Distribution of native *Mytilus trossulus* and non-native *M. galloprovincialis*（Mytilidae: Bivalvia）along the coast of Hokkaido Island, Japan

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Abstract

The distribution of two species of mytilid mussels, native *Mytilus trossulus* Gould, 1850, and non-native *M. galloprovincialis* Lamarck, 1819, was studied at 120 sites（83 harbors and 37 shores）along the coast of Hokkaido Island and on three small islands（Okushiri, Rishiri and Rebun Islands）in the Sea of Japan. *M. trossulus* occurred at 28 harbors and on one shore, all of which were located in eastern and southern Hokkaido: coastal areas of the Sea of Okhotsk, the Nemuro Strait and the Pacific Ocean. It was never found on the Sea of Japan coast including the three islands. *M. galloprovincialis* was found at 70 harbors and on three rocky shores all around Hokkaido and the three islands, predominating on the Sea of Japan coast. Additionally, mussels with inner shell morphology intermediate between those of the two species were found at 26 harbors and on one rocky shore almost only in eastern and southern Hokkaido, the distribution being very similar to that of *M. trossulus*. The relative abundance of *M. trossulus* individuals among these three mussel types was greater on the Nemuro Strait coast and eastern Pacific coast and tended to decrease westward. The relative abundance of *M. galloprovincialis* individuals among the three mussel types was 100% at almost all harbors along the Sea of Japan coast and tended to decrease eastward. Salinity and the scale of shipping traffic at the harbors did not show any relation to the occurrence and relative abundance of the three mussel types.

【Keywords】 distribution, Hokkaido Island, *Mytilus galloprovincialis*, *Mytilus trossulus*, non-native species

I. Introduction

Biological invasions by human-mediated introduction and the resultant hybridization between native and non-native congeners are global concerns in the conservation of biological diversity at both local and global scales（Lowe *et al*., 2000）. A representative of this in the marine context is the marked range expansion of the mytilid mussel *Mytilus galloprovincialis* Lamarck, 1819 and hybridization among members of the *Mytilus edulis* species complex（McDonald *et al*., 1991）, which consists of *M. edulis* Linneaus, 1758, *M. trossulus* Gould, 1850 and *M. galloprovincialis*. *M. edulis* is distributed in the temperate zones of northern Atlantic Ocean in Europe and North America. *M. trossulus* has a more boreal distribution, extending over

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the northern Pacific Ocean, northern Atlantic Ocean, and Baltic Sea. *M. galloprovincialis* is native to the Mediterranean Sea, but has been introduced into the Atlantic Ocean, Pacific Ocean and Indian Ocean via hull fouling and ships' ballast water probably since the late 19th century (Hilbish *et al*., 2000). *M. galloprovincialis* has now established populations and formed extensive hybrid zones with *M. edulis* and *M. trossulus* in the areas in which it has been introduced (e.g. Skibinski *et al*., 1978; Geller *et al*., 1994; Suchanek *et al*., 1997; Rawson *et al*., 1999; Braby & Somero, 2005; Brannock *et al*., 2009). The decline of native mussel populations by the invasion of *M. galloprovincialis* has been revealed or suggested in some regions (Geller, 1999; Hanekom, 2008), and thus this species has been ranked as one of the top 100 of the world's worst invasive alien species (Lowe *et al*., 2000).

Around Japanese waters, *M. trossulus* inhabits only Hokkaido Island (hereafter referred to as Hokkaido), the most northerly of Japan's main islands (Kuwahara, 1993, 2001; Suchanek *et al*., 1997; Iwasaki *et al*., 2012, 2017). The non-native *M. galloprovincialis* was first recorded at Hyogo Port (N34° 40', E135° 10'), western Honshu Island, in 1932 (Uchihashi, 1939), and has extended its distribution northward to Hokkaido, southward to Shikoku Island, and westward to Kyushu Island (Otani, 2002; Iwasaki *et al*., 2004; Iwasaki, 2006)

On Hokkaido, records on the distribution of both species have been much fewer than those on Honshu Island (Otani, 2002; Iwasaki *et al*., 2004), and the original distribution of native *M. trossulus* and the history of invasion of *M. galloprovincialis* have not yet been revealed. Kuwahara (1993, 2001), who examined the inner shell morphology of dry mussel specimens collected on Hokkaido from the 1900s to the 1990s, revealed 9 localities with *M. trossulus* and 15 localities with *M. galloprovincialis*. Additionally, Kuwahara (2001) reported the occurrence of mussels with morphology intermediate between those of the two species (hereafter referred to as Intermediate type) at four sites of the eastern and southern Hokkaido, suggesting them to be hybrids between the two species. However, Kuwahara (1993, 2001) did not report the year of collection for most of the specimens. Iwasaki *et al*. (2012), who examined dry shell specimens collected in the late 1970s and 1980s by the same method as Kuwahara (2001), reported the occurrence of *M. trossulus* at 4 sites, *M. galloprovincialis* at 10 sites, and the Intermediate type at 4 sites. Inoue *et al*. (1997) analyzed mussel adhesive protein genes and found hybrids between the two species at two sites in the southern Hokkaido. Moreover, Brannock *et al*. (2009), who examined the genetic structure of the mussels at 26 sites in 2004 and 2006, revealed two distinct hybrid zones in northern (the Sea of Okhotsk) and southern (the Pacific Ocean) Hokkaido. They also argued that the distribution of the two species and the hybrid zones had been stable for at least a decade from the mid-1990s to the mid-2000s and was determined not by ongoing displacement of *M. trossulus* by *M. galloprovincialis* but by environmental factors such as coastal current circulation patterns. On the other hand, Iwasaki *et al*. (2012), taking into account the previous records on the distribution of the two species before the 1990s, suggested the decline of the native *M. trossulus* populations in western and southern Hokkaido and the expansion of *M. galloprovincialis* populations in these areas. However, all of these records are still too sparse to reveal the spatiotemporal distribution patterns of both species, particularly the range extension of non-native *M.*

galloprovincialis and possible decline of native *M. trossulus* populations.

Surveys on the distribution of both species were conducted at 120 sites along the coast of Hokkaido, as well as at three islands（Okushiri, Rishiri, and Rebun）in the Sea of Japan, from 2010 to 2014. In the present paper, detailed patterns of their occurrences, including that of the Intermediate type, are presented, and the possibility of ongoing range extension or decline of both mussels on Hokkaido is discussed, by comparison with previous records on their distribution.

II. Study sites and methods

Hokkaido（83,450 km^2）has a coastline of 2676 km. As the mussels were reported to occur more abundantly and frequently at harbors than on shores（Iwasaki, 2017a, 2017b, 2018）, 62 harbors were selected as study sites based on the criterion of having at least one study site along each stretch of 50 km of coastline: 8 harbors along the Sea of Okhotsk coast; 4 and 2 in Lake Saloma and Lake Notoro with brackish water, respectively; 5 along the Nemuro Strait coast; 24 along the Pacific coast including Tsugaru Strait;

