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Marine macroinvertebrate fauna of the shallow coastal waters of the Shiretoko Peninsula, a World Natural Heritage at Hokkaido, Japan

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Abstract: The Shiretoko Peninsula, located at the southernmost point of the Sea of Okhotsk, was registered as a World Natural Heritage in 2005 in recognition of its rich biodiversity and an example of the interaction between marine and terrestrial ecosystems. However, there is insufficient information on its marine biota, which is an essential component of this ecosystem. This study was conducted from 2006 to 2019 to clarify the macroinvertebrate fauna along the shores of the Shiretoko Peninsula. A total of 299 species from 11 phyla were identified, including 118 mollusks, 107 crustaceans, 34 annelids, 24 echinoderms, and 16 species from other taxa, including two species recorded in Japan for the first time [*Oregonia kurilensis* (Decapoda: Brachyura) and *Henricia alexeyi* (Asteroidea: Echinasteridae)]. In addition, five species, including one new species of Isopoda, have been firstly reported from Japan based on the material collected by this project. Faunal similarity and biogeographical features differ between the Sea of Okhotsk side and the Nemuro Strait side of the peninsula, probably because of the effects of warm and cold currents, coastal topography, and drift ice pressure on the shore in winter. The macroinvertebrate fauna of the Shiretoko Peninsula is located at the boundary of different marine biogeographic provinces and is organized by environmental factors unique to the Sea of Okhotsk. Therefore, it is important to monitor the marine biota around the peninsula shores as these species act as bio-indicators of environmental changes.

Key words: intertidal macroinvertebrate fauna, North Pacific, ocean current, coastal topography, drift ice

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Supplementary materials may be found in the online version of this article.

Introduction

The Shiretoko Peninsula is located at the southern point of the Sea of Okhotsk, which is the southern limit for drift ice in the northern hemisphere. The elongated peninsula is approximately 70 km long and 15–25 km wide and features a series of volcanoes above 1200 m elevation along its central axis. The distance from the central mountain ridge to the coastline is short, and the mountains that make up the central part of the peninsula have been uplifted from the sea floor. Therefore, the coastline of the Shiretoko Peninsula is based on lava from prior intense volcanic activity (Gochi 2008) and has a complex and diverse topographical shape owing to wave erosion and the impact of drift ice, thus forming a characteristic coastal topography.

The coastline of the Shiretoko Peninsula is affected by a complicated ocean current system (Fig. 1). On the Sea of Okhotsk side of the peninsula, the Soya Warm Current, which increases in the summer, moves southward along the Hokkaido coast (Matsuyama et al. 1999), while the East Sakhalin Current, which increases in the winter, transports colder water from the northwestern shelf of the Sea of Okhotsk (Ohshima 2013). In contrast to the Sea of Okhotsk side, the Nemuro Strait side is strongly affected by another cold current, the Oyashio Current, which flows southwestward along the Kurile Islands from the subarctic North Pacific Ocean, during the spring and summer, as well as the East Sakhalin Current, which dominates in the winter (Mori et al. 2010). Moreover, the shore of the peninsula is physically disturbed by drift ice brought about by the East Sakhalin Current between January and March. The impact of this ice on the shore is stronger on the Sea of Okhotsk side and weaker on the Nemuro Strait side (Ohmura 2000, Gochi 2008). This is because the Shiretoko Peninsula extends to the northeast, and the shore on the Sea of Okhotsk side is more strongly affected by drift ice for a longer period by the prevailing northwesterly winds and the increasing flow of the East Sakhalin Current in winter (Gochi 2008). These oceanographic features create diverse and unique coastal environments on the Shiretoko Peninsula.

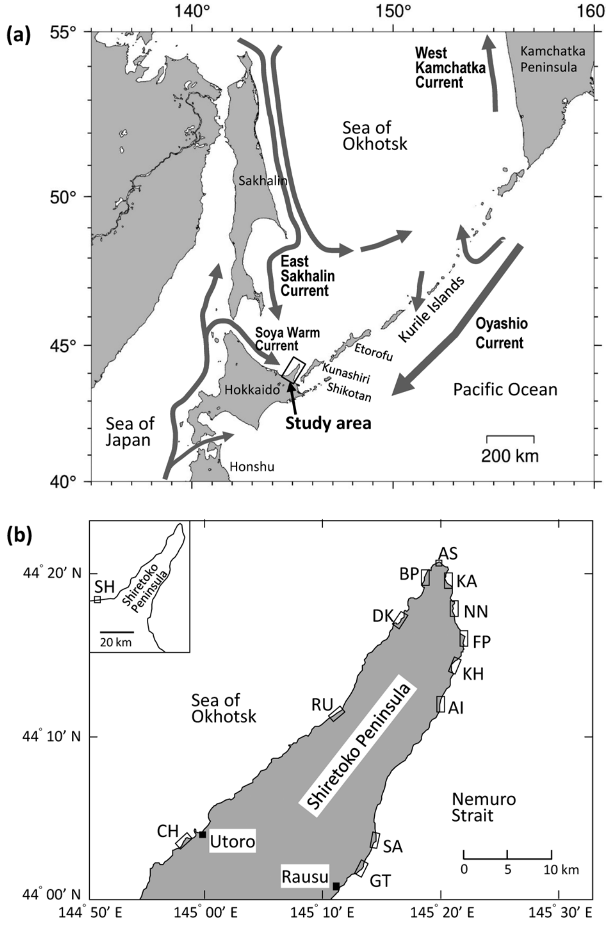


Fig. 1. Study area (a) and the survey stations (b). See details of the stations in Table 1. Gray arrows in (a) indicate the major ocean currents (Modified from Ohtani 1991 and Ohshima 2013).

The North Pacific Ocean, including the Sea of Okhotsk, is one of the most productive areas in the world and has abundant marine resources; therefore, various marine biological surveys have been conducted (Lapko & Radchenko 2000). Russian research institutes have been engaged in various oceanographic studies on the Sea of Okhotsk and its surrounding waters, and many of these have focused on intertidal organisms. Thus, the general features of the intertidal biota in the Russian territory have been reported (e.g., Kussakin 1975, Kafanov et al. 2004, Ivanova & Tsurpalo 2012, Yamazaki et al. 2015). However, in Japan, at the southernmost coastline of the Sea of Okhotsk, there are reports on molluscan fauna by Yamazaki (2011) and Nobetsu & Yamazaki (2011, 2020), and fish fauna by Nobetsu et al. (1998) and Shinohara et al. (2012), but our understanding of the entire species composition is still far from satisfactory.

The Shiretoko Peninsula and its coastal waters were registered as a World Natural Heritage Site in 2005. The unique ecosystems of this region, encompassing land and sea interactions, local biodiversity, and rare species, were the main drivers for this decision. Because the surrounding waters were included in the evaluation, the Shiretoko World Natural Heritage Area Science Committee, which was formed to create a management plan for heritage areas, has devised a sea area working group (Sakurai 2006). However, there is still little clarity regarding the entire biota, particularly for the sea area of the Shiretoko Peninsula. Konno (1988) reported on marine invertebrate fauna at the tip of the peninsula, but no peninsula-wide survey has been conducted to date. Therefore, the Ministry of the Environment created the Shiretoko World Natural Heritage Area Ecosystem Monitoring Research Project, which has resulted in various studies being conducted on land, rivers, and seas (Shiretoko Nature Foundation 2010). As part of this project, the present study aimed to clarify the marine macroinvertebrate fauna of the coastline, which is centered on the natural heritage area of the Shiretoko Peninsula. This study organizes and finalizes the results of five reports (Sonoda et al. 2008, 2009, 2010, 2018, 2020) issued during the 2006–2019 study period.

