned basins, e.g. the Atlantic, the Antarctic as well as the Sea of Japan.

The contribution of particular Peracarida orders to the bathyal and pseudo-abyssal macrobenthic community of the Sea of Japan is consistent with the results published for non-isolated deep-sea areas (see above) with the prevalence of the isopods and amphipods and a smaller share of other orders. Decreasing abundance with depth, and depth-related patterns of peracarid taxa have been observed by some authors previously (Birstein, 1963; Brökeland et al., 2007; Hessler, 1974). These have also reported that isopod diversity increased with depth from the lower bathyal to the abyssal (with the maximum at 4,000–5,000 m in compared open deep-sea areas) while amphipod diversity decreased (Birstein, 1963; Brökeland et al., 2007; Hessler, 1974). Cumacea and Mysida generally do not reveal similar strong differences in abundance and show stable distributional patterns. For instance, in the lower bathyal and abyssal of the Antarctic their shares in the total number of Peracarids were relatively higher in the depth interval from ~2,000 to 3,000 m (Brökeland et al., 2007), while in the Sea of Japan their numbers strongly decreased with depth. Tanaidacea show the similar depth-related patterns at the compared depths of the Antarctic and the Sea of Japan with the maximal representation at ~2,000–3,000 m (Brökeland et al., 2007).

Distribution

The low diversity and species richness in the bathyal and abyssal depths of the Sea of Japan were previously reported for many benthic groups including Peracarida (Derjugin, 1933, 1939; Nishimura, 1966, 1968, 1969; Zenkevitch, 1963) and our results generally support those conclusions.

In the Sea of Japan, a high diversity and species richness of many higher taxa (brachiopods, bivalves, echinoids, crustaceans, fish) in shallow waters, which decreased sharply with depth were documented by Zezina (1970), Kafanov (1991), Kafanov and Kudryashov (2000) and Lutaenko (2003, 2006). For Isopoda the vertical distribution of about 70.0% of previously recorded species was shown to be confined to the shelf zone, i.e. above ~200 m depth (Golovan and Ivin, 2008; Kussakin, 1973). In the bathyal (> 200 m) the number of species decreased with increasing depth, but at ~500 m depth the local maximum of species richness (see Kafanov and Kudryashov, 2000), indicating the overlapping of vertical distributional boundaries, was recorded (Golovan and Ivin, 2008). Around these depths, the boundary between the surface water and the deep-sea water mass of the Sea of Japan may be placed (Leonov, 1960; Luchin and Manko, 2003; Tyler, 2002). Thus, the high diversity, species richness and abundance observed at these depths during SoJaBio can be explained by an overlap with the shallower (and richer) species-complex of the upper bathyal.

On the steep continental slope below 500 m the peracarid fauna was much poorer. Here the upper bathyal species still prevailed, but they were scarcely represented and their number gradually decreased with the depth. These findings, as well as the second maximum in abundance at the pseudo-abyssal stations along the base of the slope, are probably due to the sedimentary processes triggered by organic material which is washed down from the shelf to the steep slope and accumulates below its base, providing food for organisms living there. Thus, among the contents of the C-EBS samples from the stations situated near the base of the slope, a large amount of the sea-grass debris remains and other allochthonous organic matter was observed. Therefore, despite the similar hydrological conditions, the abundance at the seaward pseudo-abyssal stations was lower.

The general character of the continental slope, as a transit zone from where the sediments are washed down (in the contrast to the abyss, where cumulative processes prevail) was previously pointed by many authors (e.g. Zenkevich, 1977). A decrease in abundance due to

declining food availability, i.e. depending on depth, has also been mentioned previously (Brökeland et al., 2007; Hessler, 1974).

At the continental slope base of open deep-sea areas, as in the adjacent Kuril-Kamchatka trench, an increase in diversity and species richness of many high taxa as well as changes in the taxonomic composition of the benthic communities were observed at the depth interval ~2,500–3,000 m (Zenkevitch, 1977). The appearance of many abyssal taxa below these depths was pointed out. This allowed some authors to draw the line between the bathyal and abyssal at 3,000 m depths (e.g. Vinogradova, 1955, 1958). The depths between 2,500 and 3,500 m according to them should be considered as an intermediate interval between the bathyal and abyssal zones (Zenkevitch, 1977).

The patterns of the distribution of Peracarida in the Sea of Japan is consistent with previous investigations in terms of abundance, although the Pleistocene isolation undoubtedly had an influence leading to its present low diversity in the abyssal. Most of the deep-sea taxa which are highly diverse in the open abyssal (e.g. the primarily deep-sea isopod families Haplomiscidae, Ischnomesidae, Macrostylidae, and some genera of other deep-sea asellote families, occurring at comparable depths in the Kuril-Kamchatka trench) (Birstein, 1963; Kussakin, 2003) were not found in the Sea of Japan. However, three peracarid species from mostly deep-sea tanaidacean and isopod families (which thrive in open deep-sea areas) demonstrate a direct correlation between abundance and depth. The tanaidacean *Chaulioleona hansknechti* (Akanthophoreidae) was known previously from the low shelf and upper bathyal (Pacific Ocean off Honshu, 169–574 m) and was found in the Sea of Japan at ~450–2,600 m. The Isopod *Eurycope spinifrons* (Munnopsidae) is endemic to the bathyal and pseudo-abyssal of the Sea of Japan, where it occurs at depths from 300 m (rare) to 3,660 m (extremely high abundance). Finally, *Paratyphlotanais japonicus* (Typhlotanaidae) is apparently an abyssal endemic of the Sea of Japan, where it was found at depths of ~2,500–3,400 m. The last two species completely dominated in the pseudo-abyssal of the Sea.

Hence, these apparently endemic species from the primarily deep-sea families of Tanaidacea and Isopoda are especially adapted to the soft deep-sea sediments, and have begun successful colonization of the pseudo-abyssal environments of the Sea of Japan, where they thrive in the absence of competition for food sources.

The munnopsid genus *Eurycope* has radiated mostly in the deep sea (see Kensley et al., 2004). But some species of the genus inhabit shelf depths, mainly in cold-water regions. The same situation has been documented for some other genera of the primarily deep-sea asellote

families: for these taxa this represents a secondary colonization of shallow waters, demonstrating the considerable ecological adaptability of this group (Malyutina et al., 2013) (**Chapter 9**). This adaptability may allow them to distribute geographically, and to overcome shallow barriers to disperse further in deep-sea zones. Thus, despite the fact that no *Eurycope* species has yet been found in the rich, diverse and highly competitive shelf macrobenthic communities of the Sea of Japan, *E. spinifrons* completely dominates at the abyssal depths of the Sea. The population structure and reproductive biology of this species have been described by Elsner et al. (2013) (**Chapter 7**).

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Author's contribution:

I assisted with the sample sorting and species identification to species level of the Isopoda. Furthermore, I assisted with the data analysis and proofread the original manuscript for grammar, spelling and style.

Borderland: isopod biodiversity in the deepest basin of the Sea of Japan

Marine Biodiversity (to be resubmitted)

Chapter 5: Borderland: isopod biodiversity in the deepest basin of the Sea of Japan

Nikolaus O. Elsner, Angelika Brandt

Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany

Abstract

The Sea of Japan is a marginal sea in the Northwest Pacific and its deep-sea basins are isolated from adjacent deep-sea basins. In August 2010, the Russian research vessel *Akademik M. A. Lavrentyev* sampled 9,782 isopod individuals at 13 stations (459–3649 m). These individuals were assigned to 17 different species. 16 of these 17 species only occurred between 459–1,360 m. The one species occurring at all stations was *Eurycope spinifrons* Gurjanova 1933 (Munnopsidae). The most abundant families were Munnopsidae and Desmosomatidae. Our results confirm the hypothesis that, in the special case of the Sea of Japan, increasing depth leads to a decrease in diversity along the continental slope (459–1,360 m). We compared our samples with samples taken by the Russian research Vessel *Vityaz* in the 1950s. Of these, we chose 13 stations in the same depth range as our samples for a comparison. The rarefaction curve of our samples from the deep Sea of Japan is clearly approaching an asymptote, while the rarefaction curve plotted from the *Vityaz* samples is not, even though considerably fewer individuals were sampled and these were assigned to far more species. This result confirms our hypothesis that the isolation of the deep Sea of Japan has led to a decrease in diversity compared to adjacent deep-sea basins. This is most likely due to the fact that organisms in the deep Sea of Japan became extinct because of anoxia until about 8000 years ago and due to the lack of deep-water straits, the deep basins are slowly being recolonized by eurybathic shelf species.

Keywords: Isopoda; benthos; epibenthic sledge; Japan Basin; continental slope

Introduction

Diversity is hypothesized to be an important factor for ecosystem stability (Ives and Carpenter, 2007; McCann, 2000). Communities with higher biodiversity show increased ability to cope with changing environmental conditions and perturbations (Stachowicz et al., 2007; Tilman et al., 2006). This also applies to marine environments, (Worm et al., 2006) where humanity creates disturbances, amongst others, via the fishing industry (Roberts, 2002) or manganese nodule exploration (Ahnert and Schriever, 2001; Veillette et al., 2007). Biodiversity in the deep sea is among the highest in any habitat (Hessler and Sanders, 1967; Ramirez-Llodra et al., 2010). It is lower on hard substrate than on soft sediment. For hard substrate communities, whale falls have the highest diversity (Amon et al., 2013; Baco and Smith, 2003; Smith, 2006), where many species thrive off the locally high input of organic matter. Hot vent communities, with their high input of inorganic matter, have lower diversities but a high amount of biomass (Jollivet, 1996; Ramirez-Llodra et al., 2007). In contrast, soft-sediment communities in the deep sea seem to be high in species richness but low in numbers of individuals (Grassle and Maciolek, 1992).

However, our knowledge of biodiversity, especially in the deep sea, is far from being complete. Although the deep-sea floor covers, with about 60%, the largest surface on earth, only about 0.01% of this surface has been studied in detail so far (Ramirez-Llodra et al., 2010). Of the roughly 9 million species supposedly living on earth, only about one tenth has been taxonomically described so far (Mora et al., 2011). The percentage of described species is higher for terrestrial than for marine organisms and therein higher in shelf areas than in the deep sea due to easier accessibility of specimens. Despite the large area of the deep sea, by far fewer samples have been taken in this area than in shallow shelf areas for this reason. Marginal seas as those found in the Northwest Pacific provide a good opportunity to study marine diversity in relatively isolated areas. In particular, the deep Sea of Japan provides the opportunity to study a semi-enclosed deep basin. The bottom water in this marginal sea has been reported to have been repeatedly anoxic and even euxinic in the past two million years (Tada, 1994). During the last glacial maximum, a eustatic sea-level fall of up to ~130 m (Clark et al., 2009) isolated the Sea of Japan completely, assumedly disrupting circulation and oxygenation of the bottom water (Gorbarenko and Southon, 2000; Oba et al., 1991; Tada et al., 1999). The Sea of Japan is connected to the East China Sea, the Okhotsk Sea and the open Pacific via four shallow-water straits with a maximal depth of 130 m. Because of the repeated periods of anoxia in the bottom water, the benthos underwent massive extinction between

85,000 and 8,000 years ago (Oba et al., 1991). Most likely, this is the reason for an impoverished deep-sea fauna which cannot be replaced by immigration due to the shallowness of the straits. It has been supposed that the deep-sea is being colonized from the shelf by eurybathic species (Zenkevitch, 1963).

Therefore, the deep Sea of Japan provides a rare opportunity to study the succession of a deep-sea benthic community. This is important in order to understand the effects, impacts and recovery potential of perturbations in the deep sea, whether created by humans or natural causes. The deep-sea expedition SoJaBio (Sea of Japan Biodiversity Studies) took place in the summer of 2010 and was designed to take samples in different depths from the continental slope to the abyssal plain at the northern slope of the Japan basin. In these samples, Isopoda have been found at all depths and in relatively high numbers (Brandt et al., 2013; Golovan et al., 2013), but only one isopod species was collected below the depth of 2,465 m (Elsner et al., 2013) (Chapter 7). The aim of this study was to assess the biodiversity of all sampled stations (459–3,649 m). As the species richness between 2,465–3,649 m is limited to one species, we focus on the four stations. Before the expedition, we hypothesized that the isolation of the deep Sea of Japan leads to decreased biodiversity with regard to adjacent deep-sea basins and that the number of species will decrease with increasing depth. Furthermore, we hypothesize that the isopod community will be dominated by the families known to be abundant in the deep sea. We compared our results to samples taken by the Russian research vessel *Vityaz* about 50 years ago (Bogorov, 1973) which have been studied in detail by Birstein (1963). He determined and described the isopods of these samples. We limited the comparison to stations in the same depth range as our samples.

Material and methods

Benthos samples were collected during the SoJaBio expedition (Sea of Japan Biodiversity Studies) with the Russian RV *Akademik M. A. Lavrentyev* from 11th of August to 5th of September 2010 in the Sea of Japan (Fig. 5.1). We sampled 13 stations on the continental slope and adjacent bathyal in the Japan basin with a camera-equipped epibenthic sledge (C-EBS) (Brandt et al., 2013). The Isopoda of the epi-net fractions, collected 25–60 cm above the seafloor, of the first haul from each of the 13 stations were included in the analysis and determined to species level. Station depths ranged from 459 to 3,649 m (Tab. 5.1). We determined a single depth value for each deployment by using the median of the minimum

and maximum depth values during the trawl of each deployment according to the sledge's CTD.

Tab. 5.1: Station characteristics of the stations included in this study. The isopod individuals were sampled by an epibenthic sledge (C-EBS) during the SoJaBio expedition in the Sea of Japan. The letter of each station refers to the transect (A–D), the first number to the station on the respective transect and the second number to the gear deployment at the station. The depth was deduced from the pressure measured by the CTD attached to the sledge (depth = pressure/ ρ (standard value of saltwater) – atmospheric pressure (standard value)). Values for temperature ($SD \leq 0.02^\circ\text{C}$) and oxygen concentration ($SD \leq 2.2 \mu\text{M}$) refer to bottom measurements only. Biodiversity indices refer to Isopoda only. N: number of individuals; S: number of species; ES (200): Hurlbert index; J': Pielou's evenness; H': Shannon index.

Station	Date	Median depth	Trawling line from-to	Temperature	O ₂ -conc.	N	S	ES	J'	H'
	2010	(m)	(Decimal degrees)	(°C)	(μM)	(100 m ²)		(100)		
A2-10	14.08.	459	44.9487°N 137.1982°E– 44.9503°N 137.1998°E	0.8	259.4	540.6	17	11.9	0.8	2.3
A3-10	14.08.	1360	44.831°N 137.2333°E– 44.838°N 137.237°E	0.2	226.4	42.5	9	4	0.7	1.6
A6-7	16.08.	2465	44.3238°N 137.4033°E– 44.3124°N 137.4009°E	0.2	225.5	33.3	1	1	n/a	0
A7-8	17.08.	3276	44.0148°N 137.4964°E– 44.0132°N 137.5046°E	0.3	223.9	17.8	1	1	n/a	0
B1-7	19.08.	3649	42.2592°N 136.7213°E– 42.2662°N 136.7148°E	0.3	222.6	0.8	1	1	n/a	0
B4-7	21.08.	3273	43.0251°N 135.4408°E– 43.0166°N 135.4362°E	0.3	225.0	92.6	1	1	n/a	0
B5-7	23.08.	2604	43.0283°N 135.0881°E– 43.029°N 135.0995°E	0.2	226.1	9.1	1	1	n/a	0
B6-6	25.08.	943	43.1773°N 135.0141°E– 43.1712°N 135.0133°E	0.4	240.1	187.5	7	4	0.6	1.1
B7-6	25.08.	576	43.2237°N 135.0705°E– 43.2268°N 135.0732°E	0.7	264.5	160.6	12	8	0.6	1.6
C1-8	27.08.	2705	42.4431°N 133.1525°E– 42.4455°N 133.1624°E	0.2	227.2	40.6	1	1	n/a	0
C3-3	28.08.	3402	42.0224°N 133.1624°E– 42.0176°N 133.165°E	0.3	223.5	56.3	1	1	n/a	0
D1-3	30.08.	3335	41.4725°N 131.7782°E– 41.4651°N 131.771°E	0.3	224.2	222.3	1	1	n/a	0
D2-7	01.09.	2478	42.1195°N 131.3518°E– 42.1143°N 131.3497°E	0.2	227.9	30.8	1	1	n/a	0

In comparable studies (e. g. Brandt 1993; Elsner et al. submitted; Kaiser et al. 2009) the abundance data was standardized to 1,000 m trawling distance (equals 1,000 m²). In the present study, standardization was more complicated, because of the imprecise winch and ship speed values and the indistinct data from the ship's analog tension meter.

Following equation 2 from Brenke (2005), the trawling distance is calculated by multiplying the speed (winch and/or ship) by the time the epibenthic sledge (EBS) is located on the ground. The latter value is derived from the tension meter (start haul of the EBS to EBS left the ground). Both factors are necessary for the standardization. But due to the imprecise data onboard the RV *Akademik M. A. Lavrentyev*, it has been previously stated that a calculation of the EBS trawling distance by any of the known equations (Brenke 2005) would be too vague for standardization (Brandt et al. 2013; Golovan et al. 2013).

However, in order to enable statistical analysis of our data, we developed a calculation method for deployments of the C-EBS equipped with a Seaguard CTD (Brandt et al. 2013). To determine the time, we analyzed the depth, direction and current measurements of the SEAGUARD RCM. The analysis of the changes of the values of these parameters gave a highly precise time for EBS start trawl to EBS left the ground. For the speed we use the average winch and/or ship speed during this time. With this new calculation method, we achieve an error rate of about 15% derived from the standard deviation of the speed calculation. This error rate is in the range of error which has to be expected from deep-sea deployments of the EBS (Brenke 2005) and the calculated trawling distance can therefore be used for standardization. We decided to standardize to 100 m trawling distance, because the trawling distance of 10 of the 13 sampled stations was below 1,000 m and abundance values should not be extrapolated (pers. comm. V. Siegel).

The samples were sieved on board through 300 µm sieves and promptly fixed in 96% precooled ethanol (-20°C) and re-fixed after a fixation period of at least 48 hours in 96% ethanol and kept at -20°C. The samples were sorted on ice and determined to species level under a dissecting microscope.

We used PAST (PAleontological STatistics) Version 3.01 (Hammer et al., 2001) to statistically analyze our data. We used the Cosine similarity index in order to plot a non-metric multidimensional scaling plot (nMDS) (Taguchi and Oono, 2005) using the standardized abundance values (standardized to 1,000 m²). With regard to the error in the trawling distance and the semi-quantitative nature of the EBS, we decided to use the Cosine similarity index which is favorable for more “qualitative” data (Pfeifer et al., 1998). The

rarefaction curves (Fig. 5.7) were calculated on the basis of the total amount of individuals collected for each species across all hauls. The non-parametric Kruskal-Wallis test (Kruskal and Wallis, 1952) was performed using IBM SPSS Statistics 20 in order to test the two groups (459–1,360 m and 2,465–3,649 m) for statistical significance and for descriptive statistics. The exact significance was used for the Kruskal-Wallis test. We used Primer Version 6.1.6 to determine the following biodiversity indices (Clarke and Gorley, 2006): S (n species), N (n individuals), J' (Pielou's evenness) (Pielou, 1975), ES (100) (Hurlbert's rarefaction (Hurlbert, 1971) index for expected number of species) and H' (Shannon index) (Shannon and Weaver, 1949).

The data presented in Birstein (1963) was used for comparing the deep Sea of Japan with an open Pacific bathyal area (Fig. 5.1). Only 13 stations from Birstein (1963) were used for comparison, because these stations are in the same depth range as our stations (975–3,107 m). Birstein's benthic samples were taken with different trawls (the "Sigsbi-Gorbunov" trawl and the "Galathea" trawl) and the "Okean" grab. The mesh size of these sampling devices is not specified, but the samples were sieved on board with 714 µm sieves. The trawling distance was not recorded. In order to check for difference in species composition, the species diversity found in the SoJaBio and *Vityaz* samples was compared.

Tab. 5.2: *Vityaz* station details in the same depth range as the SoJaBio samples according to Birstein (1963). S and N were calculated based on the species-abundance matrix extracted from Birstein (1963). The ES (100) value equals the S values. N: number of individuals; S: n species; Hurlbert index; J': Pielou's evenness; H': Shannon index.

Station	Depth (m)	Longitude	Latitude	Year	Gear	N	S	J'	H'
141	2207	46°41'N	151°26.3'E	1949	Petersen Grab	1	3	n/a	0.0
2078	1050–1070	44°09'N	148°38'E	1953	Trawl	5	34	0.5	0.8
2124	950–1000	47°35.7'N	153°3.7'E	1953	Trawl und Ocean Grab	5	8	0.9	1.4
2133	1226	48°23.7'N	154°17.6'E	1953	Ocean Grab	1	1	n/a	0.0
2210	2430–2670	50°1.8'N	157°39.2'E	1953	Trawl	2	2	1	0.7
2220	2940	43°25.2'N	147°41.2'E	1953	Trawl	4	8	0.8	1.1
3184	2917–2887	45°07.6'N	145°30.9'E	1954	Trawl	1	1	n/a	0.0
3223	1693	39°45.1'N	143°22.1'E	1955	Ocean Grab	2	3	0.9	0.6
3271	3107	51°06.1'N	158°55'E	1955	Ocean Grab	1	4	n/a	0.0
3364	2867–3015	48°21.2'N	168°54.1'E	1955	Trawl und Ocean Grab	2	3	0.9	0.6
3475	1406	31°21.8'N	150°53.4'E	1955	Trawl	1	1	n/a	0.0
3577	2700–3042	38°40.1'N	143°29.3'E	1957	Trawl und Ocean Grab	1	1	n/a	0.0
3578	1641	38°35'N	142°53.3'E	1957	Trawl	3	5	0.9	1.0

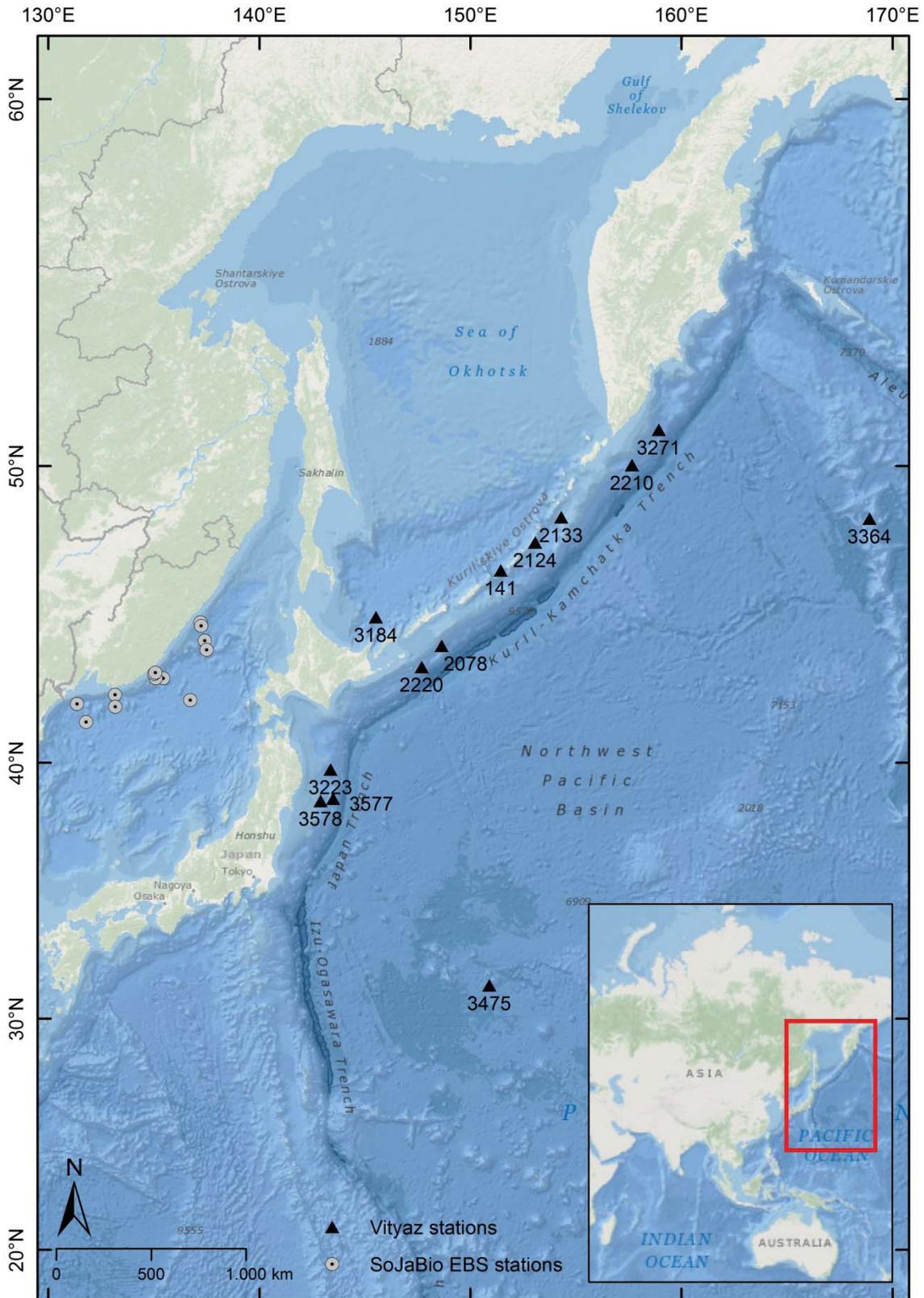


Fig. 5.1: Stations of the SoJaBio-expedition where the epibenthic sledge was deployed (circles) and Vityaz stations in the same depth range according to Birstein (1963) (triangles). The map was created using Esri ArcGIS 10.2 by T. Springer.

Results

During the SoJaBio expedition, we sampled 9,782 isopod individuals belonging to 17 species, 11 genera, 6 families and 2 suborders. Of the 17 species sampled, 7 species (41.2%) are not scientifically described to date. The majority of individuals belong to the suborder Asellota (98.7%), only 1.3% belong to the suborder Cymothoidea.

Species richness (S) generally decreases with depth: we found the highest S at 459 m where all 17 species occurred. Between 459 and 1,360 m depth, S is reduced from 17 to 7 (Fig. 5.2). At all nine stations below 2,465 m, only the species *Eurycope spinifrons* Gurjanova, 1933 (Munnopsidae) was found. This species is the most numerous species at every station.

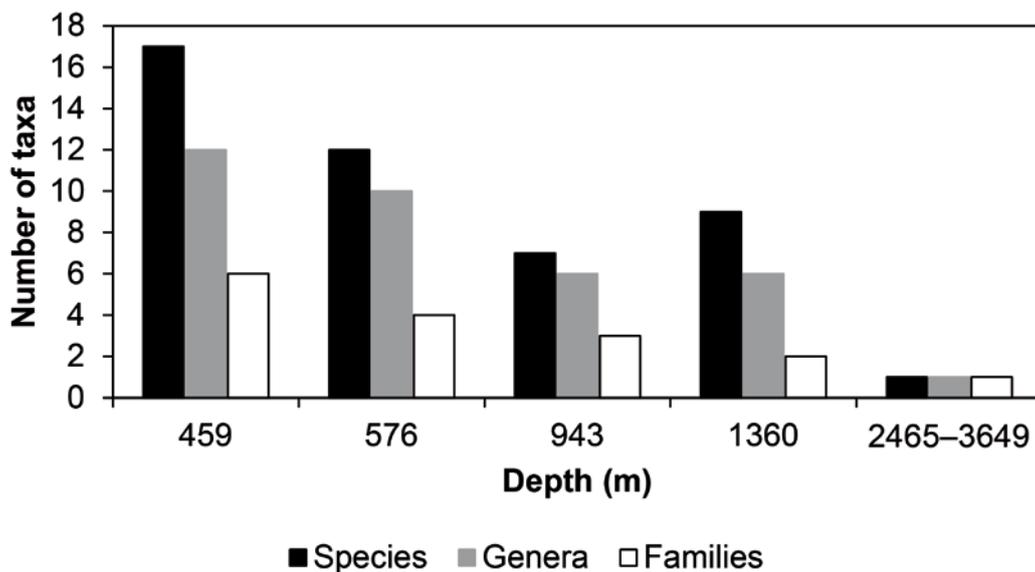


Fig. 5.2: Depth dependent number of families (black), genera (grey) and species (white) per station.

On family level, Munnopsidae (71.1%) dominated overall in the samples, followed by Desmosomatidae (17.7%), Paramunnidae (9.3%), Gnathiidae (1.8%), Bopyridae (0.05%) and Munnidae (0.02%) (Fig 5.3 B). The shallowest station A2-10 at 459 m yielded the highest number of isopod individuals (37.7% of all isopods), followed by station C-3-3 at 3,402 m depth (15.5%). The smallest numbers of individuals were retrieved from station A6-7 at 2,465 m (0.1%) and station B5-7 at 2,604 m (0.6%). On average, 110.4 ± 148 isopod individuals were sampled per station.

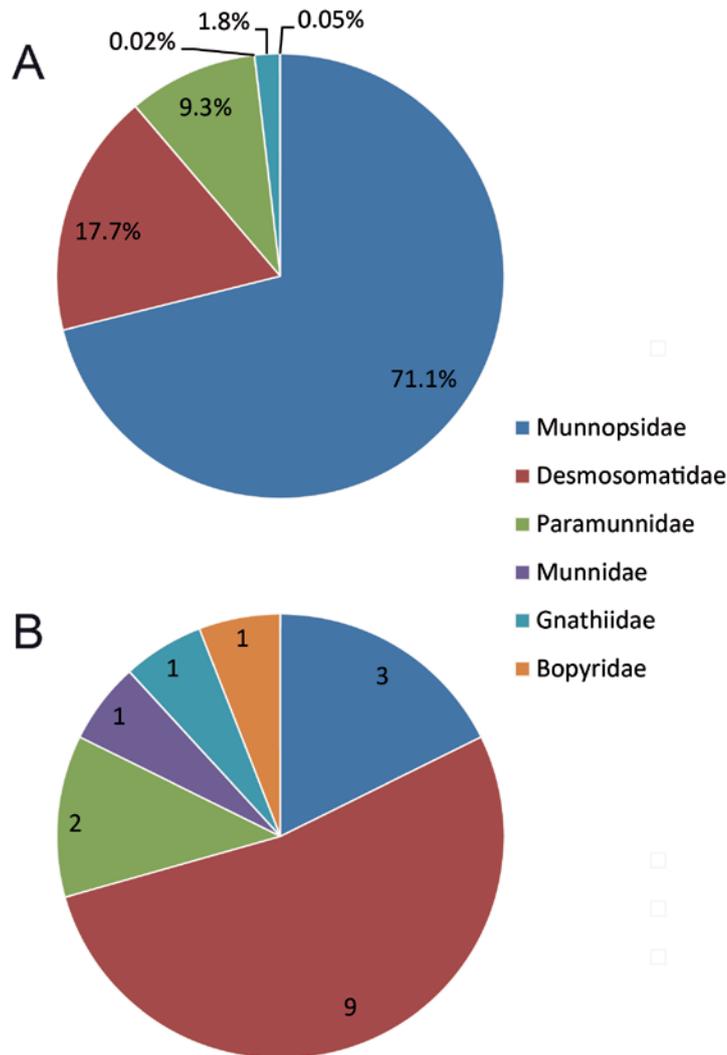


Fig. 5.3: Percentage of individuals (A) and number of species (B) per family.

The overall family composition differs between stations: Munnopsidae generally dominate, but at station A2-10 at 459 m depth, Desmosomatidae (42.4%) are more abundant than Munnopsidae (28.8%) and Paramunnidae (24.3%). At station B7-6 at 576 m and station A3-10 at 1,360 m, Desmosomatidae are the only other abundant family except for Munnopsidae. Overall, *Eurycope* Sars, 1848 (64.7%), *Pleurogonium* Sars, 1864 (9.3%) and *Desmosoma* Sars, 1864 (7.5%) are the most abundant genera. The overall species composition differs between stations (Fig. 5.4). The shallowest station sampled (459 m) differs most and shows the greatest evenness (Tab. 5.1). At 576 m depth, *E. spinifrons* is clearly more abundant than any other species. At 943 m, *Baeonectes brandtae* Maljutina, Golovan, Elsner 2013 and at 1,360 m *Eugerdia fragilis* (Kussakin, 1965) are additionally found in comparably high percentages. Overall, *E. spinifrons* makes up 64.7% of all sampled individuals and is followed

by *Desmosoma ochotense* Kussakin, 1965 (Desmosomatidae) with 6.5% and *Pleurogonium* aff. *kyushuense* Shimomura, 2009 (Paramunnidae) with 5.9%.

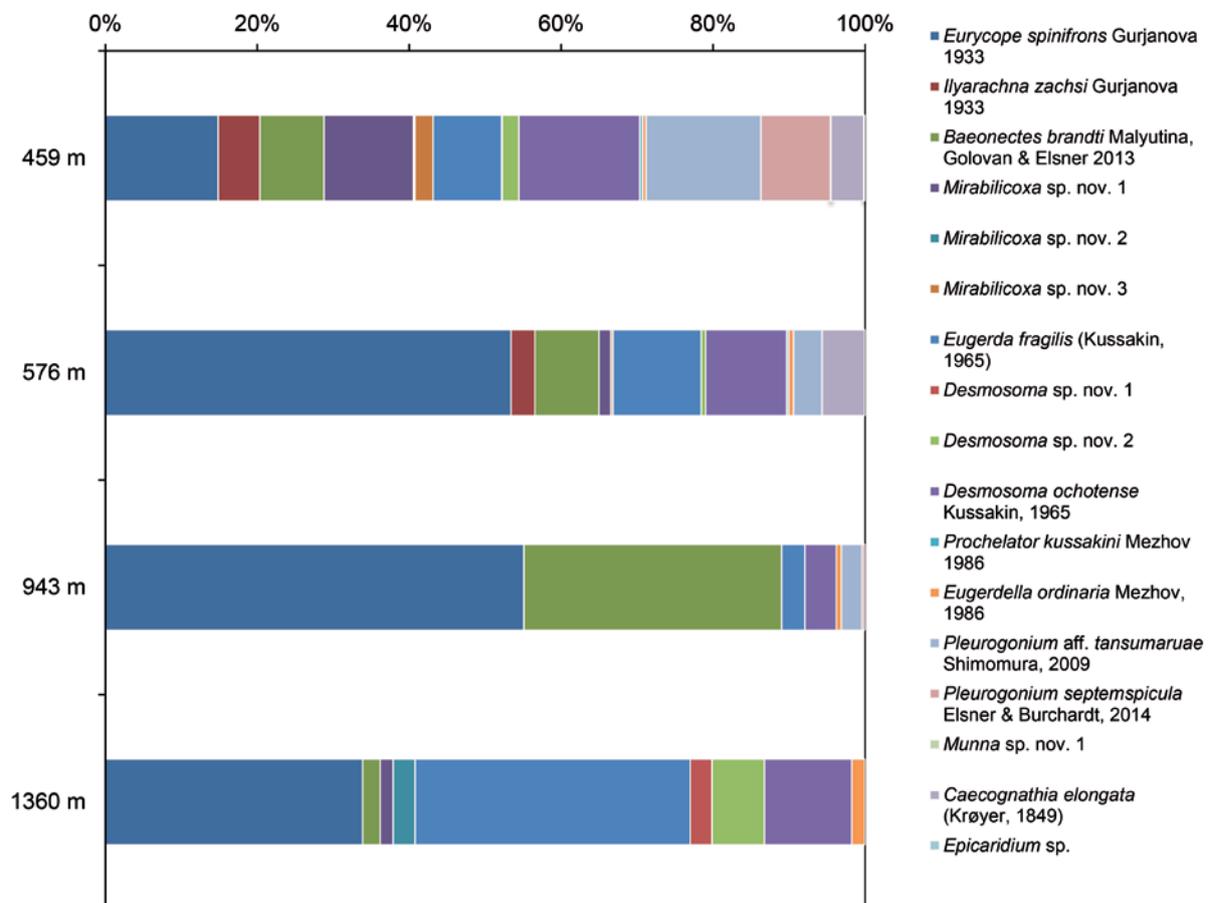


Fig. 5.4: Species composition of the shelf-bathyal stations (459–1,360 m). The percentage of each of the 17 species is shown for each of these stations.

Apart from the clear dominance of Munnopsidae and *E. spinifrons*, it is striking that few families, genera and species occur in high percentages and a high number of genera and species occur in low percentages. The rank abundance diagram (Fig. 5.5) illustrates this pattern and the correlation yielded a R^2 -value of 0.93 on species level.

The nMDS plot (Fig. 5.6) shows that the shallowest station A2-10 at 459 m is more different from the other stations than any of these among each other. Not surprisingly, the stations from 2,465–3,649 m depth are all placed on the same spot in the plot. According to the Kruskal-Wallis test, there is a significant difference between the two groups 459–1,360 m and 2,465–3,649 m ($p = 0.001$).

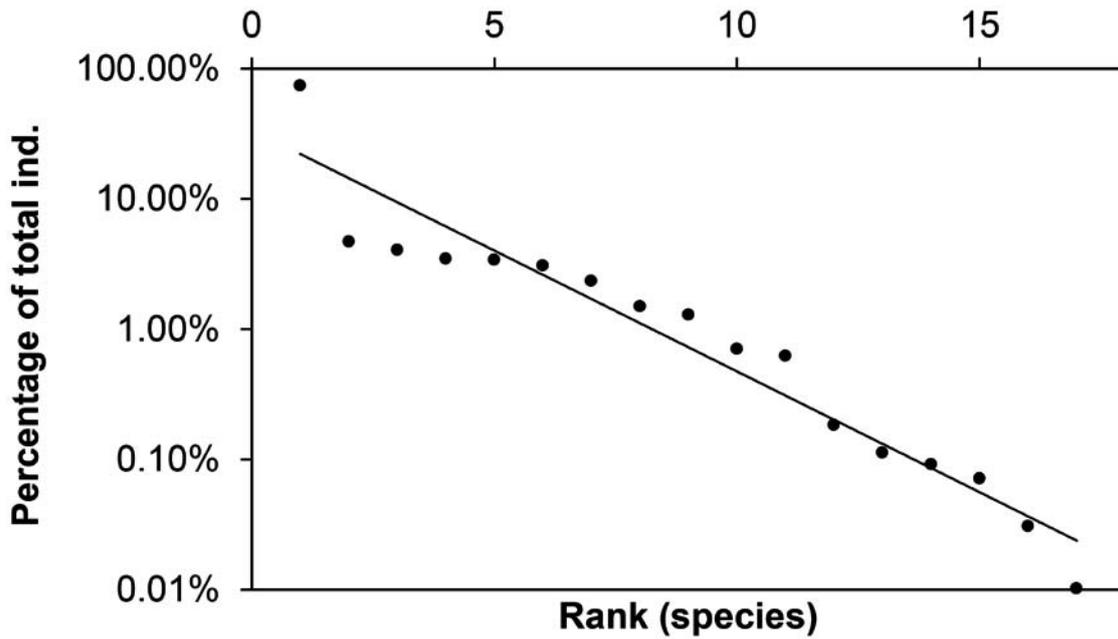


Fig. 5.5: Rank abundance diagram of all stations. The ranked species (most abundant to least abundant) and number of individuals (log 10 scale) are shown. $R^2 = 0.93$.

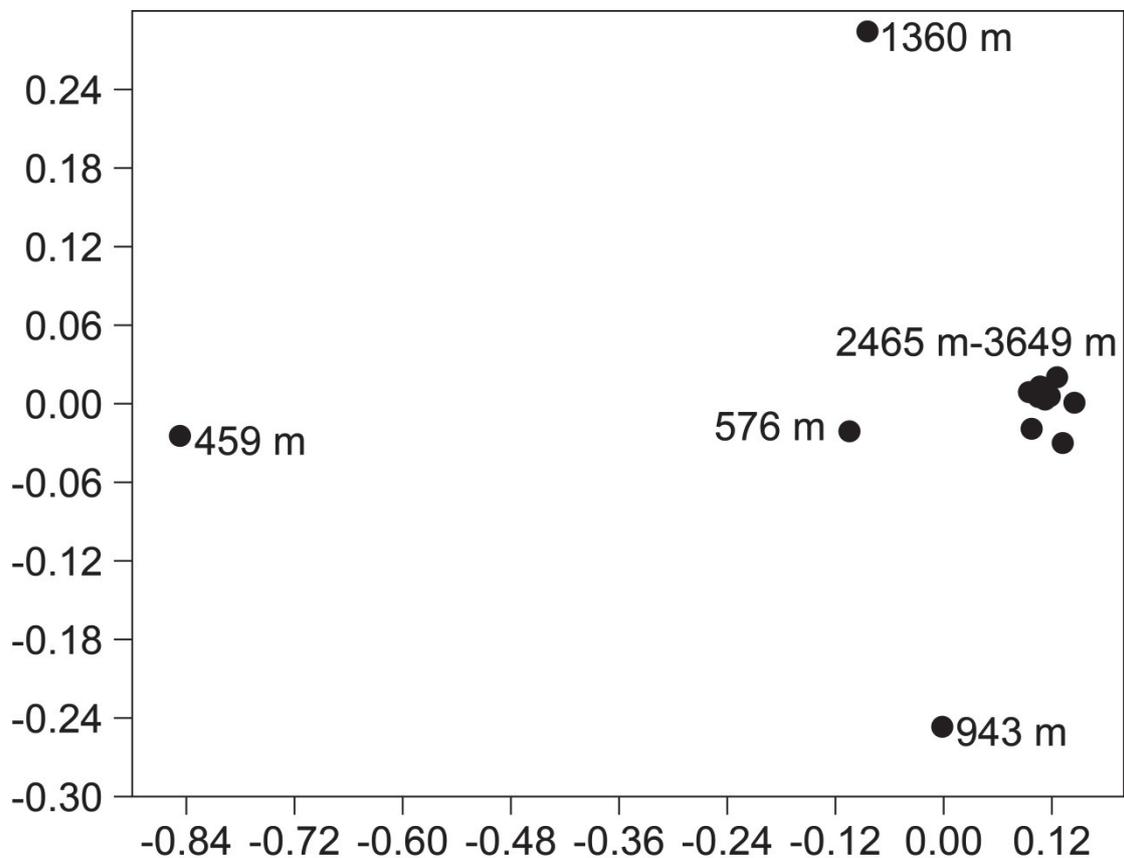


Fig. 5.6: Non-metric multidimensional scaling plot of all studied stations on the basis of the Cosine similarity index. Stress: 0.17.