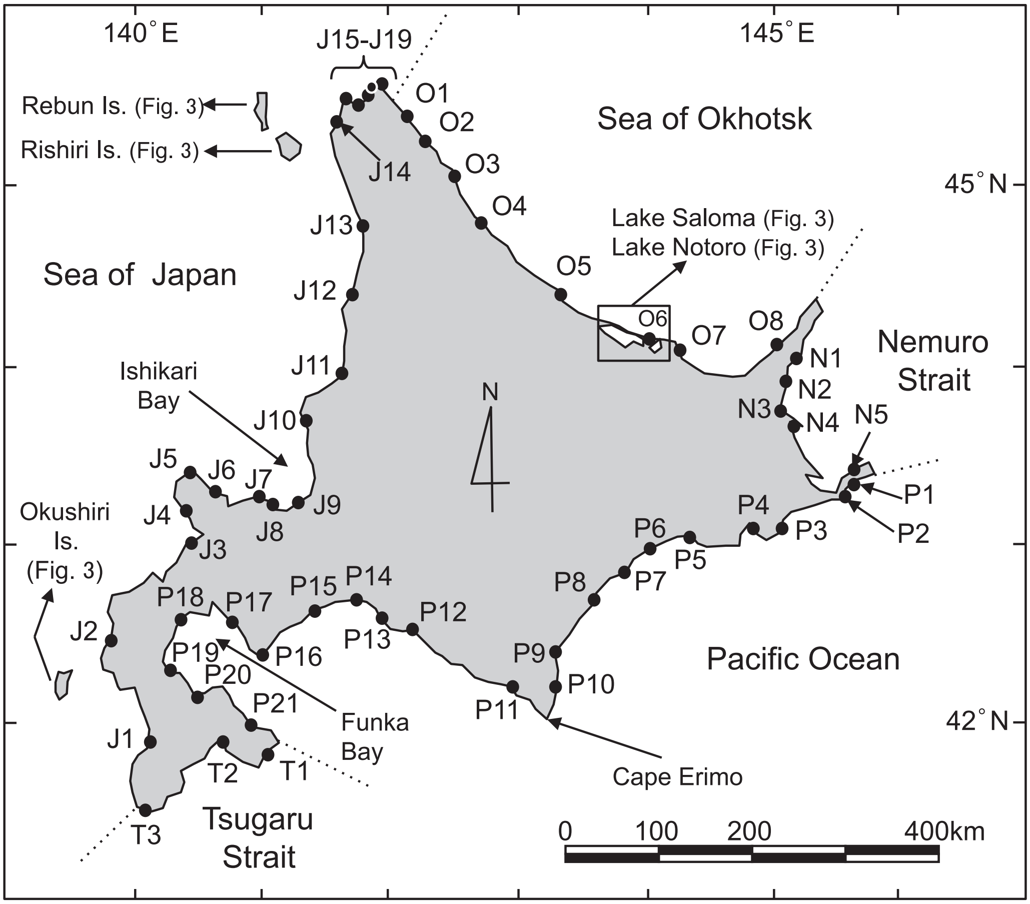

Fig. 1 Study sites around Hokkaido Island. See Appendix for site names.

and 19 along the Sea of Japan coast (Fig. 1, Appendix). Furthermore, 21 harbors on three small islands in the Sea of Japan were surveyed: 4 on Okushiri Island (143 km^2), 9 on Rishiri Island (182 km^2), and 8 on Rebun Island (81 km^2) (Fig. 2, Appendix). Additional surveys were conducted on 37 rocky or boulder shores just adjacent to the 37 surveyed harbors (half-toned sites in Appendix). Most surveys were conducted at ebb tides on spring-tide days in early or mid-September in 2010, 2012 or 2013 on Hokkaido, and in June and August in 2014 on the three small islands.

Thirty-minute searches for mussels in the intertidal and upper subtidal zones up to a depth of 50 cm were conducted at the study sites, and mussels were qualitatively collected using a scraper or "Mussel Collector" (15-cm aperture, 7-cm depth, 6-cm height with a 2-mm nylon net, No. 548, Siyouei, Co. Ltd., Tokyo, Japan), the latter of which was attached to the tip of a 3-m fishing rod. Attempts were made to collect at least 30 mussels at each site, but actually fewer than this were obtained at 45 of the 120 sites (see Results). The salinity of surface water was also measured using a refractometer (S-millE, Atago Ltd., Tokyo, Japan).

In the laboratory, the mussels were dissected and classified into *M. trossulus*, *M. galloprovincialis* and Intermediate type (hereafter referred to as the "three mussel types" altogether), based on the morphological criteria reported by Zolotarev & Shurova (1997) and Kuwahara (2001) regarding the disposition among ligament, prismatic layer, and nacreous layer coating inner shell valves. The authors discriminated the two specimens with nacreous layers connecting directly to ligaments as *M. galloprovincialis* and those with prismatic layers between nacreous layers and ligaments as *M. trossulus*. Additionally, the authors suggested that the Intermediate type with narrow nacreous layers under the ligaments (i.e., specimens with prismatic layers partially intruding between nacreous layers and the ligaments) was a hybrid between the two species. Then their shell lengths were measured to the nearest 0.1 mm by a slide caliper. However, juvenile mussels smaller than 6 mm in length were not examined because their shells were too fragile to dissect. Thus the present study showed the results for only mussels larger than 6 mm.

Port index (PI) was used to estimate the geographical range of shipping traffic for each surveyed harbor. The shipping traffic data were converted into numbers from 1 to 5 according to the following criteria: 1: a small-scale fishing port of Type 4 Fishing Port Code (hereafter FPC) provided by the Fisheries Agency of Japan (a fishing port located on an isolated island or rural area, and used as a refuge, or to develop new fishing grounds), 2: a fishing port of Type 1 FPC (used for only local fisheries), 3: a middle-scale fishing port of Type 2 FPC (used more widely than a Type 1 fishing port, but not as large as a Type 3 fishing port), 4: a fishing port of Type 3 FPC (used nationwide), and 5: a larger-scale fishing port of Type Special 3 FPC (especially important to the development of national fisheries) and a commercial port. Then, the occurrences of each mussel type at the harbors were analyzed using multivariate logistic regression (present : 1, absent: 0) on four variables (PI, salinity, latitude, and longitude at each harbor), using Mac Multivariate Analysis ver. 2.0 (Esumi Co., Ltd., Tokyo, Japan).

The influence of water temperature on the mussels' potential distributional ranges was examined using the mean water temperature data for the coldest (February or March from 1906 to 2003) and hottest (August from 1906 to 2003) months at the sea surface in 20 regions of coastal water each corresponding to a square of 1° latitude and 1° longitude offshore at the survey areas, all of which were obtained from the Japan Oceanographic Data Center (2018). Additionally, the influence of long-term change in water temperature on the spaciotemporal distribution of the three mussel types was examined using the annual mean water temperatures in winter (from January to March) and summer (from July to September) in the northeastern Sea of Japan (comparable to offshore along the Sea of Japan coast) (from 1902 to 2014) and offshore of Kushiro (comparable to offshore of the eastern Pacific coast, P1–P10 in Fig. 1 and Appendix) (from 1929 to 2014 in winter, from 1908 to 2014 in summer), and in three seasons except winter offshore of Abashiri (comparable to offshore of the Okhotsk coast: no data in winter due to the drift-ice berth) (from 1964 to 2009), which were obtained from the Japan Meteorological Agency (2018).

III. Results

Mytilus trossulus was found at 28 out of 83 harbors surveyed (Table 1). The percentage of harbors where the species occurred was 50.0% on the Okhotsk coast, 80.0% on the Nemuro Strait coast, 66.7% on the Pacific coast including Tsugaru Strait, and 5.3% on the Sea of Japan coast. No *M. trossulus* was found at 21 harbors on the three small islands in the Sea of Japan. The Intermediate type was discovered at 26 harbors, and the distribution and percentage of occurrence were similar to those of *M. trossulus*: 57.1% on the Okhotsk coast, 60.0% on the Nemuro Strait coast, 62.5% on the Pacific coast, 5.3% on the Sea of Japan coast, and 0.0% on the three small islands in the Sea of Japan. *M. galloprovincialis* was found at 70 harbors, and the percentage occurrence exceeded 60% in all coastal areas. The rocky shores where the mussels occurred were very few; only one on the Okhotsk coast for each of *M. trossulus* and the Intermediate type,

Table 1 Number of sites studied, number (No.) and percentage (%) of sites where each mussel type (*Mt: Mytilus trossulus*, It: Intermediate type, *Mg: M. galloprovincialis*) was found, and the relative abundance in number of individuals (RA% mean ± SE, harbors with less than 10 individuals were excluded) among the three mussel types at the harbors in each coastal area. OK: Okhotsk including Lake Saloma and Lake Notoro, NS: Nemuro Strait, PT: Pacific Ocean and Tsugaru Strait, SJ: Sea of Japan, IJ: islands in the Sea of Japan (Okushiri, Rishiri and Rebun).

