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Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact

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ABSTRACT: A common littoral barnacle, *Balanus glandula* Darwin, 1854 (Crustacea, Cirripedia) from the west coast of North America has become established in the mid-littoral zone of harbors on the Pacific side of northern Honshu, Japan. The new immigrant occupies space in the lower half of the *Chthamalus* spp. and *Balanus albicostatus* zones, and in the upper fringe of the *Semibalanus cariosus* zone. However, the species has not been detected in harbors along the Sea of Japan, south of the Ozika Peninsula, northern Honshu, and to the north and east of Kushiro, Hokkaido. Considering its present distribution, shell sizes, and abundance, it is most likely that it was introduced into 3 separate port areas in NE Honshu, Japan, during the last 20 to 40 yr, probably by anthropogenic activities. It was apparently also introduced to the La Plata estuary, Argentina, during the same period. *B. glandula* is becoming a dominant littoral zone species, especially in embayments, largely at the expense of the tropical endemic *B. albicostatus* in the upper littoral fringe. Taking into account the biogeographical distribution of common Japanese barnacles in relation to water temperature, the future distribution of the newly introduced species is considered.

KEY WORDS: *Balanus glandula* · Introduced species · Distribution · Annual mean water temperature · Biogeography · Anthropogenic activities

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INTRODUCTION

The introduction of marine organisms around the world by ocean-going ships has affected domestic biotas mainly in competition for food and space. The arrival of the Australasian barnacle *Elminius modestus* Darwin to Europe is the first well documented transoceanic barnacle invasion (Bishop 1947, Crisp & Chipperfield 1948, Stubbings 1950, Crisp 1958). A more recent example of transoceanic spread is the invasion of Hawaiian shores by the western Atlantic species *Chthamalus proteus* (Southward et al. 1998). Earlier, *Balanus eburneus* Darwin, common along the east coast of North America, had been introduced to Rochelle, France, by shipping (Pilsbry 1916). Although *E. modestus* has not yet been found in Japanese waters, *B. eburneus* has appeared during the last 50 yr, as well as *B. improvisus* Darwin, which is common along estuaries in western Europe. The latter 2 warm-water species were first recorded in central Japan, but are now found throughout Japan (except Hokkaido), where they are dominant forms in embayments (Kawahara 1963, Utinomi 1966, Yamaguchi 1977, 1989).

On the NE coast of Honshu, the endemic littoral barnacle fauna includes *Semibalanus cariosus*, *Chthamalus dalli*, *C. challengeri*, *Tetraclita japonica*, *Balanus albicostatus*, and *Capitulum mitella*. Of these, *S. cariosus* and *Chthalmus dalli* are the only cold-water species. No introduced barnacles have been known to inhabit the littoral zone in northern Japan. In May 2000, however, we found an abundant but hitherto unknown (in this area) barnacle, *B. glandula* Darwin, 1854 in this habitat (Ofunato Bay, Iwate Prefecture; see Stn 24 in Table 1).

Balanus glandula is a common cold-water littoral barnacle along the western coast of North America

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(Pilsbry 1916, Henry 1942, Newman & Abbott 1980, Foster et al. 1991). Darwin (1854) noted that it ranged from the northern Pacific to California, i.e. from the Aleutians (Bering Sea) to Baja California (Newman & Ross 1976). While this species has not previously been recorded from the eastern side of Asia, it was recently reported to be established in Mar del Plata, Argentina (Young 1995, Vallarino & Elias 1997).

Following the discovery of *Balanus glandula* (Fig. 1) in Japan in 2000, several surveys were conducted along the northern coast to clarify the actuality of its invasion. The present work reports on its distribution and abundance and its ecological and biogeographical relationships with the endemic barnacles; the time and the route of the introduction is also discussed.

MATERIALS AND METHODS

Ecological surveys of the littoral zone were conducted along the coast of northern Japan from June to August 2000 (39° 50′ N along the coast of the Sea of Japan, and north of 38° 20′ N along the coast of the Pacific Ocean and the Sea of Okhotsk). About 50 fishing ports with concrete mooring slopes and adjacent quay walls were selected as survey stations because of ease of access and uniformity of the substratum, i.e. concrete.