Materials and Methods

Sampling

The faunal investigation was conducted seasonally from 2006 to 2019 at 13 survey stations, including the base of the Shiretoko Peninsula (Fig. 1). Details of the locations, shoreline features of the survey stations, and dates of the surveys are shown in Tables 1 and 2. For the survey around the tip of the peninsula, we moved to Bunkichi Bay (station BP) by chartered boat from Aidomari fishing port (station AI) and set up a base camp there. The survey was conducted during spring tide period, with three to five investigators at a time, for a total of approximately 4 hours, 2 hours before and after low tide on each survey day. Marine macroinvertebrates were observed throughout the intertidal zone on the shore of the survey site, and the specimens were collected by hand, landing nets, or shovels. In addition, some specimens were collected in the subtidal zone (water depth shallower than 20 m) via diving surveys. The collected specimens were fixed, stored in 70% ethanol or 10% neutral formalin, and taken to the laboratory for identification.

Identification and data processing

Taxonomic identification of the collected specimens was conducted by the persons in charge (Table 3) to the species level where possible. Identified specimens were deposited in the collections listed in Table 3. The invertebrate fauna identified in this study was compiled according to the scheme of two marine taxonomic databases (BISMaL

Table 1. Details of the survey stations.

Survey stations	Code	Latitude, longitude	Shoreline features
Shari Beach	SH	43°55′06.4″N, 144°40′19.7″E	sandy shore
Chashikotsu	CH	44°04′08.2″N, 144°58′39.4″E	wide rocky bench with holes, boulder, cobble shore
Rusha	RU	44°11′32.7″N, 145°10′56.0″E	cobble, boulder shore
Dairin-banya–Kan-non-iwa	DK	44°17′30.5″N, 145°16′50.5″E	cobble shore, rocky bench
Bunkichi Bay–Poromoi Bay	BP	44°19′55.9″N, 145°18′50.7″E	rocky bench, cobble shore
Aburako Bay–Shiretoko Cape	AS	44°20′32.5″N, 145°20′22.1″E	rocky bench, cobble shore, sand flat in inner side of offshore bench
Kabuto-iwa–Aka-iwa	KA	44°19′18.4″N, 145°20′53.5″E	cobble, pebble shore
Nihon-daki–Nenbutsu-iwa	NN	44°18′20.4″N, 145°20′53.3″E	cobble, boulder shore
Funadomari–Pekin-no-hana	FP	44°16′17.1″N, 145°21′56.6″E	cobble, boulder shore
Kaseki-hama–Moireushi	KH	44°15′20.1″N, 145°21′52.4″E	cobble, pebble shore
Aidomari	AI	44°11′27.0″N, 145°19′42.1″E	rocky bench, boulder, cobble shore
Sashirui Cape	SA	44°04′05.1″N, 145°14′42.7″E	rocky bench, boulder, cobble shore
Gaizu-iwa–Tate-iwa	GT	44°02′13.9″N, 145°13′22.2″E	boulder, cobble shore

Table 2. Details of the survey dates and stations. See station code in Table 1.

Survey date	Station												
	SH	CH	RU	DK	BP	AS	KA	NN	FP	KH	AI	SA	GT
22–29 Jul 2006		*		*	*	*		*	*	*	*		
4–21 Nov 2006		*			*	*					*		
30 May–6 Jul 2007	*	*		*	*	*		*		*	*	*	*
24–30 Aug 2007	*	*	*		*	*	*			*	*	*	*
16–21 Jun 2008	*	*			*	*				*	*	*	*
12–17 Sept 2008		*	*		*	*			*		*		
11–15 May 2009	*	*			*	*	*		*		*		
18–22 Aug 2009	*	*			*	*	*				*		*
18–22 Aug 2017	*	*			*	*					*		*
7–22 Nov 2017		*									*	*	
3–8 Jun 2019	*	*			*	*					*	*	
Total no. of survey	7	11	2	2	10	10	3	2	3	4	11	5	5

