Geographic distribution of nonindigenous marine invertebrates on 64 islands in Japanese waters

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日本の 64 の島嶼における外来海産無脊椎動物の地理的分布

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Abstract

Surveys of nonindigenous marine invertebrates（NMI）were conducted at 424 sites（218 harbors and 206 rocky, boulder, or embanked shores outside of the harbors）on 64 inhabited islands in Japanese waters from 2014 to 2017. Eleven species of NMI were discovered during the surveys: the calyptraeid slipper snail, *Crepidula onyx*; three mytilid mussels, *Mytilus galloprovincialis*, *Perna viridis*, and *Xenostrobus securis*; five balanid barnacles, *Amphibalanus amphitrite*, *A. eburneus*, *A. improvisus*, *Balanus glandula*, and *Perforatus perforatus*; the portunid crab, *Carcinus aestuarii*; and the ascidiid ascidian, *Ascidiella aspersa*. One or more species of NMI were found at 177 sites on 55 islands. In total, one or more species of NMI were present at more than 40% of the study sites and more than 85% of islands surveyed. They occurred exclusively at the harbors（148 out of 206 harbors）, while they were rarely found on the shores（29 out of 206 shores）. Multiple Poisson regression analysis revealed that the latitude, the index of artificial environment, and the number of indigenous sessile invertebrate species at a site had positive relationships with the number of NMI at a site, and the number of indigenous motile invertebrate species at a site had a negative relationship with the number of NMI. This suggested that high latitude, a higher degree of artificial environment, and higher species abundance of indigenous sessile invertebrates had positive effects on the occurrence of NMI, and the species abundance of indigenous motile invertebrates had a negative effect on NMI.

Keywords: Geographic distribution, Human-mediated introduction, Japanese islands, Marine invertebrates, Nonindigenous species

I Introduction

The human-mediated introduction of marine organisms beyond their native ranges has long been of great

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interest to marine biologists. Since the early 20th century, a marked increase in the number of many species of nonindigenous marine organisms and rapid expansions of their distributional ranges have been reported in several countries, including Japan, sea areas and continents[1)–5)]. Information on other aspects of the biological invasions[6)], e.g., vectors from donor to recipient areas, the physiology and ecology of nonindigenous organisms, and the impacts of nonindigenous organisms on native ecosystems and industries, has been steadily accumulated to elucidate the patterns and processes of invasions, develop risk assessments, and manage marine invasions[7),8)].

It is well understood that the native terrestrial fauna and flora on many oceanic islands is unique and endemic to each of these islands and are thus vulnerable to biological invasions[9)]. In contrast, there have been very few reports about marine biological invasions of islands relative to reports on terrestrial invasions of islands and on marine invasions to mainland coasts. Exceptions include reports of marine biological invasions on Guam[10)], American Samoa[11)] and the Hawaiian Islands[12)–15)]. Environmental and biogeographic factors affecting the presence or absence of nonindigenous marine organisms and their species abundances on islands have not been revealed, again with the exception of Hawaii[13)].

Japan has many islands, including both oceanic and continental islands; these islands have various origins such as coral-reef upheaval, volcanic orogenesis, crustal folding, and land erosion. For the four large main islands (Hokkaido, Honshu, Shikoku, and Kyushu Islands; hereafter referred to as the Main-islands), which have large-scale international ports, the occurrence of nonindigenous marine organisms has been revealed by many researchers since the 1950s[3)–5)]. For the remaining islands and archipelagos, however, there were no systematic biogeographic studies on the distribution of nonindigenous marine species until the early 2000s, although there were isolated reports of one or more nonindigenous species during studies of native coastal fauna at various islands and island groups. Examples include Sado Island[16)–18)], the Nansei Islands[19)–22)], and the Ogasawara Islands[23)]. All occurrences on the Nansei and Ogasawara Islands were considered to have been temporary and ephemeral, having arisen due to stranded driftwood or plastic buoys.

Since 2014, the author has conducted surveys of the geographic distribution of nonindigenous marine invertebrates (hereafter referred to as NMI) at 424 sites on 64 inhabited islands (excluding the Main-islands) in Japanese waters. The results of the surveys performed on the Izu Islands in the Pacific Ocean, four small islands in the Sea of Japan (Tobishima, Awashima, Hegurajima, and Mishima), and the Koshikishima Islands in the East China Sea, have been published elsewhere[24)–26)]. All of these surveys revealed that the species abundance of NMI was much greater in harbors compared with shores outside of the harbors. However, the environmental and biological factors affecting the number of NMI species differed among the island groups.

In the present study, NMI were found during every survey of all 64 islands. Factors affecting the species abundance of NMI at each study site were investigated, based on six variables: the location of the study site (latitude and longitude), salinity, the degree of artificiality of the environment, and the number of indigenous invertebrates (both sessile and motile). Overall trends for the occurrence of NMI on Japanese islands are discussed, focusing on the effects of latitude and the artificial and biological environments at the study sites.

II Study sites and methods

Surveys were conducted on 64 inhabited islands from May 2014 to May 2018 (Fig. 1). The dates of the surveys, the area of each island, and the number of sites surveyed on each island are shown in Tables 1 & 2. The names of the islands in English are based on the uniform standard as coordinated by the Geospatial Information Authority of Japan in March 2014, and the area of the Sea of Japan is delimited in accordance with the definition of the International Hydrographic Organization. Most islands with a population of more than 500 people and located more than 10 km apart from the Main-islands (except for ten islands in the Nagasaki, Kagoshima and Okinawa Prefectures) were surveyed. The majority of islands located within 10