To assess the present extent of the invasion by *Balanus glandula*, at each site a sampling location with a high population density of *B. glandula* was selected, regardless of shell size and age. Using 1 of 4 quadrats (5 × 5, 10 × 10, 25 × 25, 100 × 100 cm), depending on the visually estimated density, the density of *B. glandula* at each sampling site was measured 2 or 3 times, and the maximum value recorded. Population zone width and height above mean sea level were also investigated at each station at low tide. Minimum brooding size was examined for about 20 individuals <8 mm in diameter at each site by noting the presence of brooding embryos inside the mantle cavity. As an indicator of reproductive potential of this species, the possibility of self-fertilization was checked by comparing a population of 24 solitary settled individuals (>10 cm apart) with a population of 104 gregariously settled individuals, by examining specimens with >7.8 mm rostro-carinal diameter at Shimanokoshi (Fig. 2, Stn 14) on 20 June 2000.

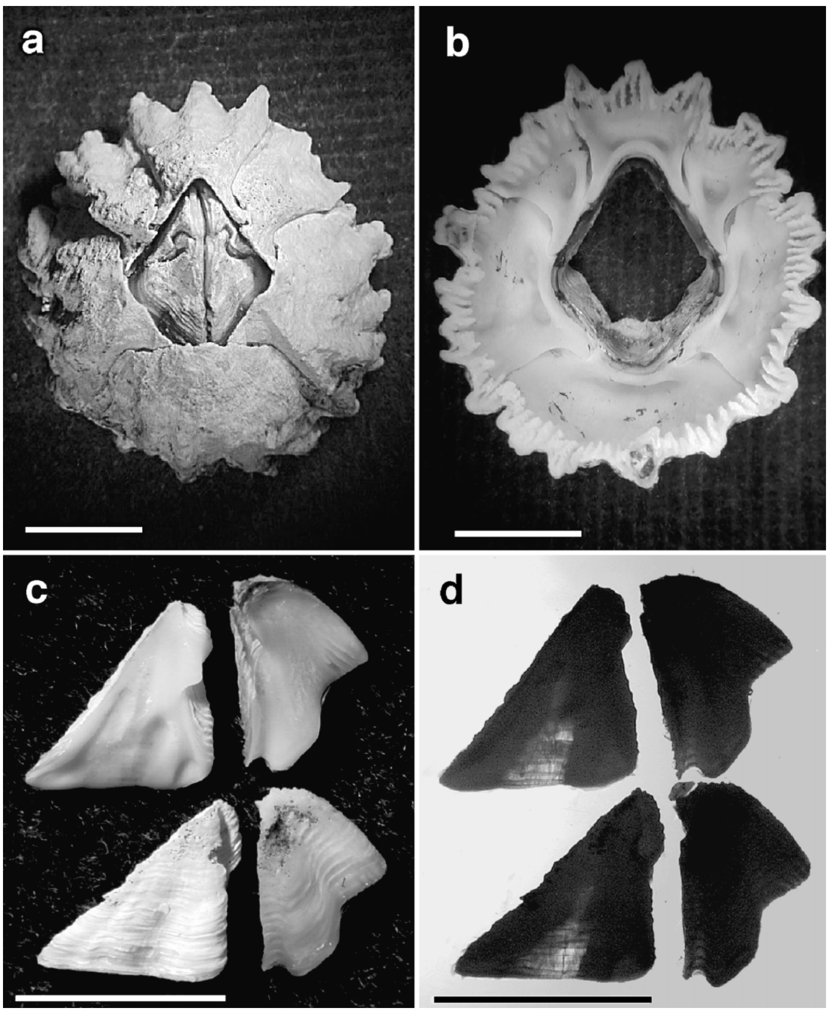

Fig. 1. *Balanus glandula* from Orikasa, Yamada Bay, Iwate Prefecture. External and internal view of (a), (b) parietes and (c) valves. (d) Translucent central portion of scutum viewed with transmitted light. Scale bars = 5 mm

RESULTS

Balanus glandula was found at most stations on the Pacific side of Japan, north of Aikawa, from Oppa Bay (Fig. 2: Stn 29) to Hokkaido (Stn 41). Densities at stations where the barnacle occurred varied from 1 m^{-2} (Shinhama, Kamaishi Bay) to 40 000 m^{-2} (Tamanowaki, Kuji Bay) (Table 1). At Tamanowaki (Fig. 2: Stn 13), rock surfaces adjacent to concrete mooring slopes were almost completely covered by this species, which occurred there in 3 size classes (2 to 3, 7 to 8, 12 to 13 mm: Fig. 3). The largest individual was found at Orikasa, Iwate Prefecture

(Fig. 2: Stn 16) and was 22.7 mm in rostro-carinal diameter. *B. glandula* was not detected in Sakihama, Okkirai Bay (Fig. 2: Stn 22), located 13 km NE of Kamihira or Sasazaki, Ofunato Bay (Fig. 2: Stn 24), but was abundant 6 km south of Konpaku, Yoshihama Bay (Fig. 2: Stn 21).