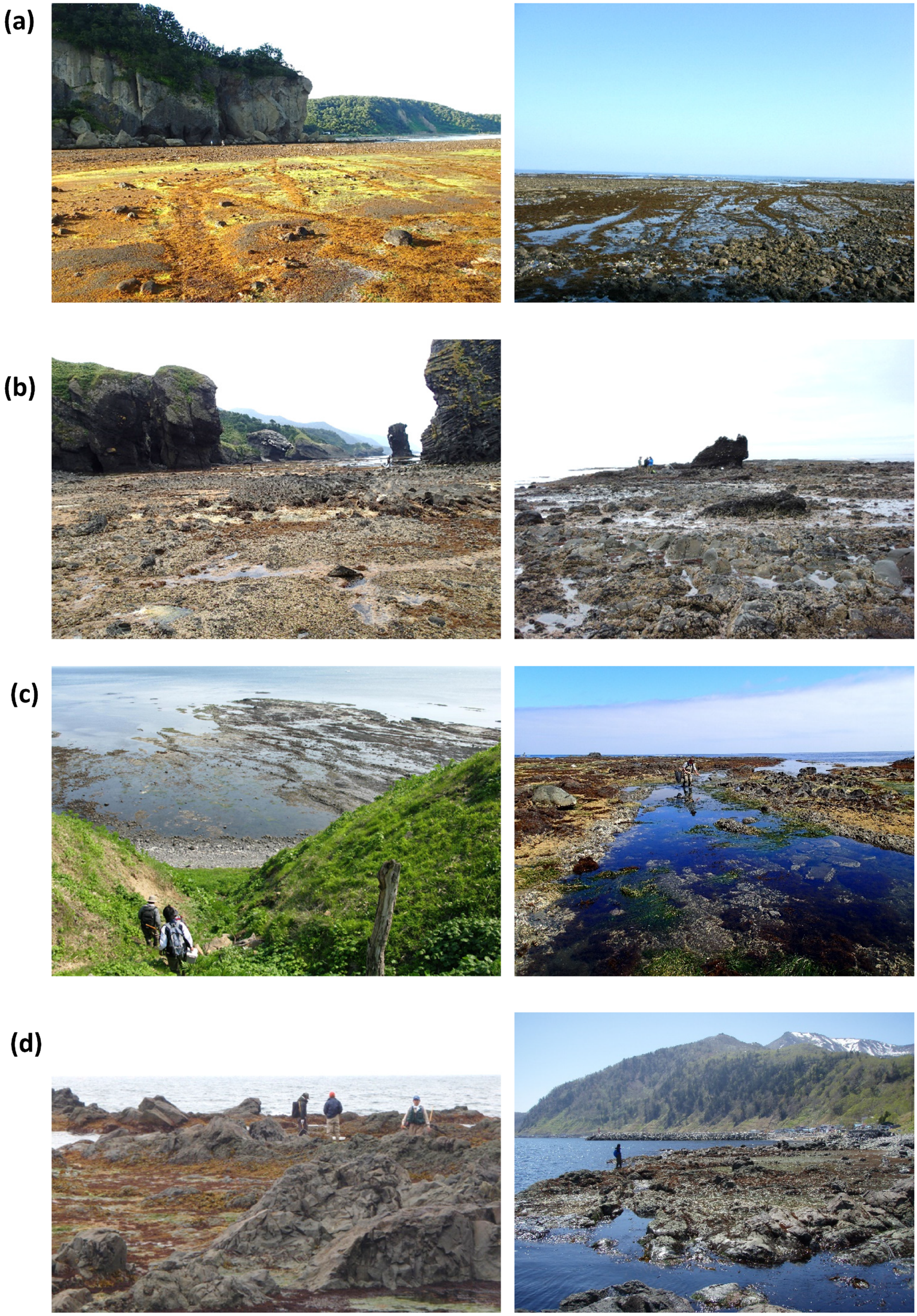


Fig. 2. Photographs of the typical landscapes at the 4 survey stations analyzed in Fig. 3.
(a) Chashikotsu (b) Bunkichi Bay (c) Shiretoko Cape (d) Aidomari

Table 3. Taxonomic group, identification and specimen storage in this study.

Taxonomic group	Taxonomic identification	Specimen storage location
Porifera	Goshima, S.	1, 3
Cnidaria	Goshima, S.	1, 3
Ctenophora	Goshima, S.	1, 3
Platyhelminthes	Goshima, S.	1, 3
Brachiopoda	Goshima, S.	1, 3
Nemertea	Sonoda, T.	3
Mollusca	Yamazaki, T., Goshima, S.	2
Annelida	Sonoda, T.	3
Arthropoda, Crustacea, Sessilia	Chiba S, Goshima S	3
Arthropoda, Crustacea, Amphipoda, Caprellidae	Ito, A., Hosono, T.	7
Arthropoda, Crustacea, Amphipoda, except Caprellidae	Tomikawa, K.	6
Arthropoda, Crustacea, Isopoda	Nunomura, N., Shimomura, M.	8, 9
Arthropoda, Crustacea, Tanaidacea	Kakui, K.	1
Arthropoda, Crustacea, Decapoda	Komai, T., Chiba, S., Goshima, S.	3, 4
Echinodermata	Fujita, T., Kobayashi, I., Goshima, S., Fujiya, H.	5
Chordata	Goshima, S.	1, 3

Specimen storage location: 1. Hokkaido University, 2. Shellfish Museum of Rankoshi, 3. Tokyo University of Agriculture, 4. Natural History Museum and Institute Chiba, 5. National Museum of Nature and Science, 6. Hiroshima University, 7. Japan Agency for Marine-Earth Science and Technology, Global Oceanographic Data Center, 8. Kanazawa University, 9. Kyoto University

(Japan Agency for Marine-Earth Science and Technology 2023) and WoRMS (WoRMS Editorial Board 2023)) and modified as necessary based on the latest taxonomic research results. Based on the taxonomic identification results, the collected data were summarized for each survey station. Furthermore, the characteristics of each taxon were examined, along with all new findings.

Comparison of macrofauna among stations

In this study, owing to various conditions, such as the difficulty of approaching survey points, samples were collected from Chashikotsu (CH) and Aidomari (AI) for all 11 surveys (Table 2). Subsequently, samples from Shiretoko Cape (AS) and Bunkichi Bay (BP) for 10 surveys were collected, except the one for November 2017 (Table 2). Although the method used in this study was qualitative, samples from the four stations were collected with similar sampling efforts. In addition, these stations are located at the tip of the Shiretoko Peninsula, on the Okhotsk Sea side, and on the Nemuro Straits side, respectively (Fig. 1). Therefore, for mollusks and crustaceans, which have the largest number of collected species, the similarity in species composition at these four stations was calculated using the Sørensen index (Sørensen 1948). The obtained results were subjected to cluster analysis using the group average method, and the similarity of fauna among the stations was examined (Southwood & Henderson 2016). For mollusks, for which the biogeographical data is both extensive and well organized, the distributional composition at the four stations was created following Nobetsu & Yamazaki (2020), using the geographical distribution classification by Higo et al. (1999). Comparisons were made with the data from the Kunashiri and Etorofu Islands (Nobetsu & Yamazaki 2020), Akkeshi Bay (Yamazaki 2011), and Shikotan Island (Nobetsu & Yamazaki 2011), where molluscan distributional compositions have been generated using the same method.

Table 4. Number of identified taxon from the Shiretoko Peninsula shores.

Phylum	Class	Order	Family	Genus	Species
Porifera	1	1	1	1	1
Cnidaria	4	4	5	6	6
Ctenophora	1	1	1	1	1
Platyhelminthes		1	1	1	1
Brachiopoda	1	1	1	2	2
Nemertea	1	1	1	1	2
Mollusca	4	16	59	94	118
Annelida		10	17	20	34
Arthropoda	2	6	38	58	107
Echinodermata	4	11	15	20	24
Chordata	1	1	2	2	3
Total	19	53	141	206	299

Results

Identified species of each major taxon and survey station

Table 4 shows the number of identified species, genera, families, orders, and/or classes for each phylum, Table 5

Table 5. Number of identified taxon in each station. ▲ denotes the Shiretoko Cape. See station code in Table 1.

Taxon	Station code												
	SH	CH	RU	DK	BP	AS	KA	NN	FP	KH	AI	SA	GT
Porifera		1				1							
Cnidaria		3			1	2	1		2		3	1	1
Ctenophora		1			1								
Platyhelminthes		1											
Brachiopoda					2								
Nemertea						2				1	1	1	1
Mollusca	28	61	17	4	63	37	30	1	24	2	46	23	24
Annelida	4	11	1		12	7					19	10	3
Arthropoda	20	54	7	4	44	37	10	11	9	18	45	21	13
Echinodermata	1	13			13	3	7	1	3	3	9	5	13
Chordata					2	1							
Total no.	53	145	25	8	138	90	48	13	38	24	123	61	55
No. of survey	7	11	2	2	10	10	3	2	3	4	11	5	5
Location of the station	The Sea of Okhotsk side of the peninsula				←	▲	→	The Nemuro Strait side of the peninsula					

presents the number of identified species per phyla at each station, and Appendix 1 (with the same electronic table Appendix ES 1) is a list of all identified species. A total of 299 species from 11 phyla were identified. The most species rich taxa were Mollusca (118 species) and Crustacea (106 species), which accounted for 75.5% of all identified species (Table 4). In addition, there were 34 species of annelids, 24 species of echinoderms, and 16 species from other phyla.

In terms of the number of species identified by the most frequently surveyed stations, the largest number of species was found in CH (145 species), followed by 137 species in BP, 123 species in AI, and 89 species in AS (Table 5). Next, we describe the results of the survey for each major taxon.