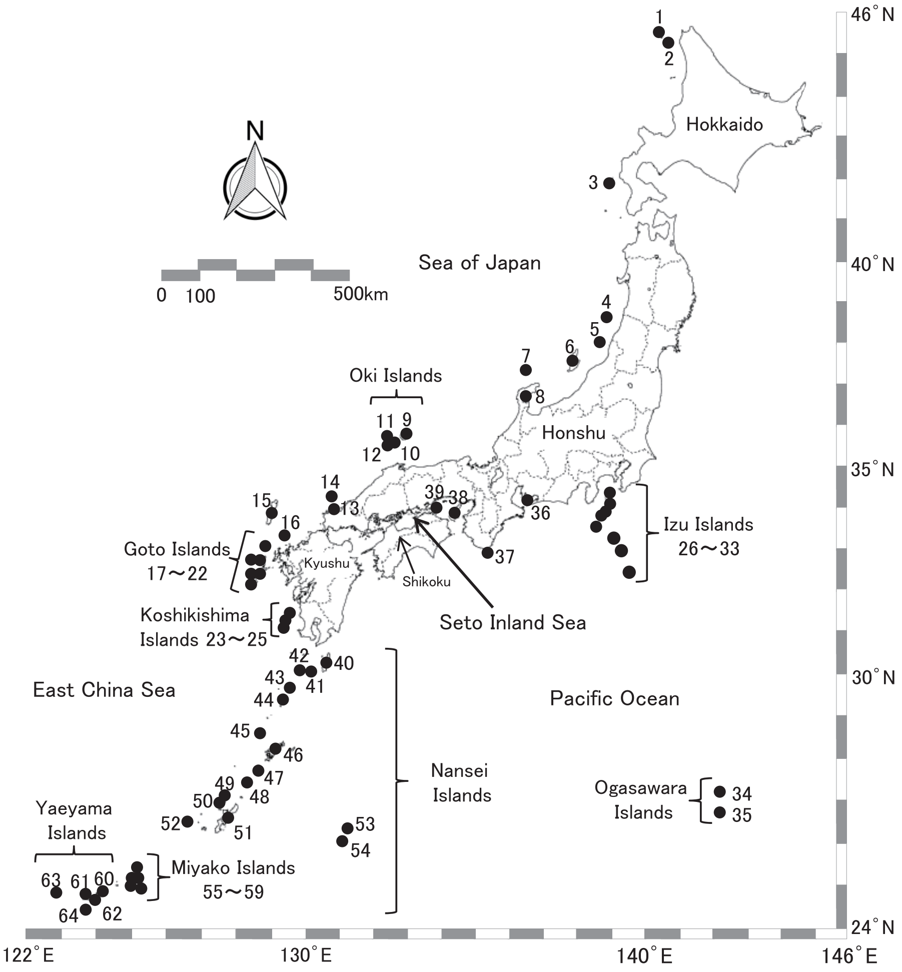

Fig. 1 Sixty-four islands surveyed. See Tables 1 & 2 for island names.

km of the Main-islands were not surveyed for two reasons; 1) they are numerous, 2) planktonic larvae of NMI can easily reach the islands from the Main-islands due to natural dispersal by coastal currents, and

Table 1 Thirty-nine islands surveyed in the Sea of Japan, East China Sea and Pacific Ocean. ECS: East China Sea, SIS: Seto Inland Sea, NMI: nonindigenous marine invertebrates, Co: *Crepidula onyx*, Mg: *Mytilus galloprovincialis*, Pv: *Perna viridis*, Xs: *Xenostrobus securis*, Aa: *Amphibalanus amphitrite*, Ae: *A. eburneus*, Ai: *A. improvisus*, Bg: *Balanus grandula*, Pp: *Perforatus perforatus*, Ca: *Carcinus aestuarii*, As: *Ascidiella aspersa*.

Sea	No.	Island name	Area (km^2)	Date of survey	No. sites	NMI found on each island	Mean no. NMI
Sea of Japan	1	Rebuntou	81.3	Jun. 4-6, 2014	16	Mg	0.44
	2	Rishiritou	182.1	Jun. 6-8, 2014	18	Mg	0.50
	3	Okushiritou	142.7	Aug. 28-29, 2014	8	Mg, Bg, Pp, As	0.88
	4	Tobisima	2.7	Jul. 25-26, 2014	6	Mg, Aa, Ai	1.00
	5	Awashima	9.7	Sep. 22, 2014	6	Mg, Aa, Ai, Pp	1.17
	6	Sadogashima	854.8	Sep. 19-21, 2014	18	Co, Mg, Aa, Ae, Ai, Pp	1.56
	7	Hegurajima	0.6	May 26, 2017	7	Mg, Aa	0.57
	8	Notojima	46.6	May 27, 2017	4	Mg, Xs, Aa, Ae,Ai	2.25
	9	Dogo	241.5	Sep. 5-6, 2016	8	Mg, Aa, Ae, Ai	0.75
	10	Nakanosima	32.3	Sep. 6, 2016	6	Mg, Aa, Ae	1.17
	11	Nishinoshima	55.8	Sep.8, 2016	5	Mg, Aa, Ae	1.40
	12	Chiburijima	13.0	Sep.7, 2016	5	Mg	0.60
	13	Omishima	14.0	May 3, 2014	3	Mg, Aa	1.00
	14	Mishima	7.8	May 1-2, 2014	7	Aa, Ae	1.00
	15	Tsushima	695.7	Jul. 24-25, 2015	10	Mg, Aa, Ai	1.50
	16	Iki	134.6	Jul. 26-27, 2015	8	Mg, Aa, Ai	1.25
	17	Ukujima	24.9	Sep. 29, 2015	4	Mg	0.25
	18	Ojikajima	12.3	Sep. 29, 2015	2	Mg, Aa,	2.00
	19	Madarajima	1.6	Sep. 29, 2015	2	Mg,	0.50
	20	Nakadorijima	168.4	Sep. 28-30, 2015	8	Mg, Aa, Ae, Ai	1.00
	21	Wakamatsujima	31.1	Sep. 28, 2015	2	Mg	0.50
	22	Fukuejima	326.3	Sep. 26-27, 2015	8	Mg, Aa, Ae, Ai	1.63
ECS	23	Kamikoshikishima	44.2	Oct.13-14, 2017	8	Mg, Pv, Aa	0.88
	24	Nakakoshikishima	7.3	Oct. 14, 2017	2	Mg, Aa	1.00
	25	Shimokosikishima	65.6	Oct. 13, 2017	6	Mg, Aa	1.00
Pacific Ocean	26	Izuoshima	90.7	Jul. 3-4, 2015	8	Co, Mg, Aa, Ai	0.75
	27	Toshima	4.1	Jul. 5, 2015	2	Mg	0.50
	28	Niijima	23.0	Sep. 26, 2015	6	Mg	0.33
	29	Shikinejima	3.7	Sep. 27, 2015	7	Mg	0.14
	30	Kozushima	18.2	Sep. 28, 2015	4	Mg	0.25
	31	Miyakejima	55.2	May 2-3, 2015	11	Aa	0.09
	32	Mikurajima	20.5	May 1, 2015	4	—	0.00
	33	Hachijojima	69.1	Apr. 29-30, 2015	9	Aa	0.38
	34	Chichijima	23.5	Jun. 23-24, 2017	8	Mg, Aa	0.25
	35	Hahajima	19.9	Jun. 25, 2017	4	Aa	0.40
	36	Sakushima	1.7	Sep. 3, 2017	6	Co, Mg, Aa, Ae, Ai	2.00
	37	Kiioshima	9.5	Sep. 21, 2017	3	Mg, Pv, Aa, Ae, Ai	2.33
SIS	38	Awajishima	592.5	Sep. 5-6, 2017	9	Co, Mg, Aa, Ae, Ai, Ca	2.00
	39	Shodoshima	153.3	Mar. 28-29, 2018	6	Co, Mg, Aa, Ae, Ai, Ca	2.00