No *Balanus glandula* were detected at stations along the Honshu coast facing the Sea of Japan, but the south and west coast of Hokkaido have yet to be surveyed.

Balanus glandula tends to occur between the mean high-water spring and extreme low-water spring tides, depending on the degree of exposure and the presence of other organisms (Fig. 4). It generally occurs together with at least 1 of 4 endemic barnacles: *Chthamalus* (i.e. *C. challengeri* and/or *C. dalli*), *Semibalanus cariosus*, and *B. albicostatus* (Fig. 4). The first 3 of these species were common at stations close to the open sea. *B. glandula* overlapped with both *Chthamalus* spp., which usually occur on higher levels of the shore, and with *S. cariosus*, which is always found on lower levels. On the other hand, *B. albicostatus* was the only barnacle occurring together with *B. glandula* in the littoral zone in semi-enclosed bays such as Ofunato (Fig. 2: Stn 24) and Yamada Bay (Fig. 2: Stn 16). The density of *B. albicostatus* was not high in comparison with that of the other barnacles in the same area. *B. amphitrite* also occurred in Ofunato Bay, but was uncommon. *B. glandula* at these stations exceeded *B. albicostatus* in abundance, but did not range as high into the intertidal. Where the 4 barnacles co-occurred, as at Akahama (Fig. 2: Stn 17) and Tarou (Fig. 2: Stn 15), they were generally distributed, from the top to the bottom of the shore, in the order *C. challengeri*, *B. albicostatus*, *B. glandula*, and *S. cariosus*. East of Tomakomai (Fig. 2: Stn 38), especially at Hiroo (Fig. 2: Stn 41), *C. dalli* dominated the upper to middle littoral zone, where it settled heavily in late July and early August of 2000, apparently to the detriment of *B. glandula* (these 2 species as well as *S. cariosus* co-occur naturally along the Pacific coast of North America).

At the stations with no *Balanus glandula*, the littoral habitats were dominated by *Chthamalus challengeri* (Honshu) or *C. dalli* (Hokkaido) in the upper and middle zones or by *B. albicostatus* in sheltered harbor areas (Honshu only) in these zones, and by *Semibalanus cariosus* in the lower zone. *S. cariosus* in Okkirai Bay has decreased remarkably in biomass over the past 4 yr, while biomass of the oyster *Crassostrea gigas* has increased (R. Kado unpubl. data).

The minimum reproductive size of *Balanus glandula* was 5.8 mm carino-lateral diameter. None of the 24 solitary settled individuals was brooding embryos, while 30 % of the gregariously settled individuals were brooding.