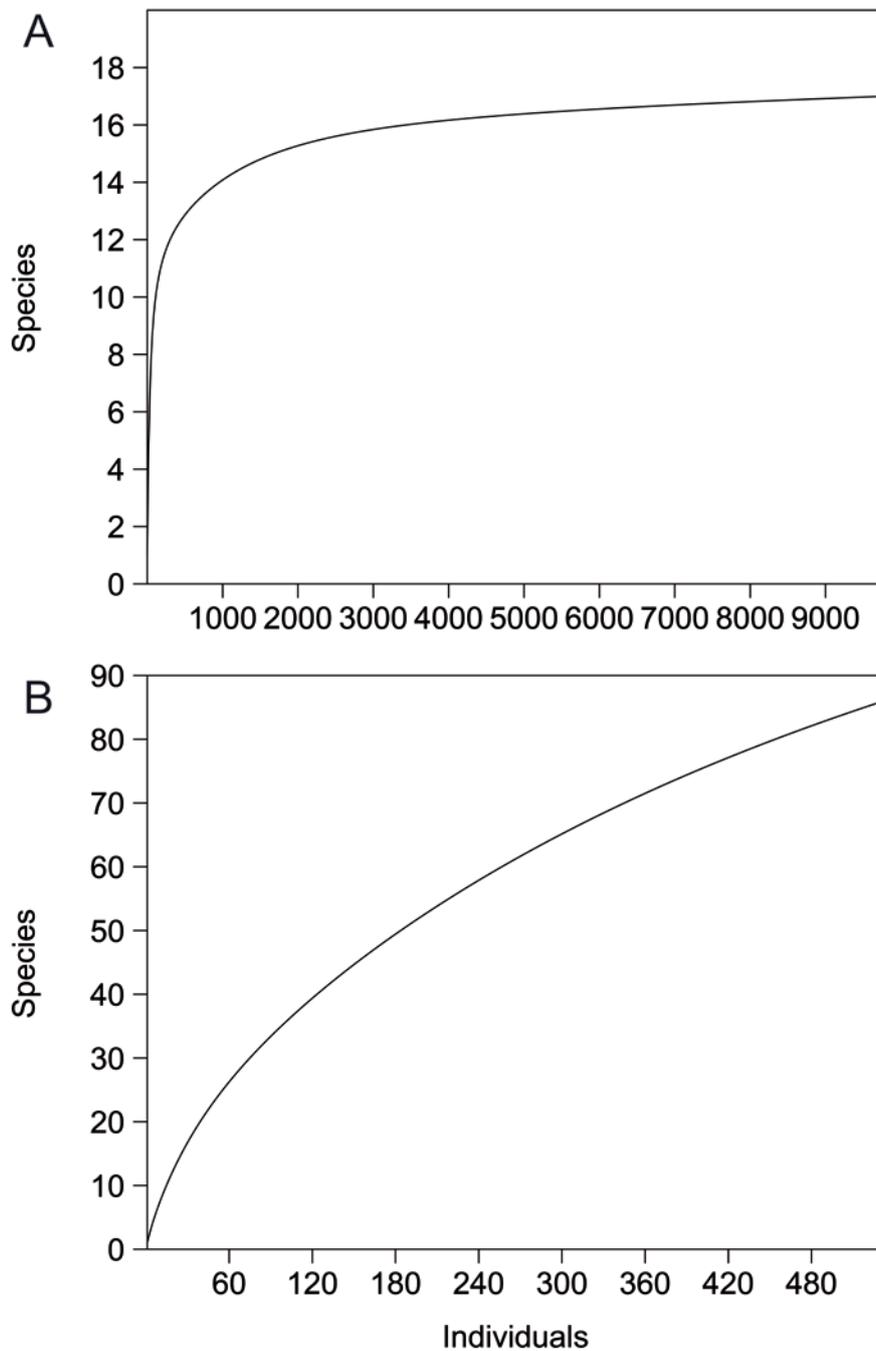


Fig. 5.7: Rarefaction curve for the SoJaBio samples of this study (A) and *Vityaz* stations in the same depth range of Birstein (1963) (B).

Within the shelf-slope group (459–1,360 m), we found an average of $S = 11.3 \pm 4.3$ per station. Concerning the number of species per family, Desmosomatidae dominated with 9 species, followed by Munnopsidae with 3 species and Paramunnidae with 2 species. Gnathiidae, Bopyridae and Munnidae were represented by one species each in the samples (Fig. 5.3 A). Within the slope-bathyal group (2,465–3,649 m), we only collected one single species, *E. spinifrons* (Munnopsidae) with 801 individuals on 900 m².

The rarefaction curve of our data (Fig. 5.7 A) is clearly approaching an asymptote. The rarefaction curve plotted from Birstein's species determination (1963) is not approaching an asymptote (Fig. 5.7 B). Note the much smaller number of individuals, but much higher number of species in the latter curve. The correlation between temperature and depth (Fig. 5.8 A) shows a decrease in temperature from 465–1,372 m and thereafter a slight increase. The correlation between oxygen concentration and depth (Fig. 5.8 B) shows a decrease from the shallowest to the deepest station.

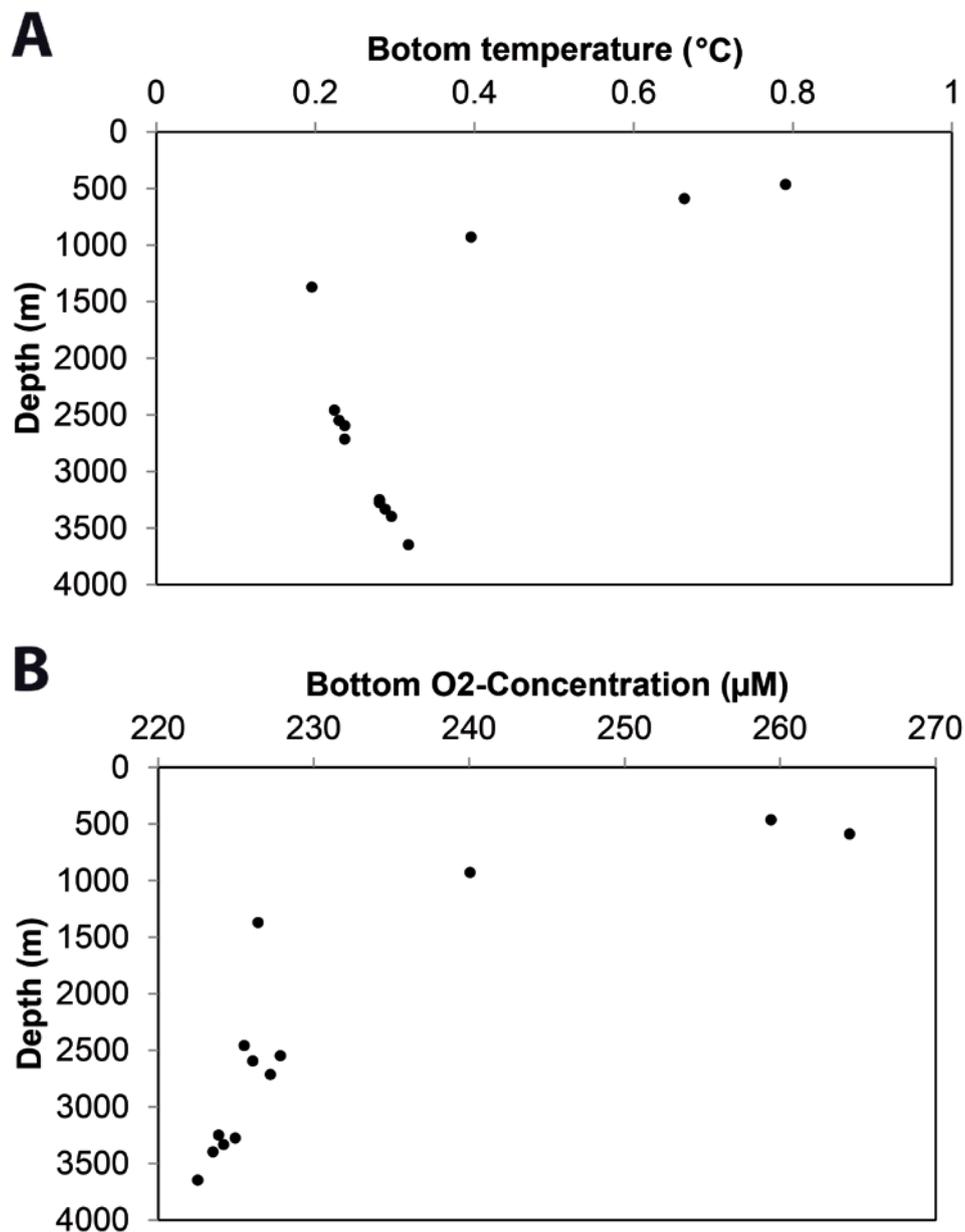


Fig. 5.8: Bottom measurements of the C-EBS associated CTD for temperature (A) and oxygen concentration (B) at the different stations during trawling.

Tab. 5.3: Species abundance data of the epi-net fractions of the SoJaBio stations (Fig. 1 & Tab. 1). The number of the two groups (459–1,360 m and 2,465–3,649 m) and of all stations in total are shown right of the horizontal line. The abundance data is standardized to 100 m trawling distance.

Family	Species	Depth (m)											Depth range (m)				
		459–576	576–943	943–1360	1360–2465	2465–2478	2478–2604	2604–2705	2705–3273	3273–3335	3335–3402	3402–3649	459–1360	2465–3649	Total		
Munnopsidae	<i>Eurycope spinifrons</i> Gurjanova 1933	80.4	22.7	18.4	6.0	0.8	92.6	9.1	187.5	160.6	40.6	56.3	222.3	30.8	127.5	800.5	928.1
Munnopsidae	<i>Ilyarachna zachsi</i> Gurjanova 1933	29.6	1.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	30.9	0.0	30.9
Munnopsidae	<i>Baeonectes brandti</i> Maljutina, Golovan & Elsner 2013	45.9	3.6	11.3	0.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	61.2	0.0	61.2
Desmosomatidae	<i>Mirabilicoxa</i> sp. nov. 1	63.7	0.7	0.0	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	64.7	0.0	64.7
Desmosomatidae	<i>Mirabilicoxa</i> sp. nov. 2	0.9	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	1.4	0.0	1.4
Desmosomatidae	<i>Mirabilicoxa</i> sp. nov. 3	13.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.2	0.0	13.2
Desmosomatidae	<i>Eugerdella fragilis</i> (Kussakin, 1965)	48.7	4.9	1.0	6.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	61.1	0.0	61.1
Desmosomatidae	<i>Desmosoma</i> sp. nov. 1	0.4	0.0	0.0	0.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.9	0.0	0.9
Desmosomatidae	<i>Desmosoma</i> sp. nov. 2	12.0	0.3	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	13.4	0.0	13.4
Desmosomatidae	<i>Desmosoma ochotense</i> Kussakin, 1965	85.9	4.5	1.4	2.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	93.8	0.0	93.8
Desmosomatidae	<i>Prochelator kussakini</i> Mezhov 1986	2.2	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	2.3	0.0	2.3
Desmosomatidae	<i>Eugerdella ordinaria</i> Mezhov, 1986	2.4	0.3	0.2	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	3.2	0.0	3.2
Paramunnidae	<i>Pleurogonium</i> aff. <i>kyushuense</i> Shimomura, 2009	81.7	1.6	0.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	84.2	0.0	84.2
Paramunnidae	<i>Pleurogonium</i> sp. nov. 1	49.6	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	49.7	0.0	49.7
Munnidae	<i>Munna</i> sp. nov. 1	0.2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.2
Gnathiidae	<i>Caecognathia elongata</i> (Krøyer, 1849)	23.5	2.4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	25.9	0.0	25.9
Bopyridae	Gen. sp. 1	0.7	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.7	0.0	0.7
Total		540.6	42.5	33.3	17.8	0.8	92.6	9.1	187.5	160.6	40.6	56.3	222.3	30.8	634.2	800.5	1434.7
Taxa		17	12	7	9	1	1	1	1	1	1	1	1	1	17	1	17

Discussion

Isopoda have been recorded to be abundant and diverse in the deep-sea benthos (Brandt et al., 2007; Hessler et al., 1979). The genus *Eurycope* Sars, 1848 is with 54 described species (Schotte et al., 1995 onwards) both species-rich and widely distributed (Kussakin, 2003; Malyutina and Brandt, 2007). We therefore use Isopoda as a model taxon for biodiversity studies and comparison with the *Vityaz* samples from the same depth range.

Munnopsidae have been recognized as the most abundant family of Isopoda in the deep-sea benthos: they commonly comprise half of the sampled individuals and about $\frac{1}{3}$ of the sampled species (Brandt et al., 2007; Malyutina and Brandt, 2007; Schnurr et al., 2014). In our samples Munnopsidae are the most numerous family at almost every station (Tab. 5.3) as well. In most benthic communities, Munnopsidae are followed by Desmosomatidae in percentage of sampled individuals (Brenke et al., 2005; Brix, 2007; Kaiser and Brix, 2007; Malyutina and Kussakin, 1996; Svavarsson, 1987).

Our results show a decline in species richness (S) between 459–1,360 m (Fig. 5.2) and thus confirm our hypothesis. This decrease has been reported earlier for the Sea of Japan (Zenkevitch, 1963) and was generally confirmed by the SoJaBio expedition (Malyutina and Brandt, 2013). This pattern applies to the taxa present on class level (Brandt et al., 2013) as well as to the Peracarida on species level (Golovan et al., 2013). Golovan et al. (2013) found three assemblages based on multivariate statistics limited to peracarid crustaceans. In this study, we analyzed the isopod fauna which makes no exception to this pattern and found two distinct groups. The intermediate assemblage between 2,511–2,725 m stated in Golovan et al. (2013) for peracarid crustaceans does not seem to exist for isopods (Fig. 5.6). Furthermore, our result of a threshold depth between 1,360–2,465 m is consistent with studies from the North Pacific: Kussakin (1990) found a distinct difference regarding Isopoda in shallow-water fauna above 1,500 m and deep-sea fauna below 2,000 m in the North Pacific Boreal Region.

The observed decline in isopod diversity with depth in the Sea of Japan most likely can be explained by the recent geological history of the Sea of Japan. The bottom water became anoxic repeatedly and a large part of the benthos became extinct (Oba et al., 1991; Tada, 1994; Tada et al., 1999). Although Isopoda have been shown to be able to cope with hypoxic conditions (Hagerman and Szaniawska, 1988), no macrofaunal organism can live and reproduce in prolonged hypoxic or anoxic conditions (Diaz and Rosenberg, 1995; Wu, 2002). The Sea of Japan is only connected to adjacent marginal seas and the Pacific through shallow-

water straits (max. depth 130 m). As a result, the deep-sea fauna which became extinct could not be replaced by immigration, leading to the decline in diversity with depth we find in the deep benthos today. Supposedly, the deep-sea fauna is now in the process of being replaced by eurybathic organisms (Zenkevitch, 1963). The high abundance of individuals at a depth of 459 m can be explained by the fact that this station is located on the upper continental slope. At this station, all sampled species occur which explains the fact that this station clusters the farthest from the other station in our analysis. The decline of the sampled amount of isopod individuals along the slope (2,465–2,705 m) most probably is caused by the steep slope itself where food does not accumulate; in contrast to the abyssal plain. On our pictures and in our samples of the deepest stations, pieces of seagrass are visible to the unaided eye (Brandt et al., 2013; Fig. 5). There, isopod abundance is high (Tab. 5.1). We cannot determine the exact threshold depth (between 1,360–2,465 m) at which *Eurycope spinifrons* becomes the only isopod species present, there most likely is a transition zone (cp. Kussakin (1990) for the North Pacific).

Though data of the Northwest Pacific and adjacent seas are sparse, expeditions with the RV *Vityaz* in the 1950s covered the area of the Northwest Pacific south of the Kuril islands (Bogorov, 1973). Birstein (1963) studied samples from an even larger area and focused on Isopoda (Tab. 5.2). These samples yielded significantly lower numbers of individuals in comparison with our samples, which is due to the fact that on board the RV *Vityaz*, grabs were used in addition to trawled gear, the former of which sample a much smaller area than the latter. Additionally, the samples were sieved onboard with a bigger mesh size (714 μm), resulting in the loss of small macrofaunal organisms. However, in 13 of the 48 studied stations from the same depth as our samples (975–3,107 m), he found 24 isopod species from a total of only 74 individuals. These 24 species belonged to 17 genera and 12 families. There is no correlation between species richness and depth ($R^2 = 0.1$). The highest species richness was 5 on two stations around 1,000 m depth (Tab. 5.2).

The rarefaction curve plotted from the deep Sea of Japan data (Fig. 5.7 A) is distinctly different from the one plotted from the 13 *Vityaz* stations in the same depth range (Birstein, 1963) from the Northwest Pacific (Fig. 5.7 B). The former is clearly approaching an asymptote. Excluding the data from the station between 2,465–3,649 m depth does not change the general shape of the curve. This means that repeated sampling in the area will not lead to an increase in the recorded diversity, because most of the species occurring in the area have been sampled during SoJaBio. On the contrary and despite the considerably lower number of collected individuals and the much higher number of species, the curve of the *Vityaz* samples

from the Northwest Pacific is not at all close to approaching an asymptote. These results are in accordance with the results concerning the diversity of isopods from the KuramBio (Kuril-Kamchatka Biodiversity Studies) expedition to the Northwest Pacific southeast of the Kuril Islands and the Kuril-Kamchatka Trench (Elsner et al., submitted) (**Chapter 6**). Both rarefaction curves confirm our hypothesis that the isolation of the deep Sea of Japan leads to a decreased diversity in regard to adjacent deep-sea basins.

According to Birstein's (1963) data, Munnopsidae are the dominant family in species richness ($S = 4$). Antarcturidae are the dominant family in number of individuals ($N = 29$), of which 27 were collected at a single station. In species richness, Munnopsidae are followed by Idoteidae and Janiridae. Concerning number of individuals, Antarcturidae are dominant followed by Haploniscidae and Janiridae. Munnopsidae is the only family also present in our samples. Only Munnopsidae and Gnathiidae are present in both studies. Only one genus, *Ilyarachna*, was found in both studies. We did not find any of the species collected by the *Vityaz* in the same depth range as our samples in the deep Sea of Japan. This indicates that the deep-sea of Japan fauna is isolated from adjacent deep-sea basins and that this fauna exhibits a high level of endemism.

In conclusion, our study about the isopod fauna of the deep Sea of Japan shows that diversity decreases with increasing depth. Furthermore, we document an impoverished isopod fauna in the Japan basin in comparison with adjacent deep-sea basins limited to a single species below 2,465 m. This is most likely due the geologically recent mass extinction in the deep Sea of Japan. Munnopsidae and Desmosomatidae are, as previously recorded for different deep-sea areas, the most abundant families. We chose the catchphrase "Borderland" to linguistically illustrate the distinctness of both the isolated deep Sea of Japan as well as the distinct reduction to one species on the continental slope of the Japan basin.

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Author's contribution:

I determined all Isopoda to species level, conducted the statistical analyses on the base of discussion and advice from the coauthors and created the graphs. I wrote and rewrote the initial draft on the basis of the reviewer's comments.

**Deep down: Isopod biodiversity of the Kuril-Kamchatka abyssal area
including a comparison with data of previous expeditions of the RV Vityaz**

Deep-Sea Research II (In Press, Accepted Manuscript)

Chapter 6: Deep down: Isopod biodiversity of the Kuril-Kamchatka abyssal area including a comparison with data of previous expeditions of the RV *Vityaz*

Nikolaus O. Elsner^a, Marina V. Malyutina^{b,c}, Olga A. Golovan^b, Nils Brenke^d, Torben Riehl^a, Angelika Brandt^a

^a*Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany*

^b*A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, 17 Palchevsky St, Vladivostok, 690041, Russia*

^c*Far East Federal University, Oktiabrskaya Str, 29, Vladivostok 690600, Russia*

^d*German Center for Marine Biodiversity Research (DZMB), Senckenberg Research Institute, Südstrand 44, 26382 Wilhelmshaven, Germany*

Abstract

This study focusses on the isopod biodiversity in the abyssal area southeast of the Kuril-Kamchatka Trench which is itself located southeast of the Kuril Islands between Hokkaido and Kamchatka. The KuramBio (Kuril-Kamchatka Biodiversity Studies) expedition in summer 2012 collected altogether 10,169 isopods from 21 C-EBS hauls at 12 stations, belonging to 19 families, 73 genera and 207 species from the depth range between 4,830–5,780 m. Munnopsidae and Desmosomatidae were the most abundant and species-rich families, *Eurycope* (Munnopsidae) and *Macrostylis* (Macrostylidae) the most abundant genera. An nMDS plot on the basis of the Cosine similarity index reveals no clear pattern and all hauls to be different from each other. We compared our data with 12 stations from the same depth range sampled by the Russian RV *Vityaz* about 50 years ago and were able to identify several species collected by the RV *Vityaz*. The identified isopod species belonged to the families Munnopsidae, Macrostylidae, Haploniscidae, Desmosomatidae, Ischnomesidae and Nannoniscidae. Of the 333 individuals collected by the RV *Vityaz*, Haploniscidae and Munnopsidae were the most abundant families. Desmosomatidae were only represented by < 1% of the isopod individuals. However, the rarefaction curves of both the KuramBio and the

Vityaz samples are not approaching an asymptote, indicating that even after repeated sampling just a part of the local fauna has been recorded so far.

Keywords: deep sea; macrofauna; Kuril-Kamchatka Trench; epibenthic sledge; rank abundance

Introduction

Deep-sea isopod biodiversity has been intensively studied around the world. As a consequence, Isopoda is one of the best-studied taxa in the generally little investigated deep sea biota (Rex and Etter, 2010). Various recent deep-sea expeditions in the Atlantic (Brandt et al., 2005; Brenke et al., 2005; Brix, 2007; Schnurr et al., 2014), the Pacific (Malyutina, 2011; Malyutina et al., 2013) and the Southern Ocean (Brandt et al., 2007c; Malyutina and Brandt, 2007) have revealed high isopod diversity down to abyssal depths (Brandt et al., 2009; Hessler and Sanders, 1967; Sanders, 1968).

Isopoda occupy different benthic habitats in the deep sea including whale falls, manganese nodule fields and hydrothermally active areas (Linse et al., 2014; Malyutina, 2011; Riehl et al., 2014), but predominantly soft sediments (Hessler et al., 1979) that dominate the vast abyssal plains (Ramirez-Llodra et al., 2010). Regarding frequency, abundance and diversity, Isopoda is an important component of the deep-sea benthos (Brandt et al., 2007a; Brandt et al., 2013; Grassle and Maciolek, 1992; Hessler and Jumars, 1974; Wolff, 1977). Thus, Isopoda seem to be a suitable model taxon for comparative deep-sea benthic biodiversity studies. On the background of increasing efforts for deep-sea mining (Bluhm, 1994; Borowski and Thiel, 1998) and deep-sea fishery (Koslow et al., 2000; Ramirez-Llodra et al., 2011; Roberts, 2002), it becomes increasingly important to understand and possibly predict impacts of deep-sea disturbances. Estimating regional biodiversity represents an important step towards this goal.

The Northwest Pacific is mainly characterized by the subduction zone between Pacific plate and the North American plate. At the subduction zone, deep-sea trenches form, like the Izu-Bonin Trench, the Japan Trench and the Kuril-Kamchatka Trench. Through this, the resulting back-arc basins are marginal seas which are connected with the Pacific via deep (Okhotsk Sea) or shallow water (Sea of Japan; 15–130 m) straits (Tyler, 2002). The Pacific abyssal plain itself lies at about 5000 m depth (Zenkevitch, 1963), generally without drastic change in

elevation. The area southeast of the Kuril Islands is mainly influenced by the Oyashio, a cold surface current flowing southwestern direction along the Kamchatka Peninsula and the Kuril Islands. It meets the Kuroshio, a warm surface current flowing eastward from the Japanese island Honshu (Qiu, 2001).

In the second half of the last century, the deep-sea fauna of the Northwest Pacific was studied during ten expeditions onboard the Russian RV *Vityaz* (1949, 1953-1956, 1957-1958, 1966) (Shirshov, 1983). These studies covered an extensive area of the Northwest Pacific Basin and adjacent hadal systems from the Aleutian Trench in the north to the Mariana Trench in the south, ranging from the low bathyal zone off the Kuril Islands to the greatest depths of the trenches. These investigations significantly broadened our knowledge of the deep-sea fauna: more than one hundred isopod species have been found and described from these expeditions, corresponding to almost one quarter of all known deep-sea isopod species at the time (Birstein, 1957, 1960, 1961, 1962a, b, 1963, 1970, 1971; Kussakin, 1971; Mezhov, 1980, 1981). However, rather large-meshed trawls (mesh size not specified) and bottom grab-samplers were used in these expeditions (such as "Sigsbee" and "Galathea" trawls, "Okean" grab sampler). These gears are well suited for collecting megabenthos and infauna, but insufficient for macrofauna, especially small crustaceans simply because of their mesh sizes and small area covered in case of grab samplers. Birstein (1971) realized that each subsequent expedition in the same area revealed additional species even when using the same gear and that major fractions of the fauna were not sampled due to inappropriate sampling and sieving methods. As a result, this region provides an opportunity to potentially add to the already existing inventory especially with regard to smaller species. Studying the area with modern gear that already have had a worldwide application would allow for biodiversity comparisons with other areas of the world and an improved understanding of the biodiversity (species and higher taxa) from this area. Assuming that the previously reported diversity is underestimated because of the large-meshed gear used, we hypothesize that the actual isopod diversity in the Northwestern Pacific deep sea is much higher than recorded so far. Additionally, it gives us the opportunity to recognize known species in our samples which have been reported in the area some 50 years ago.

In order to resample the abyssal basin southeast of the Kuril-Kamchatka Trench, the German-Russian expedition KuramBio was conducted in August 2012 onboard the German RV *Sonne*. An epibenthic sledge (EBS) (Brandt et al., 2013) specifically designed for collecting macrofaunal epibenthos, was deployed in a standardized manner at all stations. We planned in particular to repeat some of the *Vityaz* stations which showed relatively high abundances in

the samples, e.g. station #5620 of the 39th cruise in 1966, one of the 12 stations of five expeditions of *Vityaz* in the area and with a depth range comparable to those of the KuramBio expedition. Prior to the expedition, we hypothesized to sample a high amount of isopod species new to science as well as isopod species known and described from the area. We also expected to find a relatively high diversity of the common families of janiroidean Asellota, as it has been found in other studies of deep-sea regions of the World Oceans. The focus of this study mainly lay on a determination of isopod species collected during the KuramBio expedition with special regard to the resampled species originally described on the basis of the samples of the *Vityaz* expeditions. A subsequent study will focus on regional and global distribution of Isopoda.

Material and methods

Benthos samples were collected during the KuramBio expedition (Kuril-Kamchatka Biodiversity Studies) with the German RV *Sonne* from 30th of July to 31st of August 2012 southeast of the Kuril Islands in the Northwest Pacific. We sampled 12 stations with 21 hauls on the abyssal plain south and one north of the Kuril-Kamchatka Trench by means of a camera-equipped epibenthic sledge (C-EBS) (Brandt et al., 2013). The figure before the hyphen refers to the station number (stations 1–12); the figure behind the hyphen refers to the deployment at the respective station. Together, they constitute the haul number. At stations 3, 4 and 12, only one haul was carried out. At every other station, two 2 hauls were carried out (Tab. 6.1): therefore, 21 hauls were conducted during KuramBio. By the nature of the sledge, the sample of one haul is divided into an epi-net (25–60 cm above the seafloor) and a supra-net fraction (77–112 cm above seafloor). Station depths ranged from 4,830–5,780 m (Tab. 6.1). For depth comparison between hauls, we use the median of the minimum and maximum depth values of each haul. The abundance data were standardized to 1,000 m; trawling distance was calculated on the basis of the ship and winch speed, respectively (both 1 knot), and the time from the start of the haul to the sledge leaving the seafloor according to the deployment protocol (Brenke, 2005: equation (2)). The samples were sieved on board through 300 µm sieves. Two hauls were conducted at each station: the samples of the respective first haul were fixed in 96% precooled ethanol (-20°C), the samples of the second haul in 4% formalin and subsequently preserved in 70% ethanol. After a fixation period of at least 48 hours, all samples were re-fixed with 96% ethanol. The samples were sorted and identified to species level on board, at the Zoological Museum Hamburg and at the Marine Biology

Institute in Vladivostok. The data of the Isopoda of epi- and supra-net for each haul were pooled for the analyses. All isopod individuals were determined to species level under a dissecting microscope (Tab. 6.2).

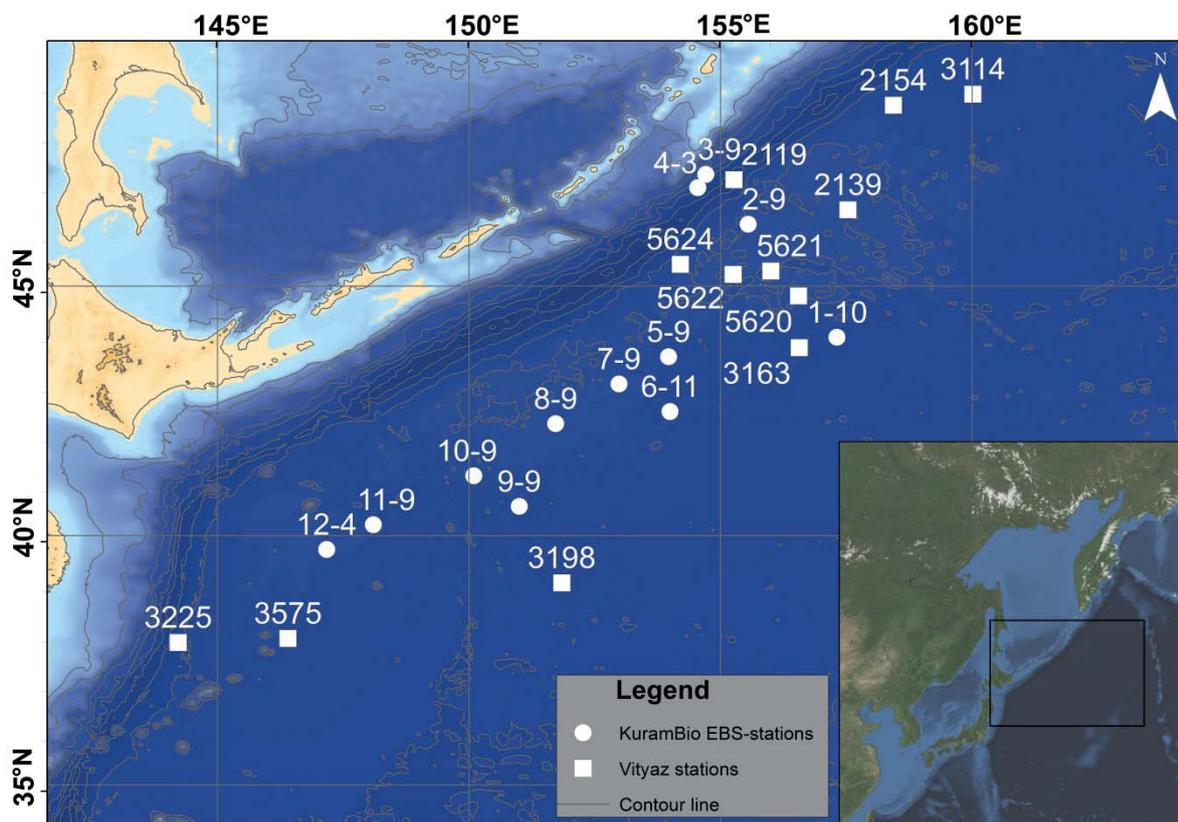


Fig. 6.1: Map of the study area showing the epibenthic sledge sample stations and number of the first haul conducted there (circles) and the *Vityaz* stations used for comparison (squares). The map was generated using ArcGIS Desktop 10 (Student Edition).

We used PAST Version 3.01 (Hammer et al., 2001) to statistically analyze our data. On the basis of the Cosine similarity index, a non-metric multidimensional scaling plot (nMDS) was plotted using the standardized abundance data (1,000 m trawling distance). Pfeifer et al. (1998) suggest the Cosine similarity index for more “qualitative” data, which is obtained by the semi-quantitative EBS. The 14 hauls with complete species data were included: 2-9, 3-9, 4-3, 5-9, 5-10, 6-11, 6-12, 7-9, 8-9, 9-9, 9-12, 10-9, 11-9, 12-4. The following hauls were excluded because of incomplete species data: 1-10, 1-11, 2-10, 7-10, 8-12, 10-12 and 11-12).

Tab. 6.1: Station list of the KuramBio expedition epibenthic sledge samples. Trawling distance was calculated using equation 2 according to Brenke (2005). All numbers and indices shown refer to Isopoda: n individuals for 1,000 m trawling distance, n families, species richness (S), J' (Pielou's evenness), H' (Shannon index), d (Margalef's species richness) and ES (100) (Hurlbert's rarefaction index for expected number of species).

Station No.	Date 2012	Depth [m]	Trawling (from - to) °	Trawling distance [m]	n / 1000 m	n families	S	J'	H'	d	ES(100)
01-10	30.07.	5424	43.9710°N 157.3278°E 43.9722°N 157.2995°E	2222	57.9	10	n/a	n/a	n/a	n/a	n/a
01-11	30.07.	5415	43.9725°N 157.3290°E 43.9768°N 157.3022°E	2161	107.4	12	n/a	n/a	n/a	n/a	n/a
02-09	03.08.	4847	46.2268°N 155.5567°E 46.2487°N 155.5428°E	3117	237.1	8	52	0.8	3.2	9.3	28.6
02-10	03.08.	4861	46.2260°N 155.5595°E 46.2499°N 155.5438°E	2932	230.4	10	n/a	n/a	n/a	n/a	n/a
03-09	05.08.	4861	47.2307°N 154.6982°E 47.2477°N 154.7197°E	2840	691.9	10	44	0.6	2.3	6.6	20.5
04-03	07.08.	5731	46.9640°N 154.5398°E 46.9747°N 154.5565°E	1574	66.1	8	23	0.9	2.7	5.4	23.0
05-09	11.08.	5378	43.5913°N 153.9647°E 43.5717°N 153.9693°E	2469	83.8	10	44	0.9	3.3	9.9	29.0
05-10	11.08.	5377	43.5912°N 153.9635°E 43.5699°N 153.9691°E	2624	42.7	10	19	0.7	2.2	4.8	10.0
06-11	15.08.	5298	42.4927°N 154.0005°E 42.4745°N 153.9943°E	2624	71.3	8	51	0.9	3.4	11.9	29.0
06-12	15.08.	5299	42.4915°N 153.9989°E 42.4704°N 153.9953°E	2562	102.3	13	48	0.8	3.2	10.3	26.0
07-09	17.08.	5220	43.0473°N 152.9905°E 43.0248°N 152.9727°E	2994	99.5	11	51	0.8	3.3	11.0	39.0
07-10	17.08.	5220	43.0463°N 152.9882°E 43.0276°N 152.9743°E	2624	95.7	11	n/a	n/a	n/a	n/a	n/a
08-09	20.08.	5133	42.2447°N 151.7351°E 42.2378°N 151.7082°E	2840	140.1	9	52	0.8	3.3	10.4	34.1
08-12	21.08.	5120	42.2453°N 151.7391°E 42.2387°N 151.7157°E	2408	64.9	9	n/a	n/a	n/a	n/a	n/a
09-09	23.08.	5404	40.5913°N 150.9987°E 40.5708°N 150.9985°E	2315	126.6	11	57	0.8	3.3	11.7	33.2
09-12	24.08.	5395	40.5918°N 150.9976°E 40.5713°N 150.9864°E	2377	56.0	13	34	0.9	3.0	8.5	21.0
10-09	26.08.	5257	41.2077°N 150.0940°E 41.1862°N 150.0933°E	2778	69.8	11	37	0.8	3.0	8.4	26.0
10-12	27.08.	5256	41.1939°N 150.0928°E 41.2169°N 150.0942°E	2778	143.2	9	n/a	n/a	n/a	n/a	n/a
11-09	29.08.	5362	40.2210°N 148.1038°E 40.2062°N 148.0905°E	2408	93.0	7	49	0.9	3.4	10.7	36.0
11-12	31.08.	5350	40.2184°N 148.1088°E 40.2018°N 148.0923°E	2346	59.2	7	n/a	n/a	n/a	n/a	n/a
12-04	31.08.	5222	39.7300°N 147.1813°E 39.7082°N 147.1562°E	2716	360.8	9	45	0.8	3.0	7.5	25.1

The rarefaction curves (Fig. 6.7) were calculated on the basis of the total amount of individuals collected for each species across all hauls. The rarefaction curve is based on species level data; therefore we could only include the 14 hauls also included in the nMDS

plots. The diversity indices S (n species), N (n individuals), d (Margalef's species richness) (Margalef, 1958), J' (Pielou's evenness) (Pielou, 1975), $ES(100)$ (Hurlbert's rarefaction (Hurlbert, 1971) index for expected number of species) and H' (Shannon index) (Shannon and Weaver, 1949) were calculated. Because these analyses are also based on species level data, results are only available for the 14 hauls included in the nMDS plots.

The rank abundance was analyzed with a linear regression using IBM SPSS Statistics 20. The pooled abundance values of all station for each species were logarithmized (\log_{10}) for the linear regression. The corrected R^2 was used as the result of this analysis.

The data set presented by Birstein (1963, 1970, 1971) for the Northwest Pacific was used for comparing the KuramBio data with known data from this area. Twelve *Vityaz* stations (Fig. 6.1, Tab. 6.3) were used for comparison because these stations were taken in the same depth range as our stations (4,830–5,780 m). Birstein's benthic samples were taken with different trawls (the "Sigsbi-Gorbunov" trawl and the "Galathea" trawl) and the "Okean" grab. The mesh sizes of these sampling devices are not specified, but the samples were sieved on board with a mesh size of 714 μm . The trawling distance was not recorded. In order to check for difference in species composition, the species found in both the KuramBio and *Vityaz* samples were compared. Mainly because no trawling distances are known for the trawled gear used onboard the *Vityaz*, we decided to refrain from any sort of statistical comparison and limit the species comparison to mere recognition of the described species (from the *Vityaz* samples) in our KuramBio samples.

Results

In total, we collected 10,169 individuals of Isopoda in the 21 epibenthic sledge samples during KuramBio (Fig. 6.1, Tab. 6.2). 99.8% of the individuals belong to the suborder Asellota; the remaining 0.2% belongs to parasitic forms of the family Bopyridae and the suborder Valvifera. Overall, 17 families of the suborder Asellota are represented in the samples (Tab. 6.2).

All collected individuals were determined to species level: they belong to the families Munnopsidae (47.4%), Desmosomatidae (20.0%), Macrostylidae (11.0%), Haploniscidae (10.0%), Ischnomesidae (7.5%), Nannoniscidae (1.5%), Thambematidae (0.6%) and Mesosignidae (0.5%) (Fig. 6.4 A; Tab. 6.2). These species could be allocated to 73 genera and 207 species. Standardized to 1,000 m trawling distance, most individuals were collected with

the haul 3-9 (692 isopods per 1,000 m²) which is one of the two hauls conducted at the upper slope of the Kuril-Kamchatka Trench (Fig. 6.2). The second most individuals were collected with the haul 12-4 (361 isopods per 1,000 m²), the haul farthest south-east of all sampled stations and closest to the Japan Trench. On average, 143 ± 147 individuals were collected per haul and 1,000 m².

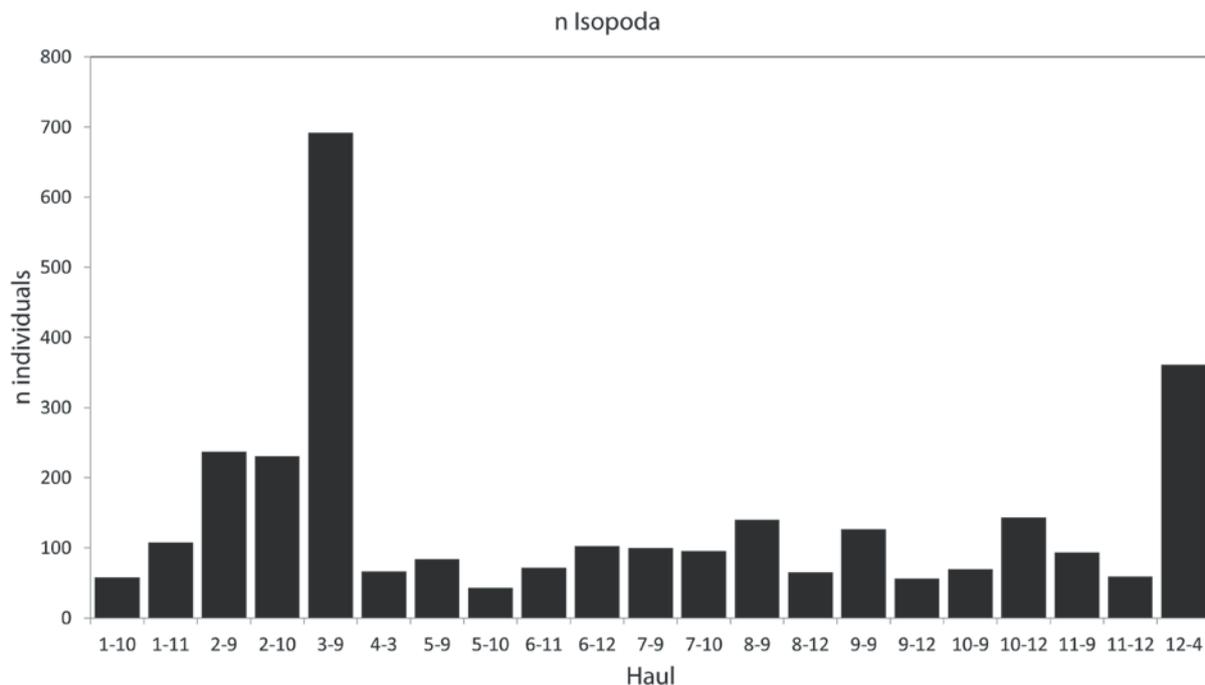


Fig. 6.2: Total numbers of collected individuals of isopods in each haul.

The overall family composition is similar between hauls (Fig. 6.3); the most frequent families are present in similar percentages at each haul. Remarkable is the high percentage of Munnopsidae at the trench's slope haul 3-9. We found a maximum of 11 families per haul of the 19 collected in total (hauls 7-9, 9-9, 9-12 and 10-9). The average number of taxa per haul is 9.0 ± 1.5 for families, 21.4 ± 6.3 for genera and 40.8 ± 13.9 for species. The three most abundant genera (Fig. 6.4 B) are *Eurycope* (Munnopsidae) (26.2%), *Macrostylis* (Macrostylidae) (26.2%) and *Haploniscus* (Haploniscidae) (6.7%). The three most abundant species (Fig. 6.4 C) are *Eurycope* sp. 1 (16.3%), *Macrostylis* sp. nov. 2 (8.6%) and *Haploniscus hydroniscoides* (5.5%). The species composition (Fig. 6.6) is similar between stations according to the nMDS based on the Cosine similarity index. Station 2-9 differs most from the rest (although it still is in the 95% concentration ellipse). The two hauls located on

the slope of the trench, 3-9 and 4-3, are also different from the rest, except for haul 7-9 on the abyssal plain and not in the vicinity of hauls 3-9 and 4-3 (cp. Fig. 6.1).