thus the process of biological invasion on the islands will be similar to that on the coastlines of the Main-islands. Only six islands within 10 km of the Main-islands（Sakushima, Notojima, Kiioshima, Awajishima, Shodoshima, and Omijima）were surveyed and included in the present study. At least three harbors were surveyed on each of the islands that had more than two harbors. All harbors were surveyed on each of the small islands that had just only one or two harbors.

Most surveys were carried out as a pair, comprising one harbor and one shore location with hard substrata（rocky, boulder, or embanked shore just outside of the harbor）at each site. The harbor or the shore is hereafter referred to as a subsite. It was not possible to conduct surveys at twelve of the shore locations due to either a shortage of survey time or the presence of strong waves. In total, 424 subsites（218 harbors and 206 rocky, boulder or embanked shores outside of the harbors）on 64 islands were surveyed（Appendices 1–3）.

At each subsite, a one-hour search for NMI was conducted in the intertidal and upper subtidal zones, at a depth of up to 50 cm, and any NMI or NMI-like species were collected from the hard substrata（i.e., concrete or rock quay-walls, buoys, ropes in the harbors, bedrock, boulders, and concrete or rock quay-

Table 2 Twenty-five islands surveyed in the Nansei Islands. See Table 1 for English names of the islands. NMI: nonindigenous marine invertebrates, Mg: *Mytilus galloprovincialis*, Pv: *Perna viridis*, Aa: *Amphibalanus amphitrite*, Ae: *A. eburneus*.

Sea	No.	Island name	Area（km^2）	Date of survey	No. sites	NMI found on each island	Mean no. NMI
East China Sea / Pacific Ocean（Nansei Islands）	40	Tanegashima	444.3	Jul. 28-29, 2016	16	Mg, Aa, Ae	0.31
	41	Yakushima	504.3	Jul 30-31, 2016	12	Aa	0.17
	42	Kuchinoerabujima	35.8	Jul.31, 2016	1	—	0.00
	43	Nakanoshima	34.4	Apr. 30, 2017	4	—	0.00
	44	Suwanosejima	27.6	May 2, 2017	4	Mg	0.25
	45	Takarajima	7.1	Apr. 29, 2017	2	Mg	1.00
	46	Amamioshima	712.4	Oct. 27-29, 2017	13	Mg, Aa	0.50
	47	Tokunoshima	247.9	Oct. 30-31, 2017	8	Aa	0.20
	48	Okinoerabujima	93.7	Nov. 1-2, 2017	7	Aa	0.33
	49	Iheyajima	20.7	Nov. 24-27, 2016	4	—	0.00
	50	Nohojima	1.1	Nov. 26, 2016	2	—	0.00
	51	Okinawajima	1207.0	Nov. 26, 2016	22	Pv, Aa	0.64
	52	Kumejima	59.5	Nov. 28, 2016	6	Aa	0.67
	53	Kitadaitojima	11.9	Apr. 29-30, 2018	6	—	0.00
	54	Minamidaitojima	30.5	May 1-2, 2018	8	Mg	0.13
	55	Miyakojima	158.9	Mar. 20-22, 2016	9	Aa	0.30
	56	Ikemajima	2.8	Mar. 20, 2016	2	Aa	1.00
	57	Irabujima	29.1	Mar. 21, 2016	6	Aa	0.17
	58	Shimochijima	9.7	Mar. 21, 2016	1	—	0.00
	59	Kurumajima	2.8	Mar. 22, 2016	1	—	0.00
	60	Ishigakijima	222.2	Apr. 28-29, 2016	8	Aa	0.56
	61	Iriomotejima	289.6	Apr. 29-30, 2016	10	Aa	0.22
	62	Kuroshima	10.0	May 3, 2016	2	Aa	0.33
	63	Yonagunijima	29.0	May 2, 2016	4	Aa	0.20
	64	Haterumajima	12.7	May 1, 2016	2	—	0.00

walls on the shores). All invertebrates were qualitatively collected using a scraper or a mussel collector (15 cm aperture, 7 cm depth, 6 cm height, with a 2-mm nylon net, No. 548, Shoeisya, Co. LTD., Tokyo), the latter of which was attached to the tip of a three-meter fishing rod. All invertebrates were preserved in 5% formalin. In addition, all native invertebrates observed during the survey were recorded. Salinity was measured at the sea surface using a refractometer (S-millE, ATAGO Ltd., Tokyo).

All specimens were taken to the laboratory and sorted, and any invertebrates more than 5 mm in length were identified according to the references 27) – 31). Indigenous invertebrates that could not be identified to the species level were classified into subgenus, genus, subfamily or family and included in statistical analyses separately as one taxon.