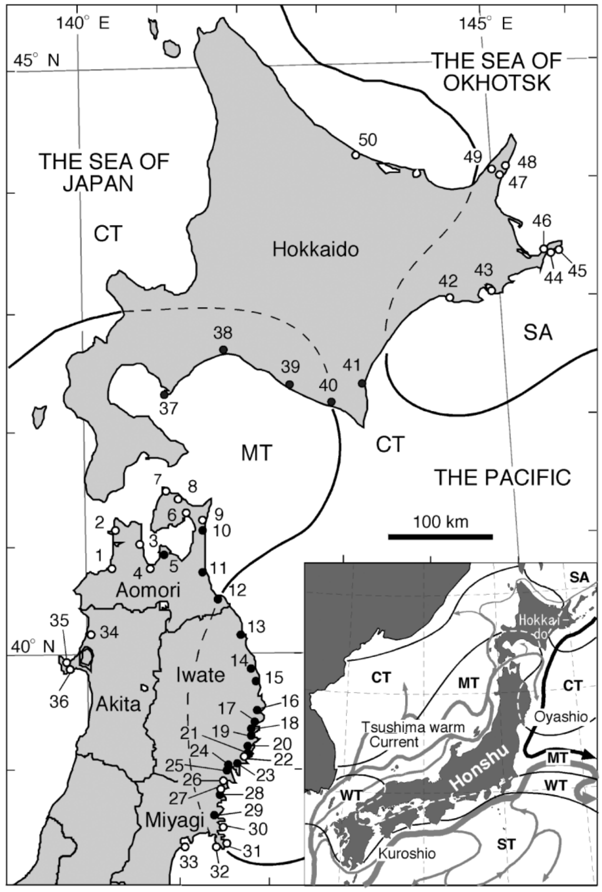

Fig. 2. *Balanus glandula.* Distribution in northern Japan. (○, ●) Stations at which *B. glandula* has not been or has been detected, respectively. Numbers indicate stations surveyed (Table 1). Inset illustrates major currents and climatic zones: ST: subtropical; WT: warm-temperate; MT: mid-temperate; CT: cold-temperate; SA: subarctic (after Nishimura 1981, 1992)

DISCUSSION

In spite of its abundance, the reason the newly discovered *Balanus glandula* was apparently overlooked for a number of years may be as follows: (1) the shape and color of *B. glandula* and *Semibalanus cariosus* are similar (both dirty white), although the latter does not occur above high tide; (2) a gradual increase in recruits of *B. glandula* to the high intertidal was probably mistaken as an increase in *S. cariosus* where *S. cariosus* was dominant. In quiet waters, *S. carious* is very rare, however, and the endemic barnacle *B. albicostatus* is found from the upper to the lower part of the littoral zone (Yamaguchi 1977). *B. albicostatus* has white narrow ribs on a dark purple shell. Therefore, unless observed closely the 2 species look similar when the shells are dirty or covered with algae. Thus, *B. glandula* became well established in the littoral zone of many harbors before it was discovered in NE Japan.

Table 1. *Balanus glandula*. Occurrence and density at stations surveyed on Pacific, Sea of Japan, and Sea of Okhotsk coasts of northern Japan in 2000. Associated barnacles are also listed. Station locations shown in Fig. 2. Nearby locations are not numbered; N: undetected, R: rare, F: frequent, A: abundant; ne: not closely examined; *Bc*: *Balanus crenatus*, *Be*: *B. eburneus*, *Bi*: *B. improvisus*, *Bm*: *B. amphitrite*, *Bl*: *B. albicostatus*, *Cc*: *Chthamalus challengeri*, *Cd*: *Chthamalus dalli*, *Sc*: *Semibalanus cariosus*