	Coastal area	No. sites studied	*Mt*			It			*Mg*		
			No.	%	RA%	No.	%	RA%	No.	%	RA%
Harbors	OK	14	7	50.0	16.4 ± 4.2	8	57.1	23.9 ± 5.2	9	64.3	59.7 ± 6.4
	NS	5	4	80.0	28.3 ± 7.0	3	60.0	36.3 ± 5.8	5	100.0	35.4 ± 11.0
	PT	24	16	66.7	12.6 ± 5.1	15	62.5	18.0 ± 4.0	22	91.7	69.4 ± 7.3
	SJ	19	1	5.3	0.1 ± 0.1	1	5.3	0.7 ± 0.7	17	89.5	99.2 ± 0.7
	IJ	21	0	0.0	0.0	0	0.0	0.0	17	81.0	100.0
	Total	83	28	33.7	8.2 ± 2.3	26	31.3	11.7 ± 2.4	70	84.3	80.0 ± 4.8
Shores	OK	5	1	20.0	—	1	20.0	—	1	20.0	—
	NS	3	0	0.0	—	0	0.0	—	0	0.0	—
	PT	6	0	0.0	—	0	0.0	—	0	0.0	—
	SJ	6	0	0.0	—	0	0.0	—	0	0.0	—
	IJ	17	0	0.0	—	0	0.0	—	2	11.8	—
	Total	37	1	2.7	—	1	2.7	—	3	8.1	—

and one on the Okhotsk coast and two on small islands on the Sea of Japan coast for *M. galloprovincialis*.

Multivariate logistic regression of the occurrences of *M. trossulus* and Intermediate type for four variables（latitude, longitude, PI, and salinity）revealed that the occurrences were correlated negatively with latitude and positively with longitude（*M. trossulus*: $\chi^2 = 46.91$, $p < 0.01$, Intermediate type: $\chi^2 = 31.22$, $p < 0.01$, Table 2）. The results indicate that the probability of occurrence of both mussel types tended to be higher towards the southeastern part of Hokkaido, but it was not affected by PI and salinity. The result for *M. galloprovincialis* showed no significant correlation with any of the four variables（$\chi^2 = 3.65$, $p > 0.05$, Table 2）.

Table 2 Results of multivariate logisitic regression analyses of the occurrence of each mussel type for latitude, longitude, Port Index, and salinity. SPRC: standard partial regression coefficient, Wald: Wald value, **: significant at 1 % level, NS: not significant at 5 % level.

Variable	*M. trossulus*		Intermediate		*M. galloprovincialis*	
	SPRC	Wald	SPRC	Wald	SPRC	Wald
Latitude	–0.467	9.95^{**}	–0.370	8.82^{**}	–0.155	1.71^{NS}
Longitude	0.516	19.17^{**}	0.404	15.15^{**}	–0.021	0.04^{NS}
Port Index	0.033	0.11^{NS}	0.103	1.03^{NS}	0.055	0.24^{NS}
Salinity	0.034	0.07^{NS}	0.020	0.03^{NS}	–0.140	1.13^{NS}
Constant	–	10.35^{**}	–	6.67^{**}	–	0.64^{NS}

Fig. 2 shows the relative abundance of the number of individuals for the three mussel types collected at each of 83 harbors on Hokkaido. The proportion for *M. trossulus* was higher on the Nemuro Strait coast（N1–N5: 0%–42%）and the eastern Pacific coast（from Cape Nemuro to Cape Erimo, P1–P10: 11%–100%）, and tended to decrease from the western Pacific coast towards the Tsugaru Strait（from Cape Erimo to Matsumae Town, P11 to T3: 0%–17%）. No *M. trossulus* was found at 7 out of 8 harbors on the Okhotsk coast and the 18 out of 19 harbors on the Sea of Japan coast, with the exceptions being Abashiri（O7）and Wakkanai（J16, located at the northern edge of the coastal area）. The distribution of the sites of occurrence and proportion for the Intermediate type were similar to those of *M. trossulus*, but the proportion was greater than that of *M. trossulus* at all of the harbors where the two mussel types co-occurred on the western Pacific coast. On the Sea of Japan coast, the Intermediate type was found at only one harbor, Takashima（J7）, in Ishikari Bay. *M. galloprovincialis* was found all around Hokkaido, but the proportion tended to be lower on the Nemuro Strait coast and eastern Pacific coast. In Lake Saloma and Lake Notoro, all three mussel types were found at all six harbors（Fig. 3A）and on a boulder shore in Lake Notoro（Notoro, SNo1 in Fig. 3A）. As for the three islands in the Sea of Japan, only *M. galloprovincialis* was found at 18 out of 21 harbors（Fig. 3B）and on 2 out of 17 rocky shores（Senhoushi and Nishiuedomari, SRi5 and SRe5 in Fig. 3B, respectively）.

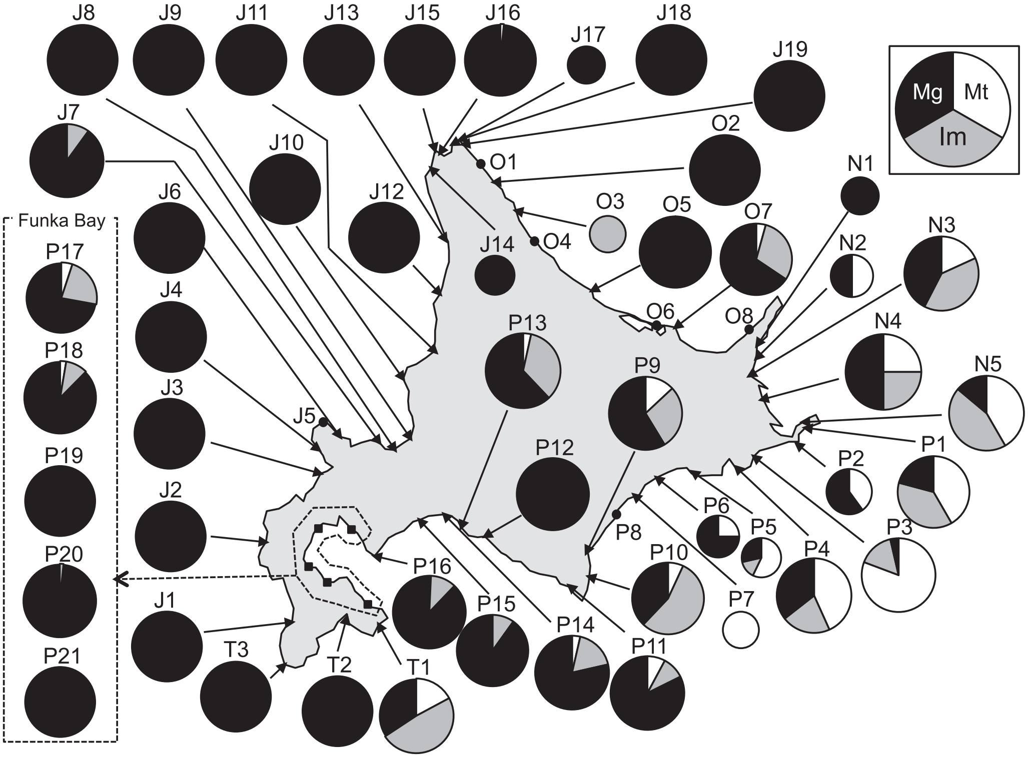

Fig. 2 Relative abundance in number of individuals for M. trossulus（Mt, white）, *M. galloprovincialis*（Mg, black）, and the Intermediate type（Im, dark）in the 62 harbors around Hokkaido Island. Small circles indicate that the number of mussels collected was fewer than 10. Dots with site numbers indicate that no mussels were collected at the sites. Location of the sites along Funka Bay is shown by black squares, and the relative abundance at the sites is shown by a broken rectangle. See Appendix for site names.