Mollusca

The most abundant mollusks were gastropods (68 species), followed by 39 species of bivalves, 10 species of chitons, and one cephalopod species (Appendix 1). Among the gastropods, 32 species of the order Littorinimorpha were the most commonly identified, of which six were from Littorinidae and another six from Buccinidae families. According to qualitative observations in the field, littorinid species were distributed throughout the shoreline of the Shiretoko Peninsula, with a large number of individuals. For Bivalvia, the order Venerida was the most frequently identified, with 15 species in five families, although nine species were collected only at one station, the sandy Shari Beach (SH). Most of the shoreline of the peninsula is composed of a rocky hard bottom; a wide soft bottom is rare (Table 1). However, many clams (*Ruditapes philippinarum*) were noted in the sandy sediment deposited in the relatively open space of the rocky bench on the AS. Apart from the order Venerida, the most common bivalves were the nine sessile epibenthic species of Mytilidae, which were distributed throughout the peninsula and comprised many individuals.

Among the identified mollusks, we were able to confirm species such as *Cerithiopsis stejnegeri* (Littorinimorph, Cerithiopsidae) that have not been reported in eastern Hokkaido. We also collected species such as *Buccinum mirandum*, *B. chishimanum*, and *B. ochotense*, which have polymorphisms in their shells and are sometimes indistinguishable from closely related species. Because the individuals we captured ranged from juveniles to adults, we were able to identify the exact species by observing morphological changes during ontogeny. In addition, *Onchidiopsis maculata* (Velutinidae) collected at CH in 2019, was found for the first time in Japan (Yamazaki 2020).

Crustacea

Among the Crustacea, order Amphipoda was the most species-rich with 54 species, followed by Decapoda (33 species), Isopoda (14 species), cirriped Balanomorpha (four species), and Tanaidacea (one species) (Appendix 1). The diversity of barnacles was low in terms of species number, but they were quite common in intertidal rocky shores across the entire peninsula, as were periwinkles and mussels. The occurrence of the alien species *Balanus glandula* was first confirmed in SH, CH, and AI in 2019.

Twenty-five gammaridean amphipods species were identified. Prior to this study, Tomikawa & Sonoda (2008, 2022) reported that our specimens included the first recorded instances of *Carineogammarus makarovi* and *Abludomelita klitinii* in Japan, while *Locustogammarus locustoides*, *Spasskogammarus spasskii*, *Mesogammarus* *melitoides* were the second recorded occurrences in Japan. Gammarids were collected from seaweed and eelgrass attached to rocks, and many were found under boulders along gravel coasts and in the interspaces inside deposited gravel. Caprellids were also confirmed at each survey station, and 18 species, including those requiring taxonomic examination, were identified.

Fourteen species of Isopoda (five families) were identified. Based on collections made by our survey, a new species of the genus *Dynoides* (Sphaeromatiae), named *D. bicolor*, was described by Nunomura (2010). Five species of Idoteidae were also collected throughout the peninsula. Nunomura (2009) updated the description of *Idotea* (*Pentidotea*) *rotundata* on the basis of specimens collected by our survey.

Regarding the Tanaidacea, *Arctotanais alascensis* was collected for the first time in Japan. Kakui et al. (2012) described the males of this species for the first time from specimens collected by our survey at FP and AI.

Caridea was the most species-rich decapod, represented by 13 species, eight of which belonged to the family Thoridae. With regard to the Anomura, it is remarkable that young individuals of the king crab *Paralithodes camtschaticus* were collected in the intertidal zone; adults of the king crab usually occur in shelf to shelf slope depths (Makarov 1938). *Oregonia kurilensis* (Brachyura: Oregoniidae) collected at AI was seen for the first time in Japan (one male and one female, deposited at the Natural History Museum and Institute, Chiba (CBM), under registration number CBM-ZC 10801).

Annelida and Nemertea

Thirty-four species from 10 orders of Annelida were identified (Appendix 1). The largest number of species were of the order Phyllodocida (15 species), followed by four species of Capitellida, and three species each of Orbiniidae and Cirratulida. *Pseudopotamilla occelata,* Sabellidae, which form colonies in depressions and crevices, were found in the rocky reef area at AS and AI. In addition, many species of Nereidae and Capitellidae were observed in the sand and mud deposited in the crevices of rocky reefs, and in the roots of eelgrass. Many sipunculid worms occupy similar microhabitats, especially in the roots of eelgrass. Nemertean worms were also frequently found in boulders on gravel shores, and our sample contained at least two species.

Echinodermata

Twenty-four Echinodermata species were identified (Appendix 1). Among them, 13 species belonging to the Asteroidea were collected in 2019 from BP, and *Henricia alexeyi* of the Echinasteridae was the first recorded instances of these organisms in Japan. Five species of Echinoidea, and three species each of Ophiuroidea and Holothuroidea were also found. A large number of *Mesocentrotus nudus* were observed along with *Strongylocentrotus intermedius* on the pier wall of the fishing port in BP at the tip of the peninsula.

Other taxa

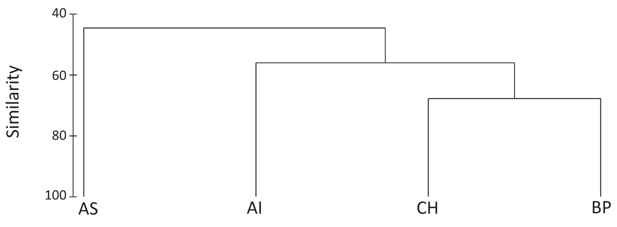
Six species of Cnidaria, including Hydrozoa, Anthozoa, and *Cyanea capillata* (Scyphozoa), were found in the tide pool at AI and identified. One species of Platyhelminthes and two species of Rhynchonellata (Brachiopoda) were also observed. In addition, sessile sponges inhabiting the entire Shiretoko Peninsula reef intertidal zone as well as three species of chordates (ascidians) were identified.

Similarity of species composition among the stations and the characteristics of geographic distribution of Mollusca

The results of the cluster analysis based on the faunal similarities of Mollusca and Crustacea among the four stations, CH (the Sea of Okhotsk side of the peninsula), BP (the Sea of Okhotsk tip of the peninsula), AS (tip of the peninsula), and AI (the Nemuro Strait side of the peninsula), are shown in Fig. 3. The cluster sequences obtained were similar between the two taxa. The stations with the highest faunal similarity were CH and BP, to which AI and AS were linked sequentially. These results show that the fauna are highly similar at the two sites on the Sea of Okhotsk side of the Shiretoko Peninsula and that the species composition on the Nemuro Strait side and the tip of the Shiretoko Peninsula differs from that on the Sea of Okhotsk.

The results of the distributional composition of molluscan fauna at the four stations, using the geographical distribution classification by Higo et al. (1999), are shown in Fig. 4. The highest percentage of distributional area of all the stations was at P10, which indicated the Pacific coast of Hokkaido. The next highest level found was at

(a) Mollusca



(b) Crustacea

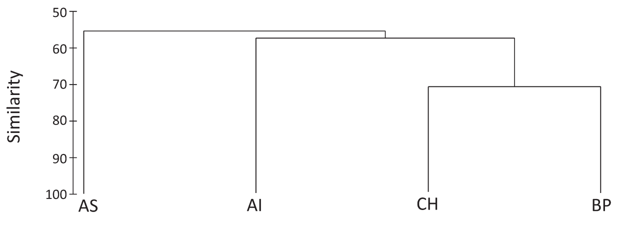


Fig. 3. Faunal similarities among the 4 survey stations. See station code in Table 1.