Station	Stn no.	Abundance	Max. density (ind. m^{-2})	Size (mm)	Other barnacles	Date
Aomori Prefecture						
Ajigasawa	1	N	–	–	*Bm*	Jul 5
Kodomari	2	N	–	–	*Cc*	Jul 5
Gousawa	3	N	–	–	*Cc*, *Bl*, *Sc*	Jul 5
Aomori	4	N	–	–	*Cc*, *Sc*	Jul 4
Asadokoro	5	N	–	–	*Cc*, *Bl*	Jul 4
Moura		R	2	6–9.5, 11–12.5	*Cc*, *Bl*	Jul 4
Oominato	6	N	–	–	*Cc*, *Bl*, *Sc*	Jul 3
Ooma	7	N	–	–	*Cc*	Jul 3
Shitafuro	8	N	–	–	*Cc*, *Sc*	Jul 3
Odanozawa	9	N	–	–	*Cc*	Jul 3
Shiranuka	10	F	500	2–3, 15–18	*Cc*, *Bl*, *Sc*	Jul 3
Misawa	11	A	1000	4–6, 11–12	*Cc*, *Bl*	Jul 2
Kofunatodaira	12	A	2000	2–5, 9–12	*Cc*	Jul 2
Iwate Prefecture						
Tamanowaki	13	A	40000	2–3, 7–8, 12–13	*Cc*, *Bl*, *Sc*	Jul 2
Hiraiga	14	A	10000	ne	*Cc*, *Sc*	Jul 2
Shimanokoshi		A	3200	ne	*Cc*, *Sc*	Jun 20
Tarou	15	A	4000	ne	*Cc*, *Sc*	Jun 20
Orikasa	16	A	3300	3–8/10–16	*Bl*	Jul 20
Akahama	17	F	384	ne	*Bl*, *Sc*	Jun 19
Ryoishi	18	A	1700	5–8, 11–15	*Bl*, *Sc*	Jun 19
Shinhama	19	R	1	8, 11	*Cc*, *Bl*, *Sc*	Jun 19
Touni	20	F	112	ne	*Cc*, *Bl*, *Sc*	Jun 19
Konpaku	21	F	200	6–8, 11–15	*Cc*, *Sc*	Jun 17
Sakihama	22	N	–	–	*Cc*, *Bl*, *Sc*	Jun 3
Urahama		R	16	ne	*Cc*, *Bl*, *Sc*	Jun 17
Nonomae		N	–	–	*Cc*, *Bl*, *Sc*	Jun 3
Tahama	23	R	300	ne	*Cc*, *Bl*, *Sc*	Jun 3
Nagasaki		F	128	ne	*Cc*, *Sc*	Jun 3
Sasazaki	24	A	10000	ne	*Bl*	Jun 2
Kamihira		A	8000	3–11, 13–16	*Bl*, *Bm*	Jun 4
Kadonohama		F	200	ne	*Cc*, *Sc*	Jun 4
Kyumikkaichi		R	1	14–15	*Cc*, *Bl*	Jun 4
Takata–Matsubara	25	R	1	12–17	*Sc*, *Bl*	Jun 4
Miyagi Prefecture						
Tadakoe		R	2	ne	*Cc*, *Sc*	Jun 18
Ooura	26	N	–	–	*Cc*, *Bl*	Jun 18
Ninoura		N	–	–	*Cc*, *Bl*	Jun 18
Amagasawa	27	N	–	–	*Cc*	Jul17
Nijuuichihama	28	R	<1	6–13	*Cc*, *Bl*, *Sc*	Jul 17
Aikawa	29	R	<1	8–13	*Cc*, *Bl*, *Sc*	Jul 17
Oura	30	N	–	–	*Cc*, *Bl*, *Sc*	Jul 17
Yagawa	31	N	–	–	*Cc*, *Bl*, *Sc*	Jul 18
Oohara	32	N	–	–	*Cc*, *Bl*	Jul 18
Shoubutahama	33	N	–	–	*Cc*, *Bl*	Jul 18
Akita Prefecture						
Noshiro	34	N	–	–	*Bl*, *Be*, *Bi*, *Bm*	Aug 6
Kitaura	35	N	–	–	*Cc*, *Bm*	Aug 6
Funakawa	36	N	–	–	*Cc*, *Bm*	Aug 6
Hokkaido						
Muroran	37	A	8000	ne	*Cc*, *Sc*	Jul 31
Tomakomai	38	A	16000	ne	*Cd*, *Sc*	Jul 31
Shizunai	39	F	500	ne	*Cc*, *Cd*, *Sc*	Jul 31
Urakawa	40	F	300	ne	*Cd*, *Sc*	Aug 1
Hiroo	41	F	300	ne	*Cd*, *Sc*	Aug 1
Katsurakoi	42	N	–	–	*Cd*	Aug 2
Akkeshi	43	N	–	–	*Cd*	Aug 2
Tokotan		N	–	–	*Cd*, *Sc*	Aug 2
Tomoshiri	44	N	–	–	*Cd*, *Sc*	Aug 2
Oineppu		N	–	–	*Cd*, *Sc*	Aug 2
Habomai	45	N	–	–	*Cd*, *Sc*	Aug 3
Nemuro	46	N	–	–	*Cd*, *Sc*	Aug 3
Rausu	47	N	–	–	*Cd*, Bc, *Sc*	Aug 4
Chienbetsu	48	N	–	–	*Cd*, Bc, *Sc*	Aug 4
Utoro	49	N	–	–	*Cd*, *Sc*	Aug 4
Monbetsu	50	N	–	–	*Cd*, *Sc*	Aug 5
Saruru		N	–	–	*Cd*, *Sc*	Aug 5