An index of Artificial Environment (IAE) was used to estimate the degree of artificial environments and the scale and quantity of ship traffic at each subsite. The IAE was converted into a numerical form from 1 to 6, according to the following criteria. 1) A rocky or boulder shore. 2) Rock quay-walls outside of a harbor. 3) Wooden or iron piers, or concrete quay-walls outside of a harbor. 4) A small scale fishing port of the Type 1 of the Fishing Port Code (hereafter referred to as FPC) provided by the Fisheries Agency of Japan (Type 1 is a fishing port that is used for only local fisheries). 5) A medium-scale fishing port of FPC Type 2 (used for fisheries more widespread than an FPC Type 1 fishing port, but does not fall into the FPC Type 3 fishing port or FPC Type 4 fishing port (located on an isolated island or in a rural area, and used as a refuge or to develop new fishing grounds). 6) A fishing port of FPC Type 3 (used for ships travelling around the nation) or commercial ports, including those that are a port-of-call for the ferries from Main-island ports.

To analyze factors affecting the species abundance of NMI at each subsite, a multiple Poisson regression analysis was performed for the number of NMI species at each subsite, using six independent variables. These were latitude (N) and longitude (E) converted into decimal values; salinity; IAE; the number of indigenous sessile invertebrate (hereafter referred to as ISI) species (sponges, bryozoans, tube-dwelling polychaetes, mussels, oysters, barnacles, and ascidians; all are competitors of NMI); and the number of indigenous motile invertebrate (hereafter referred to as IMI) species (limpets, snails, shrimps, crabs, and free-ranging polychaetes; all are predators of NMI) at the subsite. For the analysis, all the subsites were treated as independent from one another with regard to the conditions and environment involving biological invasions. The number of NMI species, IAE, and the numbers of ISI species and IMI species are integers with discrete distributions. Accordingly, the relationships between the number of NMI species and the other six factors were analyzed using multiple Poisson regression performed with a generalized linear model (GLM) using RStudio (ver. 1.2.1335, RStudio, Inc).

III Results

III–1 Nonindigenous marine invertebrates discovered in this study

Eleven NMI species were discovered in the present study. These were the slipper snail, *Crepidula onyx*

Table 3 Number of islands and study sites where nonindigenous marine invertebrates（NMI）were found.

NMI	No. islands	No. sites		
		Harbor	Shore	Total
Crepidula onyx	5	3	2	5
Mytilus galloprovincialis	39	109	15	124
Perna viridis	3	5	1	6
Xenostrobus securis	1	1	0	1
Amphibalanus amphitrite	41	98	18	116
A. eburneus	13	17	3	20
A. improvisus	14	25	0	25
Balanus grandula	1	1	0	1
Perforatus perforatus	3	9	0	9
Carcinus aestuarii	2	2	0	2
Ascidiella aspersa	1	1	0	1

Sowerby, 1814; three mytilid mussels, *Mytilus galloprovincialis* Lamarck, 1819, *Perna viridis*（Linnaeus, 1758）, and *Xenostrobus securis*（Lamarck, 1819）; five balanid barnacles, *Amphibalanus amphitrite*（Darwin, 1854）, *A. eburneus*（Gould, 1841）, *A. improvisus*（Darwin, 1854）, *Balanus glandula* Darwin, 1854, and *Perforatus perforatus*（Bruguière, 1789）; the portunid crab, *Carcinus aestuarii*（Nardo, 1847）; and the ascidiid ascidian, *Ascidiella aspersa*（Müller, 1776）（Tables 1–3）. The North American slipper snail, *C. onyx*, was found on five islands, Sadogashima, Izuoshima, Awajishima, Shodoshima, and Sakushima, the first four of which have an area larger than 50 km^2（Table 1）, and the last three of which were located in inland seas（Fig. 1）. This species occurred in three harbors（Izuoshima, Sakushima and Shodishima）and on two shores（Sadogashima and Awajishima）（Table 3）.

The Mediterranean blue mussel, *M. galloprovincialis*, occurred on 39 widely ranged islands from Rebuntou, the northernmost island in Japan, to the subtropical island of Minamidaitojima（Tables 1&2）. It predominately occurred in harbors and was rarely collected from shores（109 harbors and 15 shores）（Table 3）. The western Pacific green mussel, *P. viridis*, was collected from three islands（Kamikoshikishima, Kiioshima, and Okinawajima）, all of which are located south of 33° latitude（Fig. 1, Table 1）. The Southeast Asian black mussel, *X. securis*, was discovered on just one island, Notojima, located in Nanao Bay, a small bay off the eastern part of the Noto Peninsula（Table 1, Table 3）. The salinity of the subsite where this species occurred was 12, much lower than the mean value for all the 424 sites surveyed（35.8）.

The striped barnacle, *A. amphitrite*, originally from the tropical Pacific Ocean, was found on 41 islands, ranging from Tobishima, the northernmost inhabited island off the Honshu Island in the Sea of Japan, to the most westerly island in Japan, Yonagunijima（Table 1）. This was the only NMI species found on many of the Nansei Islands（Table 2）.

The European ivory barnacle, *A. eburneus*, and the European bay barnacle, *A. improvisus*, occurred on thirteen and fourteen islands, respectively（Tables 1–3）. Their geographic distributions were similar, and they were found exclusively on islands near the Main-islands（Fig. 1, Tables 1&2）, and but were seldom collected from the Nansei islands or the islands off Hokkaido Island. *A. eburneus* occurred in seventeen harbors and on three shores, while *A. improvisus* was only recorded at harbors（25 harbors）（Table 3）.

The North American acorn barnacle, *B. glandula*, and the European ascidiid ascidian, *A. aspersa*, were discovered on just one island, Okushiritou（Table 1）, off Hokkaido Island, and at only one site, respectively

(Table 3).

The European common acorn barnacle, *P. perforatus*, was collected from three islands located in the northern part of the Sea of Japan; Okushiritou, Awashima, and Sadogashima (Table 1). This species occurred in nine harbors in total (Table 3): one harbor on Okushiritou, two harbors on Awashima, and six harbors on Sadogashima.