Harbors on the Nemuro Strait coast had the highest mean proportions for *M. trossulus* and the Intermediate type, 28.3% and 36.3%, respectively, and the lowest mean value for *M. galloprovincialis*, 35.4%（Table 1: harbors with fewer than 10 mussels were excluded when calculating the mean values）. The mean values for *M. trossulus* and the Intermediate type decreased in the order of the Okhotsk coast, Pacific coast, Sea of Japan coast, and three small islands in the Sea of Japan, while the value for *M. galloprovincialis* increased in the same order.

The percentage proportions of all mussel types did not correlate with the PI or salinity for the 43 harbors on the Okhotsk, Nemuro Strait and Pacific coasts where all three mussel types appeared to have potentially occurred（r^2 for PI and salinity: 0.0001 and 0.014 for *M. trossulus*, 0.0001 and 0.009 for Intermediate type, 0.010 and 0.001 for *M. galloprovincialis*, respectively, all $p > 0.05$）.

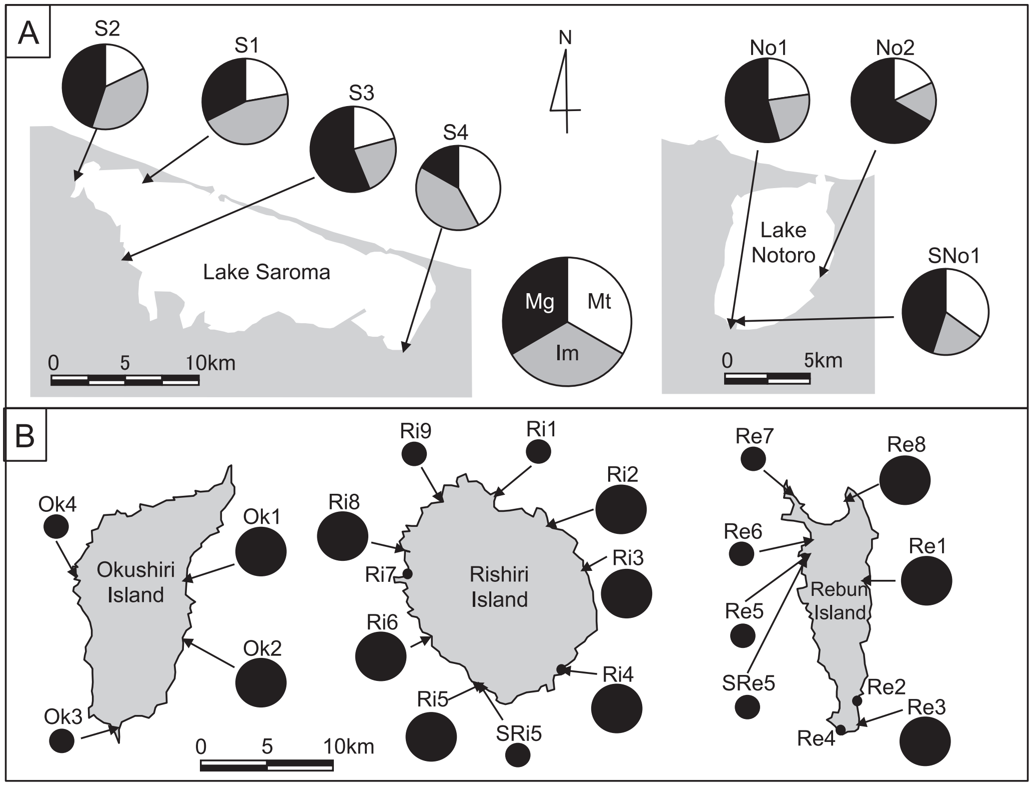

Fig. 3 Study sites and relative abundance of *M. trossulus*（Mt, white pattern）, *M. galloprovincialis*（Mg, black）, and the Intermediate type（Im, dark）at the harbors in Lake Saloma and Lake Notoro（A）, and on Okushiri, Rishiri, and Rebun（B）. SN1, SRi5, and SRe5 indicate the relative abundance on the shores near the harbors. See Appendix for site names, and Fig. 1 for small circles and dots.

IV. Discussion

Long-term change in water temperature around Hokkaido

The annual mean water temperatures offshore of the Sea of Japan coast in winter tended to increase during the 112 years from 1902 to 2014（$r^2 = 0.078$, $n = 91$, $p < 0.01$）, while those in summer did not（$r^2 = 0.002$, $n = 105$, $p > 0.05$）（Fig. 4）. The annual mean water temperatures off the eastern Pacific coast showed similar long-term changes: increasing in winter during the 85 years from 1929 to 2014（$r^2 = 0.102$, $n = 69$, $p < 0.01$）, and no significant change in summer during the 106 years from 1908 to 2014（$r^2 = 0.031$, $n = 87$, $p > 0.05$）. As for those off the Okhotsk coast in spring to fall, no significant change was detected during the 45 years from 1964 to 2009（$r^2 = 0.014$, $n = 40$, $p > 0.05$）. The long-term increase in winter temperature is considered to have potentially promoted the establishment and expansion of populations of the temperate mussel *M. galloprovincialis* in the coastal areas. On the other hand, the lack of significant change in summer or three seasons' temperature（except winter）appears to indicate that water temperature has had no effect on the long-term decline of the boreal mussel *M. trossulus* populations

（Iwasaki *et al.*, 2012）.

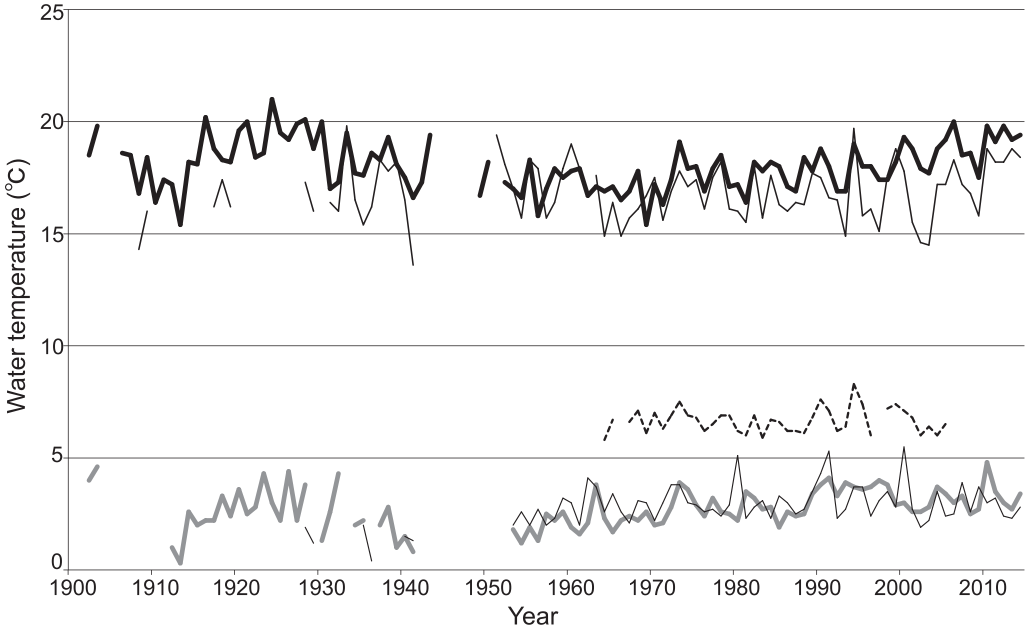

Fig. 4 Long-term change in annual mean water temperatures off the Sea of Japan coast [in the northeastern Sea of Japan as reported by Japan Meteorological Agency（JMA）, thick lines] and eastern Pacific coast（offshore at Kushiro in JMA, thin lines）in winter（gray lines）and summer（black lines）, and off the Okhotsk coast（offshore at Abashiri in JMA）from spring to fall（not winter, broken lines）.