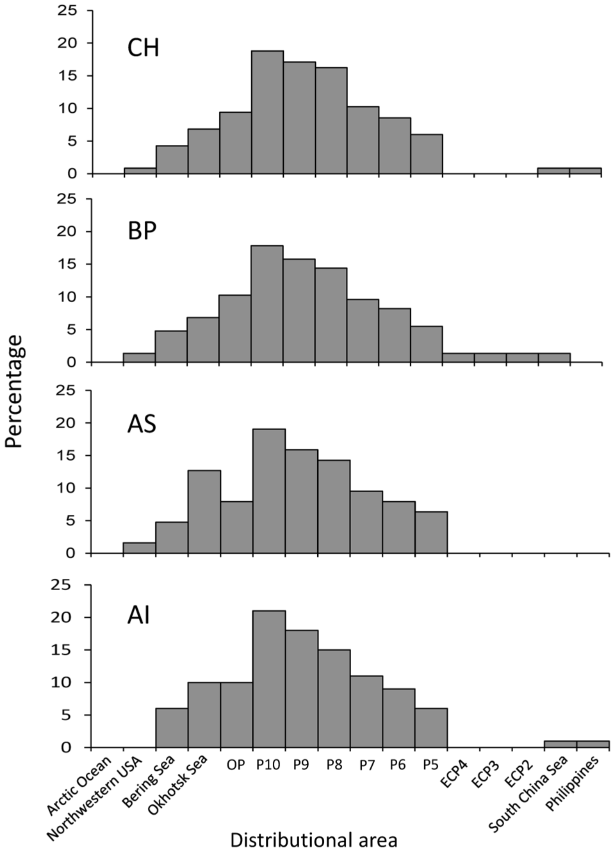


Fig. 4. Distributional composition of molluscan fauna of Shiretoko Peninsula. See station code in Table 1. Distributional area is placed in the order of decreasing latitude from left to right, generally from north to south. Distributional area abbreviations (see Higo et al. 1999 in details); OP: Northern Pacific of Nemuro Peninsula and southern Kurile Islands, P10: Pacific area between Cape Shiriyazaki and Nemuro Peninsula, P9: Pacific area between Oshika Peninsula and Cape Shiriyazaki, P8: Pacific area between Cape Inubosaki and Oshika Peninsula, P7: Pacific area between Cape Nojimazaki and Cape Inubosaki, P6: Pacific area between Cape Shionomisaki and Cape Nojimazaki, P5: Pacific area between Cape Sata and Cape Shionomisaki, ECP4: East China Sea between Takarajima Island and Cape Sata, ECP3: East China Sea around Amami Islands, ECP2: East China Sea around Okinawa Islands.

P9, followed by P8. In the distributional area indicating the northern sea, the percentage was slightly higher at station AS, the tip of the Shiretoko Peninsula, and the Sea of Okhotsk area, accounting for 14%. In contrast, in the southern distributional area, species from ECP4 and from the waters ranging from the Satsunan Islands to the Philippines were present at stations CH, BP, and AI, but the proportion of all species was small at 1%.

Discussion

This is the first comprehensive study of shallow-water macroinvertebrate fauna covering entire coast of the Shiretoko Peninsula. A total of 299 species were identified, including a number of undescribed species, as well as species which had previously never been seen in Japan or in the Shiretoko region. Although it was a qualitative survey, the data collected was valuable, especially considering the difficulties in conducting the survey at many of these points, including Cape Shiretoko, which was normally inaccessible. In the following summary, we consider the results obtained for the major taxa, and then comprehensively consider the entire macroinvertebrate fauna of the Shiretoko Peninsula shore.

Mollusca

Summarizing the current records of Mollusca reported in eastern Hokkaido, approximately 300 species inhabit the sea in this region (Yamazaki 2011). A total of 118 species were confirmed along the coast of the Shiretoko Peninsula. Many of these consisted of cold-current species (Fig. 4). When comparing molluscan fauna from the Shiretoko Peninsula with those from Nemuro Bay (Tsuchida 1998) and Akkeshi Bay (Habe 1955, 1958, Yamazaki 2011), few differences were noted. However, when comparing the habitat depths individually, it was found that species generally inhabiting deeper areas sometimes appeared in the intertidal zone of Shiretoko. *Volutharpa ampullaceal ampulacea* has been reported from a depth of 500 m off Kushiro (Habe & Ito 1980), and *Buccinum ochotense* was reported from a depth of 80 m near the mouth of Uchiura Bay (=Funka Bay) (Yamazaki 1998), whereas, in the Shiretoko Peninsula, both these were found in the lower part of the intertidal zone. Despite their geographical proximity, this difference in vertical distribution between the Shiretoko Peninsula and other waters of Hokkaido may be due to differences in the ocean currents flowing around the peninsula and its water temperature. When comparing molluscan fauna between locations in the conventional way, even if the fauna appears similar, their characteristics may differ when vertical distribution information is added; therefore, a detailed analysis is required in the future.

The family Littorinidae is widely distributed along the coast of the Shiretoko Peninsula and *Littorina* (*Neritrema*) *sitkana* is a mollusk that symbolizes this region. According to population genetic analysis, the genetic diversity of this species is particularly high in the area around the Shiretoko Peninsula, and it is speculated that this species spread from Shiretoko to the west coast of North America via the Kurile and Aleutian Islands after the last glacial period (Azuma et al. 2011, 2017). It has also been reported that cryptic species exist in some of the morphologically identified *L.* (*N.*) *sitkana* individuals collected on the coast near the station CH (Azuma et al. 2011), and it is expected that the number of littorinid species will be further increased after molecular analysis.

Mussels are a globally important group of sessile bivalves that dominate rocky intertidal zones. In this study, we found nine mussel species, including *Mytilus galloprovincialis*, *M. trossulus*, and *Crenomytilus grayanus*. *M. galloprovincialis* is an exotic species native to the Mediterranean that invaded Japan in the 1920s (Kajiwara 1985; Ishida et al. 2005). In and around the Shiretoko Peninsula, the exotic species *M. galloprovincialis* and the native species *M. trossulus* are distributed in a mixed manner, but it has been reported that this is a crossed area where natural hybrids of both species exist (Kuwahara 2001; Brannock et al. 2009). These hybrids were not confirmed in this study; however, this should be verified in future studies.

Onchidiopsis maculatae is a species of the family Velutinidae, with a type locality at the west coast of the Sea of Japan (Russian Far East), and details have been reported by Yamazaki (2020). The author clarified various morphological characteristics of this species, including the external morphology, the shell morphology buried in the soft body, and the radula morphology. Yamazaki also identified a second finding of the genus *Onchidiopsis* in Japan, after *O. nihonkaiensis*, which was found inhabiting the Sea of Japan.