The Mediterranean green crab, *C. aestuarii*, was found on two islands in the Seto Inland Sea, Awajishima and Shodoshima (Table 1), and in one harbor, respectively (Table 3).

III–2 Number of NMI species per island

The number of NMI species per island ranged from zero to six (Tables 1 & 2). Nine of the islands surveyed showed no NMI present: Mikurajima in the Pacific Ocean, and eight of the Nansei Islands (Tables 1 & 2). The numbers of NMI species per island on the Nansei Islands were in a narrow range from zero to three: one species on fourteen islands, two species on two islands, and three species on one island (Table 2). More than 85% of the islands that make up the Nansei Islands had either none or just one species of NMI. On the other hand, two or more species of NMI were found on more than 60% of the remaining islands (25 of the 39 islands other than the Nansei Islands) (Table 1). The maximum number of NMI species on one island, six species, occurred on Sadogashima, Awajishima, and Shodoshima, and five species were identifies on Notojima, Sakushima, and Kiioshima. Sadogashima is the second-largest island after the four Main-islands of Japan, and the other five islands are located within 7 km of the Main-islands.

III–3 Number of NMI species per subsite and comparison between harbors and shores

The number of NMI species per harbor ranged from 0 to 5 (Table 4): no NMI species in 70 harbors, 1 species in 79 harbors, 2 species in 35 harbors, 3 species in 18 harbors, 4 species in 12 harbors, and 5 species in 4 harbors. On the other hand, 86% of shores surveyed had no NMI species (177 of 206 shores, Table 4). In total, about 60% of the 424 subsites were free from NMI (Table 4). The numbers of NMI species in harbors were significantly greater than those on shores (Mann–Whitney U-test: $W = 35040$, $p<0.001$).

The salinity in the 216 harbors was slightly but significantly lower than that at the 208 shores (Mann–Whitney U-test: $W=26030$, $p<0.01$, Fig. 2A). The numbers of ISI species in the harbors were significantly greater than those on the shores (Mann–Whitney U-test: $W=9387$, $p<0.001$, Fig. 2B). The numbers of IMI species in the harbors were significantly lower than those on the shores (Mann–Whitney U-test: $W=28347$, $p<0.001$, Fig. 2C). The harbors had lower salinity, higher species abundance of ISI, and lower species abundance of IMI compared with the shores.

Table 4 Number of sites (harbors and shores) and NMI species found per site (No. NMI).

No. NMI	No. harbors	No. shores	Total
0	70	177	247
1	79	21	100
2	35	7	42
3	18	0	18
4	12	1	13
5	4	0	4
Total	218	206	424

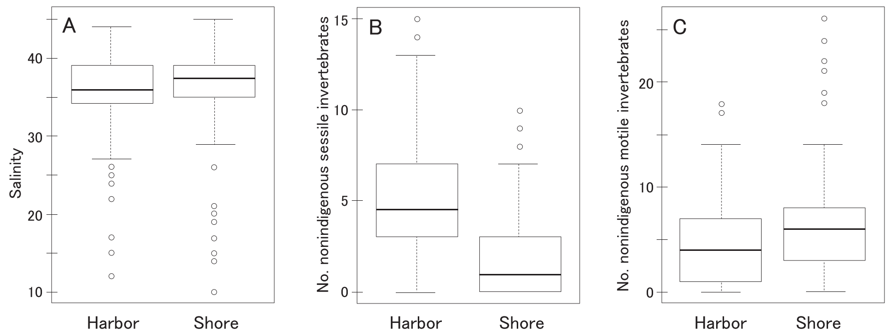

Fig. 2 Comparisons of salinity (A), number of indigenous sessile invertebrate species (B), and number of indigenous motile invertebrate species (C) between harbors and shores.

III–4 Factors affecting NMI species abundance

Table 5 shows the results of a multiple Poisson regression analysis based on the number of NMI species at each subsite against six independent variables at the subsites. The z-values for the slopes of latitude, IAE, and the number of ISI species in the regression equation were significantly positive, indicating that the species abundance of NMI increased exponentially with increasing latitude, IAE, and number of ISI species. The z-value for the slope of the number of IMI species was significantly negative, indicating that the species abundance of NMI decreased exponentially with increasing number of IMI species. The z-vales for the slopes of longitude and salinity based on the regression equation were not significant.

Table 5 Results of multiple Poisson regression for the number of non-indigenous species at each study site for six independent variables. IAE: index of artificial environment, ISI: indigenous sessile invertebrates, IMI: indigenous mortile invertebrates, Estimate: estimated slope of the regression equation, SE: standard error, ***: significant at 0.1%, NS: not siginificant at 5%.

Variable	Estimate	SE	z-value
Latitude	0.064	0.017	3.816***
Longitude	–0.024	0.017	–1.368
IAE	0.273	0.043	6.413***
Salinity	–0.017	0.010	–1.594
No. ISI	0.141	0.019	7.289***
No. IMI	–0.094	0.019	–4.828***
Intercept	–0.006	1.921	–0.003

IV Discussion

In the present study, eleven species of NMI were discovered on the 55 of 64 islands surveyed (Tables 1 & 2), i.e., more than 85% of the islands had one or more species of NMI. However, the species abundance of NMI varied widely among the islands (Tables 1& 2) and subsites (Table 4). The reasons of these differences and the factors affecting the species abundance at the subsites are discussed in the following sections.

IV‒1 Effect of indigenous motile invertebrates

The abundance of NMI species was clearly much lower on the shores than in the harbors (Table 4). Most shores surveyed were less than 100 m away from their nearest harbors, so it would seem likely that propagules such as fertile eggs or larvae of NMI could have easily spread from the harbors to the shores. However, the scarcity of NMI species on the shores suggests that there is some factor inhibiting the establishment of NMI populations in these locations.