Water temperature regime of mussels

Suchanek *et al.*（1997）, who investigated the distribution of *M. galloprovincialis* in the northern Pacific Ocean, presented the mean water temperatures in January and July at the 29 sites where the species was found: from 7.7 ℃ to 19.9 ℃ in January, and from 13.1 ℃ to 27.1 ℃ in July（Fig. 5）. Iwasaki *et al.*（2017）revealed a similar temperature regime for *M. trossulus* in the northern hemisphere（Fig. 5）: from − 2.0 ℃ to 12.8 ℃ in the coldest month, and from 7.8 ℃ to 23.6 ℃ in the hottest month.

As for the present study sites, the water temperature regime on the Sea of Japan coast（⓮ - ⓴ , in Fig. 5）, where *M. trossulus* was rarely found, ranged from 1.4 ℃（offshore at Soya, ⓴ ）to 7.8 ℃（southwestern Oshima Peninsula, ⓮）as minimum means in the coldest month, and from 20.4 ℃（⓴）to 23.6 ℃（⓮）as maximum means in the hottest month. The maximum means were within the range for *M. trossulus* in the work of Iwasaki *et al.*（2017）. This indicates that *M. trossulus* can potentially inhabit the Sea of Japan coast with regard to temperature tolerance. The water temperature regime along the Okhotsk, Nemuro Strait and Pacific coasts（① - ⑬）, where both *M. trossulus* and *M. galloprovincialis* were found, ranged from − 1.7 ℃（offshore at Abashiri, ③）to 8.0 ℃（Tsugaru Strait, ⑬）in the coldest month, and from 15.2 ℃（Nemuro Strait, ⑤）to 23.7 ℃（⑬）in the hottest month. This temperature regime is within the range for *M. trossulus* reported by Iwasaki *et al.*（2017）, but far from the lowest winter temperature（7.7 ℃）of the range for *M.*

galloprovincialis reported by Suchanek *et al.*（1997）. It is evident that, on Hokkaido, *M. galloprovincialis* has extended its distribution to much colder areas outside of its known temperature regime.

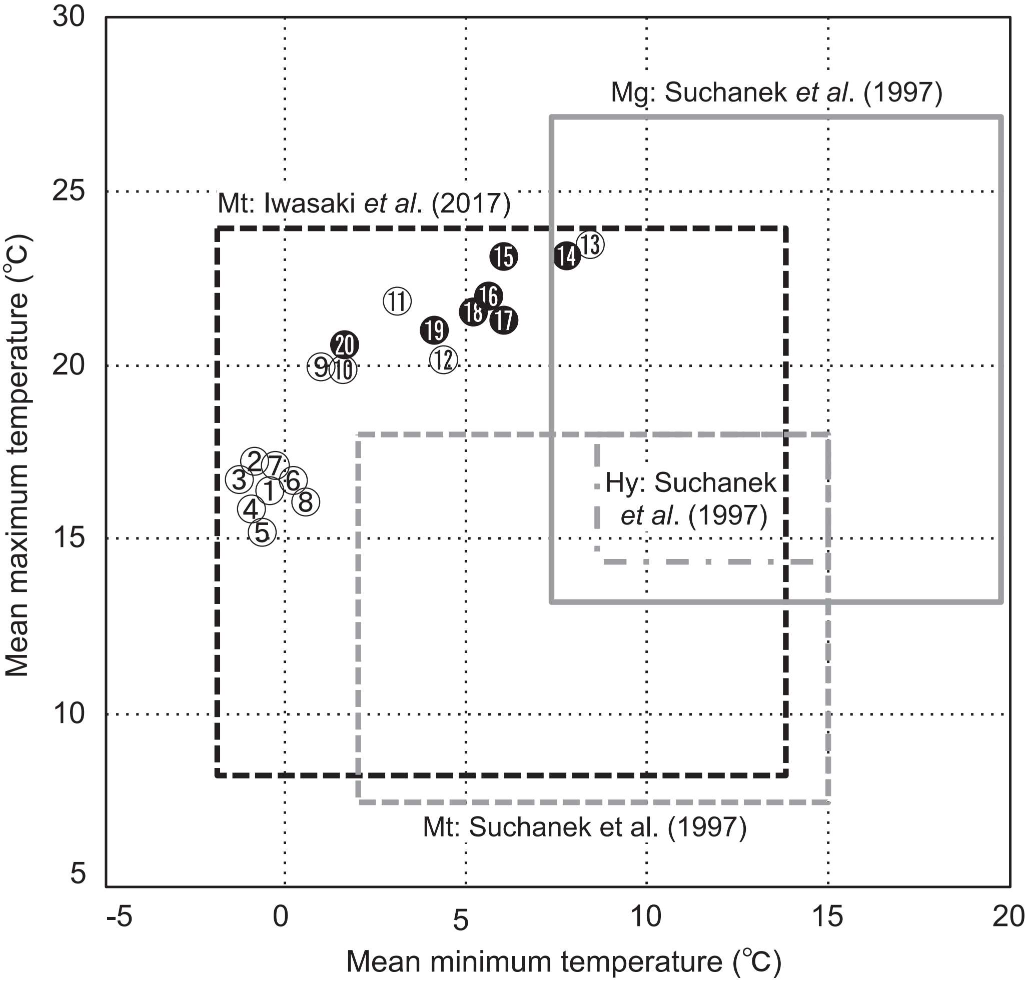

Fig. 5 Schematic water temperature regimes［mean water temperatures in January（x-axis）and July（y-axis）］for *M. trossulus*（Mt, a rectangle enclosed with gray broken lines）, *M. galloprovincialis*（Mg, a rectangle enclosed with gray solid lines）, and their hybrids（Hy, a rectangle enclosed with gray one-dot chain lines）in the north Pacific Ocean（Suchanek *et al.*, 1997）, and schematic water temperature regime［mean water temperatures in the coldest month（x-axis）and hottest month（y-axis）］for *M. trossulus*（a rectangle enclosed with black broken lines）in the northern hemisphere（Iwasaki *et al.*, 2017）. ①-⓴ indicate the mean sea surface water temperatures in the coldest month（x-axis）and hottest month（y-axis）in 20 coastal waters offshore at the present study sites（Japan Oceanographic Data Center）. White circles indicate the sites along the Okhotsk, Nemuro Strait, and Pacific coasts（1: Hamatonbetsu, 2: Monbetsu , 3: Abashiri, 4: Shiretoko（near O8）, 5: Nemuro Strait, 6: Kiritappu, 7: Kushiro, 8: Tokachi, 9: Hidaka（near P11）, 10: Tomakomai, 11: Funka Bay（P17 – P20）, 12: Oma, 13: Tsugaru Strait）. Black circles indicate the sites along the Sea of Japan coast（14: southwestern Oshima Peninsula（near T3）, 15: northwestern Oshima Peninsula（J1）, 16: Setana, 17: Shakotan Peninsula（J4 – J6）, 18: Ishikari Bay, 19: Rumoi, 20: Soya）.