The planktonic gastropods *Clione elegantissima* and *Clione* sp. were collected from the tip of the Shiretoko Peninsula. *C. elegantissima* was observed in the intertidal zone under the Cape Shiretoko lighthouse and *Clione* sp. was found near the entrance of Bunkichi Bay, showing an allopatric distribution. *C. elegantissima*, observed along the coast of the Sea of Okhotsk in June, rarely reaches the coast of Hokkaido, though it is usually observed in the colder waters offshore Hokkaido and in further adjacent waters (Nobetsu et al. 2020; Takahashi et al. 2022). The presence of this species is considered an indicator of cold water (Takahashi et al. 2022). Therefore, the observation of *C. elegantissima* along the coast of the Shiretoko Peninsula is thought to be the result of cold water from the East Sakhalin Current and/or the Okhotsk Surface Low Salinity Water reaching the coast. Similarly, *Clione* sp. is an endemic species that inhabits the intermediate to deep waters of the Sea of Japan and yet appears in the summer in the coastal/offshore areas of the Sea of Okhotsk due to the complex water dynamics of the currents and water masses around Hokkaido (Yamazaki et al. 2018, 2022; Takahashi et al. 2022). It is thought that *Clione* sp. reached the Shiretoko Peninsula after the collapse of the cold-water belt. Because *Clione* is a planktonic gastropod, it can be an indicator species of water mass on the coast of the Sea of Okhotsk (Takahashi et al. 2022).

The order Nudibranchia (commonly known as sea slugs), of which 17 species from 13 families have been confirmed, is a generally small creature with a short lifespan which settles after the planktonic larval stage. Therefore, the species composition and distribution pattern of sea slugs on the Shiretoko Peninsula may be short-term indicators of warm and cold currents reaching the area. However, because of their small size, lack of hard tissue, and loss of body color in fixed specimen, sea slugs are often overlooked in field sampling, being difficult to detect, and are difficult to be taxonomically identified in many cases. Kashio & Yamazaki (2021) reported that sea slugs in the subtidal zone of the Shakotan Peninsula, Hokkaido, have a species composition that reflects the effects of warm and cold currents, and that more than half of them are warm water species. In the Shiretoko Peninsula, if diving at fixed stations can be conducted in the future, it may be possible to obtain data on species composition that takes into account the response of sea slugs to the marine environment.

Comparing the distributional composition of molluscan fauna of the four main stations (CH, BP, AS, and AI; Fig. 4) by Nobetsu & Yamazaki (2020), it was found that the components of the four stations on the Shiretoko Peninsula were highly similar to those of Shikotan Island and Akkeshi Bay and slightly different from those of Etorofu Island and Kunashiri Island, which have many northern elements.

Crustacea

For crustaceans, remarkable results were obtained from the specimens in our survey, with one species new to science (Nunomura 2010), four species recorded for the first time in Japan. Of these newly identified four species, *Oregonia kurilensis* is reported for the first time in this paper, and the remaining three species have already been reported in other papers (Tomikawa & Sonoda 2008, 2022, Kakui et al. 2012).

Cirripedia Balanomorpha. The barnacle *Balanus glandula*, which was first recorded on the Shiretoko Peninsula in this study, originated in the Pacific coast of North America. This species was discovered in 2000 in locations ranging from the southern part of Sanriku (Oshika Peninsula) in Miyagi Prefecture to Hiroo on the Pacific coast of Hokkaido and at high densities around Muroran and Tomakomai in Hokkaido but were not found at the Shiretoko Peninsula (Kado 2003). This species was found at AI on the Nemuro Strait side of the Shiretoko Peninsula in an unrelated survey in December 2017 (unpublished). However, it was recorded at three survey stations on both sides of the Shiretoko Peninsula in 2019, suggesting that although its abundance is low, it may be distributed over a wide area of the Shiretoko Peninsula. The possible routes of invasion of this species are: (1) natural invasion from the Kamchatka Peninsula and the Kurile Islands or (2) invasion by attachment to ships. As for (1), this species has not previously been found in the eastern part of Hokkaido, and as for (2), because lumber was transported from ports on the west coast of North America, such as Vancouver and Seattle, to Ofunato, Hachinohe and Tomakomai in the 1960s, this is likely how the barnacle arrived in Japan (Kado, 2003). Alam et al. (2014) confirmed the first invasion of larvae in Akkeshi, Hokkaido in 2004 and its establishment as a population in 2006. Therefore, considering the direction and time lag of the distributional expansion of this species and the coastal ocean currents, it is likely that this population has become established in the

Shiretoko Peninsula.

Amphipoda. The superfamily Gammaroidea, *Carineogammarus makarovi* from the northern Primorskaya Oblast, Kamchatka Peninsula, and Alaska, was found in this study for the first time in Japan at AI. In addition, second records of *Locustogammarus locustoides* (the first record has an unknown locality), *Spasskogammarus spasskii* (the first record is from Akkeshi Bay), and *Mesogammarus melitoides* (the first record is from Muroran) have been identified in Japan (Tomikawa & Sonoda 2008). *Abludomelita klitinii* (Hadzioidea, Melitidae), which was originally described at the southwestern shelf of Sakhalin Island, was recorded at AI (Tomikawa & Sonoda 2022). This is the first record of *A. klitinii* in Japan. The geographical distribution of these four species ranges from the northern part of the Sea of Japan to the Sea of Okhotsk and the Bering Sea, but these species are also distributed in the Shiretoko Peninsula, which is the southernmost tip of the Sea of Okhotsk. The sampling station where all four species were collected was station AI, whereas fewer species were found at Nihondaki (Station NN) and Kaseki-hama (Station KH), all on the Nemuro Strait side of the Shiretoko Peninsula. This may reflect the topographical characteristics of the coast of the study site as well as the fact that the Nemuro Strait side of the Shiretoko Peninsula is more strongly affected by the Oyashio Current, which circulates from Alaska along the Aleutian and Kurile Islands. As a result of this study, we were able to obtain a valuable confirmation of the habitat distribution of small crustaceans, such as Gammarida and Caprellidae. Further detailed investigations, including various types of microhabitats, are expected to increase the number of newly identified species and new discoveries.

Isopoda. Based on the material collected in our investigation, a new sphaeromatid species *Dynoides bicolor* has been described by Nunomura (2010). This species was distinguished from its congeneric species in characteristic and easily recognizable color of the dorsal surface: black in the anterior part and white in the posterior part (Nunomura 2010). It is known that of many species of the genus *Dynoides* are commonly found in mussels or seaweed beds in rocky intertidal zones (Li 2000, Espinoza-Perez & Hendrick 2002). Further comparative ecological survey, such as life cycles, microhabitat selection and feeding behavior on the genus *Dynoides* will be necessary to understand their ecological niche partitioning in the Shiretoko Peninsula and its surrounding areas.

Tanaidacea. *Arctotanais alascensis* is a species of the family Tanaididae and suborder Tanaidomorpha. Its distributional area was from the western part of the Aleutian Islands to the Kurile Islands. Kakui et al. (2012) reported this species for the first time in Japan based on our specimens from station FP and station AI, as well as individuals from Oshoro and Muroran. Later, it was also reported from Rishiri Island and Otsuchi (Iwate Prefecture) in Japan (Kakui et al. 2014). Further studies should provide more detailed information on the geographic distribution and ecology of these rare species in Japan.