Several authors have demonstrated a negative correlation between the number of nonindigenous marine species and the number of indigenous marine species, either in laboratory experiments[32] or in specific sea areas[1, 2, 33, 34]. These authors have suggested that indigenous organisms have negative effects on nonindigenous ones through competition, predation, or grazing activities. The multiple Poisson regression analysis used in the present study revealed similar results: that IMI exert some type of negative effect on NMI. IMI species identified in the present study are snails, crabs, and free-ranging polychaetes, which may exert negative effects on NMI by acting as predators or grazers. The species abundance of IMI was greater on the shores than in the harbors (Fig. 2C), therefore this is likely to have been one of the factors inhibiting the establishment of NMI on the shores.

IV‒2 Effect of latitude

The multiple Poisson regression analysis suggested that higher latitudes, higher IAE, and greater number of ISI species promote the abundance of NMI species (Table 5). With regard to latitude, the native ranges of nine NMI species (the exceptions being *P. viridis* and *A. Amphitrite*) are temperate or boreal sea areas[3, 4, 35, 36], whose latitudes are similar to or north of the areas in the present study. The native ranges of both *P. viridis* and *A. amphitrite* are suggested to be tropical shores of the southwestern Pacific Ocean and the Indian Ocean[37, 38], farther south of the sea areas in the present study. In fact, many of the subtropical islands that form the Nansei Islands were inhabited by just one NMI species, *A. amphitrite* (Table 2). Accordingly, the greater abundance of NMI species with temperate or boreal origins in the present study must have been responsible for the positive relationship between the number of NMI species and latitude. Conversely, higher temperatures may inhibit the establishment of many NMI populations on the islands south of the Main-islands, i.e., the Izu Islands, the Ogasawara Islands, and the Nansei Islands.

IV‒3 Effect of degree of artificial environment

The positive relationship between IAE and the number of NMI species suggests that a larger area of artificial environment and/or greater shipping traffic promote the species abundance of NMI. Marine species inhabiting large international ports in their native sea areas are considered to have been exclusively transported via ocean-going vessels to become nonindigenous species in recipient areas[1, 2]. Thus, many nonindigenous marine organisms will have a tolerance for or even a preference to artificial environments in and around such large ports. Greater volumes of shipping traffic will provide more propagules of NMI to the ports on the islands, resulting in an increased probability of invasion success[39].

Many researchers have reported that the species abundance of nonindigenous marine organisms is greater in inner bays or estuaries with lower salinity compared with outer bays or exposed shores with higher salinity[1),2),33),34),40)]. Salinity, however, did not seem to affect the species abundance of NMI in the present study. There were no large bays or estuaries on any of the 64 islands surveyed, and the salinity at many subsites fell within a narrow but high range, from 33 to 39 (Fig. 2A). This narrow but high range of salinity may have been responsible for the lack of a significant relationship between salinity and species abundance of NMI.

IV–4 Effect of indigenous sessile invertebrates

The positive relationship between ISI and NMI seems initially curious, because ten of the eleven NMI species, with the exception of the crab, *C. aestuarii*, are either sessile or adhesive organisms, and therefore should compete with ISI for space for attachment. However, three of the nonindigenous barnacle species, *A. amphitrite*, *A. eburneus*, and *A. improvisus*, are known to frequently attach themselves to the shells of large bivalves and barnacles[41)]. Sessile organisms such as oysters, mussels, and barnacles have been suggested to promote the settlement and survival of juvenile *X. securis* during their secondary settlement, presumably by providing refuge from strong waves, desiccation, high temperatures, competitors, and predators[42)]. Mytilid mussel beds create complex habitats and a variety of physical and biological micro-environments, and thus harbor a diverse fauna including sessile organisms[43)]. These biological processes that remake habitat structures, now referred to as ecosystem engineering[44)], are considered to be prevalent forces along intertidal and shallow subtidal shores[44)–46)]. Thus, ISI may have promoted the abundance of NMI species on many islands, particularly in harbors (Fig. 2B), through their ecosystem engineering.

There is another hypothesis to explain the positive relationship between NMI and ISI. Most sessile invertebrates are suspension-feeders, and their requirements for survival and their preferred environments (e.g., high levels of plankton and other particulate organic matter, weaker wave action, and more stable substrata for attachment) are similar to one another irrespective of whether they are an indigenous or a nonindigenous species. Accordingly, the numbers of both NMI and ISI species could increase at the same subsites provided with such requirements for survival and preferred environment. From this perspective, many harbors can be considered to offer a preferential environment for sessile invertebrates compared with shores, which would explain the greater abundance of NMI species in harbors compared with the abundance of these species on the shores.

IV–5 Low abundance of NMI species on the Nansei Islands

Coles et al.[13)], who conducted a review of the research into the distribution of nonindigenous marine organisms in the Hawaiian Islands, Guam and American Samoa, reported the occurrences of between two and forty-two species at individual sites on coral reefs around the islands. In the present study, however, very few to no NMI species were found on many of the Nansei Islands (Table 2), several of which have coral reefs on and around their shores. There have been very few reports about nonindigenous marine organisms having invaded the Nansei Islands, except for the barnacle *Amphibalanus zhujiangensis* Ren, 1989[47], and some *M. galloprovincials* stranded on driftwood or plastic buoys[19)–22]. Less shipping traffic into the Nansei Islands, which have few international ports[48], combined with the higher temperatures described above, may be responsible for the scarcity of NMI on the Nansei Islands.

IV−6 Island biogeography of NMI

The present study treated all the subsites as independent from one another with regard to the conditions involving biological invasions. However, such conditions may be similar among the subsites within an island and different among those on different islands, because each island might have its own anthropogenic and biogeographic conditions of marine invasions. For example, nonindigenous marine organisms on islands are most likely to have been introduced exclusively from large ports on other continents via shipping[15]. Then, the distance between large ports on the Main-islands and recipient ports on the islands will be crucial to the success of any invasion of the islands, because the mortality of propagules of nonindigenous organisms during the voyage could be high and positively correlated with increasing distance[49]. Additionally, the amount of shipping traffic an island receives and the number of commercial ports it has will be important for invasion success, because these factors will affect the supply of propagules to the islands, with the amount of propagules closely linked to invasion success[39]. Additionally, the frequency of occurrence on the islands differed greatly among NMI species（Table 3）, suggesting that factors affecting the geographic distribution of NMI or their ability to invade islands also varied among species. Analyses of the effects of such attributes, of both islands and species, on the distribution and species abundance of NMI are essential to elucidate the overall island biogeography of nonindigenous marine organisms in Japanese waters. These effects will be explored in further papers.