Spaciotemporal distribution of *M. trossulus*

There were very few specimens and records of *M. trossulus* on Hokkaido before the 1980s. Kuwahara (2001) reported that dry specimens identified as *M. edulis* by Iwakawa (1919) and Kinoshita and Isahaya (1934) were *M. trossulus*. The locality of the former was simply "Hokkaido", and the localities of the latter were Ishikari Bay on the Sea of Japan coast, Tsugaru Strait, and Funka Bay on the Pacific coast (closed triangles in Fig. 6A). Since then, although several authors have reported or suggested the occurrence of *M. galloprovincialis* on Hokkaido (e.g., Hosomi, 1989), it has been unclear whether the species was *M. trossulus* or *M. galloprovincialis* because of the absence of specimens. Iwasaki *et al.* (2012) examined dry specimens collected in the late 1970s and 1980s and showed four localities of *M. trossulus*: Oshoro (near J7) in Ishikari Bay (open and closed squares in Fig. 6A), Lake Saloma on the Okhotsk coast, and Akkesi on the Pacific coast (closed squares in Fig. 6A). Suchanek *et al.* (1997) collected this species at Akkeshi

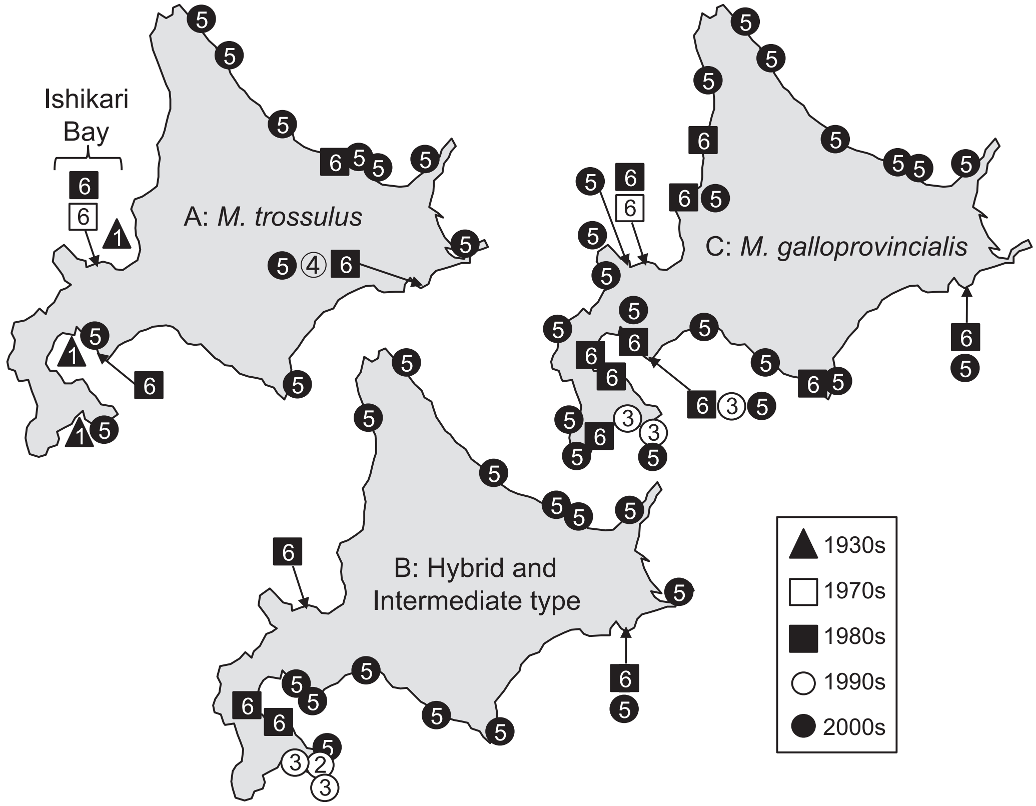

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Fig. 6 Years, sites, and references of *M. trossulus* (A), hybrids or Intermediate type (B), and *M. galloprovincialis* (C) collected around Hokkaido. Closed triangle: 1930s, open square: 1970s, closed square: 1980s, open circle: 1990s, closed circle: 2000s. 1: Kinoshita & Isahaya (1934) in Kuwahara (1993, 2001), 2: Inoue *et al.* (1995), 3: Inoue *et al.* (1997), 4: Suchanek *et al.* (1997), 5: Brannock *et al.* (2009), 6: Iwasaki *et al.* (2012).

in 1992（open circle in Fig. 6A）, and Brannock *et al*.（2009）found this species at 8 sites on the Okhotsk coast, 1 site on the Nemuro Strait coast, and 6 sites on the Pacific coast in 2004 and 2006（closed circles in Fig. 6A）. It is thus certain that *M. trossulus* inhabited Ishikari Bay of the Sea of Japan in the 1930s and Oshoro in the bay in the 1970s and 1980s.

In the 2000s, however, Brannock *et al*.（2009）could not find this species at any of the eight sites on the Sea of Japan coast, including Yoichi close to Oshoro. In the present study, it was not found at 39 sites on the Sea of Japan coast including Takashima（J7）near Oshoro and the three islands with the exception of Wakkanai（J16, the northern edge of the coast）. It is therefore suggested that, on the Sea of Japan coast, this species was originally very low in abundance and with a small distribution or has become very rare or extinct since the 1990s. In considering whether global warming has caused the decline of the populations since the 1990s, the summer water temperatures along the Sea of Japan coast during the 25 years after 1990（from 1990 to 2014）were significantly higher than those during the 25years before 1990（from 1965 to 1989）（Steel-Dwass's multiple comparison test: $t = 3.64$, $P < 0.01$）, but were not significantly different from those during the 25 years from 1915 to 1939（$t = 1.42$, $P > 0.05$）（Fig. 4）. Taking into account that this species survived the hot period of the 1920s-1930s and its populations persisted to the 1980s in the Ishikari Bay, high summer water temperatures since the 1990s should not have decreased *M. trossulus* populations to near extinction levels. On the other hand, it is certain that populations of this species persisted at many sites in Lake Saloma and Lake Notoro, and on the Nemuro Strait and eastern Pacific coasts into the 2010s.

Hybrids and Intermediate type

Inoue *et al*.（1997）found the hybrids between *M. trossulus* and *M. galloprovincialis* at Hiura and Hakodate on the Tsugaru Strait coast in 1993 and 1995（open circles in Fig. 6B）. Brannock *et al*.（2009）showed the occurrence of the hybrids at 14 sites（closed circles in Fig. 6B）in 2004 and 2006. Although the maximum life span of the hybrids has remained unknown, these findings suggest that hybridization between the species had occurred in the 1990s at the latest and progressed in the 2000s.