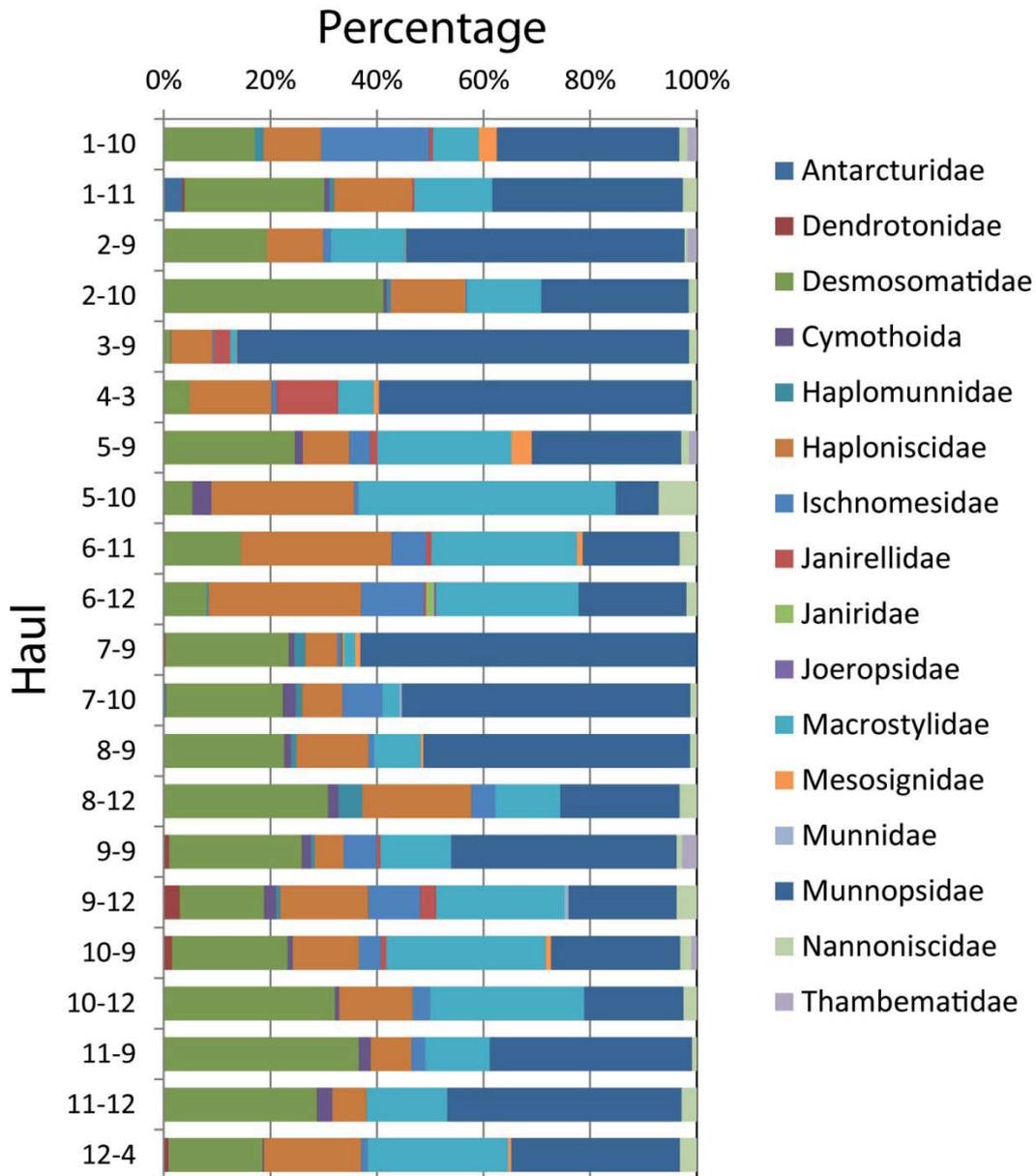


Fig. 6.3: Percentage of individuals of each family of Isopoda present in the samples for each haul. The families are in alphabetical order (left to right).

In the same area and depth range as our samples, 333 individuals of 55 species of isopods belonging to 11 families and 28 genera were sampled at the 12 *Vityaz's* stations (Birstein, 1963, 1970, 1971). In these samples, Haploniscidae (24.9%) were the most abundant family, followed by the Munnopsidae (22.8%) and Macrostylidae (14.4%). The Desmosomatidae, in

contrast to our results, represented only 0.9% of the sampled Isopoda. *Haploniscus* (20.1%), *Macrostylis* (14.4%) and *Eurycope* (10.5%) were the most abundant genera.

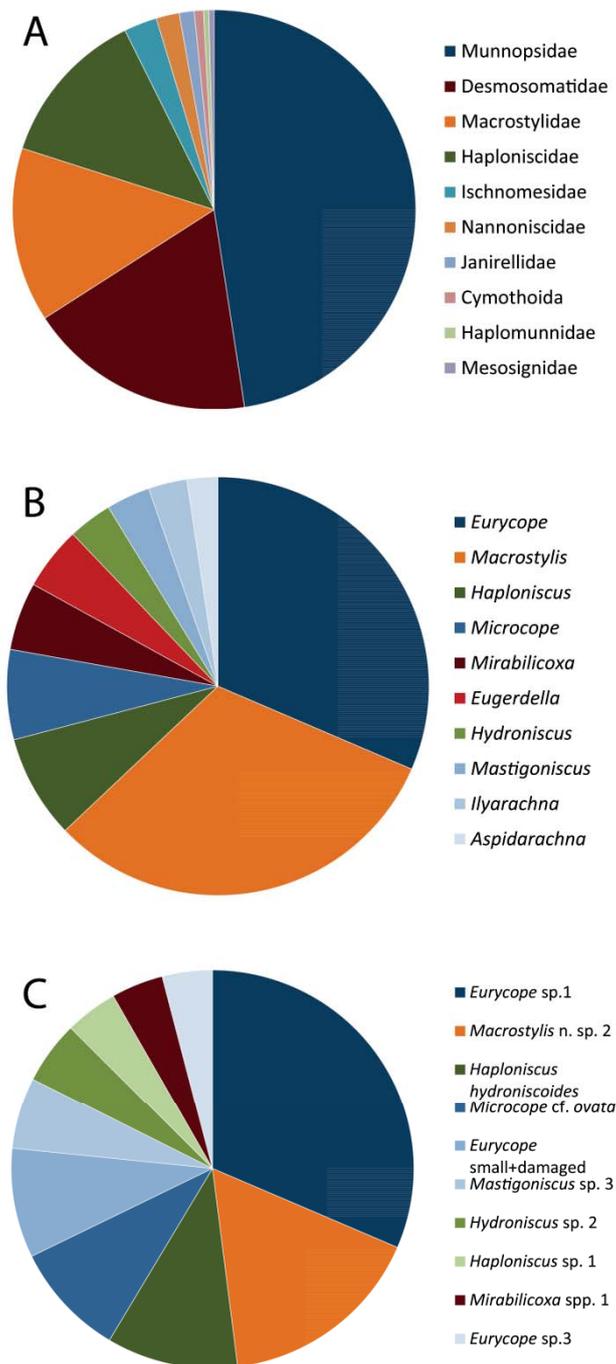


Fig. 6.4: Pie charts showing the overall percentage of n individuals of the 10 most abundant families (A), the 10 most abundant genera (B) and the 10 most abundant species (C). The three most abundant families and their genera and species are colored as follows: Munnopsidae blue, Desmosomatidae red, Macrostylidae orange and Haploniscidae green. Subsequent genera and species in the same family are colored in different intensities.

About half of all isopods collected at the 12 comparable *Vityaz* stations (Fig. 6.1) (Tab. 6.3) have been collected at station 5620. 144 specimens belonging to 33 species of 18 genera have been collected there; only 14 species collected at this station have already been recorded for the area earlier (Birstein, 1960, 1963). The other 21 species have been described as new to science (Birstein, 1970, 1971).

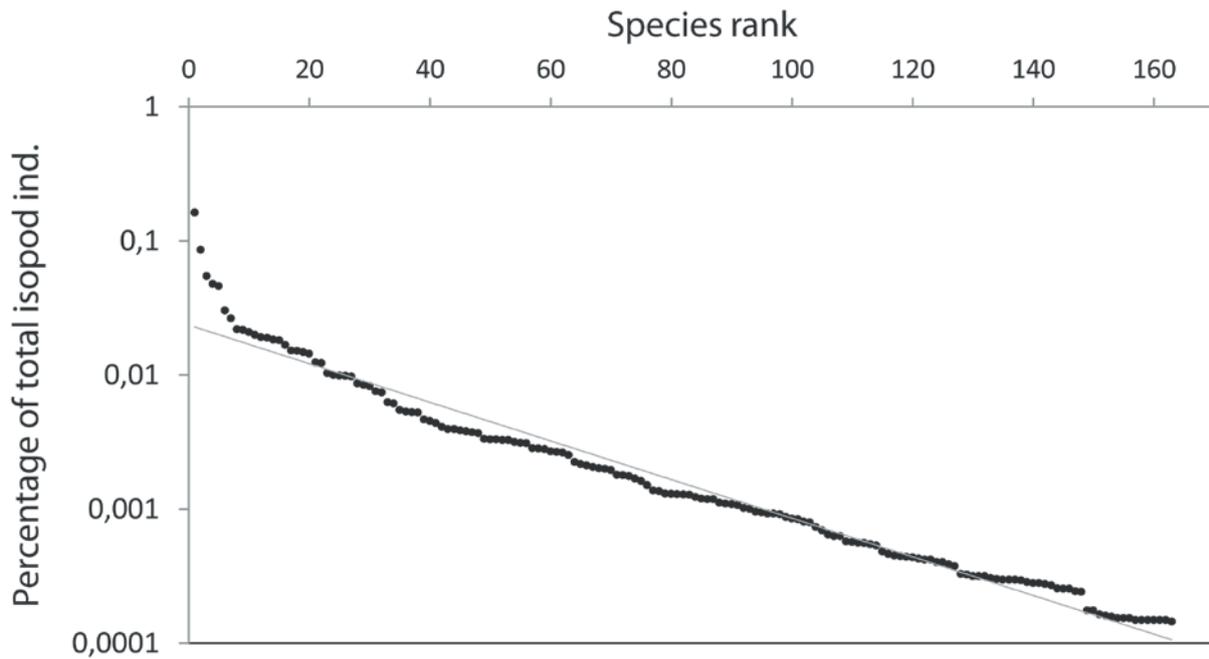


Fig. 6.5: Rank abundance diagram of the total percentage of all sampled species. The species are plotted in ranked order (from the most abundant (1) to the least abundant (187) against the percentage of the total number of isopod individuals for this species. The y-axis is plotted in a semi logarithmic scale to clarify the strict exponential correlation. $R^2=0.96$.

In all KuramBio samples, 272 isopod individuals occurred as singletons; 117 occurrences with 2 individuals per haul and 428 with more than 2 individuals per haul. Many species (64) occurred only in one haul. A total of 89 species occurred in 2–7 hauls and only 32 species in 8–20 hauls. The only species to occur in 20 of the 21 hauls was *Macrostylis* sp. n. 2, the second most abundant species of all KuramBio samples. *Eurycope* sp. 1, the most abundant species by far, occurred at 17 stations. The 4 species which occur at the most stations are 2 Macrostylidae and 2 Haploniscidae. Of the 20 species which occur at the most stations (10–20 stations), only 6 are Munnopsidae which are able to swim and therefore presumably have a larger distribution than species restricted to crawling.

We identified a relatively high abundance for few families, genera and species respectively contrasted by a high number of similarly ranked taxa with relatively low abundances. We therefore plotted a rank abundance diagram (Fig. 6.5). We plotted the pooled abundance of all isopod species of all stations against all recorded species ranked from most abundant to least abundant. We noticed an exponential decline from the abundant taxa to the less abundant taxa. The linear regression yielded a corrected R^2 of 0.96.

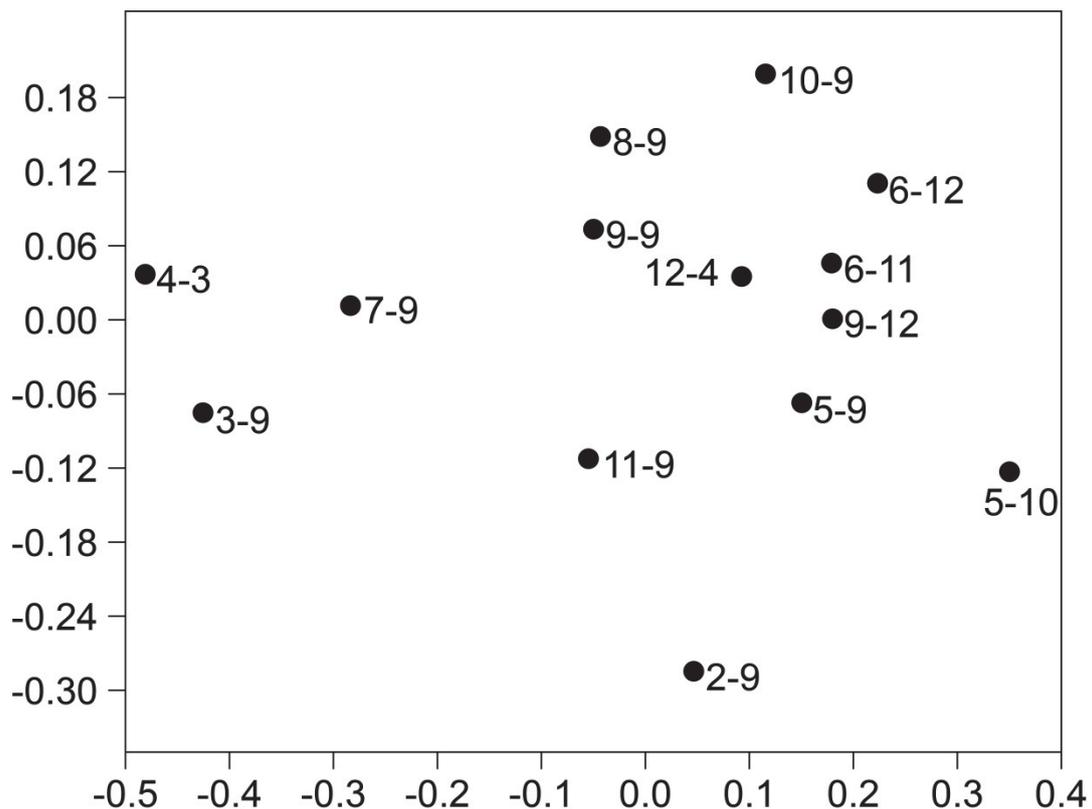


Fig. 6.6: Non-metric MDS plot of the 14 hauls where species level data was available from.

The rarefaction curve of both the KuramBio samples (Fig. 6.7 A) and the *Vityaz* samples (Fig. 6.7 B) show a similar shape: they both have a steep slope. In order to test whether depth is a relevant factor for species richness, we correlated the data ($R^2 = 0.03$). There is no correlation; depth is not a relevant factor for species richness in our samples.

A comparison with the data collected by Birstein (1963, 1970, 1971) has to be done with great care. *Vityaz* samples were collected with grabs and trawling gear different from those methods applied during KuramBio and trawling distances were not recorded during the Russian cruises. However, we think that a comparison of the species presence is reasonable. Of the species found (and described) by Birstein (1963, 1970, 1971), we were able to collect and

identify three species of Desmosomatidae, four species of Haploniscidae, two species of Ischnomesidae, six species of Macrostylidae and one species of Nannoniscidae (Tab. 6.4): However, in several cases, e.g. for the macrostylids, the type material was not available for comparison and species identification based on the original descriptions and illustrations has to be treated with care.

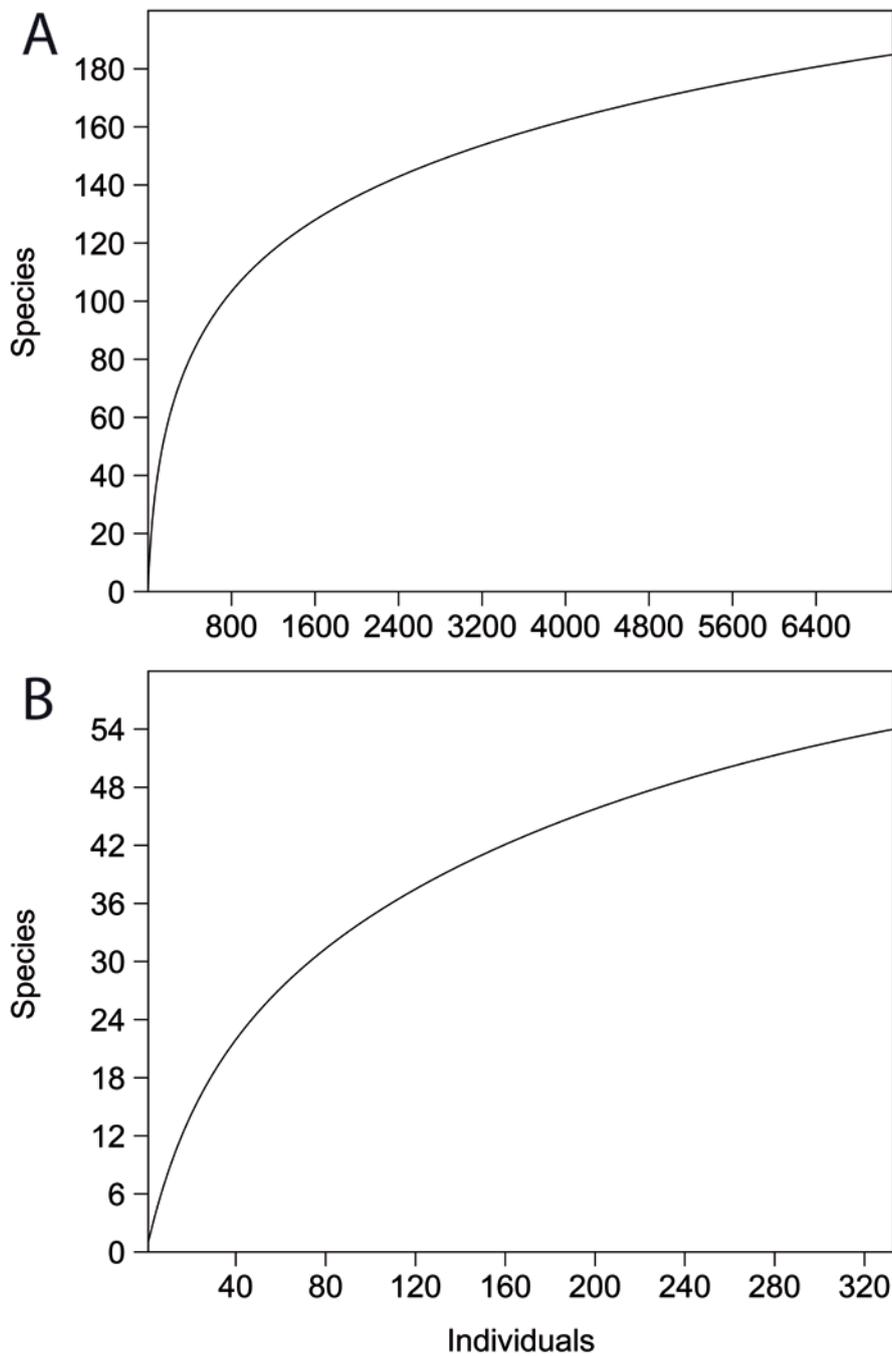


Fig. 6.7: Rarefaction curve of the KuramBio samples analyzed in this study (A) and of comparable *Vityaz* samples (B).

Tab. 6.2: List of isopod families present in the KuramBio samples. Total number of individuals in all samples (n), corresponding percentage of the isopod fauna (% of n Isopoda) and in how many hauls each family was present (at n hauls) are shown for all families. Number of genera and species are additionally shown for the families determined to species level (*).

Family	n genera	n species	n	% of n Isopoda	at n hauls
Arcturidae	1	1	4	0.04%	1
Dendrotionidae	1	2	20	0.2%	6
Desmosomatidae	8	28	2022	20.0%	21
Haplomunnidae	2	4	10	0.1%	10
Haploniscidae	3	11	1006	10.0%	21
Ischnomesidae	6	24	757	7.5%	21
Janirellidae	1	7	91	0.9%	11
Janiridae	1	2	5	0.05%	2
Janiroidea incerta sedis	3	3	4	0.04%	3
Incerta sedis (fam nov.?)	1	1	1	0.01%	1
Katianiridae	1	2	2	0.02%	2
Macrostylidae	1	18	1116	11.0%	21
Mesosignidae	1	2	50	0.5%	16
Munnidae	1	1	1	0.01%	2
Munnopsidae	28	80	4787	47.4%	21
Nannoniscidae	10	14	151	1.5%	20
Paramunnidae	1	1	4	0.04%	1
Thambematidae	2	2	62	0.6%	11
Bopyridae	2	2	16	0.2%	16
Σ	74	205	10109		

Tab. 6.3: *Vityaz* stations which lie in the same area and depth range as the KuramBio samples and which are used for comparison. T: trawl; DO: bottom dredger “Okean”.

Station No.	Expedition No.	Depth [m]	Mean depth [m]	Longitude °N	Latitude °E	Year	Sampling gear
2119	14	5070-5090	5080	47.13	155.2667	1953	T + DO
2139	14	4852	4852	46.5267	157.5333	1953	DO
2154	14	5529	5529	48.6233	158.26.3	1953	DO
3114	19	5670-5680	5675	48.8467	160.0167	1954	T + DO
3163	19	5441	5441	43.7617	156.5667	1954	DO

3198	19	5807-5817	5812	39.0483	151.8433	1954	T
3225	20	5290	5290	37.8533	144.2167	1955	T + DO
3575	24	5461-5495	5478	37.9333	146.4	1957	T + DO
5620				44.8	156.55		
5621				45.3	156		
5622				45.2333	155.25		
5624				45.4333	154.2		

Tab. 6.4: List of species described from specimens collected by the RV *Vityaz* and recollected with the RV *Sonne* in 2012.

Family	Species
Desmosomatidae	<i>Mirabilicoxa coxalis</i> (Birstein, 1963)
Desmosomatidae	<i>Mirabilicoxa</i> cf. <i>tenuipes</i> (Birstein, 1963)
Desmosomatidae	<i>Pseudomesus</i> cf. <i>similis</i> Birstein, 1963
Haploniscidae	<i>Haploniscus</i> cf. <i>belyaevi</i> Birstein
Haploniscidae	<i>Haploniscus</i> cf. <i>menziesi</i> Birstein, 1963
Haploniscidae	<i>Haploniscus hydroniscoides</i> Birstein, 1963
Haploniscidae	<i>Hydroniscus vitjazi</i> Birstein, 1963
Ischnomesidae	<i>Fortimesus</i> cf. <i>concinnus</i> (Birstein, 1960)
Ischnomesidae	<i>Fortimesus</i> cf. <i>profundicolus</i> (Birstein, 1971)
Ischnomesidae	<i>Gracilimesus</i> cf. <i>insignis</i> Hansen 1916
Macrostylidae	<i>Macrostylis curticornis</i> Birstein, 1963
Macrostylidae	<i>Macrostylis grandis</i> Birstein, 1970
Macrostylidae	<i>Macrostylis longula</i> Birstein, 1970
Macrostylidae	<i>Macrostylis ovata</i> Birstein, 1970
Macrostylidae	<i>Macrostylis reticulata</i> Birstein, 1963
Macrostylidae	<i>Macrostylis zenkevitchi</i> Birstein, 1963
Munnopsidae	<i>Acanthocope</i> cf. <i>curticauda</i> Birstein, 1970
Munnopsidae	<i>Aspidarachna</i> cf. <i>glabra</i> (Birstein, 1971)
Munnopsidae	<i>Betamorpha acuticoxalis</i> (Birstein, 1963)
Munnopsidae	<i>Eurycope</i> cf. <i>affinis</i> Birstein, 1970
Munnopsidae	<i>Ilyarachna distincta</i> Birstein, 1971
Munnopsidae	<i>Ilyarachna kussakini</i> Birstein, 1963
Munnopsidae	<i>Microcope ovata</i> (Birstein, 1970)
Munnopsidae	<i>Munnopsoides tattersalli</i> Birstein, 1963
Munnopsidae	<i>Syneurycope affinis</i> Birstein, 1970
Munnopsidae	<i>Vanhoeffenura chelata</i> Birstein, 1957
Nannoniscidae	<i>Panetela tenella</i> (Birstein, 1963)

Discussion

Deep-sea isopods are known to be abundant and species-rich in the benthos (Brandt et al., 2005; Brandt et al., 2007a; Brandt et al., 2009; Hessler and Sanders, 1967). Therefore and since the most abundant families and even some genera (e.g. *Eurycope*, *Macrostylis* and *Haploniscus*) are cosmopolitan (Brökeland, 2010a; Riehl and Brandt, 2010; Wilson and Hessler, 1981) they are a useful and convenient model taxon for comparative biodiversity studies.

Munnopsidae has regularly been found the dominating family amongst samples of deep-sea macrobenthos where they often make up for about 50% of the total isopod individuals and about 30% of the species (Brandt et al., 2007a; Lörz et al., 2013; Malyutina and Brandt, 2007; Schnurr et al., 2014). Desmosomatidae are abundant in the deep sea as well and frequently constitute the second-most frequent isopod family (Brenke et al., 2005; Brix, 2007; Brix, 2006; Hessler, 1970; Kaiser and Brix, 2007; Kussakin, 1999; Malyutina and Kussakin, 1996; Svavarsson, 1987).

The genus most abundant in our samples, *Eurycope*, is the species-richest genus within the Munnopsidae and one of the most widely distributed within the family (Kussakin, 2003; Malyutina and Brandt, 2007; Malyutina and Golovan, 2010; Schotte et al., 1995 onwards; Wilson, 1982). This genus is known from the adjacent deep Sea of Japan: during the SoJaBio expedition to the northern slope and the deep-sea basin of the Sea of Japan (Malyutina and Brandt, 2013), *Eurycope*, represented by one species, *E. spinifrons* Gurjanova, 1933, was the most abundant and frequent isopod genus sampled at each station (Elsner et al., 2013; Golovan et al., 2013; Malyutina et al., 2013). Macrostylidae is monotypic (Riehl and Brandt, 2010; Riehl et al., 2014) possibly due to high degrees of convergence and a consequently uniform morphology (Riehl et al., 2014) obscuring superspecific lineages to be recognized as genera, which may, in part, explain the high abundance of the genus *Macrostylis*. Nevertheless, *Macrostylis* is a frequent component of the deep-sea soft-sediment macrofauna and has been found amongst the most frequent or abundant taxa in other regions as well, such as the Gulf of Mexico (Wilson, 2008) and the Southern Ocean (Brandt et al., 2011; Brandt et al., 2007a; Kaiser et al., 2009; Lörz et al., 2013). Interestingly, one of the most common species in Birstein's samples, *M. affinis*, could not be collected during KuramBio.

The third most abundant genus in our samples, *Haploniscus*, is relatively speciose (> 70 species) (Schotte et al., 1995 onwards) which may be due to the fact that *Haploniscus* is not a

monophyletic group but comprising all species of Haploniscidae which according to the current classification could not be allocated to any of the well-defined genera (Brökeland, 2010b). As a result, *Haploniscus* is species-rich and widely distributed. *Microcope* Malyutina 2008 is the fourth most abundant genus in our samples with two species, *Microcope ovata* (Birstein, 1970) and *M. stenopigus* sp. nov. Malyutina (submitted). The genus contains five described species: 2 species in the Northwest Pacific, one in the Southwest Pacific and 2 in the South Atlantic (Malyutina, submitted).

The most abundant species in our samples, *Eurycope* sp. 1, seems to be a new species, because it does not fit to any *Eurycope* species described by Birstein from the whole Northwest Pacific, but it requires a careful examination and comparison with the types of known species of *Eurycope* of this area. Only one species of *Eurycope*, *E. affinis* Birstein, 1970, is described from the comparable *Vityaz* stations (found at three stations, most abundant with 22 individuals at station 5620). The genus *Eurycope* is the most speciose munnopsid genus in the KuramBio samples with at least 17 species: some of the species that are treated as single species in this paper have the potential to be a complex of several species with minute morphological differences (M.V. Malyutina, unpublished data). The second most abundant species, *Macrostylis* sp. nov. 2, also is a previously undescribed species. Preliminary molecular results (T. Riehl, unpublished data) suggest that while morphologically indistinguishable, at least two distinct and co-occurring lineages are present which is an indication for cryptic species (Held, 2003). The third most abundant species, *Haploniscus hydroniscoides* Birstein, 1963, was recollected from the same area and depths from which it had been described. It is known from relatively large geographical and depth ranges covering the Kuril-Kamchatka, Japan and Izu-Ogasawara Trench and the adjacent abyssal plain at depths between 4,790 and 8,120 m (Birstein, 1963, 1971). This species was found in all hauls at all Kurambio stations except for station 7. The fourth most abundant species, *Microcope ovata* (Birstein, 1970), was found in 16 hauls. Birstein described the species based on two specimens collected at the most species-rich station 5620 and one specimen from the nearby station 5624.

In our samples, we found all of the 12 families recorded by Birstein (1963, 1970, 1971) and additionally 4 more: Haplomunnidae, Dendrotionidae, Katianiridae and Joeropsidae. We collected all 16 genera recorded by Birstein (1963, 1970, 1971). Comparison on species level is difficult, because unambiguous species determination requires comparison with type material which is partially not available. About two thirds of the species we collected during KuramBio are new to science. This supports one of Birstein's (1971) observations: even

repeated sampling in the same area will yield a high amount of species not previously collected. In the samples of eight *Vityaz* expeditions in the Northwest Pacific, 67 species of Isopoda were discovered; then, as a result of the sampling at 29 stations > 1,000 m during the 39th *Vityaz* cruise in 1966, 76 species of isopods were determined. Most of the species were new to science, less than half of the collected species was known, previously described from this area, though. The material was collected and sieved in the same manner and determined by the same person. As known, many deep-sea species occur patchily, like singletons in the samples (e.g. Kaiser et al., 2007, 2009; Brandt et al., 2007a-c), which confirms that even repeated hauls in close vicinity at the same station brought different numbers and composition of isopods in the samples. In all KuramBio samples, 272 isopod individuals occurred as singletons (117 occurrences with 2 individuals per haul and 428 with more than 2 individuals per haul). Keeping this in mind, we consequentially can predict that additional samplings with the fine-meshed epibenthic sledge and more careful sieving might reveal more species and we can approximately estimate the real biodiversity of isopods of the Kuril-Kamchatka Trench area. This assumption is further supported by the rarefaction curves (Fig. 6.7). The curve of the KuramBio samples (Fig. 6.7 A) shows almost the same shape as the curve of the comparable *Vityaz* samples (Fig. 6.7 B), although the number of individuals is more than twentyfold in the former compared to the latter. A curve approaching the asymptote would indicate that the majority of species has been recorded for an area.

The haul 3-9, conducted on the upper slope of the trench, differs from the other hauls in total abundance of individuals (Fig. 6.2) and species composition (Fig. 6.3), but not in the total number of species. Note the high abundance in haul 3-9 on the slope of the Kuril-Kamchatka Trench. Unlike haul 3-9, haul 4-3, which is also located on the upper slope of the trench, does not show such a high number of individuals. This was undoubtedly due to the fact that on haul 4-3, the C-EBS was retrieved completely wrapped in a nylon fishing net and the plankton net disconnected from the epi-net cod end. It is unclear how exactly the ghost net impacted the sampling but we did not get an epi-net fraction for this deployment and the overall result of this deployment must thus be considered biased. Both hauls conducted at the upper slope of the trench show a higher abundance of Munnopsidae and a lower abundance of Desmosomatidae than all other hauls.

Abiotic factors measured *in situ* with the C-EBS (temperature, oxygen content and bottom current) are listed in detail in Brandt et al. (submitted). Temperature ($1.5 \pm 0.03^\circ\text{C}$ across all hauls) and oxygen content ($157.0 \pm 1.5 \mu\text{M}$) only vary slightly between stations and we therefore deem these two abiotic factors not influential to the diversity pattern.

The rank abundance diagram of species for all stations (Fig. 6.5) is in accordance with the species abundance model (Fisher et al., 1943) and shows a lognormal series (Whittaker, 1972). Such a pattern is known in the deep sea for bivalves in a canyon system off the coast of Portugal (Gage et al., 1995).

The rarefaction curves (Fig. 6.7) are not approaching the asymptote. This is not surprising: in the Southern Ocean, the same intermediate result is observed after 40 bathyal and abyssal stations (Brandt et al., 2007a). Generally, a greater sampling effort is required for areas with few abundant and many rare species (Thompson and Withers, 2003), which is the case in our samples.

The KuramBio expedition has revealed and confirmed the Kuril-Kamchatka Trench area to be species-rich as recorded and further anticipated after the *Vityaz* expeditions. The high diversity may well be caused by the nutrient-rich waters brought into this area by the Oyashio Current originating in the Bering Sea. Sampling of the trench itself and further sampling of the area will undoubtedly improve our knowledge of the trench and the local fauna in detail and help understanding deep-sea diversity and patterns in general, both abyssal and hadal.

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Author's contribution:

I determined all Isopoda of the families Ischnomesidae, Haploniscidae Mesosignidae and Thambematidae to species level, conducted the statistical analyses and created the graphs. I wrote and revised all of the manuscript during the submission process including the comments of the coauthors concerning the initial draft.

Alone in the dark: Distribution, population structure and reproductive mode of the dominant isopod *Eurycope spinifrons* Gurjanova, 1933 (Isopoda: Asellota: Munnopsidae) from bathyal and abyssal depths of the Sea of Japan

Chapter 7: Alone in the dark: Distribution, population structure and reproductive mode of the dominant isopod *Eurycope spinifrons* Gurjanova, 1933 (Isopoda: Asellota: Munnopsidae) from bathyal and abyssal depths of the Sea of Japan

Nikolaus O. Elsner^a, Olga A. Golovan^b, Marina V. Malyutina^b, Angelika Brandt^a

^a*Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany*

^b*A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, 17 Palchevsky St, Vladivostok, 690059, Russia*

Abstract

Due to isolation and a period of severe anoxic conditions in geologically recent times, biodiversity is low in the deep Sea of Japan. Among a small group of species inhabiting depths below 2,500, only one isopod species, *Eurycope spinifrons*, was found during the SoJaBio expedition in 2010, but it was the most abundant species of all benthic taxa. *E. spinifrons* was found with remarkably high numbers of individuals at the sampled stations below 2,500 m, providing a rare opportunity to investigate aspects of population structure and reproduction of a deep-sea isopod. The distribution, population structure, fecundity and depth dependent density of *E. spinifrons* were studied. Brooding females were the longest in body size and least abundant, while mancae were the shortest and most abundant. The mean length of individuals showed little deviation among the stations below 2,500 m, ranging from 4.21 ± 0.29 mm in brooding females to 1.20 ± 0.26 mm in free-living mancae. Iteroparity is demonstrated for *E. spinifrons*. It is argued that females have continuous reproduction which increases in the summer. The length of the brooding females is positively correlated with the number of eggs in the marsupium in our sample ($r = 0.291$; $p < 0.05$). Comparing the mean length of *E. spinifrons* between different stations revealed that specimens sampled at the upper slope (460 m) were significantly smaller in every developmental stage than those from stations below 2,500 m. This finding confirms the existence of a threshold depth below which

E. spinifrons was the only isopod species found. Thus, we argue that individuals at deeper stations grow bigger due to reduced competition in the deep Sea of Japan.

Keywords: Biodiversity, Sea of Japan, *Eurycope spinifrons*, population structure, fecundity

Introduction

Sea of Japan

In the bathyal and abyssal zone of the Sea of Japan, biodiversity is low in contrast to the shelf (Derjugin, 1933, 1939; Fujikura et al., 2010). From the upper Pleistocene (85-27 ka) to the lower Holocene (10-8 ka), marine organisms there were deprived of oxygen (Oba et al., 1991) which caused a decrease if not an almost total loss of the endemic deep-sea fauna. The layer between 100 and 400 m stayed constant in salinity and oxygen content throughout this time (Kazutaka, 2004). This layer offered a refuge for the marine fauna during hostile conditions. When oxygen returned to the deep sea in the lower Holocene, the extinct deep-sea fauna was replaced by shallow-water fauna originating from North Pacific species through adaptation to the cold and high-pressure environment (Oba et al., 1991; Tyler, 2002). Recolonization by North Pacific bathyal and abyssal fauna was not possible due to the shallow-water straits with a maximum depth of 130 m. Thus, the deep Sea of Japan is still in an early state of succession. In contrast to the anoxic event in the Pleistocene and Holocene, the Sea of Japan today has an abnormally high level of dissolved oxygen in its deeper parts (Malyutina and Brandt, 2013; Min and Warner, 2005).

The low abundance of individuals usually encountered in the deep sea makes it very difficult to investigate population structure of single species. Additionally and in contrast to shallow-water fauna, husbandry of living individuals or monthly sampling in order to investigate ecological aspects in general are virtually unfeasible. Therefore, most of the available information refers to shelf organisms while knowledge on deep-sea species generally remains sparse (Sanders and Hessler, 1969). Because of its geological history, the deep-sea benthos of the Sea of Japan shows low species richness and high individual abundances, quite contrary to the general condition in the deep sea (Grassle and Maciolek, 1992; Snelgrove and Smith, 2002). The slope off the Russian mainland is steep and with our video equipment, we could observe a flat abyssal plain with lots of organics (e.g. sea-grass remains) accumulated. The only isopod species sampled below 2,500 m, *Eurycope spinifrons*, was sampled there in exceptionally large numbers (up to 2,029 ind. station⁻¹ at station C3-3; see Tab. 7.1). Thus,

this species provides a favorable opportunity to study the population structure of a deep-sea isopod.

Isopoda

The lack of larval dispersal limits the ability of peracarids to overcome geographical barriers like the shallow-water straits of the Sea of Japan. Isopoda are an important model organism in the deep sea because they are abundant and almost omnipresent in deep-sea basins. The family Munnopsidae is frequent in deep-sea samples and within this family the genus *Eurycope* occurs in all oceans with numerous species and are an important part of deep-sea benthic communities (Malyutina and Brandt, 2007; Malyutina et al., 2006; Wilson and Hessler, 1981). *E. spinifrons* was first described by Gurjanova (1933) from Peter the Great Bay at 730-3,000 m and from Vladimir Bay at 308-1,002 m, respectively. So far, it has only been recorded in the Sea of Japan (Malyutina et al., 2013).

According to Wolff (1962), isopod males have three and females six additional development stages resulting in sexual maturity. If the females are iteroparous, brooding stage (with marsupium) and preparatory stage (with developing oostegites) alternate. Molts in-between reduce the marsupial oostegites to small lobes which never completely disappear once sexual maturity is reached (Elizalde and Sorbe, 1993). For shallow-water marine Isopoda, reproduction is known to be uni- (de Alava and Defeo, 1991; Koop and Field, 1980; Shafir and Field, 1980) and bivoltine (Adcock, 1979). The mancae are released at certain time periods, usually when conditions for the offspring are favorable. However, for deep-sea Isopoda, reproduction strategies are far less well known.

To understand the vulnerability and ability of regeneration of deep-sea ecosystems (e.g. after deep-sea fishing or manganese nodule utilization), it is important to know the processes and rate at which deep-sea areas are recolonized. The deep Sea of Japan provides a natural environment in which the recolonization of such an area in isolation can be observed. Usually, regeneration is low due to certain life-history traits like late maturity and low fecundity (Devine et al., 2006). We hypothesize that biodiversity is reduced in the deep sea due to the anoxic event in contrast to the shelf fauna which was not exposed to such severe anoxia and additionally can be replaced by adjacent shelf fauna.

Here, we compare the percentage and length of every development stage among stations to detect depth dependent distribution. We also check for uni- and bivoltinity and seasonality in

the release of the mancae. Furthermore, we hypothesize that there is a correlation between female length and egg numbers.

Material and methods

Sampling area

The material for this study was collected in August-September 2010 in the deep-sea basin of the Sea of Japan during the Russian-German expedition SoJaBio (*Sea of Japan Biodiversity studies*) on board R/V *Akademik M. A. Lavrentyev*. The near-bottom macrofauna was sampled with a newly modified epibenthic sledge (C-EBS, see Brandt et al., 2013). During this survey, 13 EBS stations (with a total of 24 replicates) have been sampled at depths ranging between 455 and 3,666 m (2013). The samples were sieved using 300 µm mesh size and immediately fixed with 96% precooled ethanol or 4% buffered formalin and then re-fixed with 96% ethanol. The target species of our analysis, *Eurycope spinifrons*, was found at all of the 13 EBS stations (depth range: 455-3,666 m). In total, 6,645 specimens of *E. spinifrons* from only eight EBS stations were used for the purposes of the present work (see Fig. 7.1 and Tab. 7.1). For best comparability, all these specimens were taken from the epi-net samples of the sledge (25-60 cm near bottom water).

Tab. 7.1: Station characteristics and number *n* of *Eurycope spinifrons* specimens sampled by the epi-net of the epibenthic sledge during the SoJabio expedition in the Sea of Japan (damaged specimens excluded).