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要　旨

日本の 64 の島嶼における外来海産無脊椎動物の地理的分布

岩　崎　敬　二

日本の 64 の島嶼の 424 ヶ所（218 港湾、206 海岸）で、外来海洋生物の分布を調査した。シマメノウフネガイ、ムラサキイガイ、ミドリイガイ、コウロエンカワヒバリガイ、タテジマフジツボ、アメリカフジツボ、ヨーロッパフジツボ、キタアメリカフジツボ、ナンオウフジツボ、チチュウカイミドリガニ、ヨーロッパザラボヤの 11 種の外来種が発見された。1 種以上の外来種が発見されたのは 55 島で、1 種も発見されなかった島は南西諸島の 8 島と伊豆諸島の御蔵島、合計 9 島であった。148 の港湾と 29 の海岸で 1 種以上の外来種が発見され、発見されなかった場所は海岸の方が圧倒的に多かった。調査場所 1 ヶ所あたりの外来種数は海岸よりも港湾の方が多く、緯度が高くなるほど、調査場所の人工環境度が高くなるほど、在来固着性無脊椎動物種数が多くなるほど増加し、在来移動性動物種数が多くなるほど減少する傾向にあった。

キーワード：地理的分布、人為的導入、日本の島嶼、海産無脊椎動物、外来種

Appendix 1 Study sites on 22 islands in the Sea of Japan and East China Sea. Dark and light gray patterns indicate that survey was conducted only at a harbor and only on a shore outside a harbor, respectively. At other sites with white patterns, survey was conducted both in a harbor and on a shore outside the harbor. 1: Ojikajima, 2: Madarajima, 3: Wakamatsujima.

Island	Site name	Latitude	Longitude
Rebuntou	Shirahama	45.46	140.97
	Funadomari	45.45	141.03
	Nairo	45.39	141.05
	Kafuka	45.30	141.05
	Sashitoji	45.28	141.05
	Shiretoko	45.27	141.03
	Nishiuedomari	45.41	140.99
	Teppu	45.41	140.99
Rishiritou	Oshidomari	45.24	141.23
	Ochushinai	45.23	141.28
	Asahihama	45.19	141.32
	Oniwaki	45.14	141.31
	Senpoushi	45.11	141.21
	Randomari	45.15	141.15
	Kutsugata	45.19	141.13
	shinminato	45.21	141.14
	Hondomari	45.25	141.19
Okushiritou	Okushiri	42.18	139.52
	Akaishi	42.15	139.52
	Aonae	42.06	139.45
	Kamuiwaki	42.17	139.41
Tobi-shima	Hoki	39.20	139.56
	Nakamura	39.19	139.55
	Katsuura	39.19	139.55
Awa-shima	Uchiura	38.47	139.26
	Awashima	38.46	139.25
	Kamaya	38.45	139.22
Sadogashima	Washizaki	38.32	138.52
	Urakawa	38.20	138.49
	Ryotsu	38.09	138.44
	Matsugasaki	37.91	138.48
	Akadomari	37.87	138.41
	Ogi	37.81	138.27
	Sawada	37.96	138.34
	Himezu	38.08	138.24
	Hiranezaki	38.12	138.27
Hegurajima	Ebisu-jinjya	37.85	136.92
	Hegurakou	37.85	136.92
	Heguragyokou	37.85	136.92
	Omuta-jinjya	37.85	136.92
Noto-jima	Kamojima	37.13	136.98
	Enome	37.13	136.98
Dogo	Fuse	36.29	133.36
	Ushiki	36.28	133.37
	Saigou	36.20	133.33
	Omosu	36.29	133.21
Nakano-shima	Toyoda	36.11	133.13
	Saki	36.05	133.09
	Hishiura	36.10	133.08
Nishino-shima	Beppu	36.11	133.04
	Funakoshi	36.11	133.01
	Uragou	36.10	132.99
Chiburi-jima	Kurii	36.02	133.04
	Chibu	36.01	133.04
	Nibu	36.01	133.03
Omi-shima	Odomari	34.42	131.21
	Ohibi	34.42	131.21
Mishima	Uzu	34.78	131.14
	Utsu	34.78	131.14
	Honmura east	34.76	131.15
	Honmura north	34.76	131.15
	Honmura west	34.76	131.15
Tsushima	Hidakatsu	34.65	129.47
	Hitoe	34.53	129.45
	Izuhara	34.20	129.29
	Tsutsu	34.12	129.18
	Takeshiki	34.30	129.30
Iki	Katsumoto	33.85	129.69
	Ashibe	33.81	129.76
	Intsuji	33.74	129.76
	Gonoura	33.74	129.69
Uku-jima	Ukutaira	33.26	129.13
	Kamiura	33.25	129.09
1	Ojika	33.19	129.06
2	Madara	33.21	129.03
Nakadori-jima	Arikawa	32.99	129.11
	Narao	32.84	129.06
	Aokata	32.98	129.06
	Nama	33.02	129.07
3	Wakamatsu	32.89	129.02
Fukuejima	Fukue	32.69	128.85
	Tomie	32.62	128.76
	Kaizu	32.71	128.66
	Miiraku	32.74	128.69

Appendix 2 Study sites on 26 islands in the East China Sea, Pacific Ocean and Seto Inland Sea. See Appendix 1 for the white, dark and light gray patterns. 1 : Nakakoshikishima, 2: Shimokoshikishima, 3: Toshima, 4: Kozushima, 5: Mikurajima, 6 :Hahajima, 7: Kii-oshima, 8: Kuchinoerabujima, 9: Nakanoshima, 10: Suwanosejima, 11: Takarajima.