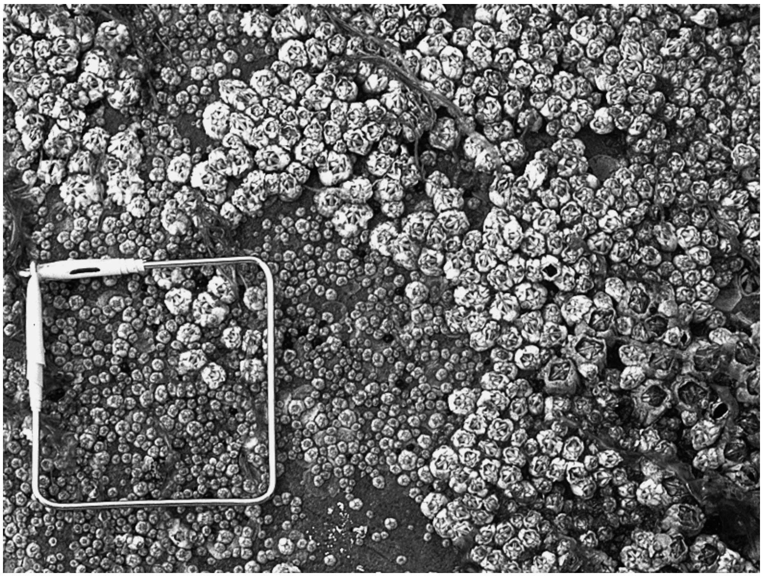

Fig. 3. *Balanus glandula* on rock surface at Tamanowaki, Kuji Bay, Iwate Prefecture. Three size classes were observed: 2 to 3 mm (lower left), 7 to 8 mm (top), 12 to 13 mm (lower right). The quadrat on the lower left is 5 cm square

Self-fertilization does not seem to occur in *Balanus glandula*, as indicated by the absence of solitary individuals, and therefore solitary brooding individuals do not contribute to its breeding population. In other words, it is essential for the species to be dense enough to ensure cross-fertilization in order to reproduce. This means that it might require a longer period to extend its distribution than species with the ability to self-fertilize. Chthamalines have a higher settlement zone than *B. glandula* (Hines 1978), so they can maintain populations despite *B. glandula* co-occupying the lower part of their range. *Semibalanus cariosus* is also subject to competition from *B. glandula*, but not as seriously as *B. albicostatus* because of its wider settlement zone, which extends into the sublittoral. In North America, *Mytilus californianus* is the best competitor for space, followed by *S. cariosus*, *Chthamalus dalli*, and seaweeds in that order (Dayton 1971). *S. cariosus* and the chthamalines display a similar pattern in Japan.

Relationship with endemic species

The vertical distributions of the endemic barnacles encountered in this survey are comparable to those in previous reports (Hiro 1938, Hoshiai 1965, Yamaguchi 1977). As shown in Fig. 4, *Balanus glandula* has invaded the habitats of *Chthamalus challengeri* and/or *C. dalli* and *B. albicostatus*, as well as that of *Semibalanus cariosus*. Because of its relatively low density, *B. albicostatus*, one of the commonest temperate to subtropical barnacles, is apparently suffering the greatest impact from *B. glandula*, especially in sheltered waters such as Ofunato Bay, where the open-coast species *S. cariosus* and *C. challengeri* are rare. *B. albicostatus* is free from competition only at the upper fringe of the zone. *B. glandula* apparently dominates *B. albicostatus* because it can breed at a small size (6 mm rostro-carinal diameter) and settles from early spring to early summer in high densities (Barnes & Barnes 1956, Hines 1978, R. Kado unpubl. data). It therefore becomes established in available open spaces before *B. albicostatus* recruits arrive. This is probably one of the reasons why *B. glandula* succeeded in becoming established in this region.

In the lower littoral zone, the mussels *M. galloprovincialis* and/or *Septifer virgatus* and the oyster *Crassostrea gigas* compete for space with *Semibalanus cariosus*. Therefore, they are also likely to be in competition with *B. glandula*. Since *B. glandula* frequently