Kuwahara（2001）found the Intermediate type at four sites; Muroran on the western Pacific coast, Lake Saloma, Abashiri, and Rausu on the Okhotsk coast. Iwasaki *et al*.（2012）reported four localities of the Intermediate type collected in the 1980s, Oshoro on the Sea of Japan coast, Kuroiwa, Mori, and Akkeshi on the Pacific coast（closed squares in Fig. 6B）. Muroran, Abashiri, Rausu, and Akkeshi were 4 of the 14 sites where Brannock *et al*.（2009）found hybrids. The present study showed the occurrence of the Intermediate type at 28 sites（Figs. 2 & 3）, whose distribution pattern was similar to that reported by Brannock *et al*.（2009）. Incidentally, I have found no Intermediate types at 304 sites along the coast of the Hoshu Island（Iwasaki, unpublished）where *M. trossulus* has never been discovered but *M. galloprovincialis* is abundant（Suchanek *et al*., 1997; Kuwahara, 2001, Iwasaki *et al*., 2012, 2017; Iwasaki, 2017b）. These results suggest that the Intermediate type is a hybrid between *M. trossulus* and *M. galloprovincialis*. In that case, *M. trossulus* populations might have continued to survive in the early 2010s in Ishikari Bay because the

Intermediate type was found at Takashima（J7）near Oshoro in the present study. Genetic analyses on the Intermediate type with comparison to *M. trossulus* and *M. galloprovincialis* are essential to identify its taxonomic existence.

Spaciotemporal distribution of M. galloprovinciali

The first reliable record of the discovery of *M. galloprovincialis* on Hokkaido was at Oshoro in 1978（Iwasaki *et al*., 2012）. However, given that the species was widely distributed by the 1980s（10 sites of closed squares in Fig. 6C）, its first invasion into Hokkaido must have occurred far earlier. Since the 2000s, this species has dominated the Sea of Japan coast and appears to have spread all over Hokkaido（Figs. 2, 3, 6C）.

The present study revealed that（i）this species predominated even on the Okhotsk coast and the western Pacific coast and（ii）its occurrence and relative abundance among the three mussel types were not affected by PI（the geographical range of shipping traffic at the harbors, Table 2）and tended to remain low on the eastern Pacific coast and the Nemuro Strait coast（Fig. 2）. The previous records and the results of the present study appear to suggest two possibilities;（i）range extension of this species from east to west has been completed on the Sea of Japan coast and western Pacific coast and has been in progress on the eastern Pacific coast and Nemuro Strait coasts, and（ii）there is some environmental or biological factor controlling its abundance, whose intensity gradually changes in the east–west direction. In connection with the latter, Brannock *et al*.（2009）, who found two distinct hybrid zones at northern（Okhotsk coast）and southern（Pacific coast）Hokkaido, suggested the importance of coastal currents in maintaining the genetic structure of *Mytilus* spp. They hypothesized that（i）Tsugaru Warm Current flowing eastward through the Tsugaru Strait provides a vector of transport of *M. galloprovincials* along the western Pacific coast,（ii）Oyashio Cold Current traveling westward provides the same for *M. trossulus* along the eastern Pacific coast,（iii）such coastal circulation plays a significant role in maintaining the genetic structure of *Mytilus* spp. and the southern hybrid zone on the Pacific coast,（iv）Soya Warm Current（a branch of Tsushima Warm Current）flowing eastward provides a vector of transport of *M. galloprovincialis* along the Sea of Japan and Okhotsk coasts,（v）East Sakhalin Current traveling southward provides the same for *M. trossulus* along the Okhotsk coast, and（vi）the interaction of the two currents causes turbulent mixing and contributes to the mosaic genetic structure of the northern hybrid zone along the Okhotsk coast.

The results of the present study appear to support their hypotheses at least on the Pacific coast because the relative abundances of the three mussel types differed between the western and eastern Pacific coasts with a noticeable shift around Cape Erimo（between P10 and P11 in Fig. 2）, as reported by Brannock *et al.*（2009）. However, the relative abundance of *M. galloprovincialis* on the Okhotsk, Nemuro Strait, and eastern Pacific coasts in the present study was higher than that in the work of Brannock et al. (2009). Even if the hypotheses proposed by Brannock *et al*.（2009）are correct, this difference might suggest that *M. galloprovincialis* has increased in abundance relative to that of *M. trossulus* in the above coastal areas from the 2000s to the 2010s. As for the Sea of Japan coast, Brannock *et al*.（2009）did not refer to the occurrence of *M. trossulus* in Ishikari Bay before 1990s（Kuwahara, 2001）. Given the occurrence of *M. trossulus* in the bay and at Oshoro in the 1970s and 1980s（Iwasaki *et al.*, 2012）and the earliest record on the invasion of *M. galloprovincialis* at Oshoro, the absence of *M. trossulus* on the Sea of Japan coast since 1990s may have been caused by the expansion of *M. galloprovincialis* populations and their competitive exclusion, which might have occurred earlier than in other coastal areas.

Micro-distribution of mussels

To my knowledge, there has been only one study showing the difference in micro-distribution of *M. trossulus* and *M. galloprovincialis* in their sympatric areas. Braby & Somero（2005）revealed that *M. trossulus* inhabits inner bay areas with lower salinity（10 – 30）than *M. galloprovincialis*（20 – 37）in San Francisco Bay. However, the present study detected no such difference in salinity（Table 2）. The scale and geographical range of shipping traffic of the ports surveyed（PI）influenced neither the occurrence nor the relative abundance of the species（Table 2）. Both species and hybrids were seldom found on natural shores out of the harbors, suggesting that there might have been some factor inhibiting the inhabitation of the mussels on the shores, such as the abundance of native competitors or predators（Stachowicz *et al.*, 1999）.

V. Conclusion

Overall comparison of the results of the present and previous studies suggests that, during the last 100 years, *M. trossulus* has been very few in number and with a limited distribution or has become very rare along the Sea of Japan coast, while *M. galloprovincialis* has invaded and extended its distribution at harbors all around Hokkaido.

Considering the recent expansion of *M. galloprovincialis* all around Hokkaido, this species may spread over natural shores and have negative impacts on native species. It will be necessary to perform monitoring and take appropriate precautionary measures to limit or prevent such negative impacts.

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和文要旨

北海道沿岸における在来種キタノムラサキイガイと外来種ムラサキイガイの分布

岩崎敬二

北海道と礼文島、利尻島、奥尻島の海岸120カ所（港湾83カ所、自然海岸37カ所）で、イガイ科二枚貝の在来種キタノムラサキイガイと外来種ムラサキイガイの分布を調査した。キタノムラサキイガイはオホーツク海沿岸、根室海峡、太平洋沿岸の29カ所で発見されたが、日本海沿岸と3つの島では全く確認できなかった。ムラサキイガイは北海道全域の沿岸と3つの島の73カ所に分布していた。殻の形態から見て両種の交雑個体と考えられる「中間型」は、キタノムラサキイガイと似た分布を示し、オホーツク海沿岸、根室海峡、太平洋岸の27カ所で発見された。両種と中間型の総個体数に占めるムラサキイガイの割合は東方に向かって低下し、キタノムラサキイガイと中間型の割合は東方に向かって増加していた。調査場所の塩分と港湾の規模（寄港する船舶の航行範囲）は、両種と中間型の生息の有無と個体数の割合のいずれについても有意な関係は検出できなかった。

【キーワード】分布、北海道、キタノムラサキイガイ、ムラサキイガイ、外来種

Appendix Study sites. Gray pattern indicates that an additional survey was conducted on a rocky shore outside the harbor.