Sea	Island	Site name	Latitude	Longitude
East China Sea	Kamikoshi-kishima	Sato Kita	31.85	129.92
		Sato Minami	31.84	129.92
		Nakakoshiki	31.84	129.86
		Urauchi	31.86	129.86
	1	Taira	31.80	129.84
	2	Nagahama	31.70	129.74
		Kashima	31.78	129.80
		Teuchi	31.63	129.71
Pacific Ocean	Izuoshima	Habu	34.69	139.44
		Okada	34.79	139.39
		Motomoachi	34.75	139.35
		Nomazu	34.73	139.35
	3	Toshima	34.53	139.28
	Niijima	Wakagou	34.41	139.28
		Habuse	34.40	139.28
		Niijima	34.37	139.25
	Shikinejima	Shikinejima north	34.32	139.22
		Shikinejima south	34.33	139.22
		Kohama	34.33	139.22
		Nobushi	34.33	139.21
	4	Miura	34.20	139.16
		Kozushima	34.21	139.13
	Miyakejima	Miike	34.08	139.56
		Okubo	34.12	139.51
		Igaya	34.10	139.49
		Ako	34.07	139.48
		Sabigaura	34.07	139.48
		Tsubota	34.06	139.54
	5	Mikurajima east	33.90	139.59
		Mikurajima west	33.90	139.59
	Hachijyo-jima	Sokodo	33.12	139.82
		Kaminato	33.13	139.80
		Yaene north	33.10	139.78
		Yaene south	33.10	139.78
		Aigae	33.06	139.82
	Chichijima	Futami north	27.09	142.20
		Futami east	27.09	142.20
		Kiyosegawa	27.10	142.20
		Futami south	27.10	142.20
	6	Oki	26.64	142.16
		Hahajima	26.69	142.15
	Saku-shima	Saku east	34.72	137.04
		Saku west	34.72	137.04
		Irigaura	34.72	137.04
	7	Nishikou	33.47	135.83
		Higashikou	33.47	135.83
Seto Inland Sea	Awajishima	Tsuna	34.45	134.92
		Shizuki	34.43	134.90
		Takenokuchi	34.35	134.89
		Yura	34.29	134.95
		Fukura	34.26	134.72
	Shodo-shima	Fukuda	34.55	134.35
		Ikeda	34.48	134.23
		Tonosho	34.49	134.18
East China Sea / Pacific Ocean (Nansei Islands)	Tanegashima	Kumano	30.46	130.96
		Takezaki	30.37	130.96
		Sunasaka	30.38	130.86
		Shimama	30.46	130.86
		Nishinoomote	30.73	130.99
		Urata	30.82	131.05
		Minato	30.81	131.07
		Anjo	30.65	131.05
	Yakushima	Miyanoura	30.43	130.57
		Koseda	30.40	130.63
		Anbou	30.32	130.66
		Kurio	30.27	130.42
		Shitoko	30.45	130.52
		Issou	30.45	130.49
	8	Kuchinoerabu	30.46	130.19
	9	Nakanoshim north	29.84	129.85
		Nakanshima south	29.84	129.85
	10	Motoura	29.61	129.70
		Kiriishi	29.61	129.71
	11	Maegomori	29.16	129.21
	Amamioshima	Usuki	28.44	129.71
		Tatsugo	28.41	129.59
		Naze	28.38	129.50
		Okuma	28.40	129.52
		Koniya	28.15	129.31
		Honohoshi north	28.13	129.37
		Honohoshi south	28.13	129.67
		Yamama	28.24	129.42
	Tokuno-shima	Hetono	27.81	128.89
		Kametoku north	27.74	129.02
		Kametoku middle	27.74	129.02
		kametoku south	27.73	129.02
	Okinoerabu-jima	Wadomari north	27.40	128.66
		Wadomari south	27.39	128.66
		China	27.33	128.57
		Inobe	27.41	128.64

Appendix 3 Study sites on 16 islands in the Okinawa Prefectures. See Appendix 1 for the white, dark and light gray patterns. 1: Iheyajima, 2: Nohojima, 3: Ikemajima, 4: Shimochijima, 5: Kurumajima, 6 :Kuroshima, 7:Yonagunijima, 8: Haterumajima.

Island	Site name	Latitude	Longitude
1	Maedomari	27.04	127.97
	Iheya	27.02	127.94
2	Noho	27.00	127.93
Okinawatou	Naha	26.45	127.80
	Tomari	26.23	127.68
	Chatan	26.32	127.75
	Onna	26.50	127.86
	Shioya	26.67	128.10
	Ginama	26.85	128.25
	Kesaji	26.60	128.14
	Nago	26.59	127.98
	Unten	26.68	128.00
	Uruma	26.43	127.83
	Nakagusuku	26.25	127.79
Kume-jima	Torishima	26.35	126.75
	Kaneshiro	26.34	126.75
	Gima	26.30	126.76
Kita-daitojima	Nishikou	25.96	131.28
	Kitakou	25.96	131.31
	Ezakikou	25.93	131.31
Minami-daitojima	Kameike	25.81	131.23
	Kitakou	25.87	131.24
	Minamidaitou	25.87	131.23
	Nishikou	25.84	131.22

Island	Site name	Latitude	Longitude
Miyakojima	Hirara	24.82	125.28
	Takano	24.77	125.40
	Bora	24.72	125.36
	Kuruma	24.73	125.27
	Hisamatsu	24.78	125.26
3	Ikema	24.93	125.25
Irabu-jima	Nagayama	24.80	125.20
	Sawada	24.85	125.16
	Sarahama	24.84	125.21
4	Nakanoshima	24.82	125.14
5	Kurumajima	24.72	125.26
Ishigaki-jima	Tonoshiro	24.33	124.16
	Inoda	24.46	124.25
	Funakoshi	24.51	124.28
	Ishigaki	24.35	124.15
Iriomote jima	Ohara	24.27	123.88
	Funaura	24.41	123.81
	Uehara	24.42	123.80
	Iriomote	24.38	123.75
	Shirahama	24.36	123.75
6	Kuroshima	24.25	124.00
7	Kubura	24.45	122.94
	Sonai	24.47	123.00
8	Hateruma	24.07	123.77