Station	Date	Depth (m)	Starting point of trawling	Ending point of trawling	n
A2-10	14.08.2010	455-465	44°56.9197'N 137°11.8947'E	44°57.0193'N 137°11.9896'E	257
A6-8	16.08.2010	2,545-2,555	44°18.6270'N 137°24.4079'E	44°18.3034'N 137°24.0370'E	195
A7-9	18.08.2010	3,340-3,347	44°00.8871'N 137°29.7822'E	43°59.9124'N 137°31.7745'E	290
B4-7	21.08.2010	3,298-3,353	43°01.5063'N 135°26.4484'E	43°00.9932'N 135°26.1730'E	716
C1-8	27.08.2010	2,670-2,681	42°26.5832'N 133°09.1471'E	42°26.7298'N 133°09.7430'E	647
C3-3	28.08.2010	3,431-3,435	42°01.3458'N 133°09.7454'E	42°01.0547'N 133°09.9003'E	2,029
D1-3	30.08.2010	3,355-3,357	41°28.3497'N 131°46.6929'E	41°27.9058'N 131°46.2575'E	764
D2-7	01.09.2010	2,619-2,637	42°07.1711'N 131°21.1091'E	42°06.8608'N 131°20.9826'E	781

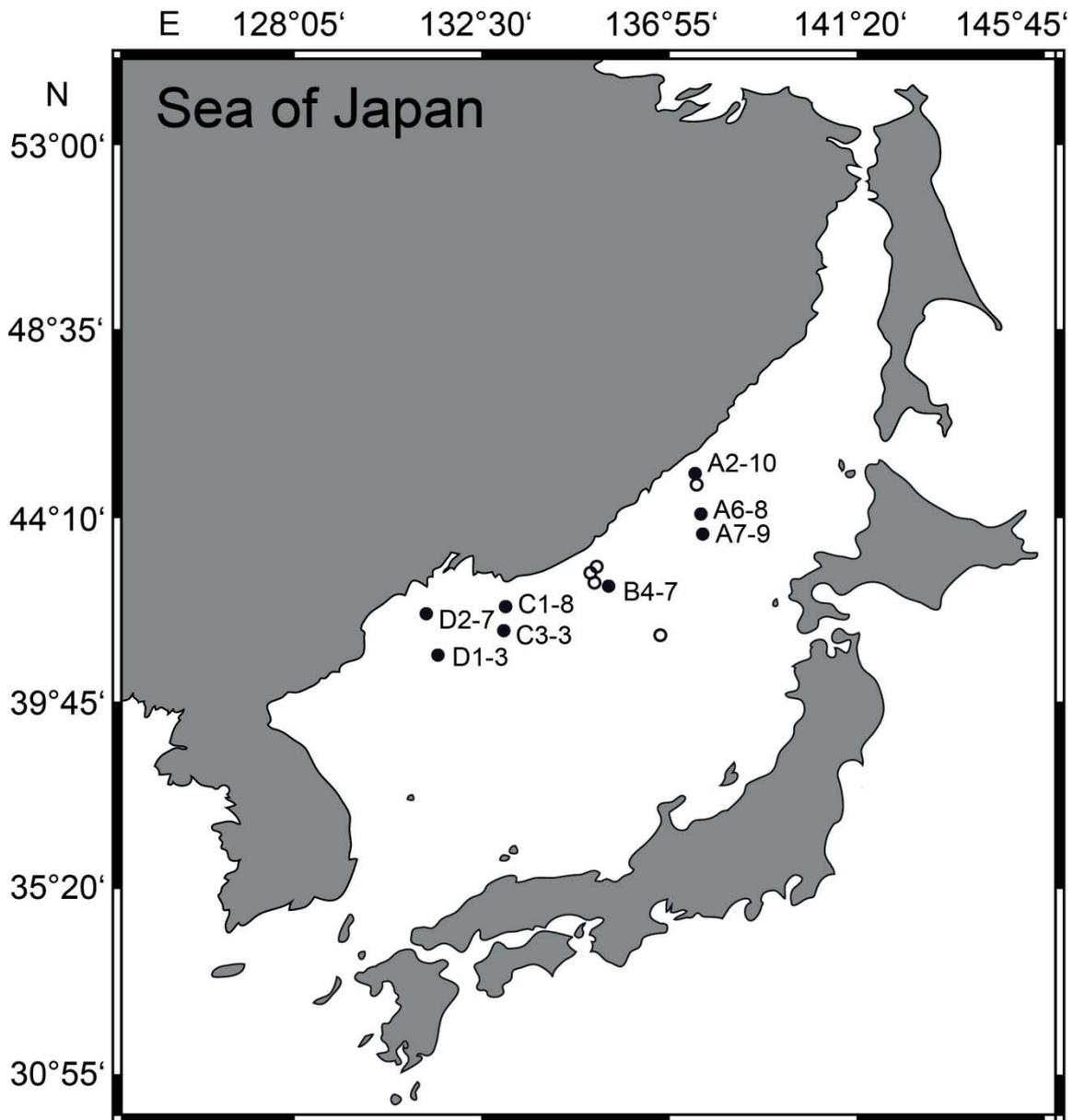


Fig. 7.1: Stations of the SoJaBio-expedition where *E. spinifrons* were used from for the present study (filled circles) and stations where *E. spinifrons* were sampled but not used for the present study (open circles).

Population structure

To characterize the population structure, the specimens of *E. spinifrons* were measured using an Olympus SZX7 and a Wild M5A dissecting microscope equipped with a micrometer eyepiece. Damaged individuals were excluded from the analyses when sex could not be determined doubtlessly or measurement of the full body length was not possible (14.5% of the total number). The six developmental stages used in this study were recognized on the basis of Wolff (1962) as follows: manca (postmarsupial): pereonite VII shorter than VI, sex not

determinable; juvenile ♂: pereomer VII as long as VI, appendix masculina visible but shorter than the pleotelson; juvenile ♀: pereomer VII as long as VI, operculum fused but coxae without oostegites; adult ♂: appendix masculina as long as the pleotelson; preparatory ♀: oostegites present on the coxae; brooding ♀: oostegites fused to form a marsupium which contains eggs or mancae (marsupial). The body length of 5,679 individuals was measured medially from the tip of the rostrum to the tip of the pleotelson.

Due to their importance in population dynamics, females in brooding and preparatory condition are shown separately in the four EBS samples in which their numbers were largest (C3-3, C1-8, B4-7 and D2-7; Fig. 7.3). In order to check for unimodal Gaussian distribution, a Shapiro-Wilk test using SPSS 20 was carried out (Shapiro and Wilk, 1965).

In order to check for seasonality in the release of the mancae, we tried to visually identify distinct normal distributions in the length-frequency histogram (Fig. 7.6). The size classes for Figs. 7.3 and 7.6 were calculated following Sturges' rule (Sturges, 1926). If seasonality occurred, we would have anticipated finding distinct normal distribution curves consisting of individuals of the same generation which share the same developmental stage (age cohort). Because molting results in stepwise growth, each age cohort should be represented by one normal distribution curve. In the case of seasonality, the width of the gap between the different curves would be determined by the time period of the molting interval and the number of broods per season. In the case of continuous reproduction, no clear cohorts would be visible because taking into account the mortality rate, there would be equal numbers of individuals in each developmental stage.

The density of individuals could not be calculated because the winch and ship speed was irregular and not recorded continuously.

Fecundity

The fecundity of *E. spinifrons* was estimated by counting the number of eggs, embryos or mancae in the marsupia of 64 brooding females. All these females were taken from the epi-net sample of station C3-3. A correlation between the number of intramarsupial individuals and the length of brooding females was calculated with SPSS 20 using Pearson's r .

Depth dependent distribution

To examine potential differences in the length of individuals at different depths, each developmental stage of every station was compared with the same developmental stages of

each of the other stations. Hence, a Scheffé test was carried out as a post hoc test following an ANOVA ($\alpha = 0.05$) using SPSS 20 (Scheffé, 1953).

Results

Distribution

In the SoJaBio material, *E. spinifrons* was found between 455-3,666 m depth. At the slope stations, it occurred together with other isopod species and was sampled in rather small numbers. At 2,500 m and deeper, it was the only isopod found. The number of collected specimens per station increased with depth below 2,500 m up to represent one of the most numerous species of the deep local macrobenthos.

Population structure

On the whole, mancae are predominant ($37.8 \pm 16.4\%$), juveniles less numerous ($33.4 \pm 11.4\%$) and adults least numerous ($28.8 \pm 8.6\%$; see Fig. 7.2). Overall, females ($38.0 \pm 9.3\%$) outnumber males ($24.2 \pm 7.8\%$). Within adults, males ($16.4 \pm 5.0\%$) outnumber females ($12.4 \pm 5.1\%$) of which, in turn, more are in the preparatory ($7.1 \pm 4.5\%$) than in the brooding condition ($5.3 \pm 1.2\%$).

In regard to the body length, brooding females were the largest individuals (4.19 ± 0.32 mm) in all of the samples, followed by preparatory females (3.77 ± 0.41 mm). Male adults (3.29 ± 0.60 mm) are shorter than female adults while juvenile females (2.24 ± 0.44 mm) and juvenile males (2.16 ± 0.26 mm) are more or less similar in length. Mancae (1.20 ± 0.26 mm) are the shortest.

In the Shapiro-Wilk test, the brooding and preparatory females of the stations C1-8 ($p = 0.636$ and $p = 0.186$) and the preparatory females of station D2-7 ($p = 0.845$) showed no significant result ($\alpha = 0.05$) indicating unimodal Gaussian distributions for these graphs (Fig. 7.3), but not for the remaining ones ($p < 0.028$).

The histogram of all developmental stages (Fig. 7.6) does not show clear cohorts for every station. For A6-8, A7-9 and D2-7, three cohorts (manca, juvenile and adult) are apparent. Two cohorts (manca/juvenile and adult) are apparent for C1-8. B4-7 lacks a manca cohort visible in all other stations. C3-3 and D1-3 on the contrary only have a manca cohort and few juveniles and adults in constant amounts each. A2-10 shows a steady decline in numbers from mancae to adults.

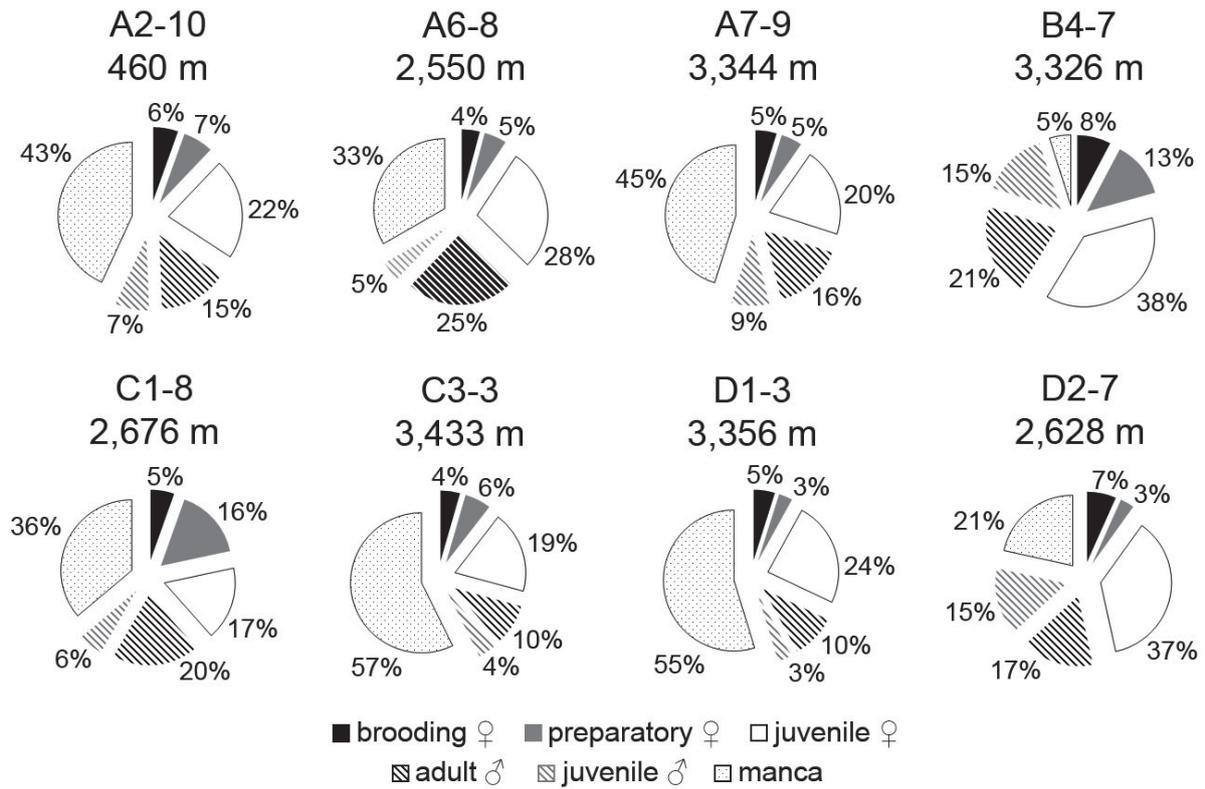


Fig. 7.2: Composition of sexes and developmental stages of the *E. spinifrons* population at eight different stations.

Fecundity

81.25% of the females analyzed were carrying rounded eggs/embryos and 18.75% were carrying mancae. The number of intramarsupial eggs correlate significantly with the body length of the brooding females ($r = 0.291$; $n = 64$; $p < 0.05$; Fig. 7.4). The mean brood size was 26.9 ± 6.5 eggs/embryos/mancae marsupium⁻¹.

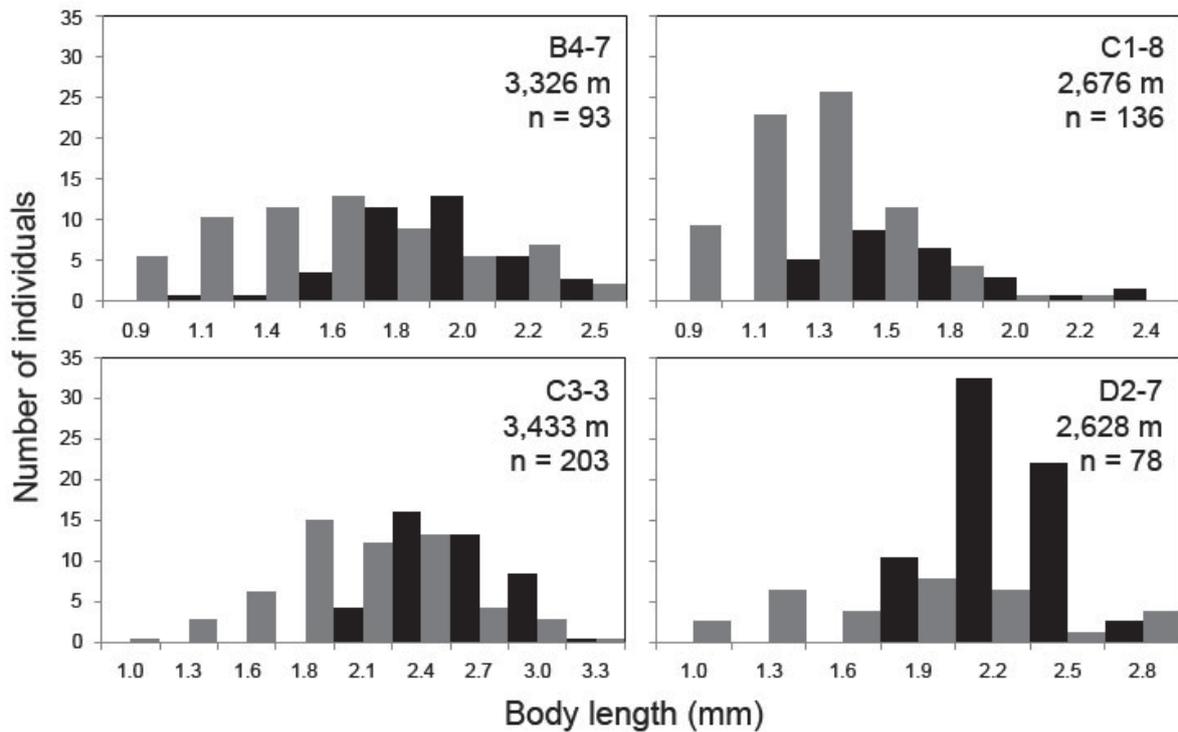


Fig. 7.3: Length-frequency histogram of preparatory (gray bars) and brooding (black bars) females of *E. spinifrons* at the four stations with the most females in these two developmental stages. Size classes: starting value on the x-axis to the value of the next size class.

Depth dependent distribution

Comparison of the developmental stages using a Scheffé test following an ANOVA (Fig. 7.5) reveals a statistically significant difference between the body length of the individuals of the shallowest station A2-10 (460 m) and all other stations (below 2,545 m). For the adult stages of *E. spinifrons*, every other station differs from the station A2-10: brooding ($p < 0.008$) and preparatory females ($p < 0.036$) and male adults ($p < 0.007$). Among the other stations few differed significantly from one another: three for brooding females ($p < 0.044$), two for adult males ($p < 0.003$) and none for preparatory females. Regarding juveniles, the difference is less apparent. The stations A6-8, A7-9 and B4-7 ($p < 0.018$) differed from A2-10 for female juveniles and stations A7-9 and B4-7 ($p < 0.008$) for male juveniles. Nine other stations differed among one another for female juveniles and four for male juveniles. For mancae, the difference is less apparent still: A2-10 differed from A6-8, B4-7 and C1-8 ($p < 0.024$) and 16 of the stations among one another.

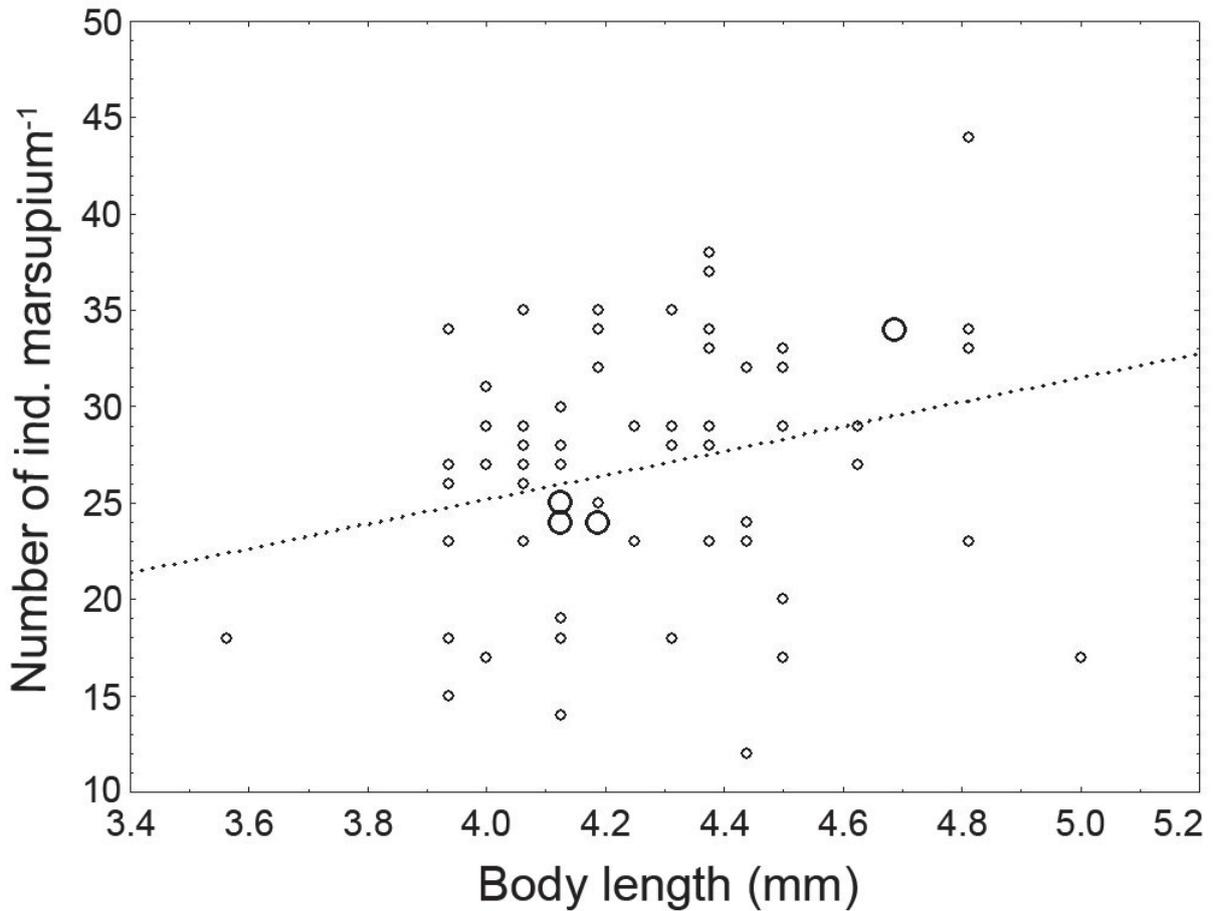


Fig. 7.4: Scatterplot and regression line showing a weak correlation ($r = 0.291$; $p < 0.05$) between the number of marsupial eggs and the length of the corresponding brooding female. The large circles show two females sharing the exact same values.

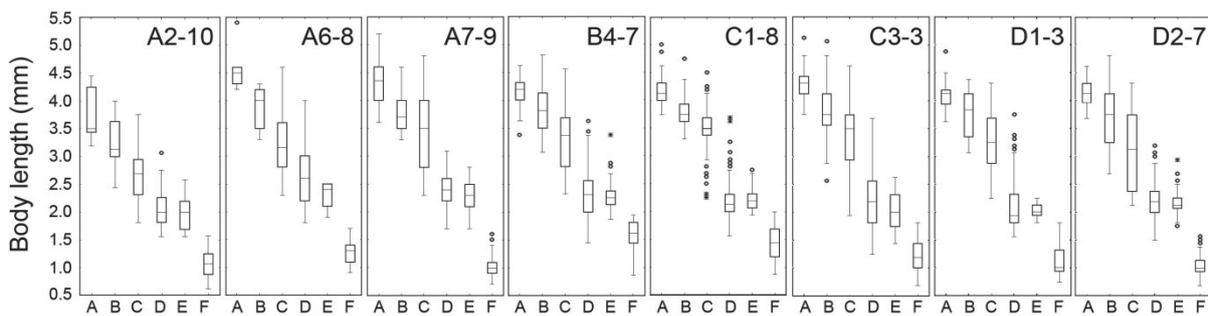


Fig. 7.5: Length (mm) of different developmental stages of *E. spinifrons* at the eight different stations. Median (line within the box), 0.25 and 0.75 quartile (lower and upper end of the box), whiskers (1x interquartile range (IQR)) and outliers (open circles; 1.5-3x IQR) are shown. A: brooding females, B: preparatory females, C: adult males, D: female juveniles, E: male juveniles, F: mancae.

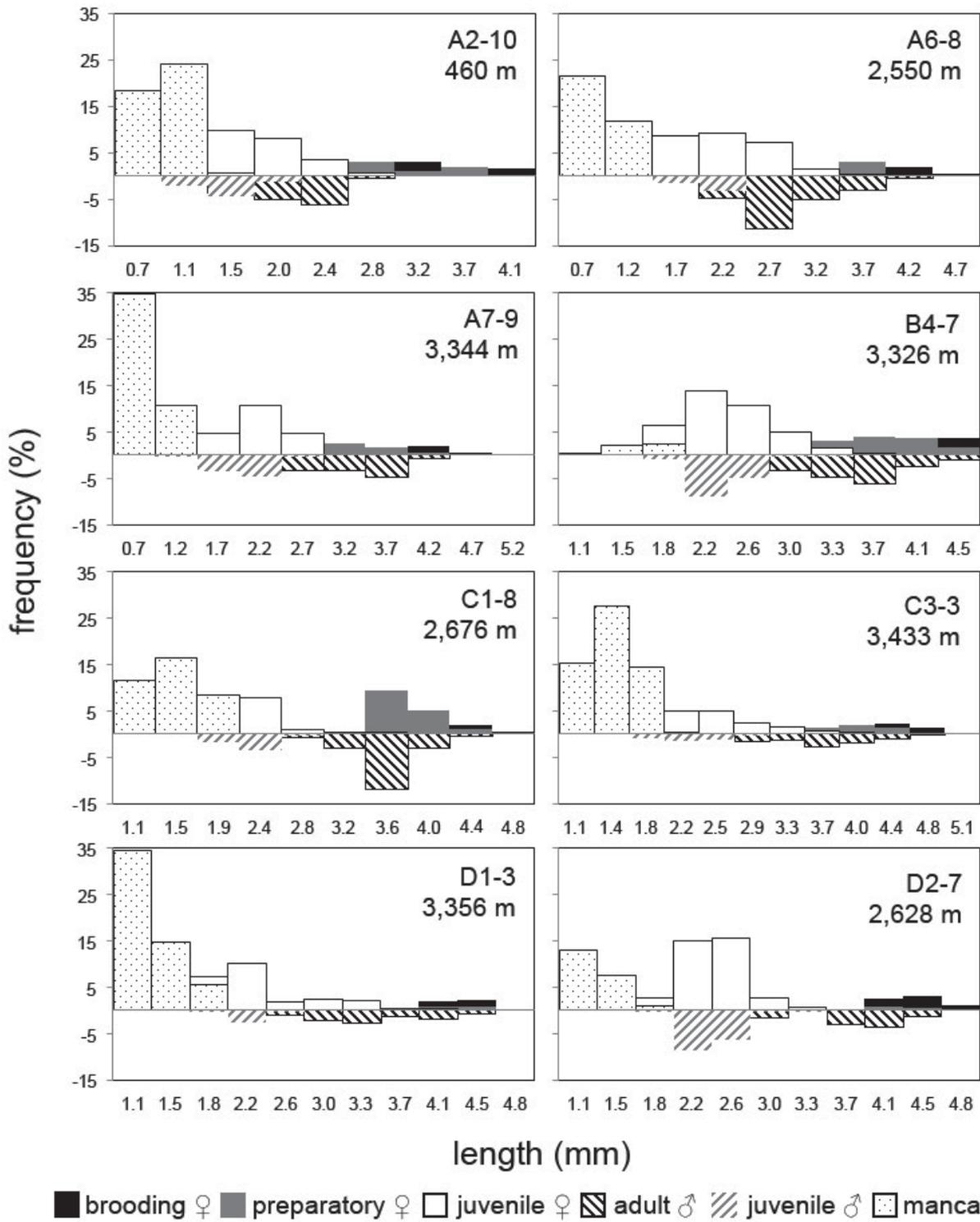


Fig. 7.6: Length-frequency histogram of the different development stages at the eight different stations. Male frequency (adults and juveniles) is given below the x-axis. Size classes: from the starting value to the value of the next size class.

Discussion

Eurycope spinifrons was previously known in the Sea of Japan from 308-3,350 m (Golovan and Malyutina, 2010; Gurjanova, 1933, 1936) and is presumed to be endemic to the Sea of Japan. In order to detect regularities and patterns, we compare our results with those of another deep-sea isopod. Although demographic analyses are scarce for deep-sea populations of isopods, we luckily can compare the population structure of *Eurycope spinifrons* with that of *Munnopsurus atlanticus* from the Bay of Biscay, France (Elizalde and Sorbe, 1993). *M. atlanticus* and *E. spinifrons* belong to different genera of the same family, occur in the northern hemisphere and in both studies sampling took place during the summer (8-9 June for *M. atlanticus*; 13 August – 1 September for *E. spinifrons*).

Population structure

Elizalde and Sorbe (1993) found a higher percentage of preparatory (19.97% at station A and 16.34% at station B) and brooding females (13.94% and 13.37%) than in our samples (cp. Fig. 7.2). Female (18.65% and 11.39%) and male juveniles (7.07% and 5.45%) and manca stages (21.29% and 16.84%) reach higher percentages in our samples while male adults (19.07% and 36.63%) are present in similar percentages in most of our samples (Figs. 7.2 and 7.6). As observed in the present study, the dominance of juveniles and females is generally interpreted as an indication of population growth under favorable environmental conditions. The only exception of this is station B4-7, but the supra-net sample of the same station and haul showed a length-frequency distribution similar to all others.

The length-frequency histograms (Fig. 7.6) do not show the exact same pattern for every station. However, they do show gaps and peaks indicating normal distribution curves and thus contradict continuous reproduction. In three of the graphs three cohorts are visible, in four graphs two and only in one graph no gaps and peaks are recognisable.

The modes of the manca stages vary (0.9-1.8 mm) which indicates that the majority of the brood has already molted and grown. Looking at all stations, the mode of mancae equals 1 mm, the mode of juveniles equals 2 mm and the mode of adults equals 4 mm. The intermolt period for isopods generally lies at around 20 days (Gruner et al., 1993) and several months in Antarctic serolid isopods (Luxmoore, 1981) which is typical for species living in cold conditions. This indicates that reproduction is not restricted to a narrow time frame, but it might still be restricted to the warm months of the year where primary production is the highest.

The length-frequency histogram (Fig. 7.6) is also not clearly multimodal which would indicate seasonality and contradict continuous reproduction. First predicted by Orton (1920), continuous breeding has been demonstrated for some deep-sea asellote isopods, including some Munnopsidae (Rokop, 1977; Sanders and Hessler, 1969), sometimes with a more intense reproductive activity in summer when food resource is abundant (Harrison, 1988). In the case of *E. spinifrons*, the absence of clear cohorts in some histograms and the high amount of mancae in almost all samples (cp. 3.2 and Fig. 7.6) suggest that this species has also continuous recruitment throughout the year.

Thus, continuous reproduction in addition to a seasonal increase in reproduction in the summer when food is most plentiful is likely. However, continuous recruitment cannot be assured with certainty on the basis of the samples from this single expedition: The fact that cohorts are apparent but not clearly distinct in the histograms could hint to continuous reproduction with an increase in the summer. Continuous reproduction could level out the minima between the different cohorts of each summer to some degree and thus explains the lack of distinct cohorts at some stations and the generally high amount of mancae in almost all samples.

Dissection of two brooding female specimens showed developing oocytes in the gonads of the females which strongly suggests iteroparity in *E. spinifrons*.

The Shapiro-Wilk test was only carried out for preparatory and brooding females each. This test showed Gaussian distribution for only two of the four tested stations for preparatory females and one of the four for brooding females (cp. section 3.2. and Fig. 7.3). Even though the remaining graphs are not normally distributed, they are nevertheless clearly unimodal and not multimodal (Fig. 7.3). Unimodality can either mean that all reproductive females are members of a single age cohort or reproduction is continuous so that distinction between cohorts is impossible due to smooth transition. We hypothesize that *E. spinifrons* lies in-between with a continuous recruitment in general, but with an increased reproduction during the summer. Thus, further research regarding deep-sea isopod reproductive biology will be necessary for a clear picture.

Fecundity

Fecundity (number of eggs/embryos marsupium⁻¹) correlates significantly with the female body length ($r = 0.291$; $n = 64$; $p < 0.05$; Fig. 7.4). This is in accordance to the investigations of terrestrial and shallow-water species, where fecundity strongly correlates with female size

(Gruner et al., 1993; Marques et al., 1994). However, in this case the correlation is weak so that other factors most likely influence fecundity as well. We found an average amount of 27 eggs per marsupium for *E. spinifrons* which matches with the numbers known for *Cirolana imposita* Barnard, 1955 from a kelp bed of 15-33 eggs per marsupium (Shafir and Field, 1980). The numbers also match for smaller specimens of the coastal *Jaera albifrons* Leach, 1814, but are considerably lower than those of the larger specimens with an average of 25 and 64 eggs at 3 mm and 5 mm length, respectively (Gruner et al., 1993). This discrepancy can be explained by the general trend that bathyal and abyssal species have fewer eggs than littoral species of equal size (Wolff, 1962).

Depth dependent distribution

Individuals from the shallowest station A2-10 (460 m) are considerably shorter than individuals from bathyal stations below 2,500 m (cf. Fig. 7.5). The adult stages clearly differ in size, while the difference in juveniles is less apparent and least apparent in mancae. The size of the eggs is genetically not fixed, but increases with higher latitudes (Clarke and Gore, 1992). However, the growth rates of juveniles and adults can be determined by various environmental factors. From marine isopods it is known that juveniles supplied with high quality and sufficient amounts of food have increased growth and survival rates (Marcus et al., 1978).

We found a considerable amount of seagrass remains in the samples of transect A in the stations below 2,000 m (visual observation), probably accumulating at such depth during summer due to the local steep slope and proximity of the Russian mainland. Contrarily, we did not find a lot of seagrass in the sample from 460 m depth. Although not quantitatively analyzed, the number of individuals per area is significantly higher at 460 m than at the deeper stations (Brandt et al., 2013; Golovan et al., 2013). The shelf and upper slope fauna would have to adapt to deep-sea conditions in order to be able to access this area where food apparently is available while competition is low. The deep-sea fauna in the Sea of Japan became extinct by an anoxic event in geologically recent history (upper Pleistocene/lower Holocene). It could not be replaced by the deep-sea fauna of adjacent deep-sea basins because the deepest connection between them (130 m) is far too shallow to allow faunal exchange especially concerning benthic brooders like peracarid crustaceans. *E. spinifrons* appears to be the only isopod species which either succeeded in adapting to the peculiar conditions of the deep Sea of Japan so far or may be the only deep-sea isopod species which survived in a

refuge. Whichever is the case, this munnopsid species meets favorable conditions in the deep sea.

We hypothesize that the difference in body size between the 460 m station and the stations below 2,500 m is caused by reduced competition rather than lower temperature in the deep-sea stations. Low temperature is believed to be a major factor for gigantism in the deep sea (Thiel, 1979), but most likely not the primary factor in this case as the difference in temperature is only 0.5°C (0.8°C at 460 m and 0.3°C at 3,000 m). The food available per area at deeper stations is higher than at the 460 m slope station which is a result of the cumulative process along the slope (Zenkevitch, 1977). Additionally, the lower density of individuals further increases the amount of food available for each individual. For *Stymphalus dilatatus* (Perty, 1833), a costal species, it is known that growth is faster when food is more plentiful (Koop and Field, 1980). Therefore, we assume that growth at the deeper stations may be induced by the higher food availability per individual which is caused by the steep slope off the Russian mainland, causing relatively high food input for a deep-sea area.

E. inermis from the North Atlantic is known to consume benthic Foraminifera (Svavarsson et al., 1993) which in turn consume detritus (Goldstein and Corliss, 1994; Gooday et al., 1992). The gut content of two brooding females and one adult male were filled which demonstrates that food is plentiful for *E. spinifrons*. The guts contained mainly diatoms and some ciliates, flagellates and plant fibers, possibly sea grass. This strongly suggests that this species mainly consumes phytodetritus.

Thus, it appears that food is readily available for *E. spinifrons*. The relatively low density of individuals due to the recent extinction event in the deep sea results in reduced competition. Consequently, *E. spinifrons* meets favorable conditions in the deep Sea of Japan.

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Author's contribution:

I determined the sex and developmental stage and measured all individuals. I conducted the statistical analyses on the basis of discussion and advice from the coauthors, wrote the initial draft and did the revision during the submission process.

Population structure of two species of *Pleurogonium* Sars, 1864 (Isopoda: Paramunnidae) from the northern continental slope of the Sea of Japan

Unpublished manuscript

Chapter 8: Population structure of two species of *Pleurogonium* Sars, 1864 (Isopoda: Paramunnidae) from the northern continental slope of the Sea of Japan

Nikolaus O. Elsner

Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany

Abstract

Population structure is an important aspect of reproductive biology. In order to study seasonality in breeding, the focus of this study lies on the size-frequency distribution of two species of *Pleurogonium* Vanhöffen, 1914 (Isopoda: Paramunnidae) collected at one station on the northern slope of the Japan basin of the Sea of Japan during the Sea of Japan Biodiversity Studies (SoJaBio) expedition in August 2010 with the Russian RV *Akademik M. A. Lavrentyev*. One of the species is undescribed; the other was determined to be *Pleurogonium* aff. *kyushuense*. This species was originally described from Kyushu; I therefore hypothesize that the populations of the two regions are connected and that the deep Sea of Japan presumably at least partially was re-colonized through the Korean Strait. A total of 564 individuals were collected, measured and their sex determined in order to assess the reproductive mode of these two species from 459 m depth. About 30% of the individuals were brooding females with a developed marsupium. This is in contrast to other studies where the brood of different isopod species always was released in spring due to the higher amount of food available at this season. The high amount of brooding female also suggests synchronized breeding in these two species; it is therefore hypothesized that the two species of *Pleurogonium* may have a different diet than other isopod species in the region. Detailed examination of the mouth parts and gut contents in the future may support this hypothesis.

Keywords: length-frequency histogram; male-female ratio; polymodal curve; age cohort

Introduction

The Sea of Japan is a marginal sea in the Northwest Pacific. As such, it is special in the way that, in contrast to adjacent marginal seas like the Sea of Okhotsk or the Bering Sea, it lacks deep-sea straits (Tyler, 2002). Thus, the deep waters of the Sea of Japan and the adjacent marginal seas as well as the Pacific Ocean itself do not exchange. The deep sea of this therefore semi-isolated basin was anoxic over repeated periods in the past (Tada, 1994) until about 8000 years ago (Oba et al., 1991) and therefore had to be recolonized, presumably from the shelf regions (Zenkevitch, 1963). The low diversity suggests that the deep Sea of Japan is still in an early succession stage (Golovan et al., 2013) (**Chapter 4**). In regard to this recolonization, different reproductive strategies may be the cause of invasion success or lack thereof for individual species.

During the SoJaBio expedition (Sea of Japan Biodiversity Studies), epibenthic sledge samples were taken along the northern slope of the Japan basin in a depth range of 459–3649 m. At the stations between 459–1360 m, 5 different families of Isopoda were found. The family Paramunnidae Vanhöffen, 1914, belonging to the suborder Asellota, was the thirdmost abundant family and 625 individuals and 2 species were collected, representing 6.4% of all collected isopods (cp. **Chapter 5**). One of the two species of *Pleurogonium* present in our samples is a new species and will be described in a subsequent publication, the other one was determined as *Pleurogonium* aff. *kyushuense*. Paramunnidae are known to occur predominantly in the Southern Hemisphere in cold and temperate waters and are considered a shallow-water group (Just and Wilson, 2007; Wilson, 1980). However, several genera and species are also known from the cold and temperate Northern Hemisphere, especially from the Sea of Japan and Japanese waters (Malyutina and Ushakova, 2001a, b; Shimomura, 2009; Shimomura and Mawatari, 1999, 2000, 2001, 2002). Generally, little is known about the behavior of deep-sea organisms, but some aspects are known for *Pleurogonium rubicundum* Sars, 1864 collected from the Skagerrak: Individuals have been reported to walk rapidly on the sediment, to vertically burrow down into the sediment with only the pleotelson sticking out for ventilation and to feed on spinach and fresh mussel in the laboratory (Hessler and Strömberg, 1989). Paramunnidae are generally small (~0.6–3.0 mm) (Just and Wilson, 2007) and the genus *Pleurogonium* consists of 21 described species of which 6 are known from Japanese waters: *P. bifolium* Shimomura and Mawatari, 2001, *P. hispidum* Shimomura and Mawatari, 2001, *P. angustum* Kussakin, 1972, *P. inerme orientale* Kussakin, 1962, *P. tanseimaruae* Shimomura, 2009 and *P. kyushuense* Shimomura, 2009.

Studies on population structure in the deep sea are rare (Elizalde and Sorbe, 1993), but are crucial for the understanding of reproduction, especially in regard to colonization and potential re-colonization after disturbances of any kind, for example after deep-sea fishing with trawl nets (Norse et al., 2012; Roberts, 2002) or deep-sea mining (Ingole et al., 2001; Miljutin et al., 2011)). Such studies can reveal important characteristics in the reproductive biology, like seasonality (Luxmoore, 1982) or brood size (Marques et al., 1994) which are largely unknown for the deep sea. Such information may help in determining months in which the benthos (or parts thereof) may be more vulnerable to disturbances than at other times. Usually, deep-sea samples contain many singletons and species with low abundances. Therefore, the opportunity was taken to study the relatively high amount ($n = 567$) of individuals of the two species of *Pleurogonium* present in our samples in order to check for seasonality of breeding in the local population.

Material and methods

The SoJaBio (Sea of Japan Biodiversity Studies) expedition took place from the 11th of August to the 5th of September 2010 in the deep Sea of Japan onboard the Russian RV *Akademik M. A. Lavrentyev*. 13 stations were sampled with a camera-equipped epibenthic sledge (C-EBS) (Brandt et al., 2013) in the Japan basin and on its slope (Fig. 8.1). The samples were immediately fixed with 96% precooled ethanol (-20°C) and then re-fixed with 96% ethanol after 48 hours. All individuals were collected in the epi-net (25–60 cm above the seafloor). Samples were sorted on board and later at the Zoological Museum Hamburg. The individuals were determined to species level, the material then dissected under a dissecting microscope (Wild M5A), drawn under a light microscope (Leica DM 2500) equipped with a *camera lucida* and the drawings and plates prepared using a Wacom Intuos 3 drawing board and Adobe Illustrator CS5. The types will be deposited in the Zoological Museum Hamburg (ZMH) once the species will be described.

For the examination with the scanning electron microscope (SEM), several specimens of each species and sex were washed in Triton-ethanol solution (Triton X-100; non-ionic detergent) and critical point dried in a Balzers CPT Dryer with CO₂. After coating with carbon in an evaporation unit PD170AZw from Leybold-Heraeus, the specimens were observed and photographed in a LEO 1525 Field emission scanning electron microscope.

For the population structure analysis, a total of 534 individuals of *Pleurogonium* sp. nov. 1 and *P. aff. kyushuense* were measured from head to pleotelson using an ocular micrometer in a dissecting microscope (Wild M5A). All measured individuals were collected at station A2-10 (44.9487°N 137.1982°E–44.9503°N 137.1998°E) at 459 m depth on the 14th of August 2010 (0.8°C bottom temperature, 259.4 µM oxygen concentration). Additionally, the sex of each individual was determined. The stages were categorized on the basis of Wolff (1962) and in a similar way as by Elsner et al. (2013) (**Chapter 7**) with the following stages: brooding female: adult female with developed oostegites forming a marsupium (containing eggs, manca or empty); female: adult female lacking a marsupium; female juvenile: female with incompletely developed seventh pereonite; adult male: fully developed seventh pereonite and first pleopod; male juvenile: seventh pereonite and first pleopod not fully developed.