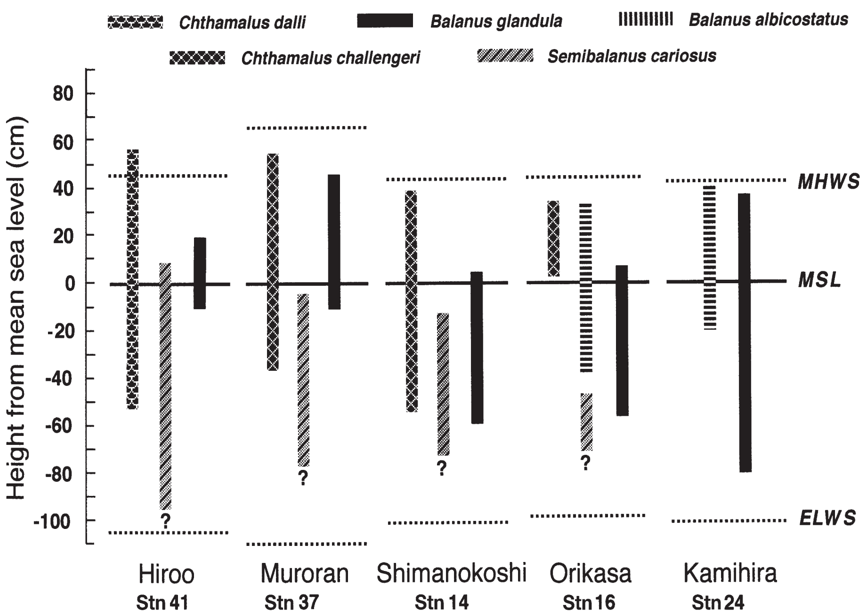

Fig. 4. Zonation of barnacles (including *Balanus glandula*) at 5 locations in northern Japan. Question marks indicate that lower limit of the species was not determined. Station numbers as in Table 1 & Fig. 2. MHWS: mean high-water spring tide; MSL: mean sea level; ELWS: extreme low-water spring tide

uses mussels as substrate, it would seem to be much more facultative than *S. cariosus*, which is rarely found on mussels.

Biogeography

On the Pacific coast of North America, *Balanus glandula* ranges through the Californian, Oregonian and Aleutian faunal provinces (warm temperate to sub-arctic regions), but is also present along the Pacific coast of Russia. The southern limit (30° 30′ N) of the species is in Baja California, at the transition zone between the Californian (warm temperate region) and Panamic (tropical/subtropical region) faunal provinces (Laguna 1990).

The annual mean water temperature at its southern limit is around 17°C (see Fig. 5 in Newman 1979), and the mean temperature in summer does not exceed 22°C (Chronological Scientific Tables 2001). Seasonal water temperatures near the outfall of a power plant in Morro Bay, California (35° 22′ 30″ N) fluctuates between 14°C in April and 30°C in September. Under such warm conditions, *Balanus glandula* is restricted to breeding between December or February and May, when the weekly mean water temperature ranges from 17 to 20/21°C (Hines 1978).

On the coasts of Japan, near 36° N (at the southern end of the mid-temperate [Nishimura 1981] region on the Pacific coast), and between 36 and 38° N (30′ north of the mid-temperate region on the coast of the Sea of Japan), annual mean water temperature is about 17°C (Fig. 5). Water temperature fluctuations at both ends of the mid-temperate region are between 11 and 23°C on the Pacific coast, and between 11 and 27°C on the Sea of Japan coast (Geological Survey of Hokkaido 1996–1999).

The southern limit of another cold-temperate littoral barnacle, *Semibalanus cariosus*, is Cape Inubo (35° 43′ N), at the southern end of the mid-temperate region on the Pacific coast (Yamaguchi 1987), whereas on the Sea of Japan coast it is around 41° N (Utinomi 1955) (Fig. 5). The southern limit of this species on the Pacific coast of North America is 37° N (Newman 1979), 6° 30′ north of the southern limit for *Balanus glandula*.

In view of the distribution of *Semibalanus cariosus* and the fact that *Balanus glandula* at Morro Bay bred at temperatures below 22°C (Hines 1978), this barnacle should be able to breed in the mid-temperate region on the Pacific coast of Japan. However, it is not likely that *B. glandula* will extend its distribution to the mid-temperate region along the coast of the Sea of Japan because of the high summer water temperatures there (Geological Survey of Hokkaido 1996–1999). On the other hand, the sub-arctic/cold-temperate barnacle *Chthamalus dalli* is distributed throughout in the North Pacific Province and co-occurs with *B. glandula* along the west coast of North America. This suggests that *B. glandula* may migrate further east along Hokkaido, and perhaps along the west coast of the North Pacific, where this species has not yet been found (Zvyagintsev 2000).

A similar biogeographical situation prevails in Argentina on the Atlantic side of South America, where introduced *Balanus glandula* have not expanded their range north or south of the transition zone where the warm Brazilian and cold Falkland currents mix (Young 1995). In Argentina, the species overwhelmingly dominates the mid-littoral zone at 2 to 3 times higher densities than in North America (Vallarino & Elias 1997).