Decapoda. Thirty-three Decapoda species were included in the collections made during our investigations. The vast majority have been previously recorded in Hokkaido. *Oregonia kurilensis* (Brachyura; Oregoniidae) was originally described at Kunashiri Island, South Kurile Islands, at a depth of 65 m (Kobjakova 1955) and was subsequently recorded from Paramushir Island, North Kurile Islands, by Komai & Yakovlev (2000). During our survey, two specimens assigned to this species were collected from the Japanese side for the first time. *Gaetice depressus* (Brachyura: Varunidae) has been recorded in the area ranging from the Oshima Peninsula to Oshoro, Rishiri, and Abashiri in Hokkaido (Komai et al. 1992), but there have been no previous records of this species in the Shiretoko Peninsula. During our survey, *G. depressus* was collected from Sashirui Cape on the Nemuro Strait side. The two congeneric species of varunids, *Hemigrapsus sanguineus* and *H. takanoi* exhibited different distributional patterns: *H. sanguineus* occurred in both the Sea of Okhotsk and the Nemuro Strait sides of the Shiretoko Peninsula, whereas *H. takanoi* was restricted to the Sea of Okhotsk side (Appendix 1). The distributional patterns of these varunid crabs may reflect different ecological traits and variations in the marine environments around the Shiretoko Peninsula. The egg brooding period and egg development duration of *H. takanoi*, which has been studied as an invasive species in Europe, become shorter at higher water temperatures, suggesting that higher sea surface temperatures increase the reproductive success of this species (Brink et al. 2013). The fact that *H. takanoi* was collected only on the Sea of Okhotsk side of the Shiretoko Peninsula, which is influenced by the Soya Warm Current, may be related to the optimal temperature of this species, and attention should be paid to future changes in its distribution.

Other taxa

Thirty-four species of polychaete annelids were identified, most of which were found in the rhizomes of eelgrass and in sand and mud deposited in reef crevices and depressions. These are common species that are widely distributed in the coastal areas of Hokkaido including the Shiretoko Peninsula. According to Kato et al. (2003) and Kobayashi et al. (2019), who conducted detailed surveys in the intertidal zone of Rishiri Island, the polychaetes collected in the intertidal to subtidal zones in that region were characterized by many groups similar to those in the Far East Russian waters; some species that were deemed absent in Japan were also found. The polychaetes collected in the Shiretoko Peninsula are also considered to share some features with those in the Far East Russian Sea, but many species in the family Capitellidae are still difficult to be identified taxonomically, and more detailed research is required on these groups.

In addition to the echinasterid sea star *Henricia alexeyi* identified in this study, several other species of the genus

Henricia were identified. It is likely that these species have not been described. However, the phylogenetic systematics of echinasterid sea stars are unclear, and further studies are required for more detailed taxonomic identification and confirmation of their distributional status.

General discussion

From a marine biogeographic perspective, the Shiretoko Peninsula and its adjacent waters can be described as a transitional or overlapping zone between warm- and cold-water species. Kussakin (1975) pointed out such remarkable biogeographic characteristics of the intertidal fauna of the Kurile Islands and stated that the Etorofu Island is a boundary. Nishimura (1992) stated that the southern part of Sakhalin Island and the eastern part of Hokkaido, including the Shiretoko Peninsula and Nemuro Peninsula, belong to the subarctic zone, whereas the northern part of Sakhalin is in the arctic zone, and the coastal area of the Sea of Okhotsk in Hokkaido belongs to the cool temperate zone. According to Nishimura (1992), the Shiretoko Peninsula is where the subarctic and cool temperate zones meet. He discussed that the main factor in defining marine biogeographic zones is ocean currents, which affect the water temperature and the transport of organisms. Briggs & Bowen (2012) noted that the western North Pacific region consists of three marine biogeographic provinces, in terms of the geological history of the seas and endemism. The Shiretoko Peninsula is located where the Okhotsk Province and Kurile Province overlap, and the Sea of Okhotsk is considered to have highly endemic fauna because of its isolation during the glacial period. Based on these marine biogeographic features, the Shiretoko Peninsula is unique in that it is located at the boundaries or overlaps of different marine biogeographic zones.

The Shiretoko Peninsula, which is located at the southern end of the Sea of Okhotsk and contains the southern limit for coastal drift ice in the northern hemisphere, is affected by the East Sakhalin Current, Soya Warm Current, and Oyashio Current (Fig. 1). Below, we discuss the major factors that influence the fauna of the Shiretoko Peninsula.

(1) Ocean current

First, we consider the ocean current factor. The distributional composition of the molluscan fauna of the Shiretoko Peninsula (Fig. 4), which reflects the influence of ocean currents, is composed of species mainly inhabiting the Pacific coast of Hokkaido and Tohoku districts. It is similar to that of Shikotan Island and Akkeshi Bay and somewhat different from that of Etorofu Island and Kunashiri Island, which have more northern elements. Therefore, while the Shiretoko Peninsula is affected by cold currents, such as the Oyashio Current and the East Sakhalin Current, the occurrence of temperate species suggests that the Soya Warm Current affects the area, and changes in the proportion of cold or cool and temperate elements would provide useful information for assessing the influence of warm currents. Ivanova & Tsurpalo (2012) described the intertidal biota of the Russian Far East and showed a trend of increasing species richness from the Kamchatka Peninsula to the Kurile Islands and a latitudinal gradient of species richness in the intertidal biota of the Sea of Okhotsk. If this trend is related to the species diversity of larvae dispersed by cold and warm currents, the ocean currents reaching the coast of the Shiretoko Peninsula may produce differences in species depending on location.

The mollusk and crustacean fauna among the sites differed between the Sea of Okhotsk side of the Shiretoko Peninsula and the Nemuro Strait side, with AS at the tip of the peninsula being different from the other sites (Fig. 3). The number of species tended to be higher on the Sea of Okhotsk side of the peninsula than on the Nemuro Strait side (Table 5). As this study is qualitative, a strict quantitative comparison was not possible. However, if we consider the above results as a qualitative pattern, the factors involved may include ocean currents that affect larval dispersal, topographic factors that affect both survival after settling and community structure organization, and coastal drift ice effects.

As shown in Fig. 4, station AS had a slightly higher proportion of boreal elements, suggesting that it was more strongly influenced by the cold current than the Nemuro Strait side. In CH and BP on the Sea of Okhotsk side of the peninsula, there are many temperate elements due to the influence of the Soya Warm Current, suggesting that the degree of influence of cold and warm currents is reflected in species composition. In fact, oceanographic monitoring data from June to August 2016 along the coast of the Shiretoko Peninsula (Ministry of the Environment Government of Japan 2017) indicates that the mean water temperature on the Sea of Okhotsk side of the peninsula is 2°C higher than on the Nemuro Strait side. This reflects the fact that the influence of ocean currents is different on both sides of the peninsula, suggesting that this is one of a factor that generates differences in fauna. Finally, these faunal features, which reflect the influence of ocean currents, are likely to be greatly affected by the peninsula. This is because the Shiretoko Peninsula extends in a northwesterly direction, blocking ocean currents from the west and acting as a barrier against the Nemuro Strait side of the peninsula. Kostina et al. (2016) found that the intertidal biota of Kunashiri Island, which is adjacent to the Shiretoko Peninsula, is dominated by warm-water species on the west coast of the Okhotsk Sea side than on the east coast of the Pacific Ocean side, and pointed out that the west coast of Kunashiri Island is more strongly influenced by the Soya Warm Current. The differences observed in the intertidal macroinvertebrate fauna of the Shiretoko Peninsula are consistent with these characteristics of Kunashiri Island.