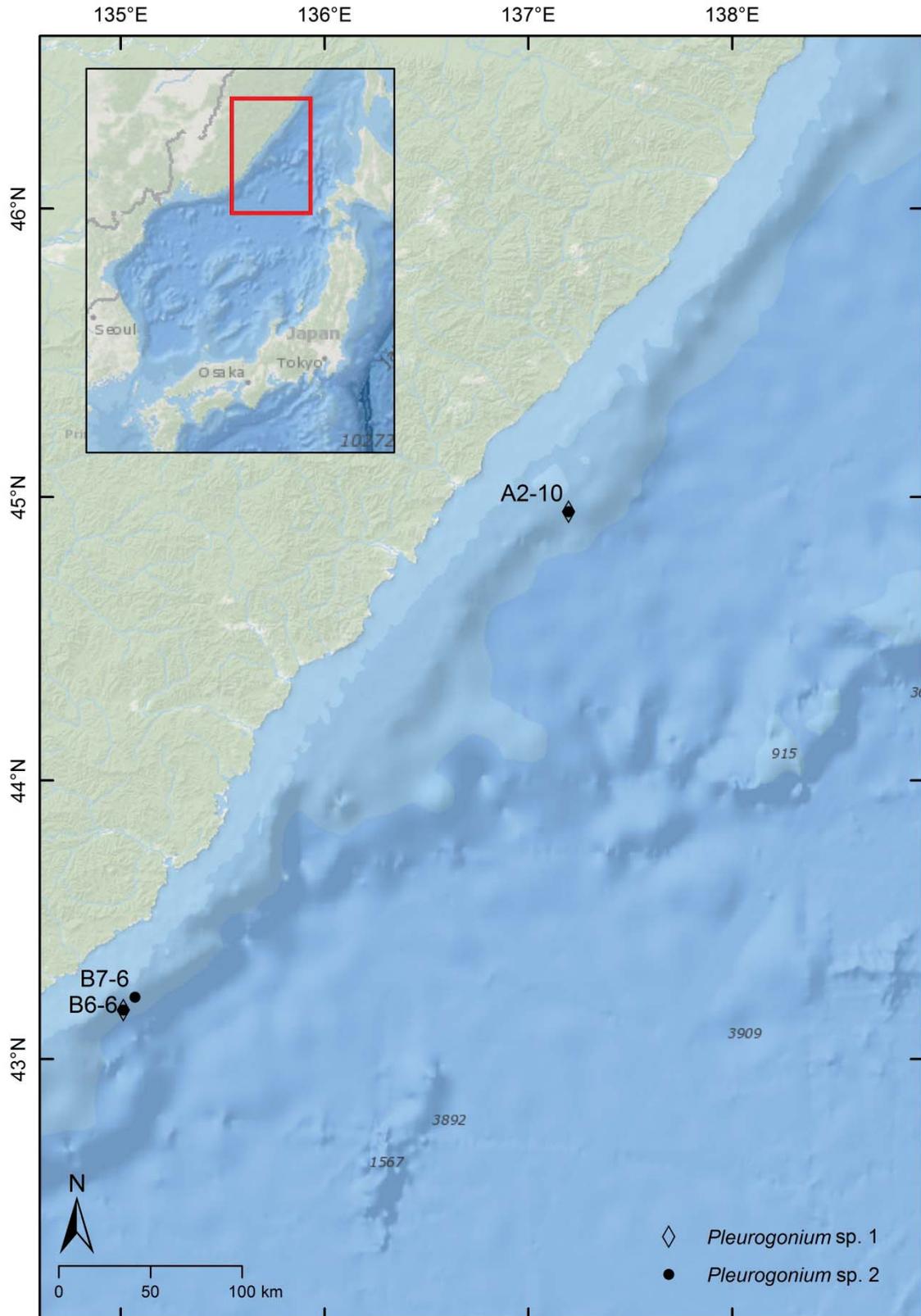


Fig. 8.1: Map of the station where both species of *Pleurogonium* were collected. The map was created using Esri ArcGIS 10.2 by T. Springer.

Results

More than 200 individuals each of both *Pleurogonium* sp. nov. 1 (Fig. 8.2 and 8.3 A, B) and *P. aff. kyushuense* (Fig. 8.3 C, D) were available from the same station. Therefore, the population structure was analyzed using a length-frequency histogram (Fig. 8.4).

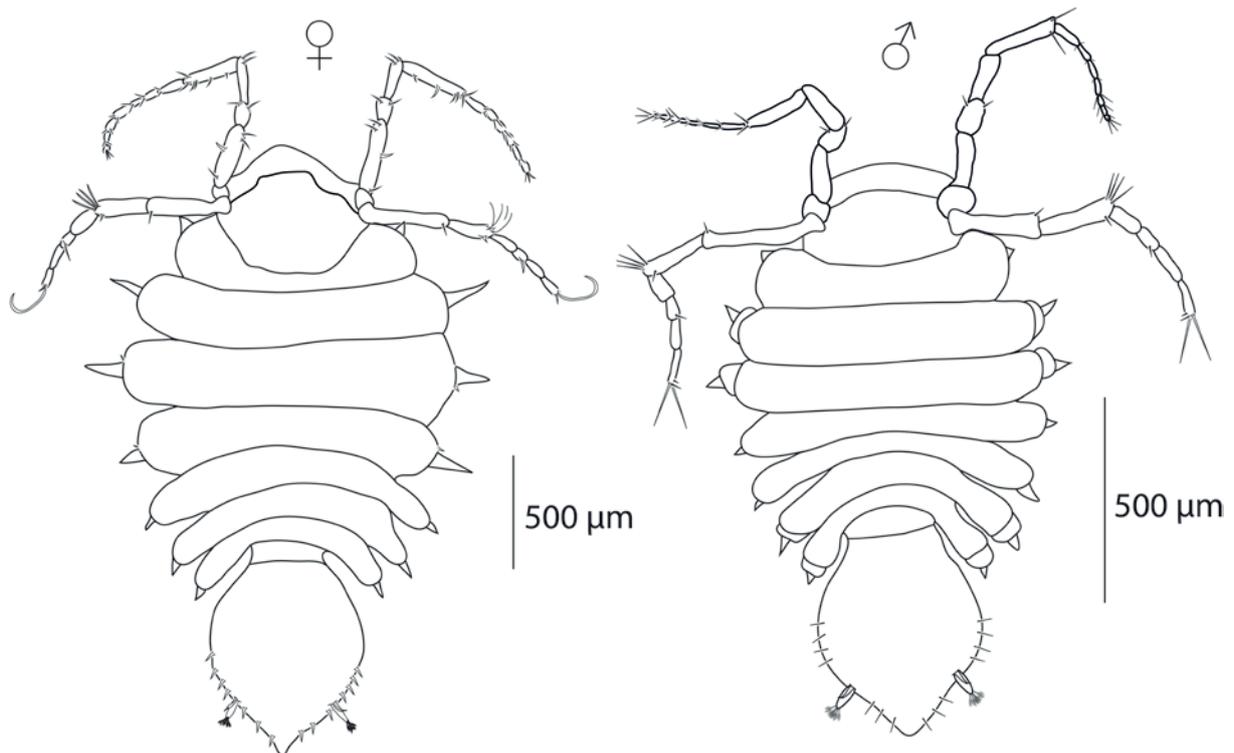


Fig. 8.2: Dorsal view of the female (A) and male (B) habitus of the new species *Pleurogonium* sp. nov. 1.

For *P. sp. nov. 1* (N = 201), brooding females comprised the largest percentage (33.3%), followed by adult males (23.4%), adult females (17.4%), female juveniles (15.4%), damaged specimens (6.0%) and male juveniles (4.5%). Brooding females measured the longest (1.6 ± 0.1 mm), followed by adult females (1.3 ± 0.1 mm), male adults (1.2 ± 0.1 mm) and male and female juveniles (both 1.1 ± 0.1 mm). The male to female ratio equals 1 : 2.4.

For *P. aff. kyushuense* (N = 366), the population structure was similar: brooding females comprised the largest percentage (31.1%), followed by adult males (27.3%), adult females (24.9%), female juveniles (9.3%), damaged specimens (5.7%) and male juveniles (1.6%). The different stages were on average all 0.1 mm shorter than the specimens of *P. sp. nov. 1*: brooding females measured 1.5 ± 0.2 mm, followed by adult females (1.2 ± 0.2 mm), male

adults (1.1 ± 0.1 mm) and male and female juveniles (both 1.0 ± 0.1 mm). The male to female ratio equals 1 : 2.3.

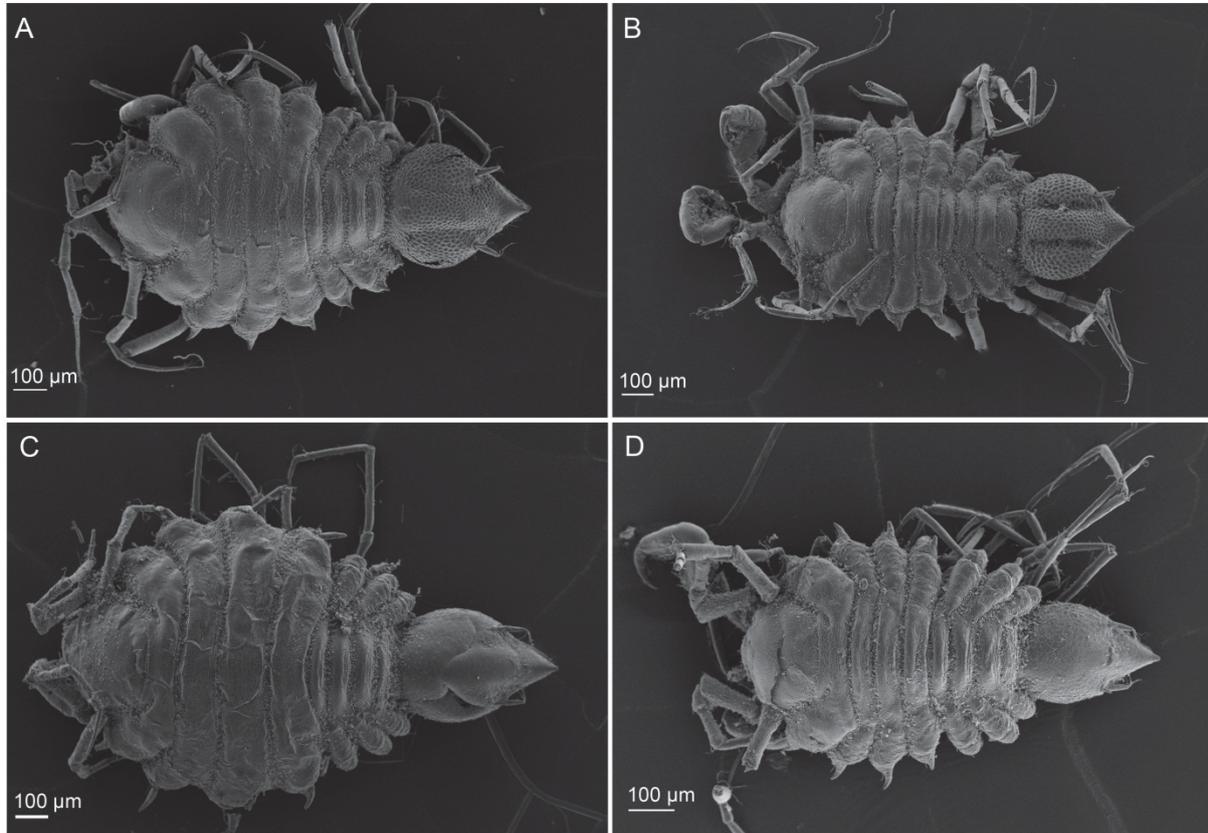


Fig. 8.3: SEM-images of both species of *Pleurogonium* present in our samples: A, B: *P. sp. nov 1*; B, C: *P. aff. kyushuense*; A, C: adult female; B, D: adult male.

This histogram shows well-defined age cohorts for each predefined stage, forming a polymodal curve. Each cohort is represented by a Gaussian distribution.

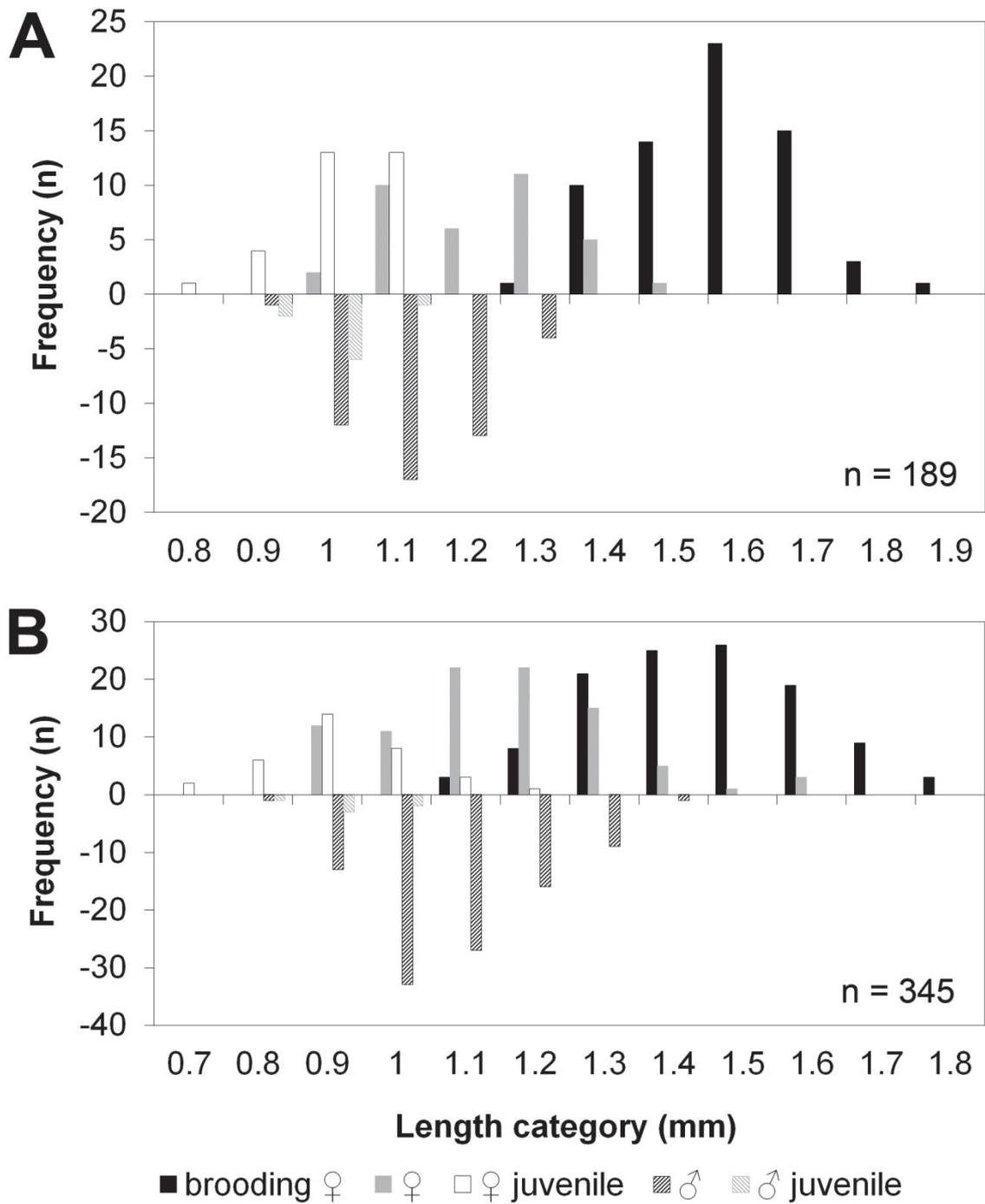


Fig. 8.4: Length-frequency histograms of *Pleurogonium* sp. nov. 1 (A) and *P. aff. kyushuense* (B), both specimens are from station A2-10 (459 m). Male frequencies are shown as negative values. Size classes are defined from the starting value to the value of the next size class.

Discussion

The species *Pleurogonium* aff. *kyushuense* from the northern slope of the Sea of Japan was collected and first described east of the eponymous Kyushu in southern Japan. In recent geological history, the Sea of Japan has been reported to have become repeatedly anoxic (Tada, 1994). Consequently, the benthos fauna became extinct between 85,000 and 8,000 years ago (Oba et al., 1991). Only a thin layer between 100–400 m remained constant in salinity and oxygen content (Amano, 2004). Therefore, the deeper parts were recolonized from the shelf and adjacent areas. The fact that *P.* aff. *kyushuense* was found east of Kyushu and now on the northern slope of the Japan basin leads us to hypothesize that at least part of the deep Sea of Japan was recolonized by the fauna of the adjacent areas south of Japan through the Korea Strait.

The high amount of individuals at the station A2-10 (459 m) of both species of *Pleurogonium* gave us the rare opportunity to analyze the population structure of these two species. Population structure analyses for deep-sea animals are scarce and the amount of individuals (N = 567) is sufficiently high to present a representative study here. From the same expedition and (amongst others) from the same station, the population structure of the munnopsid isopod *Eurycope spinifrons* Gurjanova, 1933 has already been analyzed (cp. Elsner et al. 2013; **Chapter 7**).

Most striking for both species of *Pleurogonium* is the high percentage of brooding females comprising about 33% of all measured individuals. Following the brooding females, male adults are more numerous than juveniles. The analysis of *E. spinifrons* yielded 6% brooding females at station A2-10. Additionally, postmarsupial mancae showed the highest percentage and male adults a higher percentage than brooding females (Elsner et al., 2013). In an analysis of the munnopsid isopod *E. iphthima* collected in the Atlantic at 2,506–4,327 m depth in August–September 1972, brooding females comprised about 10% and about 3% at the shallowest stations and were absent at the four deepest stations. Instars dominated in this study (Wilson, 1983). In an analysis of the munnopsid isopod *Munnopsurus atlanticus* (Bonnier, 1896) in the Cap-Ferret Trench in the Bay of Biscay at 401 m and 710 m depth in June 1991, brooding females were the least abundant at both stations (about 13% of sampled individuals) and mancae and juveniles less abundant than adults (Elizalde and Sorbe, 1993). In an analysis of the hadal amphipod *Hirondellea gigas* (Birstein & Vinogradov, 1955) in the Izu-Bonin Trench south of Japan from 8,172 and 9,316 m depth in March 2009, juveniles

were more abundant than adult males while adult females were least abundant (Eustace et al., 2013).

The results of these studies are in contrast to the population structure of the two species of *Pleurogonium* in the Sea of Japan with a high amount of brooding females and low percentage of juvenile stages. This combination suggests seasonality in brooding and a release of the mancae from the marsupium later in the year than mid-August. Harrison (1988) studied the pooled data of several asellote species in a depth range of about 1,000–3,000 m over a period of ten years and found a maximum of brooding females (25%) in winter and a minimum (5%) in summer (late July, beginning of August). Holdich (1968) states for an East Atlantic shallow-water species that the release of the mancae occurs in May/June and that the females die afterwards. The high rate of brooding females indicates synchronized breeding activity, but in all other studies of breeding behavior of isopods, whether shallow or deep, the release of the offspring is in spring. For Antarctic serolid isopods, this release of the brood is synchronized and linked to the seasonality of Antarctic primary production (Luxmoore, 1982). I hypothesize that the two species of *Pleurogonium* present in our samples presumably release their brood synchronized in autumn in contrast to other isopod species studied in order to avoid direct competition, for instance with the apparently successful species *E. spinifrons*. It may be possible that the success of *E. spinifrons* may be linked to the different reproductive strategy of this species, but future studies have to investigate this aspect in greater detail. Future studies may also show whether *Pleurogonium*, supposedly because of the much smaller size than *E. spinifrons* and other isopod species, manages to survive with less food than other species, feed off of the smaller peak of primary production in autumn or whether they have other diets (e. g. gut content analyses).

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Author's contribution:

Everything was done by me except for the drawings of male and female *Pleurogonium* sp. nov. 1 in dorsal view (courtesy L. Burchardt).

Description of *Baeonectes brandtae* sp. nov. and redescription of *Eurycope spinifrons* Gurjanova, 1933 (Crustacea, Isopoda, Munnopsidae) from the deep-sea basin of the Sea of Japan ♀

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Chapter 9: Description of *Baeonectes brandtae* sp. nov. and redescription of *Eurycope spinifrons* Gurjanova, 1933 (Crustacea, Isopoda, Munnopsidae) from the deep-sea basin of the Sea of Japan

Marina V. Malyutina^a, Olga A. Golovan^a, **Nikolaus O. Elsner^b**

^a*A.V. Zhirmunsky Institute of Marine Biology, Far Eastern Branch, Russian Academy of Sciences, 17 Palchevsky St, Vladivostok, 690041, Russia*

^b*Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany*

Abstract

A small collection of isopods of the family Munnopsidae Lilljeborg, 1864, including four species from the slope and the deep-sea basin of the Sea of Japan (Northwest Pacific), was studied. The new species *Baeonectes brandtae* sp. nov. which occurs at depths of 455–1,525 m is described. It is the second species of *Baeonectes* Wilson, 1982 described from the Sea of Japan and the deepest recorded species of the genus. *Eurycope spinifrons* Gurjanova, 1933, the only *Eurycope* species known from the Sea of Japan is redescribed. It is the most abundant species in the studied deep-sea macrobenthic communities in all samples.

Keywords: The Sea of Japan, deep sea, taxonomy, Munnopsidae, new species

Introduction

The amazing isopod species richness in the deep sea mainly consists of representatives of the deep-sea families of Asellota, with an especially importance by the natatory family Munnopsidae. This is a widespread and one of the largest isopod families, including 42 genera and around 320 species (Schotte et al., 2010 <http://www.nmnh.si.edu/iz/isopod/>). About 90% of the munnopsid species occur in bathyal and abyssal depths of the World Ocean where they are often the most abundant isopod group (Brandt et al., 2007a; Brandt et al.,

2007b; Kussakin, 2003; Malyutina and Brandt, 2007; Wilson, 1989). Species of some genera of the family inhabit shelf depths, mainly at high latitudes of both hemispheres. This is evidence for a secondary colonization of shallow waters by this primarily deep-sea family and for the considerable ecological adaptability of the group. This adaptability allowed some representatives of the deep-sea family to compete successfully in shelf communities, to spread geographically, and perhaps to overcome shallow regions that are barriers to their further dispersal in the bathyal and abyssal zones. An example for such a process could be the beginning colonization by munnopsids of the geologically young deep basin of the Sea of Japan, which is separated from the adjacent deep-sea ocean waters by shallow straits (Malyutina and Brandt, 2013).

One of the objectives of the investigation of the deep-sea fauna is the description of new and the redescription of known but poorly described species, especially of the abundant, dominant ones that characterize the fauna. Munnopsidae is a cosmopolitan, actively evolving family, and knowledge of its taxonomy and phylogeny is important for understanding the formation of the deep-sea fauna as a whole. However, the taxonomy of this large and complicated family is currently not completely resolved. Over the past 30 years, after an accumulation of new data and revisions of only one, the central munnopsid genus *Eurycope* Sars, 1864, seven new genera have been erected for some former members of this genus (Malyutina and Brandt, 2006; Malyutina, 2008; Wilson, 1982; Wilson and Hessler, 1981; Wilson, 1989). For the Sea of Japan six munnopsid species were known (Gurjanova, 1933, 1936; Kussakin, 2003): the shelf species *Eurycope pavlenkoi* Gurjanova, 1933 and *Ilyarachna kurilensis* Kussakin and Mezhev, 1979; *I. starokadomskii* Gurjanova, 1933 and *Munnopsurus minutus* Gurjanova, 1933 from depths around 500 m; *I. zachsi* Gurjanova, 1933 from depths of 105–1,002 m, and the deep-sea species *Eurycope spinifrons* Gurjanova, 1933 found at a depth range of 308–3,350 m. Revision of the old collections allowed us to clarify the taxonomic position of two of these species. *I. starokadomskii* was synonymized with *I. zachsi* as a junior synonym (Golovan and Malyutina, 2006). *E. pavlenkoi* together with *E. ochotensis* Kussakin, 1979 from the Okhotsk Sea were transferred to the genus *Baeonectes* Wilson, 1982 (Malyutina and Golovan, 2010). *B. ochotensis* was redescribed, but unfortunately, it was not possible to study *Baeonectes pavlenkoi* because the type material was lost (communication with the curator of ZIN, St.-Peterburg).

The deep-sea Russian-German expedition SoJaBio (Sea of Japan Biodiversity studies) on board R/V *Akademik M. A. Lavrentyev* in the Sea of Japan which sampled in depths between 455–3,666 m (Malyutina and Brandt, 2013) has brought extensive collections of Peracarida

(Golovan et al., 2013) (**Chapter 4**) where Isopoda was the most abundant order. The family Munnopsidae was the most frequent isopod and peracarid, but just in terms of abundance, not species richness. The new material revealed four munnopsid species - three already known from the deep Sea of Japan: *E. spinifrons*, *I. zachsi* and *M. minutus* and one species of *Baeonectes*. Two shelf species, *I. kurilensis* and *B. pavlenkoi*, were absent in our material.

The redescription of *I. zachsi* has been published previously (Golovan and Malyutina, 2006). *M. minutus* is represented only by a few juveniles in our samples. Due to the good condition of the collected specimens, we had the opportunity to study the two most numerous munnopsid species, *E. spinifrons* and the species of *Baeonectes*. Using the illustrations and descriptions of *B. pavlenkoi* of Gurjanova (1933, 1936) and Kussakin (2003) for comparison, we suggest that the specimens of *Baeonectes* from the SoJaBio collections belong to a different and new species. The description of the new species *B. brandtae* sp. nov. is presented herein besides the redescription of *E. spinifrons*. Distribution, population structure and reproductive mode of *E. spinifrons*, the most prevalent species of the deep-sea macrobenthos of the Sea of Japan, were investigated as well (Elsner et al., 2013) (**Chapter 7**).

Material and methods

Specimens were collected using a new modified camera-epibenthic sledge (C-EBS; Brandt et al., 2013 (**Chapter 2**)). The samples were washed onboard immediately with ice-cold water through sieves with a mesh size of 300 μm . Then the sample from the first deployment of each station was fixed in pre-cooled 96% ethanol for genetics and the sample from the second deployment was fixed in 4% formaldehyde for morphological studies. The material was sorted and identified using a stereomicroscope, drawings were made using an Olympus SZX7 compound microscope, equipped with a camera lucida and a LABOVAL 4 microscope with a Lomo RA-7U4.2 drawing tube.

Terminology and measurements mostly follow Wilson and Hessler (1980) and Wilson (1989). The total body length was measured medially from the tip of the rostrum to the posterior tip of the pleotelson. The dorsal view was used for measuring the width, while the length of body segments was measured in lateral view. For the description of the body and some further details the holotype was used, for mouthparts, pereopods and pleopods a male paratype was dissected and for the study of some sexual dimorphisms a female paratype was used. The type

material is deposited in the Museum of A.V. Zhirmunsky Institute of Marine Biology, Vladivostok, Russia, and in the Zoological Museum of Hamburg, Germany.

Abbreviations

C-EBS – camera-epibenthic sledge, MIMB – Museum of A.V. Zhirmunsky Institute of Marine Biology, Vladivostok, ZMH – Zoological Museum of Hamburg, An1 – antenna 1, An2 – antenna 2, bAn2 – basis of antenna 2, Hy – hypopharynx, lMd – left mandible, rMd – right mandible, Mx1 – maxilla 1, Mx2 – maxilla 2, Mxp – maxilliped, P1–7 – pereopods 1–7, Plp 1–5 – pleopods 1–5, Ur – uropod, m – male, f – female.

Taxonomy

Munnopsidae Lilljeborg, 1864

Eurycopinae Hansen, 1916

Baeonectes Wilson, 1982

Baeonectes Wilson, 1982: 3333; Kussakin, 2003: 134–135; Malyutina and Brandt, 2006: 8–15; Malyutina and Golovan, 2010: 99.

Type species: *Baeonectes muticus* (G.O. Sars, 1864), by original designation.

Baeonectes brandtae sp.nov.

(Figs 1–8)

Material examined. *Holotype*: (MIMB 27223), copulatory male (1.8 mm), SoJaBio C-EBS station B7–7, 25.08.2010, 470–528 m, 43°13N 135°04E, allotype (MIMB 27224), preparatory female (1.75 mm), from the same sample with the same locality.

Paratypes: (MIMB 27225), 245 specimens: female (1,95 mm) and male (1,9 mm) used for dissection, 94 females (1,85–2,5 mm) – 35 females brooding with eggs (7–16 eggs in brooding chamber), 3 females with embryos (15–16 embryos), 14 females with empty brooding chamber, 42 preparatory females; 78 copulatory males (1,3–2,3 mm), 73 manca and juveniles (0,7–1,2 mm), the same sample from the same locality, (ZMH 43255), 28 specimens, A2–10, 14.08.2010, 455–465 m, 44°56N 137°11E – 223 specimens (ZMH 43256).

Additional material. SoJaBio C-EBS stations: A3–11, 14–15.8.2010, 1,494–1,525 m, 44°47N 137°15E – 4 specimens; B6–7, 25.08.2010, 1,001–1,011 m, 43°10N 135°01E – 55 specimens; B7–6, 25.08.2010, 517–521 m, 43°13N 135°04E – 6 specimens.

Etymology. The species is named in honor of Prof. Dr. Angelika Brandt whose enthusiasm and efforts have contributed to the success of several deep-sea expeditions and who was the leader of the German party of the SoJaBio expedition.

Diagnosis. Rostrum of cephalon 1,4 of antenna 1 article 1 width. Antenna 1 article 3 about half of article 2 length and width. Maxilliped palp article 3 smaller than article 2. Pereopod 4 longest, twice longer than body and pereopod 1 in male and about 1,7 in female. Propodus of pereopods 5–7 with serrated dorsal margin. Male pleopod 1 distolateral lobes slender, acute, and curved to form rounded hooks at same level as distomedial lobes. Stylet of male pleopod 2 0,6 of propod length. Uropod protopod as long as wide, endopod twice longer than protopod, exopod half of endopod length.

Description. Holotype, male: *body* (Fig. 9.1) length 2,0 width, body height 0,3 body length, dorsal surface with sparse small setae. *Cephalon* length 0,45 width; rostrum length 0,9 mid-length width, 0,55 cephalon length, rostrum width 1,4 antenna 1 article 1 width; clypeus length 0,9 labrum length, width 0,6 labrum width (Fig. 9.2 F).

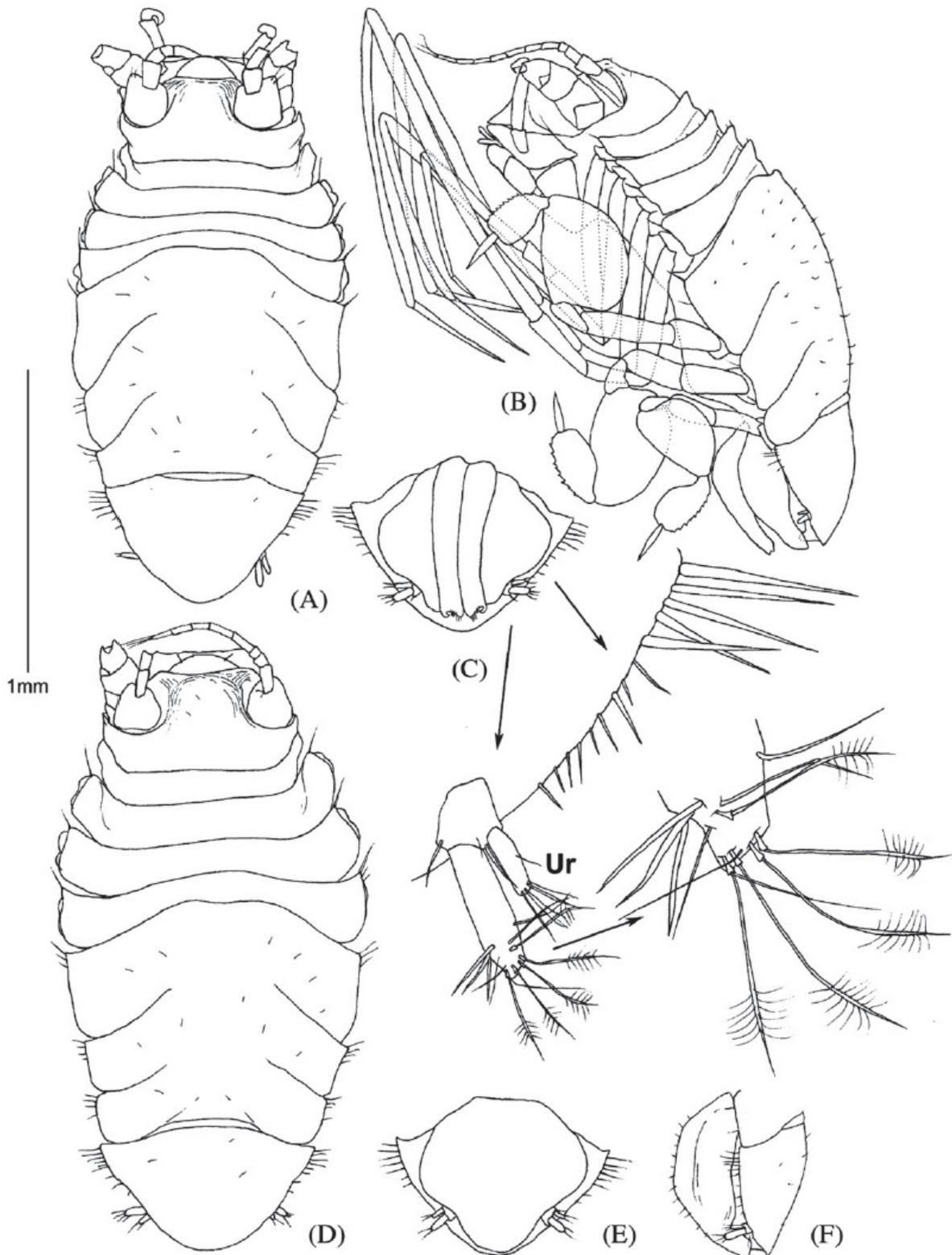


Fig. 9.1: *Baeonectes brandtae* sp.nov. Holotype, copulatory male (MIMB 27223), total view. A) dorsal view, B) lateral view, C) pleotelson, ventral view with enlarged lateral margin and uropod. Allotype, preparatory female (MIMB 27224). D) dorsal view, E) pleotelson, ventral view, F) pleotelson lateral view.

Pereonites 1-4 gradually broadening from 1 to 4, width of pereonites 1 and 4 1,1 and 1,4 cephalon width respectively; pereonites 1–4 medial length/cephalon length behind antennular sockets: 0,7;0,7; 0,5; 0,5 respectively; pereonite 1 shortest laterally, pereonites 2–4 subequal in lateral length; anterior lobes of coxae 1–4 not extended anterolaterally of margin of corresponding pereonites. *Natasome* length 0,7 body length; width 1,4 cephalon width, pereonite 5 longest, lateral length 0,9 lateral length of pereonites 6 and 7 together; pereonite 7 shortest, 0,45 of pereonite 5 length, width of fused mediodorsal part of natasome between sutures 0,4 natasome width; anterolateral margin of pereonites 2–5 pointed with long distal seta, of pereonites 6 and 7 with few setae. *Pleotelson* length 0,6 width and 0,2 body length; lateral margin in front of uropods insertion with row of setae, 5–6 distolateral setae longer than others; uropod inserted ventrally; preanal ridge low and rounded.

Antenna 1 (Fig. 9.3) 0,4 of body length, article 1 length 0,95 width, slightly extending beyond rostrum anterior margin, distolateral projection and distomedial margin with 1 broom and 1 small unequal bifid setae each; articles 2–5 length–width ratios: 1,8; 1,4; 1,0; 3,5, articles 2–5 to article 1 length ratios: 0,7; 0,3; 0,2; 0,6; article 2 with 1 broom and 2 simple distal setae; article 3 without setae; article 4 with 1 distal broom seta, article 5 as long as articles 3 and 4 together, following 6 flagellar articles subequal in length or shorter than article 5, last article with 4 aesthetascs equal in length to last 3 articles together.

Antenna 2 (Fig. 9.3) broken off from article 4 in males. Article 1 triangular in dorsal view; lateral margin of article 2 shorter than article 1; article 3 noticeably longer than article 2; scale on article 3 small, with long distal seta; article 4 slightly shorter than article 3.

Mandible (Fig. 9.3) incisor process with 4 cusps; *lacinia mobilis* of left mandible length 0,9 incisor length, with 5 teeth; spine row with 4 and 5 spines on left and right mandibles respectively; molar process stout, rounded distally, ventral margin with 2 setae; condyle length 1,7 molar process length, palp length 0,9 mandibular body length, article 2 2,4 of article 1 length, with several slender distal setae; article 3 subequal in length to article 1, weakly twisted, with 1 long and few shorter distal setae.

Hypopharynx (Fig. 9.3) outer lobes 1,2 as wide and 1,7 as long as inner lobes, with 1 stout and dense fine seta distally.

Maxilla 1 (Fig. 9.4) lateral endite 1,4 times as wide as mesial endite; 2 setae of 12 distal spine-like setae denticulate.

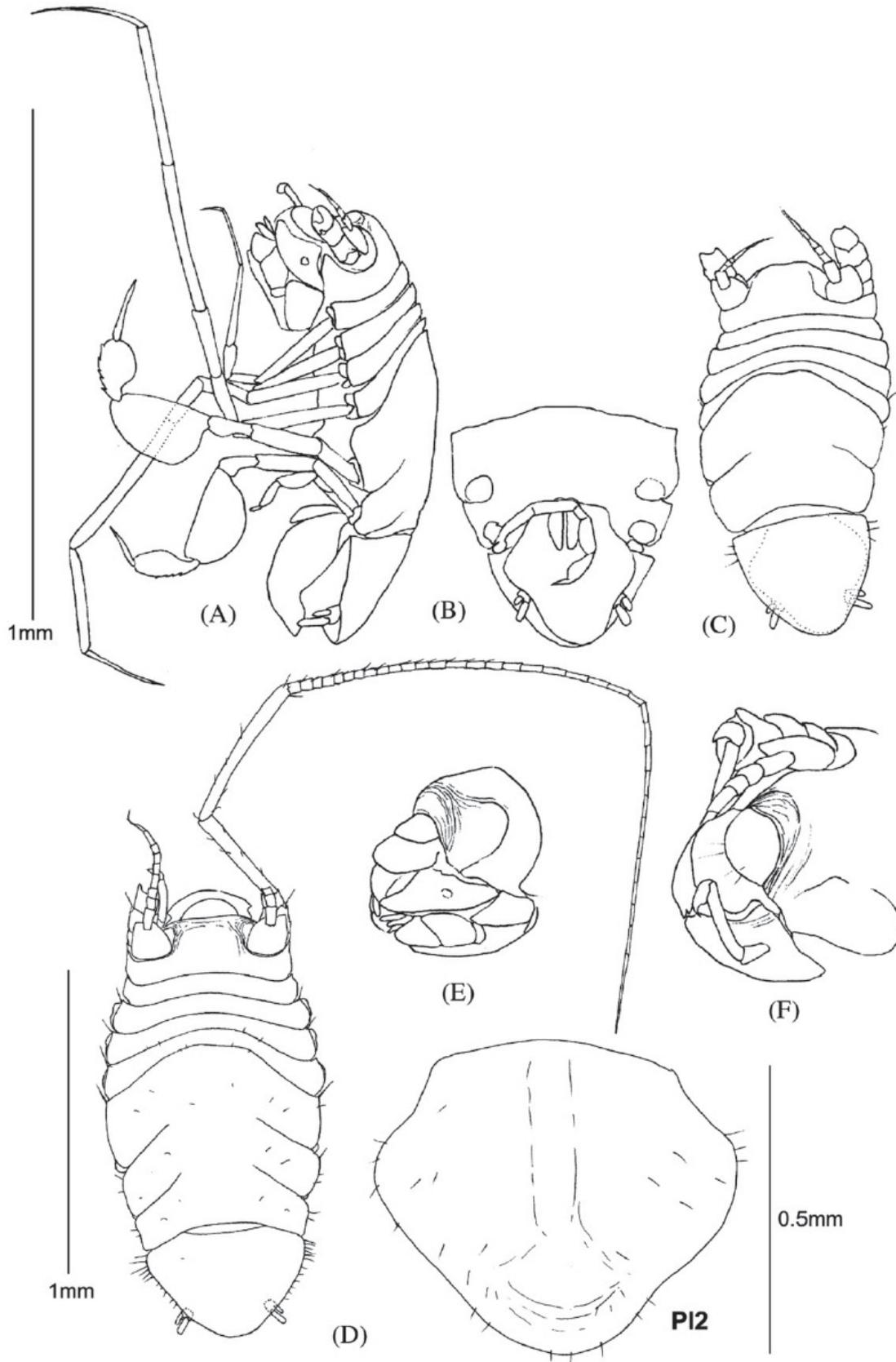


Fig. 9.2: *Baeonectes brandtae* sp.nov. Paratypes (MIMB 27225). Juvenile male at stage 4. A) dorsal view, B) ventral view of natasome. C) juvenile female, dorsal view. D) female, P12 - operculum. E) female, cephalon without antennae, oblique lateral view. F) male, cephalon, oblique dorsal view.

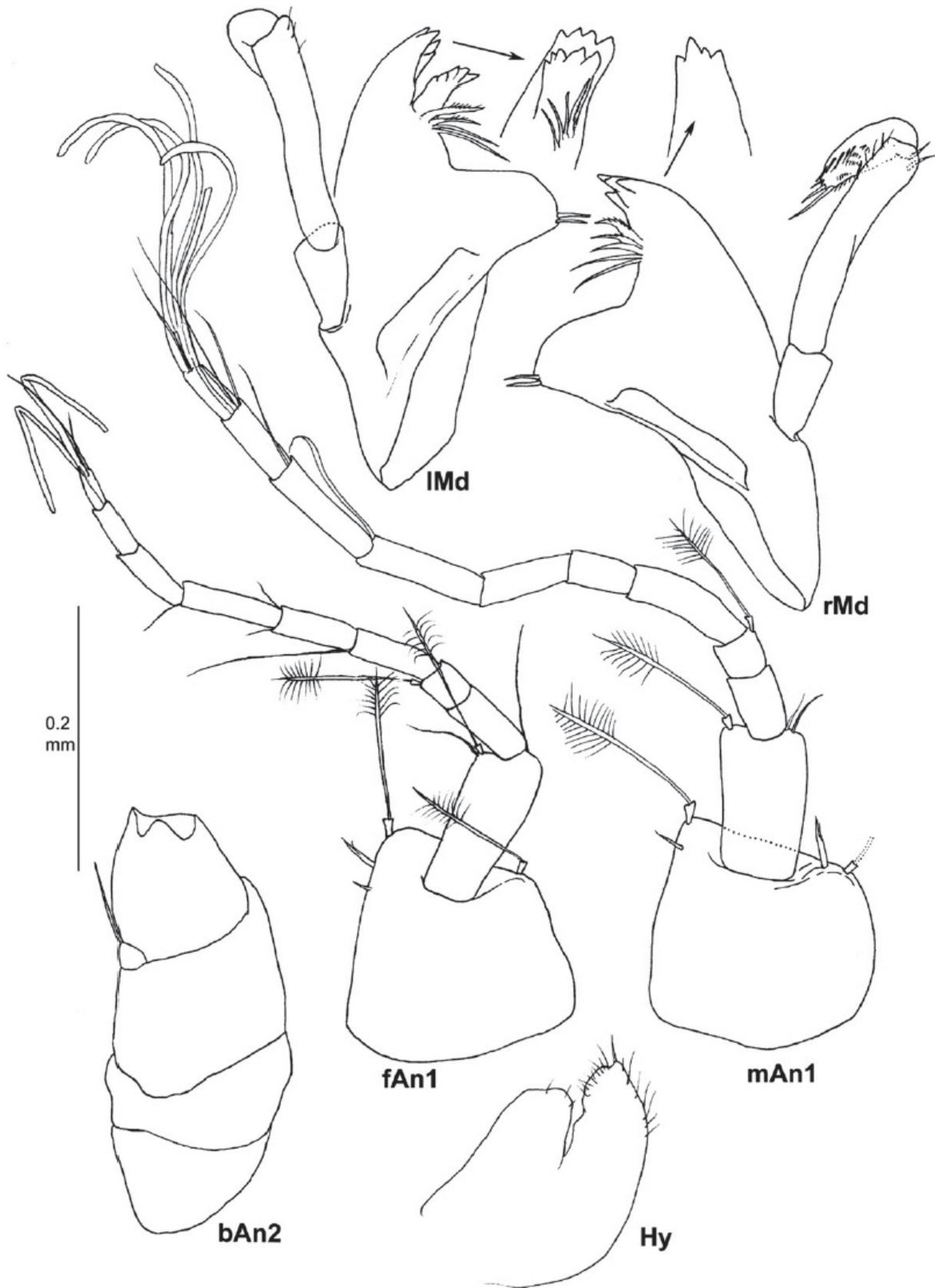


Fig. 9.3: *Baeonectes brandtae* sp.nov. Paratypes (MIMB 27226), male and female: antenna 1, basal articles of antenna 2, mandibles and hypopharynx.