Sea	Site No.	Site Name	Latitude	Longitude	Date
Sea of Okhotsuk	O1	Hamaonishibetsu	45° 28' 39"	141° 58' 32"	3 Sept. 2012
	O2	Hamatonbetsu	45° 8' 7"	142° 23' 31"	3 Sept. 2012
	O3	Esashi	44° 56' 19"	142° 35' 18"	3 Sept. 2012
	O4	Otoshibe	44° 42' 26"	142° 48' 52"	3 Sept. 2012
	O5	Monbetsu	44° 20' 44"	143° 21' 37"	3 Sept. 2012
	S1	Hamasaroma	44° 5' 31"	143° 55' 38"	4 Sept. 2012
	S2	Barou	44° 9' 0"	143° 42' 31"	4 Sept. 2012
	S3	Teinei	44° 11' 35"	143° 40' 18"	4 Sept. 2012
	S4	Toetoko	44° 11' 9"	143° 44' 32"	4 Sept. 2012
	O6	Tokoro	44° 7' 32"	144° 6' 6"	4 Sept. 2012
	No1	Notoro	44° 2' 20"	144° 10' 49"	4 Sept. 2012
	No2	Uharanai	44° 0' 54"	144° 6' 52"	4 Sept. 2012
	O7	Abashiri	44° 1' 14"	144° 16' 53"	5 Sept. 2012
	O8	Utoro	44° 4' 4"	144° 59' 23"	5 Sept. 2012
Nemuro Strait	N1	Rausu	44° 1' 17"	145° 11' 55"	5 Sept. 2012
	N2	Kunbetsu	43° 47' 41"	145° 3' 48"	5 Sept. 2012
	N3	Shibetsu	43° 40' 9"	145° 7' 41"	5 Sept. 2012
	N4	Odaitou	43° 34' 6"	145° 13' 21"	5 Sept. 2012
	N5	Nemuro	43° 20' 25"	145° 35' 9"	6 Sept. 2012
Pacific Ocean	P1	Hanasaki	43° 16' 59"	145° 34' 13"	6 Sept. 2012
	P2	Ochiishi	43° 11' 19"	145° 30' 36"	6 Sept. 2012
	P3	Kiritappu	43° 4' 55"	145° 7' 27"	6 Sept. 2012
	P4	Akkeshi	43° 2' 37"	144° 51' 15"	6 Sept. 2012
	P5	Kushironishi	43° 0' 5"	144° 19' 22"	3 Sept. 2013
	P6	Shiranuka	42° 57' 10"	144° 5' 5"	3 Sept. 2013
	P7	Atsunai	42° 48' 24"	143° 49' 17"	3 Sept. 2013
	P8	Otsu	42° 40' 39"	143° 38' 13"	3 Sept. 2013
	P9	Tokachi	42° 17' 49"	143° 19' 16"	3 Sept. 2013
	P10	Meguro	42° 7' 11"	143° 19' 1"	4 Sept. 2013
	P11	Samani	42° 7' 38"	142° 54' 50"	4 Sept. 2013
	P12	Higashishizunai	42° 19' 28"	142° 22' 16"	4 Sept. 2013
	P13	Shiomi	42° 32' 52"	141° 56' 30"	4 Sept. 2013
	P14	Tomakomaihigashi	42° 36' 42"	141° 48' 37"	4 Sept. 2013
	P15	Shiraoi	42° 31' 19"	141° 18' 49"	5 Sept. 2013
	P16	Muroran	42° 20' 8"	140° 57' 42"	5 Sept. 2013
	P17	Toyoura	42° 35' 1"	140° 42' 19"	5 Sept. 2013
	P18	Oshamanbe	42° 31' 44"	140° 23' 50"	5 Sept. 2013
	P19	Yakumo	42° 15' 16"	140° 17' 14"	5 Sept. 2013
	P20	Mori	42° 6' 40"	140° 35' 44"	6 Sept. 2013
	P21	Osatsube	41° 53' 35"	141° 0' 52"	6 Sept. 2013
Tsugaru Strait	T1	Oma	41° 44' 39"	141° 4' 31"	6 Sept. 2013
	T2	Hakodate	41° 46' 21"	140° 42' 2"	6 Sept. 2013
	T3	Matsumae	41° 25' 40"	140° 6' 39"	13 Sept. 2010

Sea	Site No.	Site Name	Latitude	Longitude	Date
Sea of Japan	J1	Esashi	41° 52' 1"	140° 7' 18"	13 Sept. 2010
	J2	Setana	42° 27' 20"	139° 50' 54"	13 Sept. 2010
	J3	Iwanai	42° 59' 6"	140° 31' 2"	13 Sept. 2010
	J4	Kawashira	43° 12' 37"	140° 20' 17"	13 Sept. 2010
	J5	Irika	43° 21' 55"	140° 28' 6"	14 Sept. 2010
	J6	Bikuni	43° 17' 54"	140° 35' 59"	14 Sept. 2010
	J7	Takashima	43° 13' 10"	141° 0' 54"	14 Sept. 2010
	J8	Otaru	43° 11' 39"	141° 0' 49"	14 Sept. 2010
	J9	Ishikari	43° 12' 39"	141° 17' 48"	14 Sept. 2010
	J10	Hamamasu	43° 34' 50"	141° 23' 11"	14 Sept. 2010
	J11	Rumoi	43° 57' 3"	141° 38' 19"	15 Sept. 2010
	J12	Haboro	44° 22' 3"	141° 41' 39"	15 Sept. 2010
	J13	Onbetsu	44° 43' 17"	141° 47' 3"	15 Sept. 2010
	J14	Bakkai	45° 18' 31"	141° 37' 9"	15 Sept. 2010
	J15	Esandomari	45° 23' 51"	141° 38' 14"	15 Sept. 2010
	J16	Wakkanai	45° 24' 31"	141° 40' 47"	16 Sept. 2010
	J17	Tomiiso	45° 27' 40"	141° 52' 41"	16 Sept. 2010
	J18	Kiyohama	45° 29' 8"	141° 52' 46"	16 Sept. 2010
	J19	Soya	45° 28' 15"	14° 50' 35"	16 Sept. 2010
Okushiri Island	Ok1	Okushiri	42° 10' 40"	139° 31' 4"	28 Aug. 2014
	Ok2	Akaishi	42° 8' 48"	139° 31' 11"	28 Aug. 2014
	Ok3	Aonae	42° 3' 36"	139° 27' 2"	28 Aug. 2014
	Ok4	Kamuiwaki	42° 10' 18"	139° 24' 38"	28 Aug. 2014
Rishiri Island	Ri1	Oshidomari	45° 14' 37"	141° 13' 40"	7 Jun. 2014
	Ri2	Ochusinai	45° 13' 31"	141° 16' 47"	7 Jun. 2014
	Ri3	Asahihama	45° 11' 37"	141° 19' 3"	7 Jun. 2014
	Ri4	Oniwaki	45° 8' 6"	141° 18' 29"	7 Jun. 2014
	Ri5	Senhousi	45° 6' 50"	141° 12' 28"	7 Jun. 2014
	Ri6	Randomari	45° 9' 15"	141° 9' 6"	8 Jun. 2014
	Ri7	Kutsugata	45° 11' 15"	141° 8' 15"	8 Jun. 2014
	Ri8	Shinminato	45° 13' 6"	141° 8' 15"	8 Jun. 2014
	Ri9	Motodomari	45° 14' 34"	141° 10' 26"	8 Jun. 2014
Rebun Island	Re1	Saioro	45° 23' 21"	141° 3' 15"	6 Jun. 2014
	Re2	Kabuka	45° 18' 7"	141° 2' 52"	6 Jun. 2014
	Re3	Sashitoji	45° 16' 46"	141° 2' 45"	6 Jun. 2014
	Re4	Shiretoko	45° 16' 29"	141° 2' 2"	6 Jun. 2014
	Re5	Nishiuedomari	45° 24' 42"	140° 59' 19"	5 Jun. 2014
	Re6	Teppu	45° 25' 2"	140° 59'247"	5 Jun. 2014
	Re7	Sukoton	45° 27' 22"	140° 58' 30"	5 Jun. 2014
	Re8	Funadomari	45° 27' 8"	141° 2' 4"	5 Jun. 2014