(2) Topography

Second, we considered topographical factors. The characteristics of coastal rocky shores are important geomorphological factors that affect faunal composition. At the tip of the peninsula (AS), a wave-cut rocky benches extend more than 300 m offshore following a shingle beach, and eelgrass and seaweed thrive in the wide open space (tide pool) of the bench where *Ruditapes philippinarum* and *Neptunea arthritica* live. In contrast, CH, BP, and AI on the side of the peninsula have relatively flat rocky benches, and their horizontal development is shorter, and the tide pool is smaller than that at the tip of the peninsula. From the tip of the bench to the offshore area, the water depth suddenly deepens, and the intertidal zone has a complex topography with relatively large rock piles. These topographic features may affect species composition.

(3) Drift ice

Third, we considered the impact of drift ice on shores. Because drift ice is first pushed by the northwesterly wind to the Sea of Okhotsk side of the peninsula and then gradually moved to the Nemuro Strait side (Gochi 2008), it is assumed that the degree of influence of drift ice on the intertidal zone differs between the Sea of Okhotsk side, tip of the peninsula, and Nemuro Strait side of the peninsula, in combination with the characteristics of the coastal topography. Regarding the effects of ice on rocky shore organisms, the number and diversity of species decreases as the pressure and scouring effects of ice become stronger. Organisms survive in topographical refugia, such as rocky crevices and depressions, where ice has a strong influence during the winter, and the upper part of the zonation is determined by the extent to which ice affects settled individuals (Bergeron & Bourget 1986, Smale 2007). The pressure of drift ice against the coast is estimated to be several to several tens of kilograms per cm^2 (Saeki et al. 1975, Gochi 2008), and small individuals that settle on rocky shores during the summer and autumn are considered to be severely affected, although the constant creation of new habitat niches by repeated disturbances may encourage the settlement of new species and increase species diversity (Connell 1978).

Konno (1988) surveyed the seashore fauna at the tip of the Shiretoko Peninsula and around Bunkichi Bay, the site of this study, from July to August 1979, and reported 76 species in 11 phyla. This study compared the Poromoi coast to the tip of the peninsula, which corresponds to Bunkichi Bay–Poromoi Bay, and observed differences in coastal topography, the status of attached organisms on the rocks facing the offshore side, the whelk *N. arthritica* found only at the tip of the peninsula, and the differences in the habitat of the fan worm *Pseudopotamilla occelata*. Based on these observations, the author stated that the differences in the impact of drift ice on the coastline were responsible for the variation in fauna. In parallel with this study, a quantitative survey of the rocky intertidal molluscan community structure was conducted in the Shiretoko Peninsula by Chiba et al. (2020), which revealed that the molluscan community of the Shiretoko Peninsula has different characteristics on the Sea of Okhotsk side (including the tip) as compared to the Nemuro Strait side. These authors also stated that the species diversity is higher on the Nemuro Strait side than on the Sea of Okhotsk side, which tends to be dominated by a few species, and that the small seaweed-attached bivalve, *Turtonia minuta*, was found only at the Nemuro Strait site. These results clearly indicate that environmental stress on the intertidal molluscan community is greater on the Sea of Okhotsk side of the Shiretoko Peninsula (Clarke et al. 2014), and that differences in the effects of drift ice pressure are reflected in the coastal biota of the Shiretoko Peninsula. The similarity of the faunal assemblages among the sites was consistent with the results obtained in this study (Fig. 3) and those of Chiba et al. (2020), suggesting that the possible influence of drift ice from the quantitative molluscan survey is a common factor in the characteristics of the seashore fauna of the Shiretoko Peninsula identified in this study.

Furthermore, Abe et al. (2010) found that the species diversity of seaweed tended to be higher on the Nemuro Strait side of the Shiretoko Peninsula than on the Sea of Okhotsk side. And they compared before and after the year of large amount of drift ice and found differences in species composition for a total of 32 species in the survey of intertidal seaweed flora at the same site as this study. Based on these results, Abe et al. (2010) stated that a certain frequency of disturbance by drift ice is necessary to maintain the seaweed flora of the Shiretoko Peninsula. The effect of drift ice on intertidal seaweed has been reported as an important factor along the Northwest Atlantic coast (Mathieson et al. 1982, Dudgeon & Petraitis 2001) and is a universal factor in the organization of the seashore community structure affected by ice in winter. The fact that the results obtained for attached seaweeds are consistent with those obtained for benthic invertebrates, which also include many attached species, strongly suggests the importance of drift ice in shaping the seashore biota of the Shiretoko Peninsula.

The issues raised by the results of this study include: 1) bias in the taxonomic groups identified, 2) the impact of alien species, and 3) the impact of global warming. Regarding the first issue, we identified 299 species in this study, but due to difficulties in taxonomic identification, there was a strong bias toward mollusks and crustaceans. Many species of other phyla, such as Porifera and Cnidaria, remain unidentified. Future surveys including more diverse taxa are necessary to document the diversity in the Shiretoko Peninsula. The second issue of concern relates to the alien barnacle species, *B. glandula*, found throughout the Shiretoko Peninsula where immigration and dispersal of the newly introduced species is ongoing, and where monitoring surveys are needed to understand its impact. The third issue, the impact of global warming, is becoming increasingly apparent every year, which might be particularly pronounced in high-latitude regions (IPCC 2007) such as the Shiretoko Peninsula; intertidal fauna are useful indicators for monitoring these effects. Ocean currents and seawater temperature are thought to have a strong influence on the dispersal and settlement of planktonic larvae of the constituent species in the organization and maintenance of the seashore invertebrate fauna of the Shiretoko Peninsula. The coastal seawater temperatures around the peninsula, based on the average coastal water temperatures off Abashiri for the 30-year period from 1981 to 2010 (Japan Meteorological Agency 2020) and the water temperature statistics for the Abashiri coast, east of AS, and the Nemuro Strait for the 5-year period from 2015 to 2019 (JMA Sapporo Regional Headquarters 2020), show an upward trend of approximately 1.0°C over the past 30 years. In this study, which focused on 13 years from 2006 to 2019, no significant changes in the seashore invertebrate fauna of the Shiretoko Peninsula were observed during the study period based on the dominant species composition. However, as the recent warming trend is also evident in seawater temperatures in the seas around Japan and changes in the distribution of coastal organisms have been reported (e.g., Inui et al. 2019), alterations may become apparent in the Shiretoko Peninsula in the future.

The results of this study indicate that the seashore invertebrate fauna of the Shiretoko Peninsula is important for marine biogeography because it lies at the boundary of two distinct marine biogeographic provinces. This means that we could recognize possible faunal changes with comparative ease, which might be expected to occur more acutely at the biogeographical boundary. The seashore biota of the Shiretoko Peninsula are bioindicators of the dynamics of the interaction between this region and the global environment and are extremely important for understanding future environmental changes. Therefore, it is essential to continue conducting surveys of seashore biota at the Shiretoko World Natural Heritage Site.

Electronic supplementary material

The online version of this article (doi: 10.3800/pbr.19.1) contains supplementary material: Appendix ES1

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