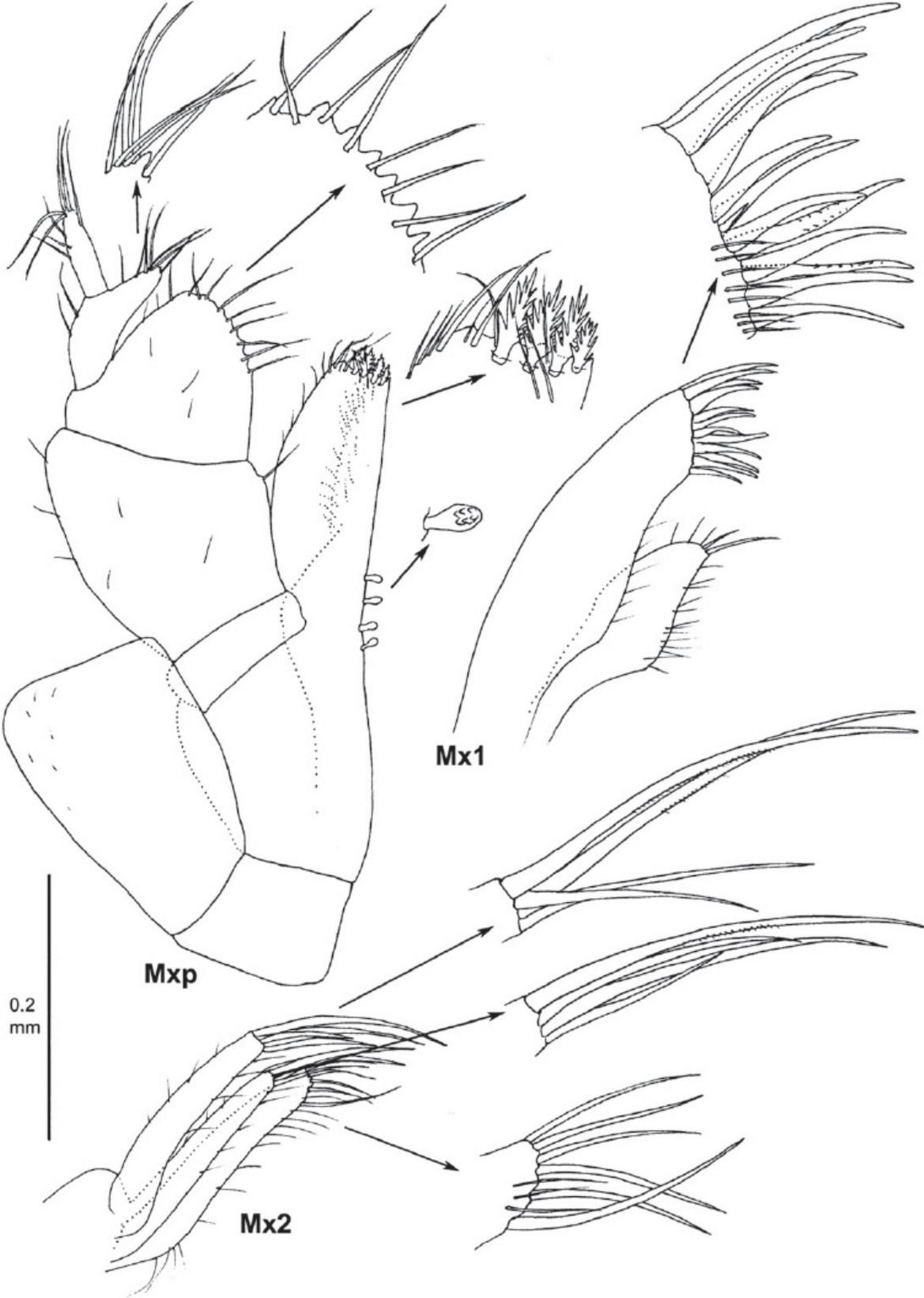


Fig. 9.4: *Baeonectes brandtae* sp.nov. Paratype (MIMB 27226), male: maxilliped and maxillae with enlarged parts.

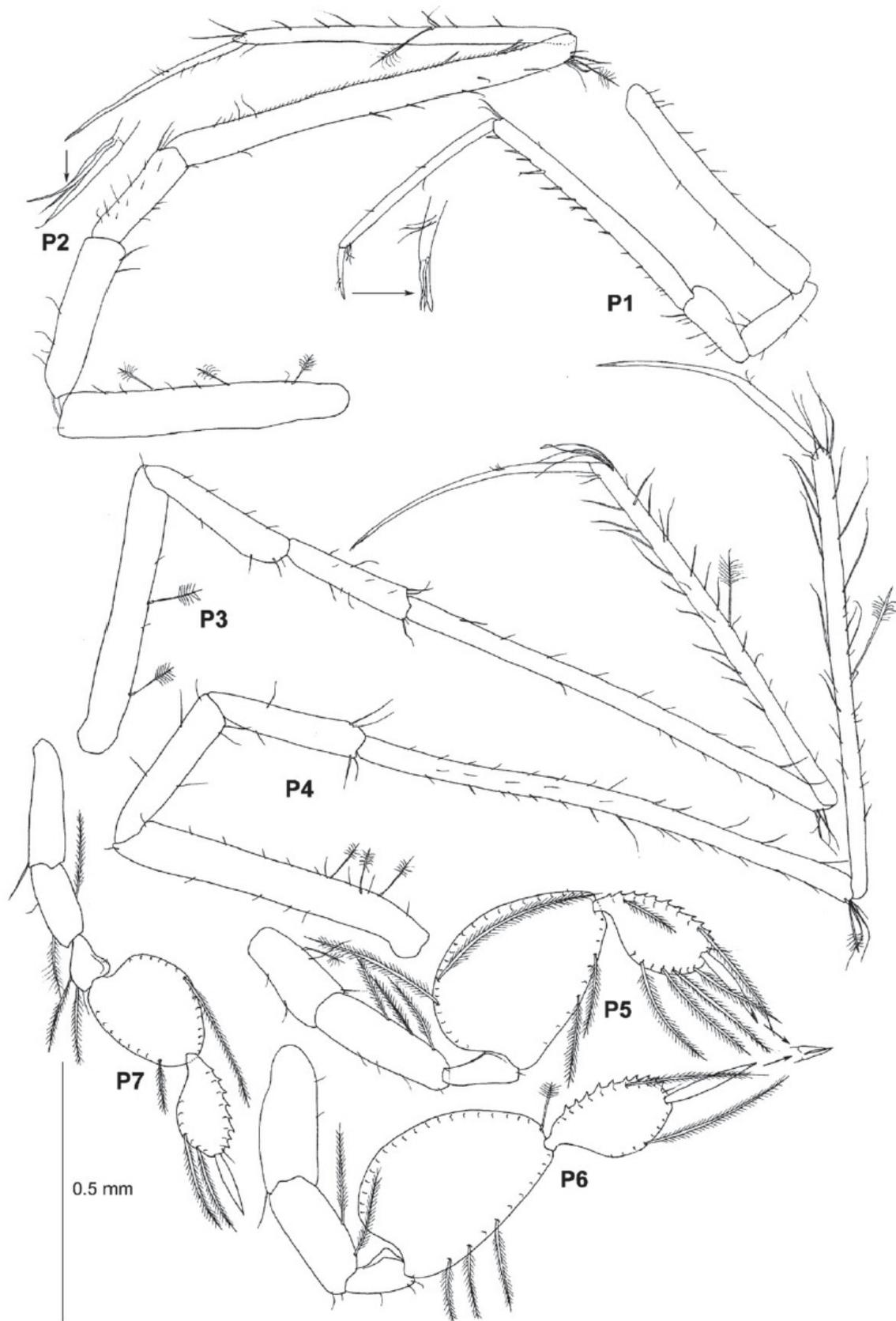


Fig. 9.5: *Baeonectes brandtae* sp. nov. Paratype (MIMB 27226), male: pereopods 1–7.

Maxilla 2 (Fig. 9.4) mesial endite longest with 6 stout and some slender distal setae; middle and lateral endites with 2 long and 2 shorter distal setae each, long setae with short comb of fine setulae; middle endite shortest.

Maxilliped (Fig. 9.4) basis length 3,0 width; endite 0,5 of basis length and width, length 2,5 width, with 3 retinaculae; distal margin with 4 fan and numerous simple slender setae; palp as long as basis; article 2 1,1 of basis width, with 1 distomedial whip seta and 3 small simple lateral setae, lateral length 1,8 medial length; article 3 0,85 of article 2 width, medial length 1,3 medial length of article 2, lateral length 0,15 lateral length of article 2; medial margin rounded, denticulate, with 12 long setae, articles 2 and 3 with sparse ventral setae; article 4 laterally twice as long as article 3 and as long as article 5; medial lobe tapering distally, with 6 long distal setae, length 0,6 article 5 length; article 5 with 8 long setae. Epipod straightly truncated distally, length 1,6 width, 0,6 basis length and as wide as basis, with few tiny setae.

Pereopods 1 to 4 (Fig. 9.5) becoming longer from 1 to 4, pereopod 1 as long as body; pereopod 4 length 2,1 body length; pereopod 1 narrowest, pereopod 2 broadest. Bases of pereopods 1–4 of similar length, with sparse simple setae and with few dorsal broom setae on pereopods 2–4, basis of pereopod 3 narrower than basis of pereopods 2 and 4, ischii and meri with several simple setae, carpus of pereopods 2–4 with set of 1 broom and 4 long whip setae distodorsally, carpus of pereopod 2 broadest; propodus of pereopods 2–4 with long broom dorsal seta on mid-length. *Pereopod 1* (Fig. 9.5) length ratios of ischium–dactylus to basis 0,4; 0,35; 1,0; 0,75, and 0,2 respectively; ischium with 2 ventral and 2 dorsal setae; merus length 2,4 width, with 6 ventral setae; carpus length 11,7 width, with 2 distodorsal and 12 ventral unequal bifid setae (5 small setae proximally and 7 stronger setae distally); propodus half as wide as carpus, with 3 distoventral setae; dactylus with three small simple dorsal setae near claws.

Pereopod 2 (Fig. 9.5) length ratios of ischium–dactylus to basis 0,6; 0,4; 1,5; 1,2, and 0,7 respectively; ischium with 2 distodorsal and 3 ventral setae; merus length 3,3 width, with 6 ventral and 4 dorsal setae; carpus as wide as merus, length 12,9 width, with 5 dorsal, 1 broom and 5 whip distodorsal setae, ventral margin fringed with setulae, 2 unequal bifid setae and 4 simple setae proximally; propodus with 8 dorsal and 3 distal setae, dactylus slender, length 3,5 of pereopod 1 dactylus.

Pereopod 3 (Fig. 9.6) length ratios of ischium–dactylus to basis 0,55; 0,45; 1,6; 1,4; and 0,8 respectively; basis with two dorsal broom setae; ischium with 2 dorsal and 3 ventral setae; merus length 4,2 width, with 3 ventral and 4 distodorsal setae; carpus length 20,0 width, with

5 dorsal, 1 broom and 4 whip distodorsal setae and 8 simple ventral setae; propodus with 1 long broom dorsal seta on mid-length, proximally with more than 10 short setae and 12 long whip setae on distal half.

Pereopod 4 (Fig. 9.5) similar to pereopod 3, but slightly longer, length ratios of ischium–dactylus to basis 0,55; 0,5; 1,6; 1,5; and 0,8 respectively.

Pereopods 5 to 7 (Fig. 9.5) similar in shape, propodi dorsal margin serrated, dactyli shorter than plumose setae of propodi, length about 0,7 propodi length, with 2 minute claws; pereopod 5 length 0,75 pereopod 1 length; pereopod 6 slightly longer than pereopod 5; pereopod 7 length 0,7 pereopod 6 length.

Pereopod 5 (Fig. 9.5) ischium–dactylus to basis length ratios 1,55; 0,75; 2,0; 1,25 and 0,8 respectively; ischium with 3 plumose dorsal setae; carpus length 1,5 width, with 24 dorsal and 10 ventral plumose setae; propodus length 1,8 width with 10 dorsal and 8 ventral plumose setae; dactylus 0,3 as long as dactylus of pereopod 4.

Pereopod 6 (Fig. 9.5) ischium–dactylus to basis length ratios 0,85; 0,5; 1,4, 0,9; and 0,65 respectively; carpus length 1,5 width, with 20 dorsal and 10 ventral plumose setae; propodus length 1,8 width, with 10 dorsal and 8 ventral plumose setae.

Pereopod 7 (Fig. 9.5) ischium–dactylus to basis length ratios 0,7; 0,4; 0,95; 0,8, and 0,5 respectively; ischium with 1 plumose dorsal seta and 2 simple ventral setae; merus with 2 plumose ventral setae; carpus 1,3 times as long as wide, with 15 dorsal and 8 plumose ventral setae; propodus length 2,1 width, with 8 dorsal and 7 ventral plumose setae.

Pleopod 1 (Fig. 9.8) significantly bent ventrally, length 2,7 basal width and 5,1 distal width; ventral surface with simple setae; distomedial lobes rounded, each with 5 distal and 6 smaller subdistal setae; distolateral lobes slender acute and curved in rounded hooks in same level as medial lobes.

Pleopods 2 (Fig. 9.8) protopod length 1,8 width; lateral projection and distoventral surface with small setae; stylet 0,6 of protopod length; sperm duct opening at midline; distal part needle-shaped; exopod distal width 0,5 endopod basal article width.

Pleopod 3 (Fig. 9.8) endopod length 1,7 width; distal plumose setae arising from medial half of distal margin, length 0,4 endopod length; exopod not reaching distal margin of endopod, 0,3 of endopod width, with slender lateral setae; distal article length 0,25 basal article length; distal plumose seta as long as endopod distal setae.

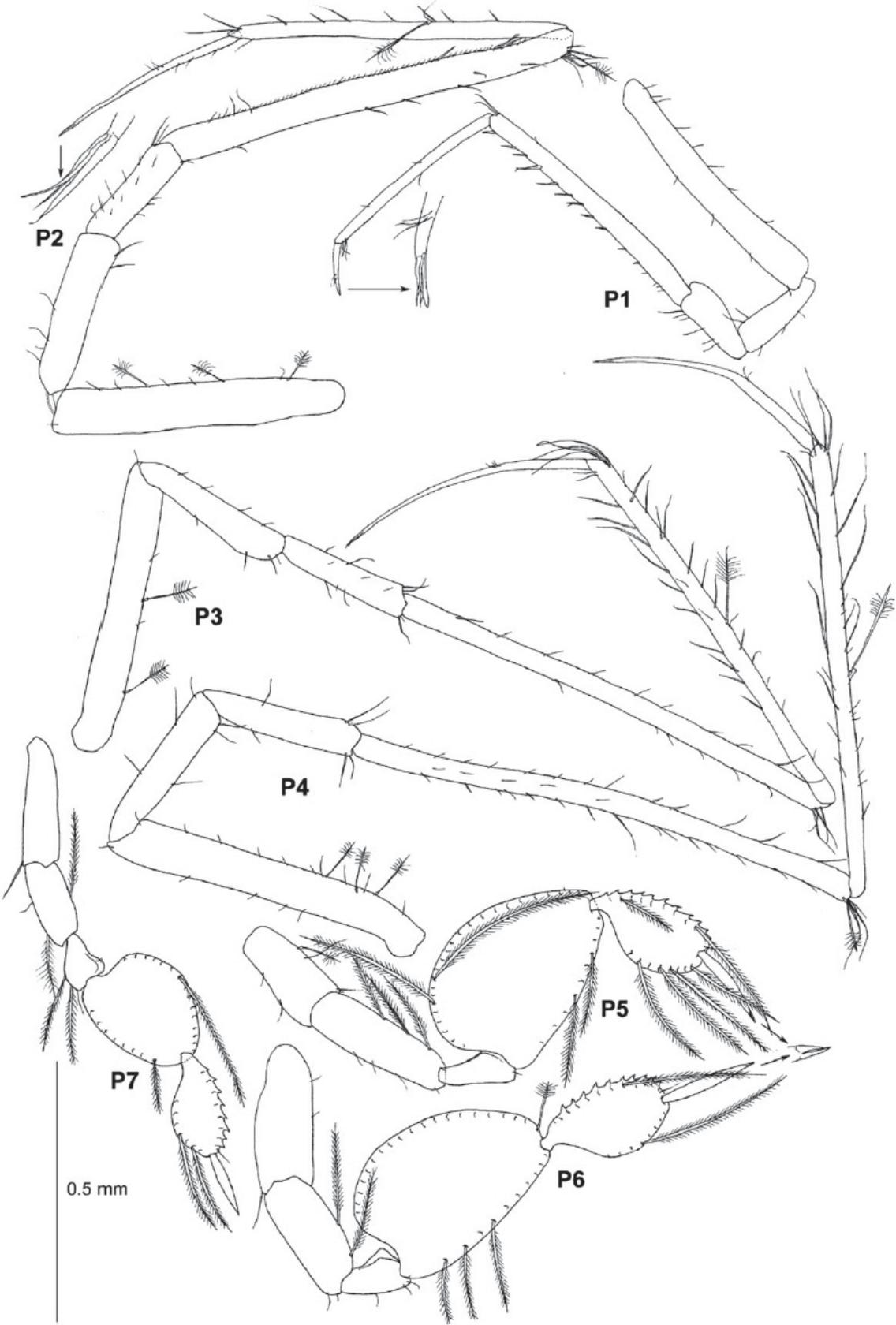


Fig. 9.6: *Baeonectes brandtae* sp.nov. Paratype (MIMB 27227), female: pereopods 1–3.

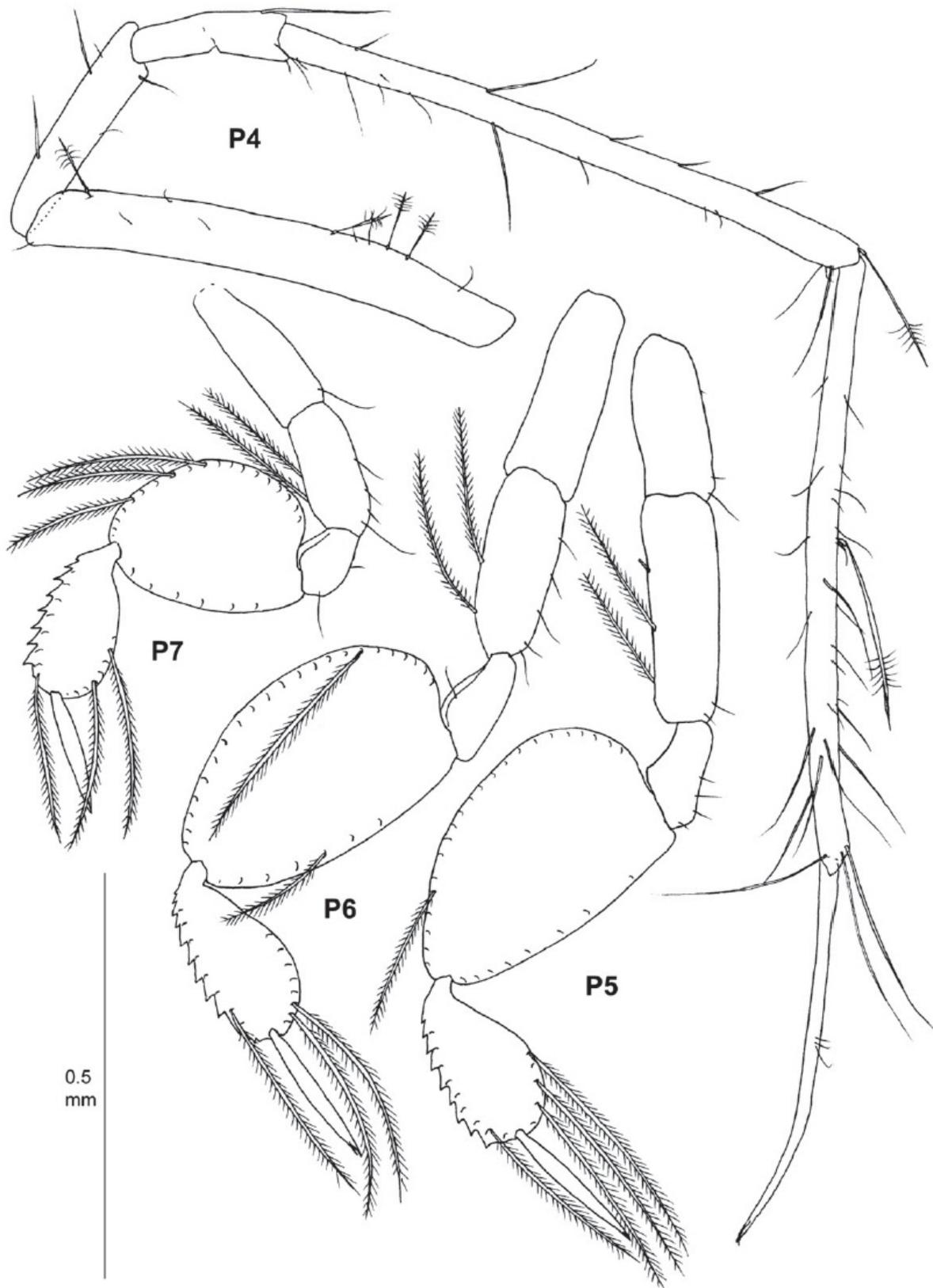


Fig. 9.7: *Baeonectes brandtae* sp. nov. Paratype (MIMB 27227), female: pereopods 4–7.

Pleopod 4 (Fig. 9.8) endopod length 1,4 width; exopod as long as endopod, distal plumose seta as long as pleopod 3 plumose setae.

Pleopod 5 (Fig. 9.8) endopod length 1,7 width.

Uropod (Fig. 9.1) length 3 pleotelson length. Protopod as long as wide, with 2 distal unequal bifid setae; endopod 0,4 width and 2,1 length of protopod, with 5 broom, 4 unequal bifid and 4 whip distal setae; exopod 0,5 length and width of endopod, with 5 distal setae.

Female. Proportions of habitus and body parts of females and juveniles (Figs 9.1, 9.2) are similar to those of males, brooding females with broader ambulosome.

Antenna 1 (Fig. 9.3) 0,35 of body length, article 1 as long as wide, not surpassing rostrum anterior margin, with 2 broom and 2 small unequal bifid setae distally; following articles more slender than in male, last article with 2 aesthetascs equal in length to last 3 articles together.

Antenna 2 (Fig. 9.2) length 2,4 body length. Peduncle articles 1–4 as in males, article 1 triangular in dorsal view; lateral margin of article 2 shorter than article 1; article 3 noticeably longer than article 2; scale on article 3 small, with long distal seta; article 4 slightly shorter than article 3, article 5 length 1,8 length of articles 1–4 together, article 6 1,5 of article 5 length. Flagellum length 2,5 of peduncle length, of about 40 articles.

Pereopods 1-4 (Figs 9.6, 9.7) of females shorter than those of males, length difference between pereopod 1 and pereopod 4 less than in male – 1,7, pereopod 3 shorter than pereopod 2, with smaller basis than that in pereopods 2 and 4. Carpus of pereopod 2 same width as in pereopods 3 and 4, whereas in male carpus twice as broad. In comparison with male, pereopod 2 carpus and especially propodus having more numerous setal armament: many stout sensory ventral setae and long broom setae. *Pereopods 5–6* (Fig. 9.7) equal to those in male.

Pleopod 2 of female (Fig. 9.2) length 0,9 width, height 0,5 length, ventral keel high, rounded; distal 1/3 of length narrowing, bent dorsally, ventral surface and distal margin covered with small simple setae.

Remarks. *Baeonectes brandtae* sp. nov. differs from other known species of the genus by the longer pereopods 1–4 and the larger difference between pereopod 1 and pereopod 4. Thus, in males of the new species pereopod 1 is as long as the body, pereopods 3–4 are twice as long as the body, whereas for *B. improvises* it is 0,9 and 1,4 times as long respectively, for *B. ochotensis* 0,8 and 1,2, for *B. pavlenkoi* it is known that “pereopods 2–4 are not too long”

(Kussakin, 2003, p. 50). *B. brandtae* sp. nov. has carpi of pereopods 2–4 of a length of about 1,5 of the corresponding bases, in contrast to the other mentioned species with the basis of pereopod 3 being subequal or slightly shorter (in *B. improvises*, *B. muticus*, *B. pygmaea*, and *B. ochotensis*) or even longer than the carpus, as in *B. pavlenkoi*. *B. brandtae* sp. nov. has article 3 of antenna 1 1,5 times as long as article 4, in *B. ochotensis* this ratio is more than twice, whereas in *B. muticus*, *B. pygmaea*, and *B. improvises* the articles 3 and 4 are similar in length. *B. brandtae* sp. nov. has a more elongate body than in the most species except *B. ochotensis*. The uropod of *B. brandtae* sp. nov. is more slender than that in other species, only *B. ochotensis* has uropods even longer and more slender than in *B. brandtae*: 0,4 of the pleotelson length, and the endopod length is 2,5 times the protopod length in contrast to 0,3 and 2,1 respectively in *B. brandtae* sp. nov. The new species has the distolateral lobes of male pleopod 1 more acute than in other species and curved into rounded hooks. By such characters as the serrated dorsal margin of the propodus of pereopods 5–7, the proportions of maxilliped palp articles 2 and 3 (article 3 is smaller than article 2), *B. brandtae* sp. nov. is more similar to *B. muticus*, *B. pygmaea* and *B. improvisus* than to the geographically closer species *B. pavlenkoi*, *B. ochotensis* and *B. abberantis*, possessing a smooth dorsal margin and a maxilliped palp article 3 equal in size to article 2. But the new species' epipod of the maxilliped is more slender than in *B. muticus*, *B. pygmaea* and *B. improvisus*.

Distribution. The species is known only from the type locality in the northwest of the Sea of Japan at 455–1,525 m depth.

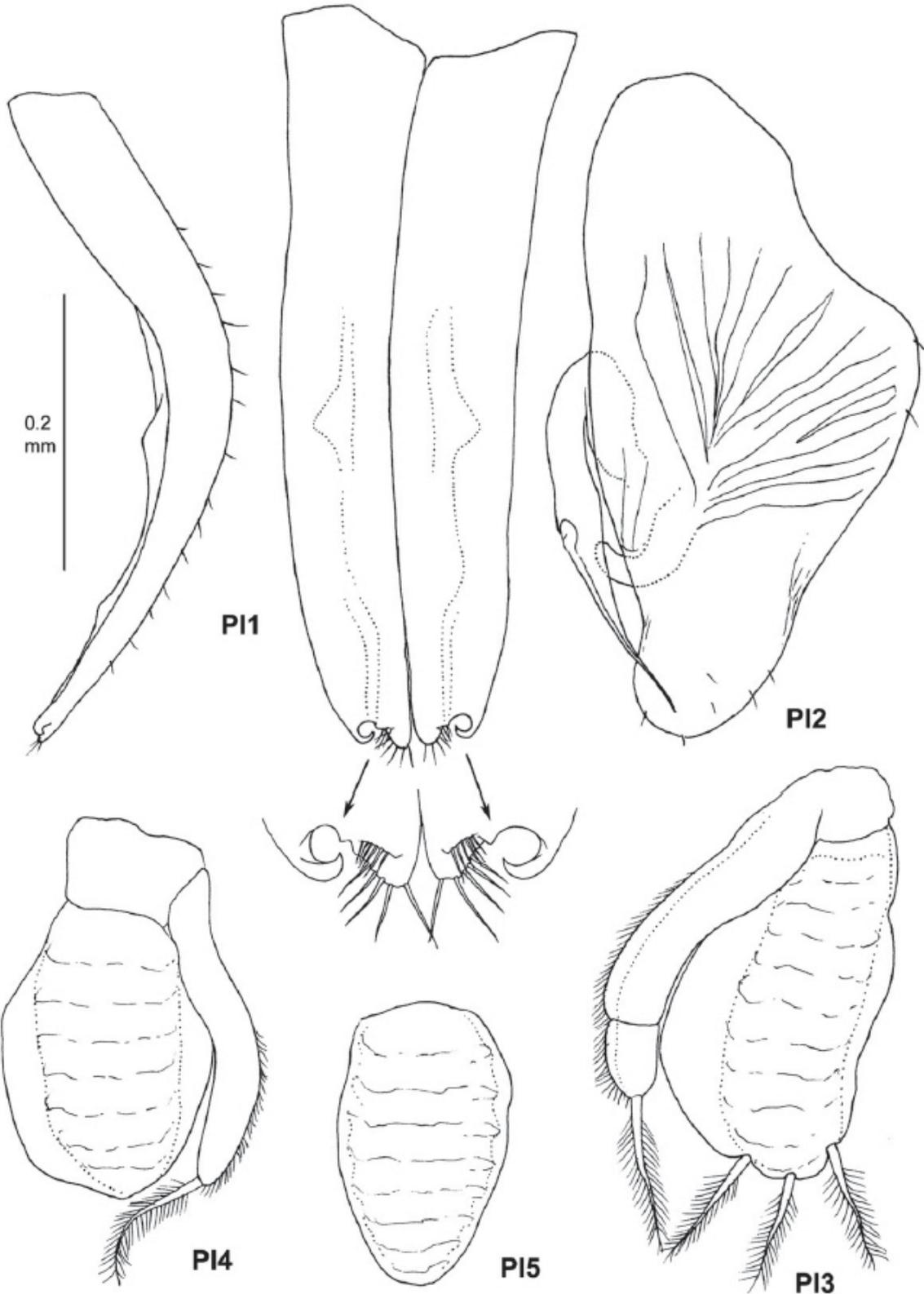


Fig. 9.8: *Baeonectes brandtae* sp.nov. Paratype (MIMB 27226), male: pleopods.

Eurycope G.O. Sars, 1864

Synonymy see: Kussakin, 2003: 21.

Type species: Eurycope cornuta Sars, 1864, by original designation.

Eurycope spinifrons Gurjanova, 1933

(Figs 9–19)

Gurjanova, 1933: 85, fig. 11a, 12a–d; 1936: 62, fig. 26; Wilson and Hessler, 1981: 404; Kussakin, 2003: 92, fig. 65; Golovan and Malyutina, 2010: 120, tabl. L.

Material examined. SoJaBio C-EBS stations: B4–7, 21.08.2010, 3,298–3,353 m, 43°01N 135°26E – 2757 specimens (2–5,5 mm), copulatory male (5,3 mm) and preparatory female (5,5 mm) with oostegites in early stages are used for dissection; A2–10, 14.08.2010, 455–465 m, 44°56N 137°11E – 18 specimens; A3–11, 14–15.8.2010, 1,494–1,525 m, 44°47N 137°15E – 29 specimens; A6–7, 14.08.2010, 2,511–2,534 m, 44°00N 137°31E – 66 specimens; A6–8, 14.08.2010, 2,545–2,555 m, 44°18 N 137°24E – 399 specimens; A7–8, 17.08.2010, 3,345–3,357 m, 44°00N 137°29E – 2,234 specimens; St. A7–9, 18.08.2010, 3,340–3,347 m, 44°00N 137°31E – 829 specimens; B1–7, 19.08.2010, 3,345–3,357 m, 42°15N 136°43E – 1903 specimens; St. B4–8, 21–22.8.2010, 3,312–3,334 m, 43°01 N 135°28E – 2,789 specimens; B5–7, 23.08.2010, 2,661–2,688 m, 43°01N 135°05E – 202 specimens; St. B5–8, 23.08.2010, 2,609–2,655 m, 43°01N 135°06E – 881 specimens; B6–7, 25.08.2010, 1,001–1,011 m, 43°10N 135°01E – 10 specimens; B7–6, 25.08.2010, 517–521 m, 43°13N 135°04E – 1 specimen; B7–7, 25.08.2010, 470–528 m, 43°13N 135°04E – 57 specimens; C1–8, 27.08.2010, 2,670–2,681 m, 42°26N 133°09E – 1,061 specimens; C1–9, 27.08.2010, 2,693–2,725 m, 42°26N 133°08E – 725 specimens; C3–3, 28.08.2010, 3,431–3,435 m, 42°01N 133°09E – 3,021 specimens; C3–4, 28.08.2010, 3,427–3,431 m, 42°01N 133°09E – 1,754 specimens; D1–3, 30.08.2010, 3,355–3,357 m, 41°28N 131°46E – 1,034 specimens; D1–4, 30.08.2010, 3,356 m, 41°28N 131°46E – 4 specimens; D2–7, 01.09.2010, 2,619–2,637 m, 42°07N 131°21E – 1,230 specimens; D2–8, 01.09.2010, 2,653–2,683 m, 42°06N 131°21E – 102 specimens.

Diagnosis. Pleotelson lateral margins bent ventrally, forming angles in dorsal view. Rostrum broad, slightly narrowing distally, not overhanging frons, anteriorly with 2 stout setae on each

side, mid-length width 0,8 antenna 1 article 1 width. Distomedial lobe of antenna 1 article 1 shorter than article 2, extending slightly beyond tip of rostrum. Antenna 1 article 3 as long as or longer than article 2. Epipod of maxilliped narrow without pronounced lateral extension. Male pleopod 1 distomedial lobes rounded, projected, length 0.1 pleopod 1 length; distolateral lobes almost not expressed, as wide as distomedial lobes. Protopod of male pleopod 2 with distomedial excavation from which exopod emerging, stylet 0,6 of protopod length. Endopod of uropod slightly longer than protopod, exopod 0,6 of endopod length.

Description

Male. Body (Fig. 9.9) length 2,3–2,7 pereonite 5 width; height at pereonites 6–7 0,2 length, dorsal surface with sparse fine setae. *Cephalon* width about 2,7 length, length 0,1 body length. Rostrum broad, slightly narrowing distally, not overhanging frons, anteriorly with 2 stout unequally bifid setae on each side, length 0,7 medial cephalic length, anterior width 0,15 cephalic width, width at base of antennae 1 0,35 cephalic width. Cephalic keels well developed. Frons (Fig. 9.9 D, E) subvertical, height equal to mouth-field depth, cephalic length behind antennae about 0,2 cephalic width; lateral spine blunt, triangular, 0,4 frons height.

Pereonite 1 length 0,2 width, and 1,1 cephalon length behind antennae; pereonites 2–7 to pereonite 1 length ratios: 0,9; 0,8; 0,7; 1,5; 1,7; 2,7; length–width ratios: 0,2, 0,1; 0,1; 0,2; 0,3; 0,4. Lateral margins of pereonites 1–6 convex, of pereonite 7 slightly concave. Coxae 1–4 similar in size and shape, in lateral view length subequal to pereonites lateral length, anterior processes in dorsal view triangular, near half of corresponding pereonites length, ending with small unequally bifid seta. *Natasome* 0,6 body length, ventral surface with cuticular ridges, medioventral area convex, pereonite 7 posterior margin overhanging base of pleotelson, with few setae, anteriorly of pereopods coxa with bulla, bearing long seta (Fig. 9.10 C). *Pleotelson* length 0,3 body length, width subequal length, lateral margins in mid-length bent ventrally into fold looking like angular protrusions in dorsal view.

Antenna 1 (Figs 9, 11) 0,7 body length, article 1 length subequal to width, slightly extending beyond tip of rostrum, with 2 medial and 1 lateral unequally bifid setae distally, distomedial projection weakly developed, not reaching distal margin of article 2; length–width ratios of articles 2–5: 1,5, 2,3, 0,7, 2,6; length ratios of articles 2–5 to article 1: 0,7 0,5 0,15 0,4; article 2 with 7 unequally bifid setae and 2 broom setae distally; article 3 with 1 distal broom seta;

article 4 with 2 broom setae, flagellum of more than 30 articles (distal articles broken off), articles 7–30 with aesthetascs.

Antenna 2 (Fig. 9.11) articles 1–6 length–width ratios: 0,6 0,5, 1,5 1,4 16,7 23,0; length ratios of articles 2–6 to article 1: 0,7 2,2 1,4 15,0 16,1; articles 1 and 2 with 1 distodorsal unequally bifid seta, article 3 with 4 distomedial unequally bifid setae and 1 medial simple seta, squama length 0,7 width and 0,4 article 3 length, article 4 with 1 distomedial simple seta, articles 5 and 6 with small unequally bifid setae more numerous on article 5.

Mandibles (Fig. 9.12) incisor with 4 cusps, on right mandible cusps 2 and 3 with one additional tip each; *lacinia mobilis* of left mandible stout, with 7 denticles; spine row with 7 spines on left and 8 spines on right mandible; molar triturative surface oval, concave, posterior margin with 5 setae. Palp length 1,1 mandibular body length, article 1 with distolateral seta; article 2 1,9 of article 1 length, with about 9 long medial setae and 2 stout distal setae; article 3 1,3 article 1 length, with about 20 marginal cleaning setae.

Maxilla 1 (Fig. 9.13) both endites with lateral fine simple setae, lateral endite with 12 distal robust serrated setae and simple slender setae on distomedial half; mesial endite 0,6 of lateral endite width, distal margin angled, with numerous fine simple setae and 1 long stout setulated seta.

Maxilla 2 (Fig. 9.13) lateral endite longest, with 2 long and 2 twice shorter setulated distal setae; middle endite shortest, with 2 long and 1 short setulated setae and slender medial seta. Mesial endite width 1,6 lateral lobe width, distal margin with 3 setulated setae and numerous fine simple setae. All endites with fine simple marginal setae.

Maxilliped (Fig. 9.13) basis length 2,4 width, with distolateral projection near palp insertion, endite length 2 width and 0,45 basis length, extending 1/3 of palp article 3 medial length, with 5 retinaculae, distal margin with 7 fan setae and some simple slender setae, lateral margin with fine simple setae. Palp 0,8 of basis length and width, articles 1–5 lateral length–width ratios: 0,5 1,1 0,4, 1,6 3,8; article 1 lateral length 1,7 medial length; article 2 width 1,5 endite width, lateral length 1,2 medial length, with 1 distomedial simple seta; article 3 as wide as article 2, lateral length 0,6 medial length and 0,35 article 2 lateral length, medial margin rounded, serrated, distally with 3 simple setae; article 4 slightly longer than article 3 laterally, medial lobe length 0,5 lateral margin length, with 5 long simple distal setae, article 5 subequal to article 4 in lateral length, with 4 simple distal setae; lateral margin of basis and palp articles 1–3 fringed with fine simple setae. Epipod subequal to basis in length and width, distal angle narrow, rounded, lateral margin weakly angular in mid-length.

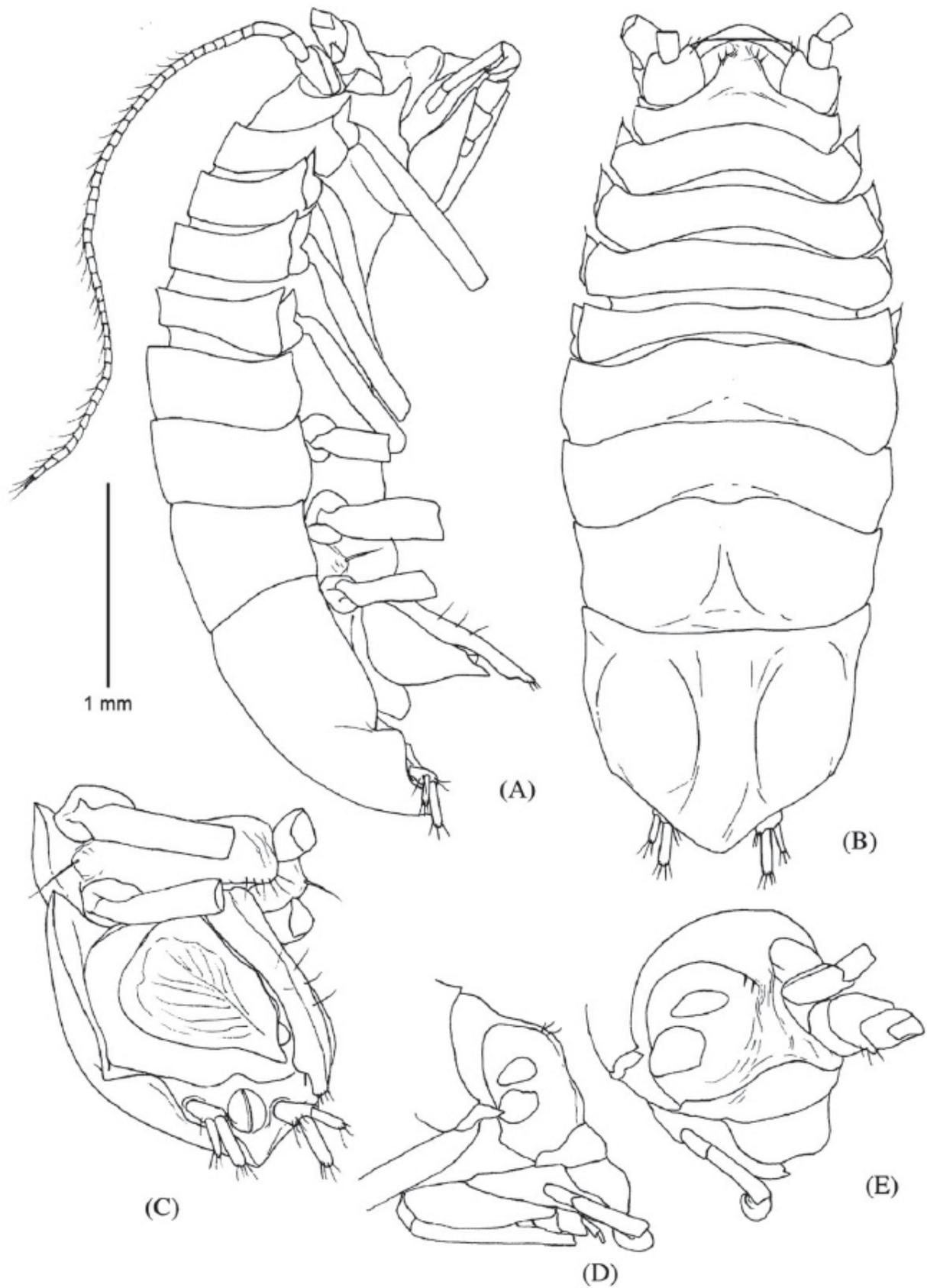


Fig. 9.9: *Eurycope spinifrons* Gurjanova, 1933. Copulatory male: A) lateral view. B) dorsal view. C) pleotelson and pleonite 7, ventral oblique view. D) cephalon, without antennae, lateral view. E) cephalon, frontal oblique view.

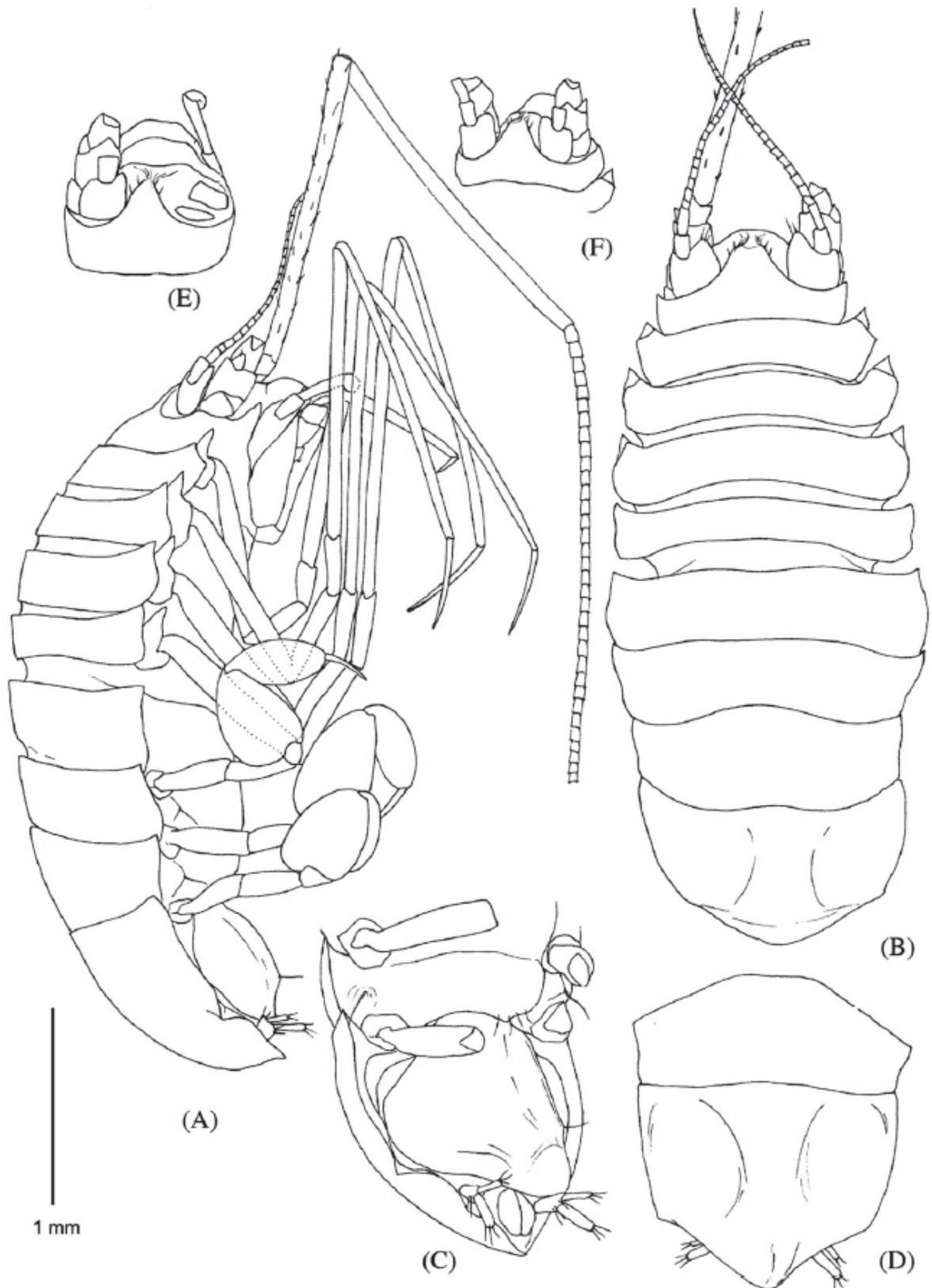


Fig. 9.10: *Eurycope spinifrons* Gurjanova, 1933. Preparatory female: A) lateral view. B) dorsal view. C) pleotelson and pleonite 7, ventral oblique view. D) pleotelson and pleonite 7, dorsal view. E, F) Cephalon of females of different sizes, dorsal view.

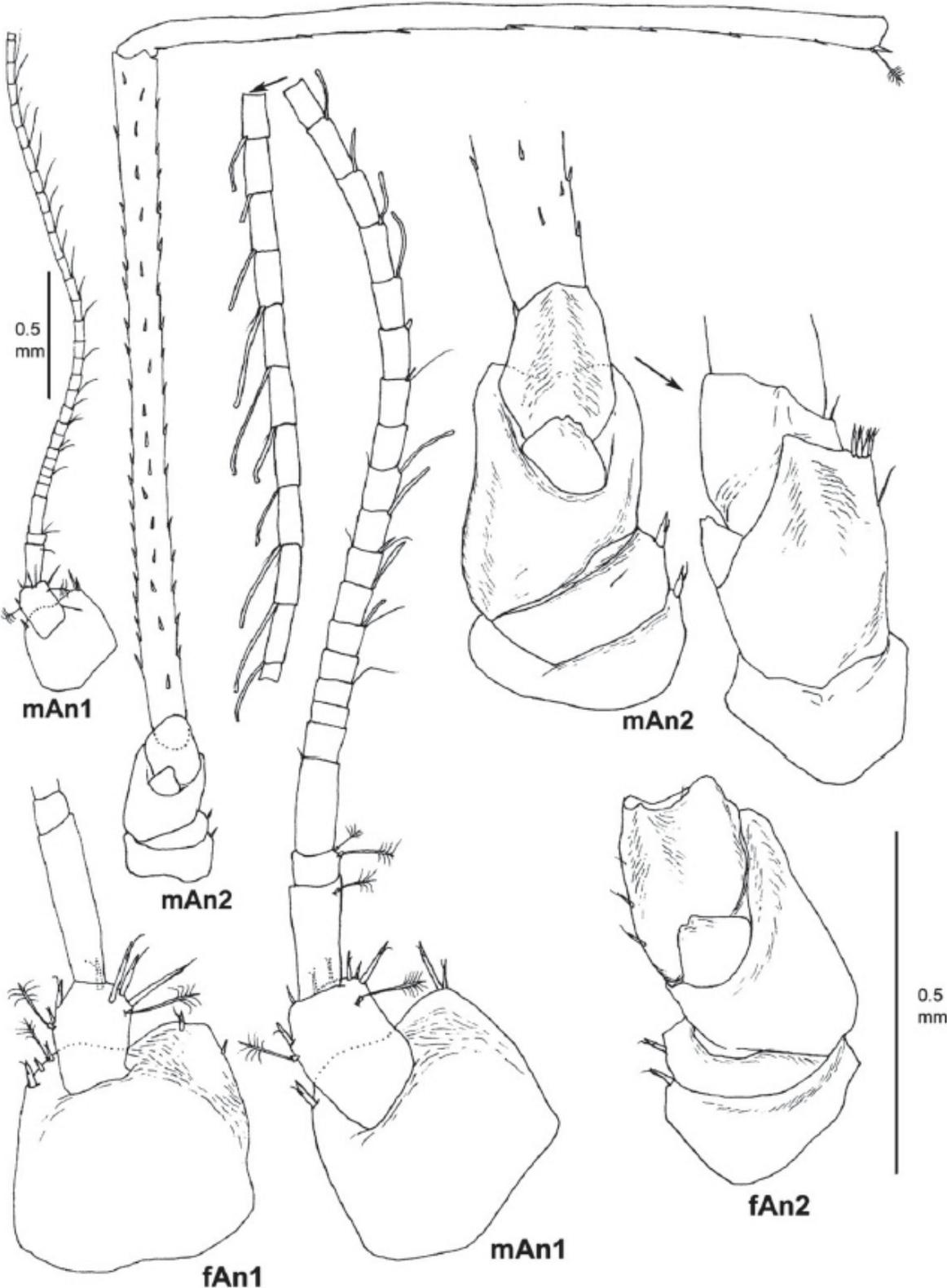


Fig. 9.11: *Eurycope spinifrons* Gurjanova, 1933. Copulatory male and preparatory female: antenna 1 and antenna 2.

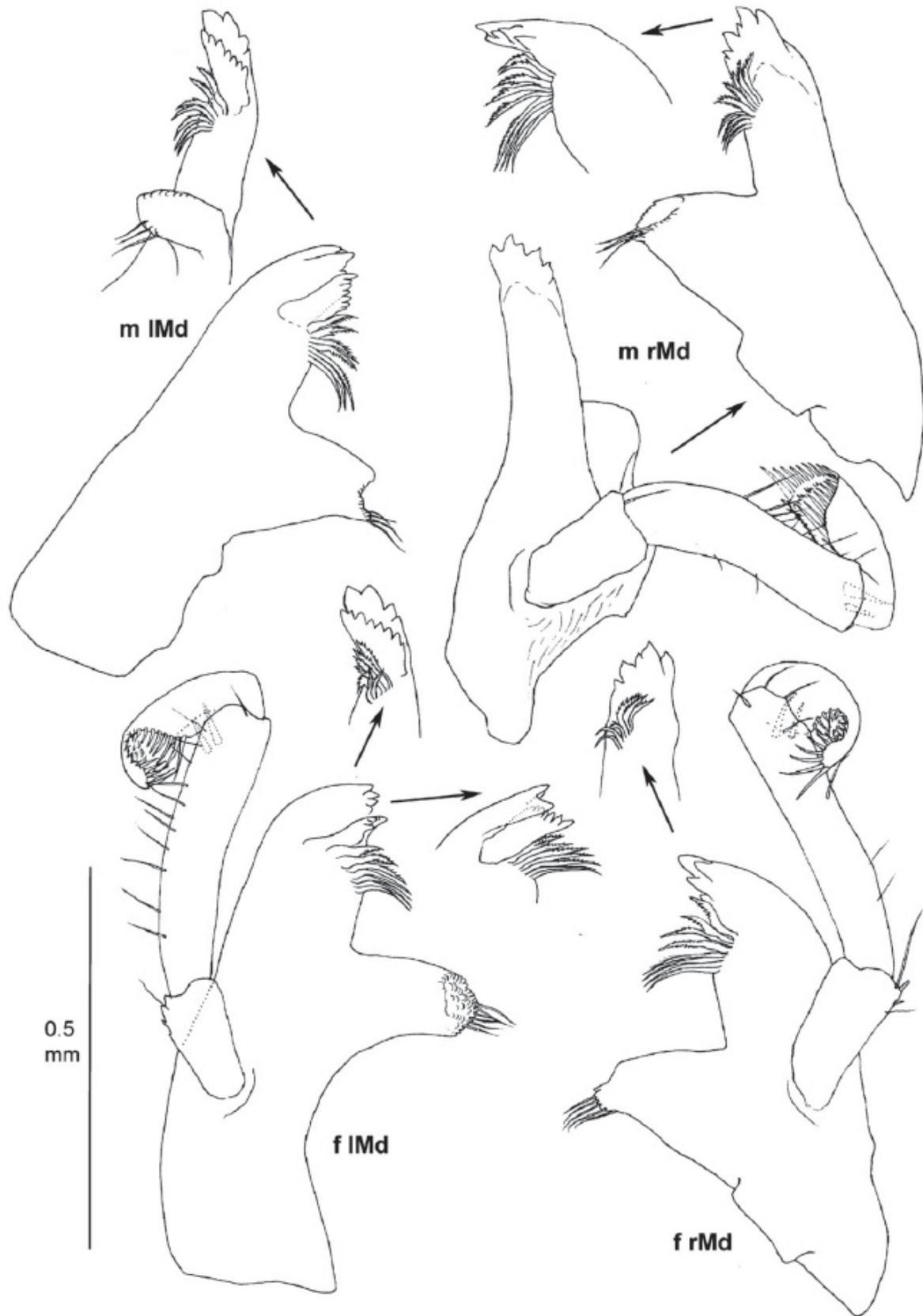


Fig. 9.12: *Eurycope spinifrons* Gurjanova, 1933. Copulatory male and preparatory female: mandibles.

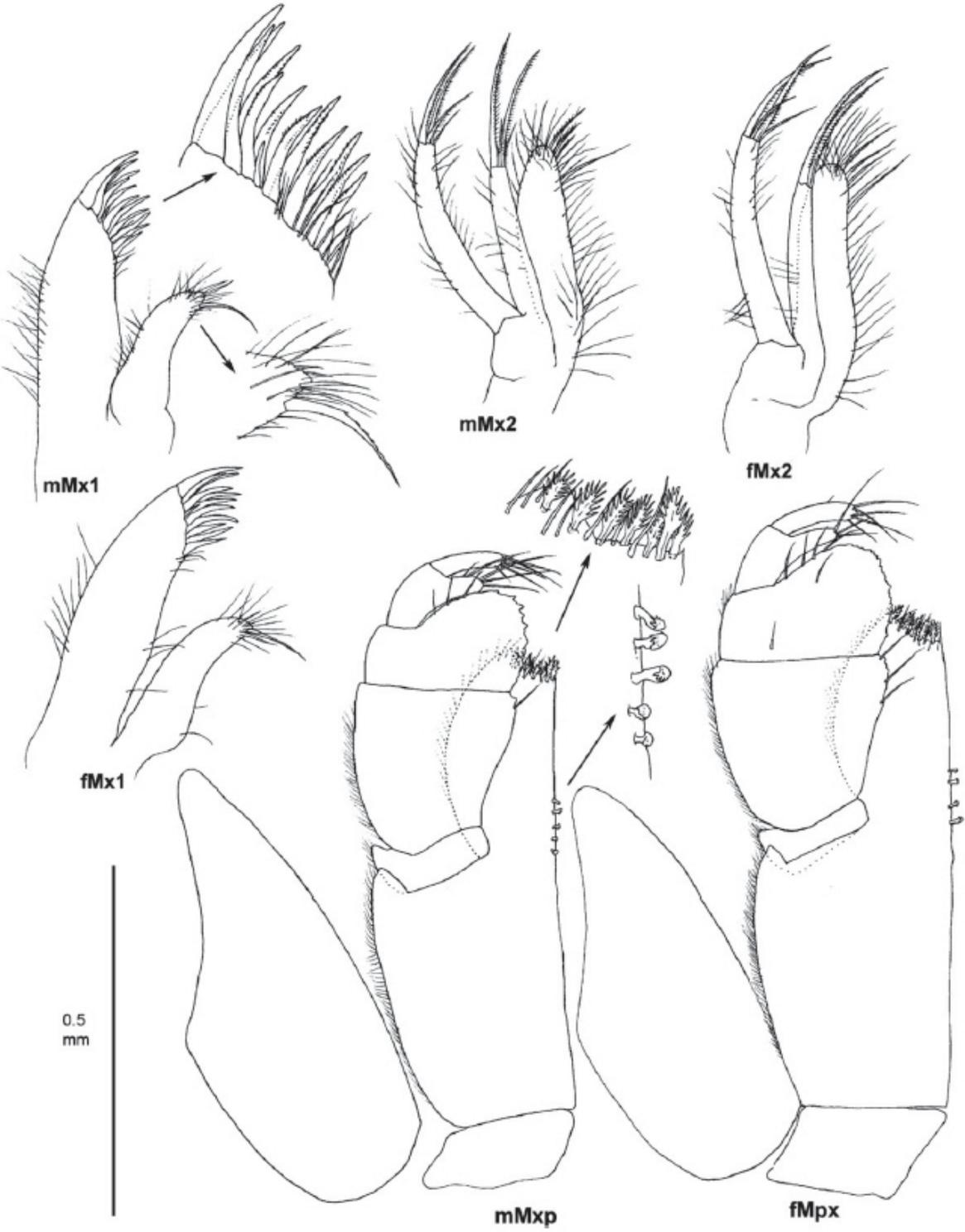


Fig. 9.13: *Eurycope spinifrons* Gurjanova, 1933. Copulatory male and preparatory female: maxillae and maxilliped.

Pereopod 1 (Fig. 9.14) basis to dactylus length–width ratios: 7,8; 4,6; 3,4; 9,6; 12,2; 5,6; length ratios of ischium–dactylus to basis: 0,5; 0,4; 1,1; 0,8; 0,2; basis with some small simple dorsal and unequally bifid ventral setae; ischium with 3 small proximal unequally bifid setae and few distal simple setae on ventral margin; merus and carpus with numerous long simple setae on ventral margin and 1–2 distodorsal setae; propodus with numerous simple setae, longest in distal part of article; dactylus with 4 fine simple seta, claws 0,3 dactylus length, ventral claw slightly longer than dorsal, 1 seta inserting between claws.

Pereopod 2 (Fig. 9.14) basis to dactylus length–width ratios: 6,3; 5,3; 2,5; 15,9; 20,0; 17,5; length ratios of ischium–dactylus to basis length: 0,6; 0,3; 1,8; 1,4; 0,6; dorsal margin of all articles with sparse fine setae; ventral margin of ischium and carpus with small unequally bifid setae, ventral unequally bifid setae of propodus longer with fringe of dense setulae in between; carpus and propodus with distodorsal set of 1 broom, few simple and unequally bifid setae; dactylus with 4 fine simple setae, claws 0,1 of dactylus length.

Pereopod 3 (Fig. 9.14) basis to dactylus length–width ratios: 7,0; 4,4; 2,4; 19,4; 38,5; 19,7; length ratios of ischium–dactylus to basis: 0,5; 0,3; 1,7; 2,0; 0,6; basis to propodus dorsal margins and merus ventral margin with sparse simple setae, basis ventral margin with sparse small unequally bifid setae, ischium, carpus and propodus ventral margins with more long and slender unequally bifid setae; carpus and propodus with a distodorsal set of 1 broom, few simple and unequally bifid setae.

Pereopod 4 (Fig. 9.14) basis to dactylus length–width ratios: 7,8; 5,4; 2,8; 17,9; 41,7; 24,0; length ratios of ischium–dactylus to basis: 0,6; 0,3; 1,9; 2,6; 0,6; ischium–dactylus ventral margins with sparse small unequally bifid setae, longest in propodus, carpus and propodus dorsal margin with fine simple setae, with distal set of 1 broom and few simple and unequally bifid setae; dactylus with 4 fine simple setae.

Pereopod 5 (Fig. 9.14) basis to dactylus length–width ratios: 2,5; 3,1; 1,7; 1,7; 2,5; 7,9; length ratios of ischium–dactylus to basis: 1,2; 0,4; 1,6; 1,4; 0,7; basis dorsally and ischium ventrally with few simple setae, ischium dorsal margin with row of 6 plumose setae; merus with 1 dorsal plumose seta; carpus with 24 dorsal and about 13 ventral submarginal plumose setae, distodorsal angle with 1 broom seta, 2 short and 1 long unequally bifid setae; propodus with about 21 dorsal and 17 ventral submarginal plumose setae, 2 distodorsal and 1 short distoventral unequally bifid setae; dactylus with 1 simple dorsal seta, claw 0.1 dactylus length, acute.

Pereopod 6 (Fig. 9.14) basis to dactylus length–width ratios: 2,5; 3,6; 0,3; 2,7; 17,8; 10,3; length ratios of ischium–dactylus to basis: 0,8; 0,3; 1,4; 1,2; 0,7; basis with few fine setae, 1 distodorsal broom seta and 1 distoventral long unequally bifid seta; ischium dorsal margin with row of 9 plumose setae, ventral margin with 6 long unequally bifid setae; carpus with 28 dorsal and 14 ventral submarginal plumose setae, distodorsally 1 broom and 4 unequally bifid setae; propodus with 2 proximodorsal, 1 stout distodorsal and 1 distoventral unequally bifid setae, 1 distodorsal broom seta, 18 dorsal and 14 ventral submarginal plumose setae; dactylus with 1 simple dorsal seta, claw 0,1 dactylus length.

Pereopod 7 (Fig. 9.14) basis to dactylus length–width ratios: 2,9; 2,3; 1,3; 1,2; 2,4; 7,0; length ratios of ischium–dactylus to basis: 0,7; 0,3; 1,1; 1,0; 0,5; basis with 1 long proximodorsal seta and 2 unequally bifid distoventral setae; ischium dorsal margin with row of 8 plumose setae, 1 distoventral unequally bifid setae; merus with 2 ventral unequally bifid and few simple setae; carpus with about 25 dorsal and 12 ventral submarginal plumose setae; propodus with 15 dorsal and 10 ventral submarginal plumose setae, 1 stout distodorsal and 1 distoventral unequally bifid setae, 1 distodorsal broom seta; claw 0,2 dactylus length.

Pleopod 1 (Fig. 9.17) length 2,9 proximal width and 3,9 “waist” width; ventral surface with 2 rows of 4 plumose setae on mid-length of each side; dorsal keels with fine simple setae on distal half; distomedial lobes rounded, projected posteriorly, length 4,1 width and 0,1 pleopod 1 length, with row of 14 fine simple subdistal setae on each lobe; distolateral lobes almost not expressed as wide as distomedial lobes, convex distally with lateral angle acute, ventral surface with tiny subdistal setae.

Pleopod 2 (Fig. 9.17) protopod length 1,5 width, with 4 submarginal setae on lateral projection and 3 distal setae, distomedial margin truncated concavely, exopod emerging from this distomedial excavation, stylet as wide as endopod basal article, length 7,5 width and 0,7 protopod length, sperm duct opening at mid-length of stylet; exopod proximal part 1,6 as wide as endopod basal article, distal part 0,6 as long and 0,5 as wide as proximal part, hook with tuft of fine setae.

Pleopods 3-5 (Fig. 9.17) endopod cupped, with convex lateral margin.

Pleopod 3 (Fig. 9.17) endopod length 1,2 width, 3 distal plumose setae about 0,3 length of pleopod 3; exopod lateral margin with fine setae, basal article length 2,4 width, equal to endopod length, distal article 0,35 length and 0,25 width of basal article, with slender simple distal seta.

Pleopod 4 (Fig. 9.17) endopod length 1.4 width; exopod length 2.2 width and 1.3 endopod length, width 0.8 endopod width, lateral and distal margins with fine setae, distal plumose seta as long as distal setae of pleopod 3 endopod.

Pleopod 5 (Fig. 9.17) endopod length 1.5 width.

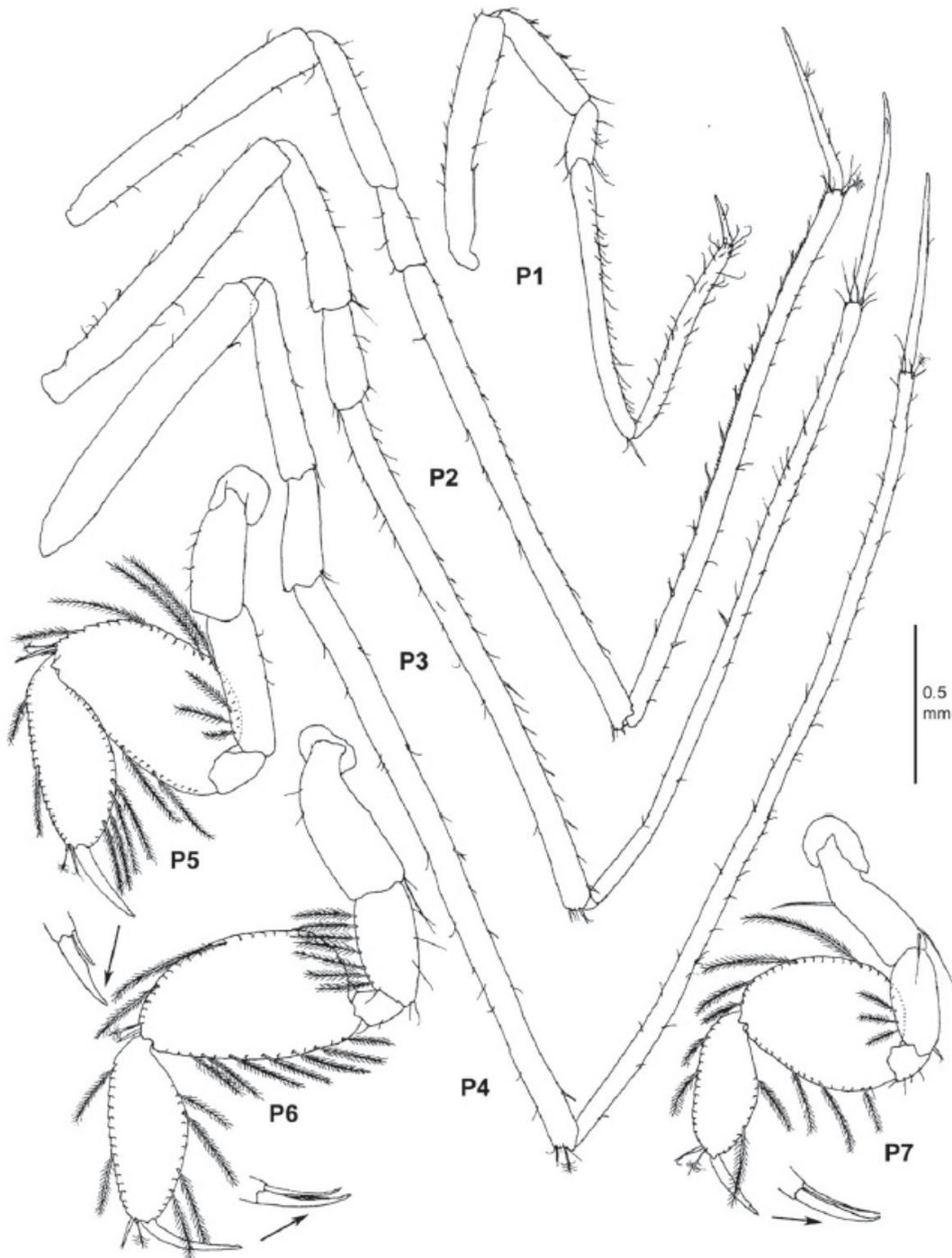


Fig. 9.14: *Eurycope spinifrons* Gurjanova, 1933. Copulatory male: pereopods 1–7.

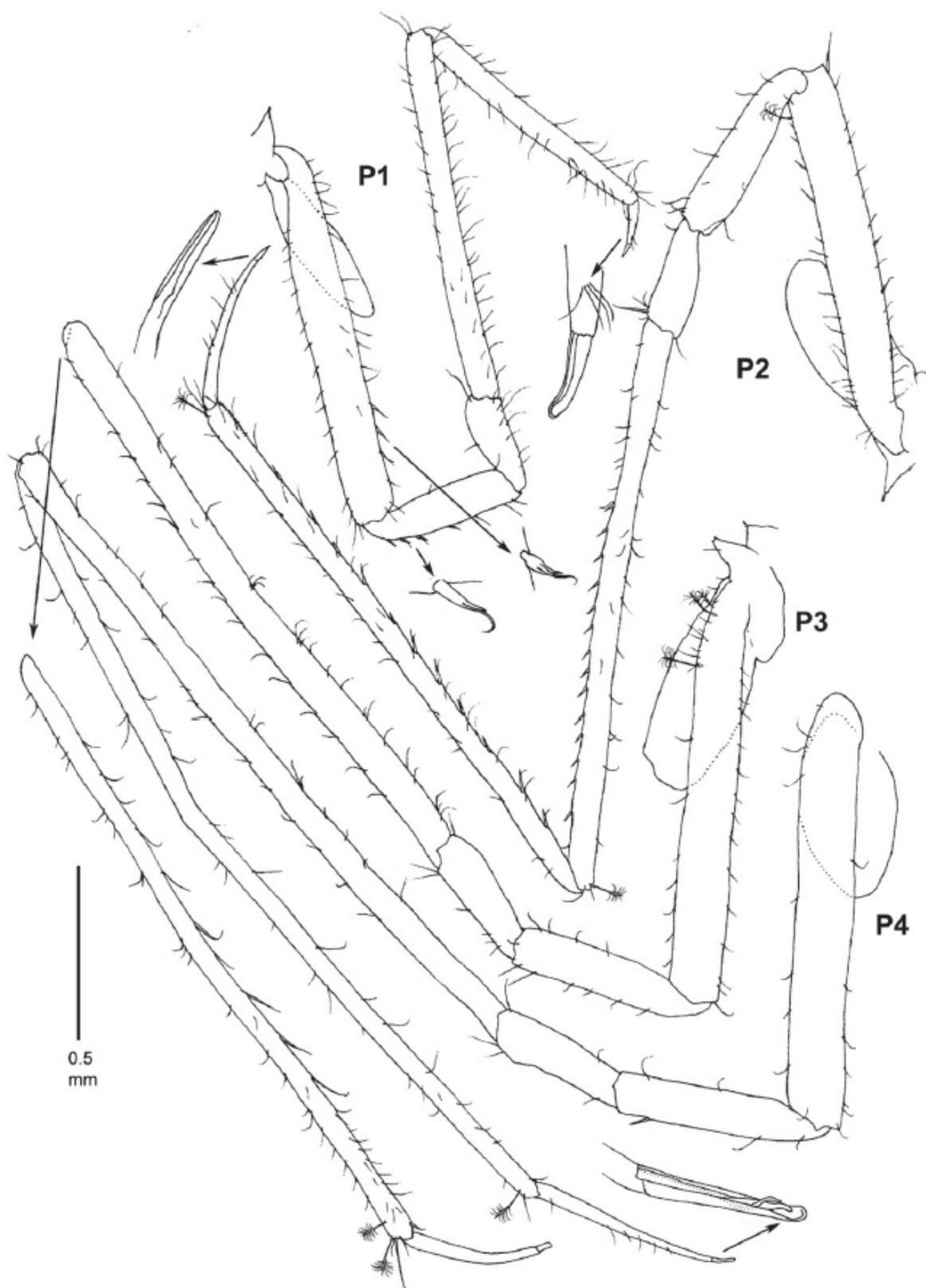


Fig. 9.15: *Eurycope spinifrons* Gurjanova, 1933. Preparatory female: pereopods 1–4.

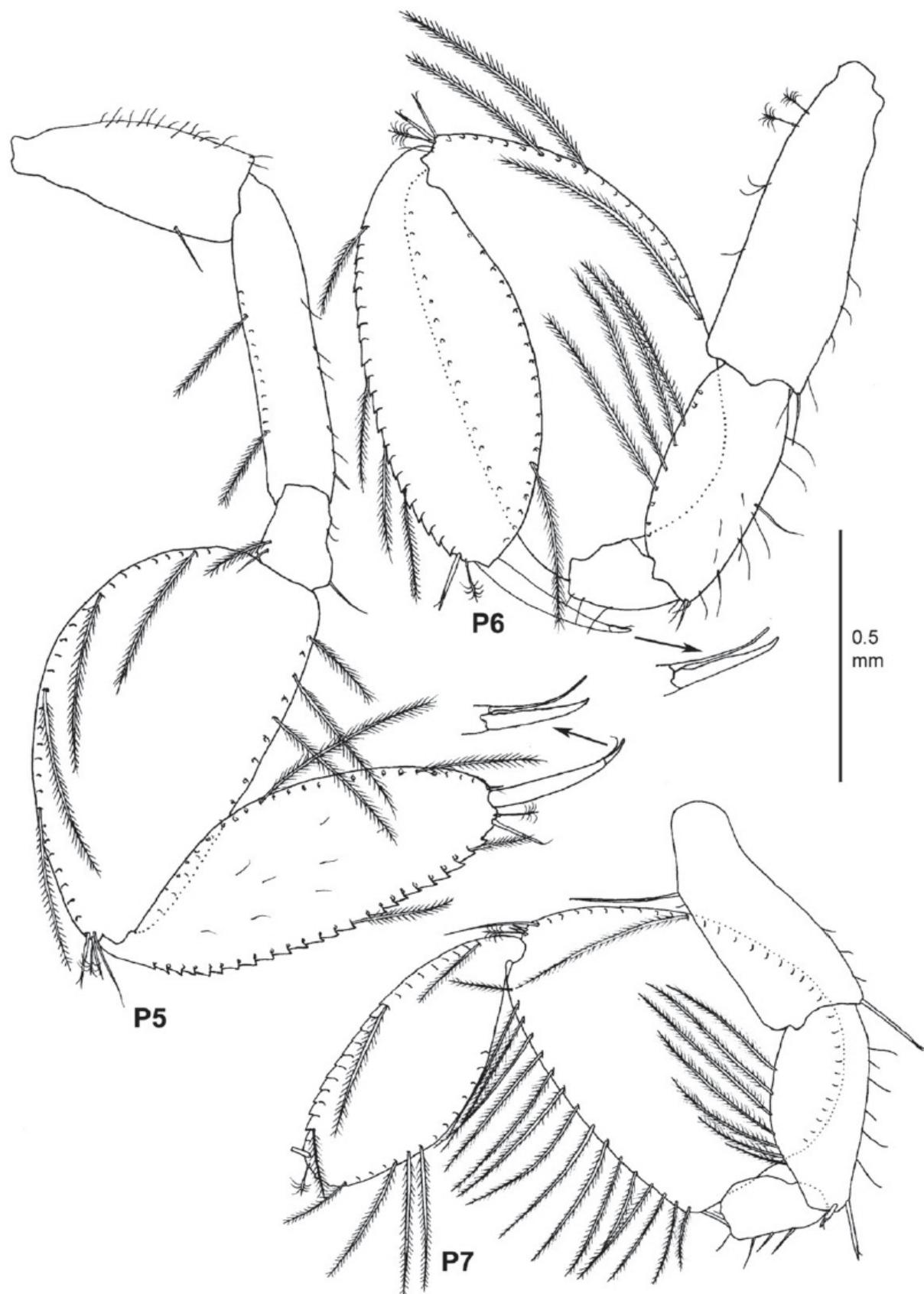


Fig. 9.16: *Eurycope spinifrons* Gurjanova, 1933. Preparatory female: pereopods 5–7.

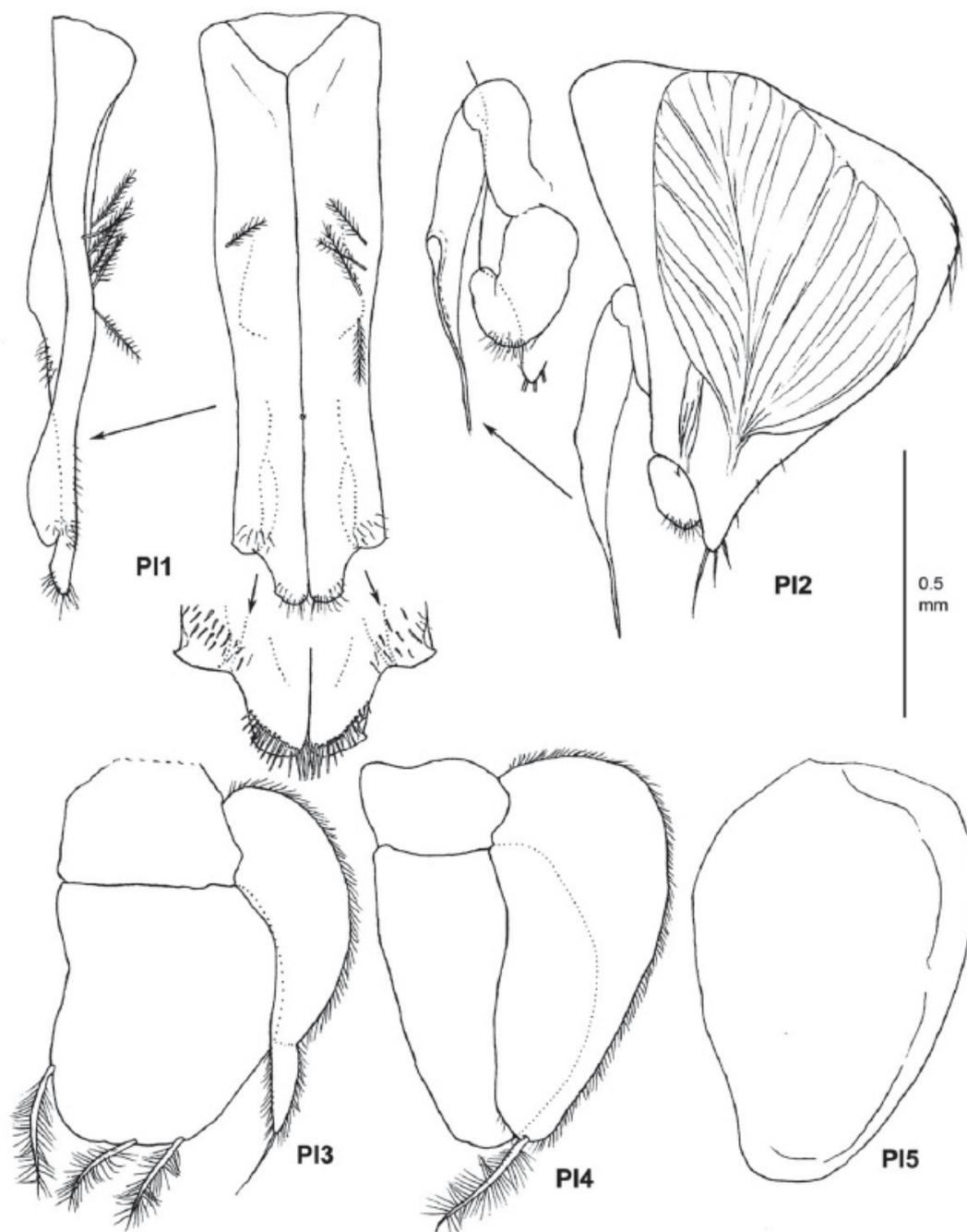


Fig. 9.17: *Eurycope spinifrons* Gurjanova, 1933. Copulatory male: pleopods 1–5.

Uropod (Fig. 9.19) protopod length 1,2 width, with 1 medial unequally bifid seta and 12 unequally bifid distal setae increasing in length towards weakly expressed distomedial angle;

endopod length 3,3 width and 1,15 protopod length, with 2 lateral and 6 distal broom setae and 7 distal unequally bifid setae, exopod length 3,5 width, 0,65 length and 0,6 width of endopod, with 1 simple lateral and 6 unequally bifid distal setae.

Female similar to male. Body (Fig. 9.10) length 2,2–2,6 width at pereonite 5; height at pereonites 6–7 0,3 length.

Antenna 1 (Fig. 9.11) shorter and more slender than that of male, about 0,4 body length, length–width ratios of articles 1–4: 1,0; 1,4; 4,1; 1,1; length ratios of articles 2–4 to article 1: 0,5; 0,75; 0,15; article 1 with 2 distomedial unequally bifid setae and 1 broom 3 and unequally bifid distolateral setae; article 2 with 5 unequally bifid setae and 2 broom setae distally.

Antenna 2 (Fig. 9.11) similar to that of male.

Mandibles (Fig. 9.12) similar to that of male, but spine row with 8 spines on left and right mandible. Length ratios of articles 2–3 of palp to article 1: 2,1; 1,1.

Maxilliped (Fig. 9.13) endite with 5 retinaculae. Remaining mouthparts (Fig. 9.13) and pereopods (Figs 9.15, 9.16) similar to those of male, insignificantly differing in proportions and number of setae.

Operculum (Fig. 9.18) subtriangular in ventral view, with rounded angles, length 0,7 width, height 0,3 length; ventral keel length 0,7 total operculum length, apex with long unequally bifid seta, ventral surface between apex and posterior margin flattened, with fine simple setae; lateral fields with 8–12 setae.

Pleopods 3–5 (Fig. 9.18) similar to those of male, but exopod of pleopod 3 without separation between articles.

Uropod (Fig. 9.19) similar to that of male, but protopod more stout, length 1,1 width, endopod length 3,5 width, 1,2 protopod length and 1,7 exopod length; exopod length 3,3 width.

Remarks. *Eurycope spinifrons* is the only *Eurycope* species known from the Sea of Japan. Besides *E. spinifrons* there are no other species of the genus recorded from the shallow waters of the northwestern Pacific, but three species, *E. affinis* Birstein, 1970 (5,009–5,900 m), *E. curticephala* Birstein, 1963 and *E. curtirostris* Birstein, 1963 (7,210–7,230 m) are known from the Kurile-Kamchatka Trench.

Morphologically, *E. spinifrons* is similar to *E. curticephala*. Both species possess a narrow maxillipedal epipod without a pronounced lateral extension and an article 1 of antenna 1 with a reduced distomedial lobe shorter than article 2. By these characters these two Pacific species are close to the longiflagrata complex from the Atlantic (Kussakin, 2003; Malyutina and Brandt, 2006; Wilson, 1983), the narrow epipod is also characteristic in *E. producta*. In all other *Eurycope* species, the epipod of the maxilliped has a more pronounced lateral extension and the antenna 1 a distomedial lobe on article 1 which is as long as or longer than article 2. Since the description of *E. curticephala* was based on female specimens and males are unknown, we cannot compare the male pleopods 1 and 2. By the shape of the uropods, the male pleopod 1 with a rounded projected distomedial lobes and the pleopod 2 with an oblique distomedial margin on the protopod. *E. spinifrons* reminds of species of the group C or the *E. inermis* cluster from the Arctic (Kussakin, 2003; Malyutina and Brandt, 2006; Wilson, 1983), but the rostrum of *E. spinifrons* is longer and broader than in members of this group, having size which is comparable to article 1 of antenna 1.

Distribution: Northwestern part of the Sea of Japan, depth range 308–3,665 m.

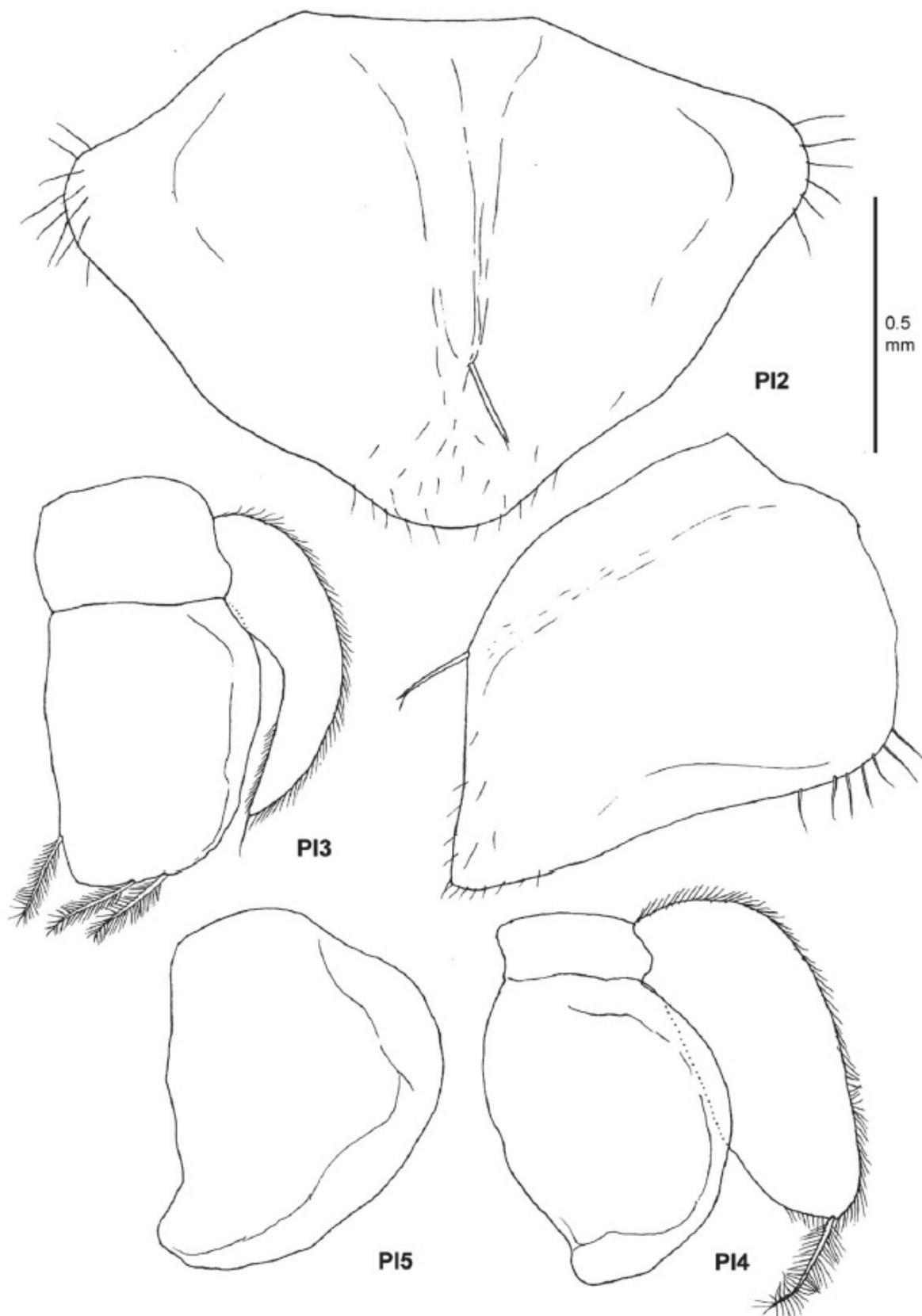


Fig. 9.18: *Eurycope spinifrons* Gurjanova, 1933. Preparatory female: pleopods 1–5.

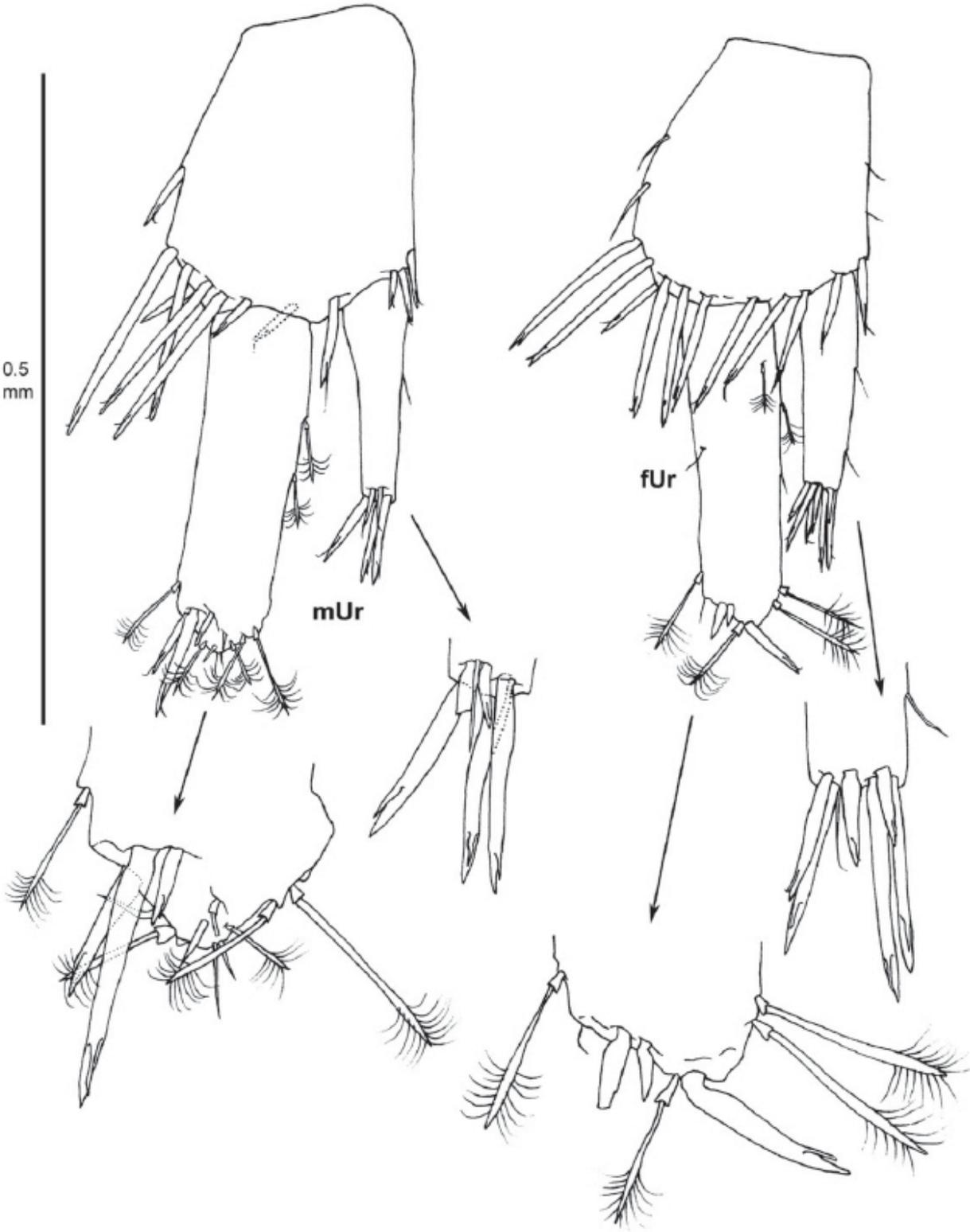


Fig. 9.19: *Eurycope spinifrons* Gurjanova, 1933. Copulatory male and preparatory female: uropod.

Ilyarachninae Hansen, 1916

G.O. Sars, 1870

Synonymy: see Kussakin 2003: 21.

Type species: Mesostenius longicornis G.O. Sars, 1864, by original designation.

Ilyarachna zachsi Gurjanova, 1933

Ilyarachna zachsi Gurjanova, 1933: 83, fig. 8 (non 7), 1936: 56, fig. 20; Kussakin, 2003: 231, fig. 165; Golovan and Malyutina, 2006: 47–60, figs.1-6; Golovan and Malyutina, 2010: 124, tabl. LII.

Ilyarachna starokadomskii Gurjanova, 1933: 83, fig. 7 (non 8), 1936: 57, fig. 21 (part); Kussakin, 2003: 221, fig. 155.

Material examined. SoJaBio EBS stations: A2–10, 14.08.2010, 455–465 m, 44°56N 137°11E – 12 specimens; B7–6, 25.08.2010, 517–521 m, 43°13N 135°04E – 2 specimens; B7–7, 25.08.2010, 470–528 m, 43°13N 135°04E – 78 specimens.

Distribution. Northwestern part of the Sea of Japan, depth range 100–1,100 m.

Incertae sedis

Munnopsurus Richardson, 1912

Synonymy: see Kussakin 2003: 357.

Type species: Munnopsurus giganteus (G.O. Sars, 1879)

Munnopsurus minutus Gurjanova, 1933

Gurjanova 1933: 84, fig. 9 (non 10), 12a–d; 1936: 61-62, fig. 25; Kussakin, 2003: 360–363, fig. 258, 259; Golovan and Malyutina, 2010: 127, tabl. LIV.

Material examined. SoJaBio EBS station B7–7, 25.08.2010, 470–528 m, 43°13N 135°04E – 3 juveniles.

Distribution. Northern part of Okhotsk Sea and northwestern part of the Sea of Japan, depth range 158–528 m.

Discussion

All four munnopsid species collected by the SoJaBio expedition occur at the shallowest stations (500 m), but most of them with a rather low abundance: with 3 specimens (*M. minutus*) or a few dozen specimens in the sample (*I. zachsi* and *E. spinifrons*). The most numerous species at those stations is *B. brandtae* sp. nov. (> 300 specimens). At the deeper stations, *M. minutus* and *I. zachsi* were not collected, though *I. zachsi* is known from depths of 105–1,002 m (Golovan and Malyutina, 2010; Kussakin, 2003). *B. brandtae* sp. nov. occurs at depths of down to 1,525 m, but significantly less frequent there than at the shallowest stations.

In contrast, the abundance of *E. spinifrons* increases with depth. The species was found at all SoJaBio stations down to 3,665 m. At the shallowest stations its abundance is moderate, with few or tens of individuals in one sample, but deeper than 2,500 m the number increases sharply, and at the deepest stations (> 3,300 m) it was the most numerous species of macrobenthos, reaching around 3,000 specimens in a sample (see also Elsner et al., 2013 (**Chapter 7**)).

The genera *Eurycope*, *Ilyarachna* and *Munnopsurus* have a worldwide distribution at a wide range of depths and include abyssal species along with some shelf and eurybathic species. *I. zachsi*, *I. kurilensis*, and *M. minutus* are subtidal-bathyal species which were found besides the Sea of Japan in the Okhotsk Sea (Golovan and Malyutina, 2010; Kussakin, 2003).

The genus *Eurycope* was not yet recorded from the Okhotsk Sea, but three species have been described by Birstein (1963, 1970) from the Kurile-Kamchatka Trench – the adjacent open ocean abyssal. The genus *Baeonectes* is restricted in its distribution to high latitudes of the Atlantic (*B. muticus*, *B. pygmaea*) and Pacific (*B. improvisus* at the northeastern Pacific coast, *B. ochotensis* and *B. abberantis* in the Okhotsk Sea and *B. pavlenkoi* and *B. brandtae* sp. nov. in the Sea of Japan). *B. brandtae* sp. nov. is the deepest recorded species of the genus, all other species except *B. abberantis* from 787–961 m in the Okhotsk Sea inhabit shelf depths (9–225 m). *B. brandtae* sp. nov. possesses the longest walking pereopods 2–4 in the genus, a typical character of deep-sea species of *Eurycope*. Obviously this feature correlates with the similar deep-sea life-style of these species on a muddy substrate.

The origin of *E. spinifrons* and *B. brandtae* sp. nov. in the Sea of Japan is yet unknown, they inhabit the sea to different degrees and at various depths. Perhaps the answer to this question will be obtained with new material from the Kurile-Kamchatka area during the planned joint expedition of the project KuramBio (Kurile Kamchatka Deep Sea Biodiversity) in 2012. Since all type specimens of Birstein's deep-sea species from the Kurile-Kamchatka Trench are in bad condition or lost and not suitable for studying, we hope that future sampling in the abyssal of the Kurile-Kamchatka area will yield new material of munnopsid species in good condition and provide an opportunity to continue the comparison and further inventory of the Munnopsidae of the northwestern Pacific.

Acknowledgment

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Author's contribution:

I partly assisted in the species determination and drawing (pencil drawings) of both species. I proofread the original manuscript for grammar, spelling and style.

Conclusions

Chapter 10: Conclusions

This study focusses on the comparison of two adjacent regions in the Northwest Pacific, namely the Sea of Japan and the abyssal plain adjacent to the Kuril-Kamchatka Trench. For this purpose, the study analyzes the samples of the two expeditions which were conducted within the respective areas.

This study contains the comparison of three topics: the comparison of macrofaunal composition at phylum, class and order level between both areas (Chapter 2 and 3), the comparison of the isopod composition at species level between both areas (Chapters 5 and 6) and finally the comparison of the population structure of three different species within the Sea of Japan (Chapters 7 and 8). Additionally, the analysis of peracarid composition (Chapter 4) gives information at intermediate taxonomic resolution about the Sea of Japan. Species descriptions and species determination are the basis for any ecological and diversity research. Therefore, one description and one redescription are included in this study (Chapter 9).

In the following, I will focus on three major topics of this dissertation: biodiversity, population structure and distribution and biogeography.

Biodiversity

Generally, the deep-sea soft sediments are characterized by low abundance and high local diversity (Brandt et al., 2007b; Grassle and Maciolek, 1992; Hessler and Sanders, 1967; Ramirez-Llodra et al., 2010). On the basis of the studies included in this dissertation, this could be confirmed for the Kuril-Kamchatka area (Chapter 6), but not for the Sea of Japan (Chapter 5). Abyssal samples retrieved from the Sea of Japan were impoverished with respect to diversity and just yielded a single species, *Eurycope spinifrons*. Patterns observed across depth were in accordance with the initial hypothesis that the deep-sea benthic fauna of the Sea of Japan was eradicated during the Last Glacial Maximum (LGM) due to anoxic conditions and, thus, is still in the process of recolonization. The preceding anoxia in the deep Sea of Japan may resemble the extensive extinction in deep sea in the mid Cenozoic (Wilson, 1999). Although this extinction was supposedly widespread, the Sea of Japan may represent a valuable model to study deep-sea recolonization following large-scale disturbance events also in the course of expected anthropogenic changes, such as seafloor mineral extraction, fisheries

and climate change (McClain and Hardy, 2010; Ramirez-Llodra et al., 2010; Roberts, 2002; Veillette et al., 2007).

In this thesis, it became obvious that data from the two expeditions, SoJaBio (Sea of Japan Biodiversity Studies) to the Sea of Japan and KuramBio (Kuril-Kamchatka Biodiversity Studies) to the Kuril-Kamchatka Trench area are technically not directly comparable. This is because the difference in depth between the deepest SoJaBio station (3,649 m) and the shallowest KuramBio station (4,847 m) is still more than 1,000 m; In the marine realm, depth and correlated factors often represent a strong driver of faunal diversity and distributions (Brandt et al., 2007a; Rex and Etter, 2010; Rex et al., 2006). However, a comparison with stations sampled by the Russian research vessel *Vityaz* in the 1950s in the Northwest Pacific (Belyaev, 1970, 1983, 1989; Birstein, 1963; Ushakov, 1952; Zenkevich et al., 1955; Zenkevitch, 1963) seems appropriate, as these were collected in the same depth range (cp. Chapter 5).

Population structure

The source-sink hypothesis is an attempt to explain bathymetric diversity gradients observed in the deep-sea benthos (Rex and Etter, 2010; Rex et al., 2005). The hypothesis assumes that certain organisms cannot reproduce in certain (abyssal) depths, but that these depths nonetheless are populated by these organisms, simply by larval dispersal and/or migration from source populations on the slope. Rex et al. (2005) furthermore suggest that these areas may be unsuitable for reproduction, but can be invaded by free-swimming larvae which are able to settle and mature there (but not reproduce). This hypothesis may partly explain why there are many rare species in the deep sea which only occur in very low abundances (Connolly et al., 2014; Ellingsen et al., 2007).

For brooding isopods, the source-sink hypothesis does not seem to hold true, which could be shown in this thesis (Chapter 7). The analysis of population structure in *Eurycope spinifrons* showed continuous reproduction throughout the year and at all depth levels investigated. Usually, reproduction is periodical in (shallow-water) Asellota, peaking in winter with about 25% brooding females (Harrison, 1988), which is also the case for other peracarid crustaceans (Bishop and Shalla, 1994; Eustace et al., 2013; Fenwick, 1985). For example, adaptation of the reproductive mode to the environment has been observed in the Southern Ocean (Luxmoore, 1982; Pearse et al., 2009; Wägele, 1987). These general patterns may apply to a

majority, but there may be exceptions. Species-specific knowledge is necessary in order to understand the (bathymetric) limitations of these species. The main factors differentiating the reproductive mode are generation time, reproduction frequency and the number of reproductions of adult females in their lifetime (semelparity/iteroparity).

In this thesis, reproduction patterns were compared between one abyssal (Chapter 7) and two slope species (Chapter 8) from the Sea of Japan, which differed markedly. Continuous reproduction in *Eurycope spinifrons* contrasted with seasonal reproduction in the two investigated *Pleurogonium* species. The two *Pleurogonium* species show a higher proportion of brooding females, than recorded in any previous study (Brandt et al., 1994).

The three species of *Eurycope* and *Pleurogonium* co-occur on the shelf area of the Sea of Japan. Sympatric occurrence may lead to a difference in depth distribution (Hill and Elmgren, 1987) or even reproduction in different seasons like winter and spring (Menge, 1975). Both species of *Pleurogonium* are additionally much smaller than *E. spinifrons* (~1.5 mm and 4 mm for brooding females, respectively). Supposedly, interspecific competition may have led each to occupy a different ecological niche concerning reproduction, but maybe also with regard to their diet. For copepods comprising different size classes it is known that the larger species has a distinctively different diet compared to the smaller one with regard to particle size (Maly and Maly, 1974). These food sources may be available at different times of year which in turn may influence the reproduction period when additional energy is needed in order to produce offspring. Further studies, focusing for instance on gut content analyses or close examination of the mouthparts and the first pereopod may further elucidate this aspect (Würzberg et al., 2011a; Würzberg et al., 2011b; Würzberg et al., 2011c).

Shelf fauna is generally more directly linked to and influenced by surface production, which in turn relates to higher biomass and abundances compared to greater depth (Grebmeier et al., 1988). Both species of *Pleurogonium* are present on the northern slope of the Sea of Japan and only occur down to a depth of 943 m. They possess a distinctly different reproductive mode from *Eurycope spinifrons* which occurs at all sampled depths. Continuous reproduction is known from several deep-sea peracarids (Rokop, 1977), and it may be a critical feature when colonizing the deep sea where food generally is sparse (Sanders and Hessler, 1969) and food falls sporadic (Stockton and DeLaca, 1982).

Distribution and biogeography

The Sea of Japan combines several extraordinary characteristics, making it a unique marine region: In addition to its geologically recent history of anoxia (Amano, 2004; Kojima et al., 2001; Oba et al., 1991; Tada, 1994; Tada et al., 1999) and the connection to adjacent regions solely through shallow-water straits (Tyler, 2002), it is divided (at roughly 40°N) by the Subpolar Front. The subarctic North is influenced by the cold water currents from the Sea of Okhotsk, while the subtropical South is influenced by the warm Tsushima Current (Ito et al., 2014; Kawabe, 1982). However, the bottom layer below 2,000 m depth is very homogeneous in terms of temperature, salinity and dissolved oxygen (Chen et al., 1999) and thus does not share this barrier.

During SoJaBio (Sea of Japan Biodiversity Studies), only stations north of the Subpolar Front were sampled. A direct comparison from within samples of this expedition between these two regions is therefore not possible.

It has been proposed that the recolonization of the deep Sea of Japan following LGM anoxia may have been achieved by the downward migration of eurybathic cold-water adapted shelf fauna (Tyler, 2002; Zenkevitch, 1963). Amano (2004) stated that there was a presumed refuge in the Sea of Japan at a depth between ~100–400 m with normal salinity and oxygen concentration during glacial minima. The occurrence of *E. spinifrons* at depths around 300 m would have enabled this species (and possibly others) to survive anoxia in the deep waters. Additionally, it keeps this species (and presumably others) endemic to the Sea of Japan, as is the case, because an occurrence no shallower than this depth would clearly prevent it from being able to pass through any of the shallow water straits with a maximum depth of 130 m (Tyler, 2002). This is even more the case for organisms lacking a free-swimming larval stage like the peracarid crustaceans.

It is not known from which shallow water strait (or straits) or shelf area the recolonization exactly happened after today's oxygen conditions were reestablished. The two species of *Pleurogonium* collected during SoJaBio were both present in considerable numbers at the northernmost station (45°N). However, both species seem morphologically most closely related to species described from east of Kyushu in southern Japan, *P. kyushuense* Shimomura, 2009 and *P. tanseimaruae* Shimomura, 2009. This leads to the hypothesis that there is at least some faunal exchange between the shelf outside of (but adjacent to) the Sea of Japan and between the subtropical southern and the subarctic northern part of the Sea of Japan

despite the supposed barrier of the Subpolar Front. Genetic analyses may further elucidate the direction of faunal colonization of the Sea of Japan and help to disentangle potential variation of faunal assemblages and recolonization patterns at the area of transition between the subarctic and Subpolar Zone.

General conclusions

The investigation area provides the rare opportunity to study the succession process of an isolated deep-sea region, the Sea of Japan, in comparison to a biogeographically well connected area, i.e. the Kuril Kamchatka region. On the one hand, the Sea of Japan represents a semi-isolated marginal sea with abyssal basins presumably being in an early succession stage concerning the deep sea. On the other hand, data from previous Russian *Vityaz* expeditions from the 1950s (Belyaev, 1970, 1983, 1989; Birstein, 1963; Ushakov, 1952; Zenkevich et al., 1955; Zenkevitch, 1963) presented a comprehensive baseline against which potential temporal changes in e.g. faunal composition and diversity could be identified. Additionally, it enabled further thorough faunal collections of the Kurile Kamchatka region, which greatly improved knowledge about the diversity and composition of deep-sea fauna in this specific region and helps to estimate the further effort which would be needed for an exhaustive investigation of this area.

It is important to understand the succession process of abyssal basins and reproductive patterns in deep-sea species with regard to deep-sea perturbations, for example deep-sea mining (Bluhm, 1994; Borowski and Thiel, 1998) and fisheries (Ramirez-Llodra et al., 2010; Roberts, 2002). In this context it may be beneficial to know about, for example, seasonality and breeding time of individual species. Local diversity and distribution may also be important factors with regard to ecosystem stability (McCann, 2000; Rooney and McCann, 2012).

Thus, this dissertation contributes to the understanding of individual reproductive modes and deep-sea diversity, biogeography and succession of an isolated deep-sea basin in comparison to an open abyssal plain with an inflow of nutrient-rich water.

Outlook

In the future, further studies will investigate the biogeographical regimes of the Northwest Pacific. A first study will analyze the distribution both bathymetrically and geographically of the Northwest Pacific and compare the diversity in the region with the Southern and Atlantic Ocean (cp. Appendix I).

Further areas of interest may be the investigation of morphologically similar but genetically different cryptic species so far combined in species complexes, which are being increasingly recognized in isopods (Brökeland and Raupach, 2008; Raupach et al., 2007; Raupach and Wägele, 2006; Wilson, 1983). A species like *E. spinifrons*, both bathymetrically and geographically widespread, may prove to be a complex of different cryptic species occurring in different depths and regions.

Sampling especially in the Sea of Okhotsk, and therein in the Kuril Basin, and in the Kuril-Kamchatka Trench itself would greatly further our knowledge and understanding of the Northwest Pacific. A comparison between the Sea of Okhotsk and the Sea of Japan would answer questions with regard to the level of connectivity enabled by the shallow-water Tatarskiy Strait and Soya Strait and the recolonization of the shelf and the deep Sea of Japan. The Kuril Basin is connected via deep-water straits with the Kuril-Kamchatka Trench, so a comparison between these two areas and the adjacent abyssal plain will give detailed information about barriers, limitations and accessibilities for deep-sea faunal organisms.

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**Uncharted: biogeography of the Isopoda in the Northwest Pacific Ocean
and diversity comparison with the Atlantic and Southern Ocean**

Unpublished manuscript

Appendix I: Uncharted: biogeography of the Isopoda in the Northwest Pacific Ocean and diversity comparison with the Atlantic and Southern Ocean

Nikolaus O. Elsner, Tanja Springer, Angelika Brandt

Biocentre Grindel and Zoological Museum, University of Hamburg, Martin-Luther-King-Platz 3, D-20146 Hamburg, Germany

Abstract

Biogeographical classifications are both of scientific and political interest and importance: They are needed in order to locate the areas of high endemic biodiversity for conservational purposes and to test hypotheses about evolutionary processes. The GOODS (Global Open Oceans and Deep Seabed) biogeographical classification was proposed in 2008. In this study, we test the hypothesis of the proposed provinces, specifically of the abyssal province “North Pacific” and the bathyal province “Northern North Pacific” on the basis of the data from the two expeditions SoJaBio (Sea of Japan Biodiversity Studies) and KuramBio (Kuril-Kamchatka Biodiversity Studies) and additional literature research. Our preliminary results suggest distinct restriction to the respective areas at least for the abundant isopod species. However, further and more detailed analysis with regard to this question is needed for a clear result. Furthermore, additional sampling in the Kuril Basin of the Sea of Okhotsk and in the Kuril-Kamchatka Trench itself would greatly add to our knowledge and understanding of the whole Northwest Pacific.

Keywords: Sea of Japan; Kuril-Kamchatka Trench; *Eurycope*, *Pleurogonium*, *Macrostylis*, *Haploniscus*

Introduction

Biogeography concerns the distribution of organisms. Research often concentrates on biodiversity hotspots, i.e. regions with high, but locally limited biodiversity like cold-seep or hot vent communities in the deep sea (Gollner et al., 2014; Nakajima et al., 2014; Tunnicliffe et al., 1998; Van Dover et al., 2002). However, other areas like the Southern Ocean also exhibit a high diversity and are biogeographically interesting (Brandt et al., 2007; Griffiths et al., 2009).

Biogeographical studies address, amongst others, questions concerning the origin and evolution of deep-sea communities and the connectivity and faunal exchange between different areas and regions (McClain and Hardy, 2010). Beside the scientific relevance, there is also a political interest to classify regions of high biodiversity and high endemism in order to permit a reasonable and meaningful conservation management. For both scientific and political reasons, a reliable classification of biogeographically distinct areas is needed. Such a classification was recently proposed with the GOODS (Global Open Oceans and Deep Seabed) biogeographical classification (O'Boyle, 2010; Vierros et al., 2008).

In this study, we test the hypothesis of the GOODS biogeographical classification with regard to the North Pacific abyssal province mainly on the basis of the isopod species data obtained from two recent expeditions: the SoJaBio (Sea of Japan Biodiversity Studies) and KuramBio (Kuril-Kamchatka Biodiversity Studies) expeditions to the Sea of Japan and the Kuril-Kamchatka Trench area, respectively. Additionally, we are conducting an ongoing literature research of the area which is mainly based on the expeditions with the Russian research vessel *Vityaz* conducted mainly in the 1950s (Bogorov, 1973; Shirshov, 1983; Zenkevitch, 1963), as these samples are the basis for our deep-sea knowledge of the Northwest Pacific prior to SoJaBio and KuramBio. The Isopoda of the *Vityaz* expedition were determined and described by Birstein (1963, 1970, 1971).

We use the obtained data for geographical and bathymetrical analyses in order to test the GOODS classification.

Material and methods

The SoJaBio expedition (Sea of Japan Biodiversity Studies) collected benthos samples with the Russian RV *Akademik M. A. Lavrentyev* from 11th of August to 5th of September 2010 in the Sea of Japan. 13 stations were sampled in the Japan Basin with a camera-equipped epibenthic sledge (C-EBS) (Brandt et al., 2013; Brenke, 2005). Station depths ranged from 459 to 3,649 m. The KuramBio expedition (Kuril-Kamchatka Biodiversity Studies) collected benthos samples with the German RV *Sonne* from 30th of July to 31st of August 2012 southeast of the Kuril-Kamchatka Trench. 12 stations were sampled with 21 hauls on the abyssal plain south and one north of the Kuril-Kamchatka Trench by means of a C-EBS. Station depths ranged from 4,830–5,780 m. In addition to the data from the SoJaBio and KuramBio expeditions, we are conducting a literature research (cp. Tab. A.1). The maps are generated using Esri ArcGIS 10.2 for Desktop (Education Edition).

Results

We analyze the distribution of different abundant isopod species from the Northwest Pacific, mainly on the basis of the species which were collected during the SoJaBio und KuramBio expeditions, respectively. Our preliminary results show a distinct difference and no overlap of the distribution between isopod species from the Sea of Japan and those from the Kuril-Kamchatka Trench area (Fig. A.1). We chose to plot the most abundant species: for the Sea of Japan *E. spinifrons* and the species so far determined as *Pleurogonium* aff. *kyushuense* (Golovan et al., 2013) (**Chapter 4**), as it closely resembles the species *Pleurogonium kyushuense* Shimomura, 2009. For the Kuril-Kamchatka Trench area, we plotted the two most abundant taxa which were also collected by the RV *Vityaz* at multiple stations.

Eurycope spinifrons Gurjanova, 1933 is endemic to the Sea of Japan (Golovan et al., 2013) and additionally only known from the northern coast of Russia. *P.* aff. *kyushuense* is confined to the North of the Sea of Japan, while *P. kyushuense* is confined to the South and West of Kyushu outside of the Sea of Japan. The species *Macrostylis zenkevitchi* Birstein 1963 and *Haploniscus hydroniscoides* Birstein 1963 were both collected in the Kuril-Kamchatka Trench area. They are not known from a locality outside this area, but *H. hydroniscoides* appears to be more widespread. In contrast to *M. zenkevitchi*, it is present at both KuramBio

stations which were sampled on the trench slope and at a *Vityaz* station southeast of the KuramBio area.

We plotted these species also according to their bathymetrical (in addition to their geographical) distribution in order to check for further differences (Fig. A.2). *P. aff kyushuense* and *P. kyushuense* show a rather shallow distribution, while *H. hydroniscoides* and *M. zenkevitchi* from the Kuril-Kamchatka Trench area show a rather deep distribution (although also stations up to a depth of 1,226 m were sampled). *E. spinifrons* shows a very large depth range (308–3649 m).

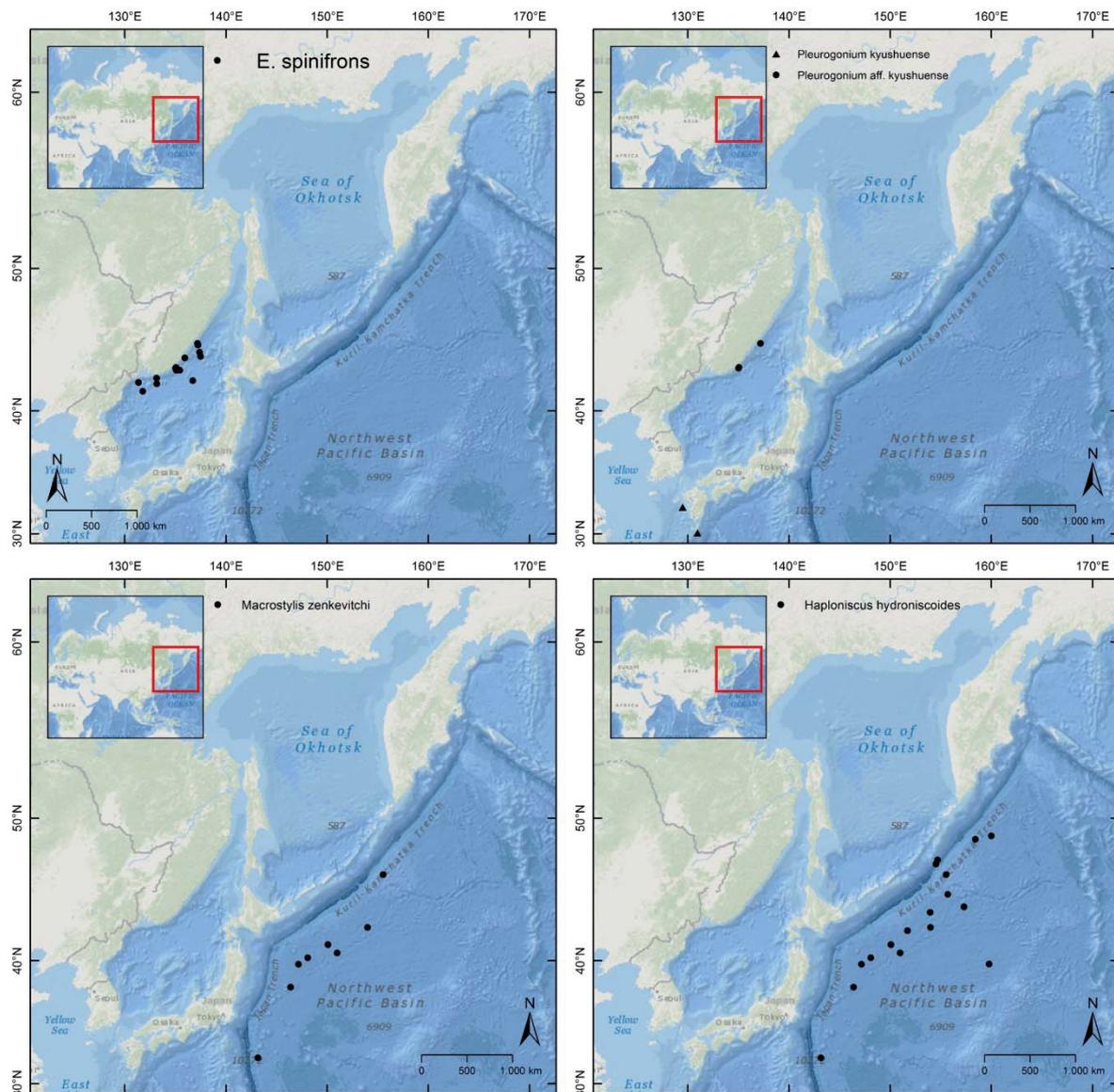


Fig. A.1: Distribution of selected species from the Sea of Japan and the Kuril-Kamchatka Trench area. Top left: *Eurycope spinifrons*; top right: *Pleurogonium kyushuense* (triangle) and *Pleurogonium aff. kyushuense* (circle; cp. Chapters 4, 5 and 8); bottom left: *Macrostylis zenkevitchi*; bottom right: *Haploniscus hydroniscoides*.

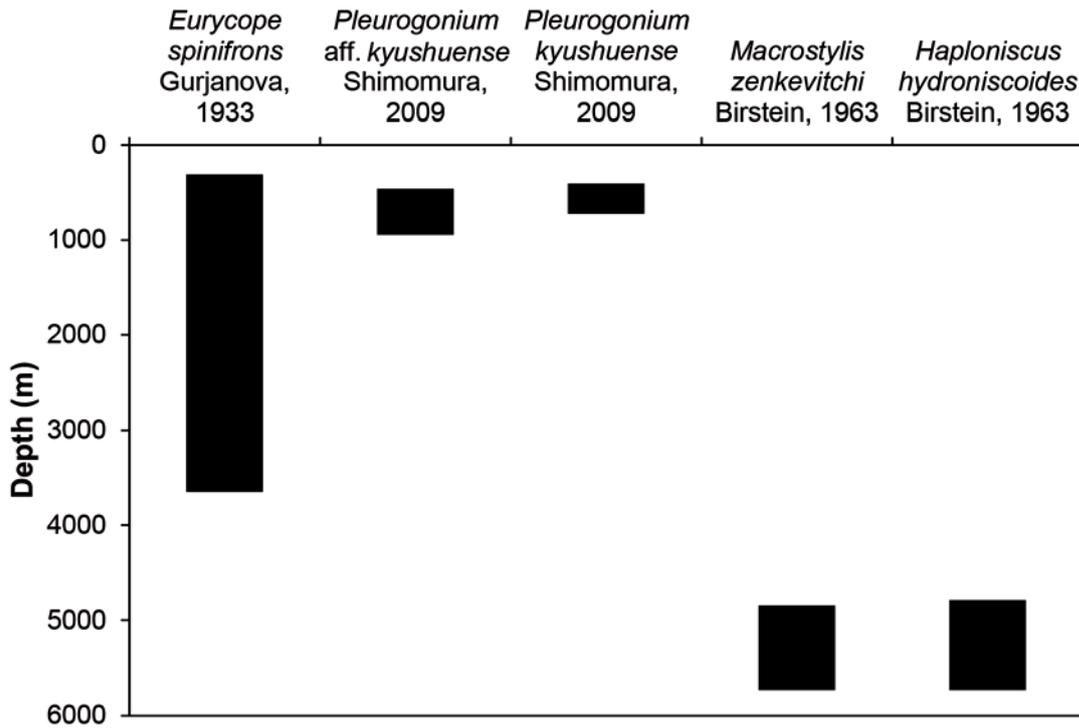


Fig. A.2: Depth distribution of five abundant species. *Eurycope spinifrons* and *Pleurogonium aff. kyushuense* are confined to the Sea of Japan, *P. kyushuense* to the South and West of Kyushu and *Macrostylis zenkevitchi* and *Haploniscus hydroniscoides* to the Kuril-Kamchatka Trench area.

Tab. A.1: Table of the localities of selected genera and species present in the Sea of Japan (ongoing literature research).

Family	Species	Latitude	Longitude	Depth
Munnopsidae	<i>Baeonectes ochotensis</i>	59°18.2'N	159°45'E	85 m
Desmosomatidae	<i>Desmosoma lineare</i>	80°28.26'N	08°10.90'E	888 m
Desmosomatidae	<i>Desmosoma plebejum</i>	71°02'N	144°55'W	1040–1540 m
Desmosomatidae	<i>Eugerda dubia</i>	74°52'N	169°47'W	230 m
Desmosomatidae	<i>Eugerda gurjanovae</i>	74°52'N	169°47'W	230 m
Desmosomatidae	<i>Eugerda intermedia</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Desmosomatidae	<i>Eugerda intermedia</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Desmosomatidae	<i>Eugerda mandibulata</i>	74°52'N	172°14'W	325–340 m
Desmosomatidae	<i>Eugerda tenuimana</i>	69°–71°22'N	129°–140°W	
Munnopsidae	<i>Eurycope complanata</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Munnopsidae	<i>Eurycope complanata</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Munnopsidae	<i>Eurycope mutica</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Munnopsidae	<i>Eurycope mutica</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Munnopsidae	<i>Eurycope pygmaea</i>	69°–71°22'N	129°–140°W	
Munnopsidae	<i>Eurycope sp.</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Munnopsidae	<i>Eurycope sp.</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Munnopsidae	<i>Ilyarachna bergendali</i>	73°51'N	162°36'W	240 m
Munnopsidae	<i>Ilyarachna bergendali</i>	74°25'N	164°08'W	420–470 m

Munnopsidae	<i>Ilyarachna bergendali</i>	74°53'N	170°11'W	230 m
Munnopsidae	<i>Ilyarachna bergendali</i>	75°09'N	170°04'W	300–330 m
Munnopsidae	<i>Ilyarachna bergendali</i>	75°52'N	171°32'W	320 m
Munnopsidae	<i>Ilyarachna hirticeps</i>	73°36'N	129°41'W	2700–1508 m
Munnopsidae	<i>Ilyarachna profunda</i>	33°12'N	118°30'W	1240 m
Munnopsidae	<i>Ilyarachna sp.</i>	69°–71°22'N	129°–140°W	
Munnopsidae	<i>Ilyarachna sp. a</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Munnopsidae	<i>Ilyarachna sp. a</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Munnopsidae	<i>Ilyarachna sp. b</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Munnopsidae	<i>Ilyarachna sp. b</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Munnopsidae	<i>Ilyarachna zachsi</i>	42°51'N	134°19'E	212–219 m
Munnopsidae	<i>Ilyarachna zachsi</i>	39°37'N	135°12'E	865–950 m
Munnopsidae	<i>Ilyarachna zachsi</i>	37°53'N	136°15'E	470 m
Munnopsidae	<i>Ilyarachna zachsi</i>	42°17'N	131°0'E	174 m
Munnopsidae	<i>Ilyarachna zachsi</i>	39°0'N	134°7'E	295 m
Munnopsidae	<i>Ilyarachna zachsi</i>	42°25'2"N	131°24'E	112 m
Munnopsidae	<i>Ilyarachna zachsi</i>	42°17'N	130°54'E	137 m
Munnopsidae	<i>Ilyarachna zachsi</i>	42°20'N	131°12'E	136 m
Munnopsidae	<i>Ilyarachna zachsi</i>	42°27'N	131°29'E	100 m
Munnopsidae	<i>Ilyarachna zachsi</i>	42°23'N	131°20'E	220 m
Munnopsidae	<i>Ilyarachna zachsi</i>	42°29'N	131°50'E	123 m
Desmosomatidae	<i>Mirabilicoxa birsteini</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Desmosomatidae	<i>Mirabilicoxa birsteini</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Desmosomatidae	<i>Mirabilicoxa fletcheri</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Desmosomatidae	<i>Mirabilicoxa fletcheri</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Desmosomatidae	<i>Mirabilicoxa kussakini</i>	42°42'7"N– 42°40'4"N	134°17'2E– 134°16'5E	510–578 m
Desmosomatidae	<i>Mirabilicoxa richardsoni</i>	57°36'N	148°36'W	3240–3330 m
Desmosomatidae	<i>Mirabilicoxa sp.</i>	84°59.7'–85°58.5'N	108°31'–122°11'W	1060–2530 m
Desmosomatidae	<i>Mirabilicoxa sp.</i>	84°13.5'–84°21.3'N	85°22.5'–86°59'W	1061–2530 m
Munnidae	<i>Munna sp.</i>	32°32'N	130°02'W	
Munnidae	<i>Munna sp.</i>	49°02'N	51°17'W	
Paramunnidae	<i>Pleurogonium inerme</i>	69°14.66'N	57°09.00'E	17 m
Paramunnidae	<i>Pleurogonium kyushuense</i>	30.073°N	130.999°W	565–723 m
Paramunnidae	<i>Pleurogonium rubicundum</i>	74°27'N	73°17'E	26 m
Paramunnidae	<i>Pleurogonium tanseimaruae</i>	29.85°N	130.928°W	1677–1769 m
Desmosomatidae	<i>Prochelator kussakini</i>	59°18'N	141°58'W	

Discussion

According to the GOODS biogeographic classification, the Kuril-Kamchatka area and the Japan Basin of the Sea of Japan belong to the abyssal province “North Pacific” (Vierros et al., 2008). The rest of the Sea of Japan belongs to the lower bathyal province “Northern North Pacific”.

Our first results indicate a distinctly different deep-sea fauna in the Sea of Japan compared with the Kuril-Kamchatka Trench area even though they are classified as the same abyssal province according to the GOODS classification. A more detailed analysis (as it is in progress) is needed to further support this hypothesis.

In addition, further expeditions are needed in order to further elucidate the connectivity between the adjacent abyssal basins in the Northwest Pacific. Of particular interest would be the Kuril Basin in the Sea of Okhotsk, because of its connection (via straits) to both the Sea of Japan and the Kuril-Kamchatka Trench area, and the Kuril-Kamchatka Trench itself in order to compare the trench fauna with the fauna of the adjacent abyssal plain.

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Author's contribution:

I wrote this initial draft on the basis of discussions with the third coauthor and help with and advice on ArcGIS by the second author.

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Confirmation for the correct use of the English language

Eric Fee
Science-Policy Advisor
International Climate Protection
German Federal Environment Agency
E-mail: eric.fee@uba.de

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To whom it may concern,

I am a U.S. citizen and native speaker of English. I have read chapters of Nikolaus Elsner's dissertation. His writing and command of English can be easily certified as excellent.



Eric Fee