Time and route of invasion

Although the growth rate of *Balanus glandula* in Japan waters is not known, the largest individual had a rostoro-carinal diameter of 22.7 cm. Applying the growth rate calculation of Barnes & Barnes (1956) and Hines (1978) for North America, it might therefore have been more than 8 yr old.

Two possibilities have been considered to account for the origin of *Balanus glandula* in Japan: (1) an

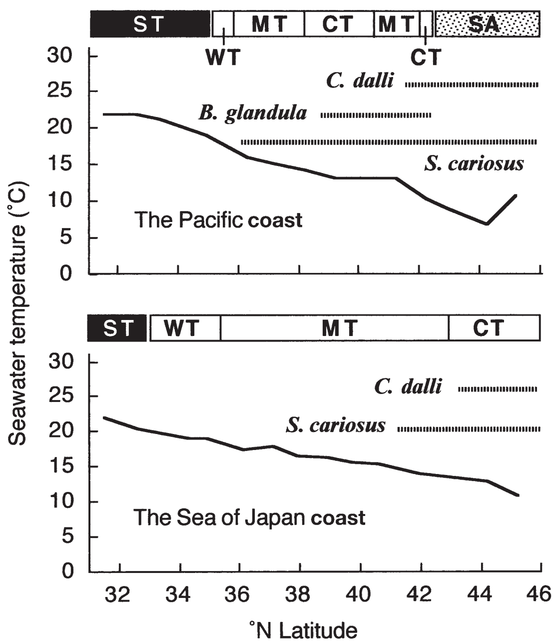

Fig. 5. Long-term temperature means (Aomori Prefectural Fisheries Experimental Station 1985–2000, Geological Survey of Hokkaido 1996–1999) along Pacific and Sea of Japan coasts of Japan. Latitudinal distributions of *Balanus glandula*, *Chthamalus challengeri*, and *Semibalanus cariosus* are shown. Abbreviations as in Fig. 2

extension of its normal distribution by larval dispersal along the shores of the Aleutians, the Kamchatka Peninsula, and the Kuril Islands, or (2) transport by ocean-going ships. The first possibility is considered unlikely because the species has not been found on the east coast of Hokkaido (Pacific and Sea of Okhotsk coasts) or in the Far East region of Russia, from where there are no reports for this species except in the Bering Sea region (Hiro 1935, Zevina 1980, Zvyagintsev 2000).

The second possibility seems more likely in view of the following circumstantial evidence. According to the records of the harbor customs offices along the north-east coast of Japan, timber has been imported on the decks of ships to Sasazaki, Ofunato Bay (Table 1: Stn 24), Hachinohe (Table 1: Stn 12) and Tomakomai (Table 1: Stn 38) in northern Japan since the 1960s from many ports such as Vancouver, Seattle, Tacoma, and Klawak etc. along the Pacific coast of North America. As a result, larvae released from fouling organisms may have settled and become established at one or more of the Japanese ports of arrival. The distribution data show that population density declines with increasing distance from these ports. For example, density (Fig. 6) is highest at Stns 13, 24 and 38, each of which is either a timber-importing port itself or close to such a port (Fig. 6). This suggests that this species has at least 3 population centers and that its introduction occurred on separate occasions. Considering that *Balanus glandula* was introduced to La Plata estuary, Argentina, despite the great thermal change it encountered when passing through the tropics (Young 1995), the moderate temperature changes across the northern Pacific are not likely to constitute a barrier to its importation by ships. If such importation has occurred, then it constitutes a further case of westward transport across the ocean by anthropogenic activities. It follows the invasion of Hawaiian shores by the Atlantic barnacle *Chthamalus proteus* (Southward et al. 1998), which also succeeded in occupying a largely vacant niche in the upper mid-littoral zone of sheltered Hawaiian shores.

The literature for Otsuchi Bay (Akahama: Table 1 & Fig. 2: Stn 17), which has the most thoroughly investigated marine biota on the NE coast of Japan, includes no reports of *Balanus glandula*, either living (Kajihara & Ura 1976, Kado et al. 1980) or in the sediments (E. Honza & T. Igarashi unpubl.). Therefore, in Otsuchi Bay, it appears that *B. glandula* was introduced less than 20 yr ago. In other areas of northern Honshu, for which few published faunal surveys exist, *B. glandula* may have been introduced within the past 40 yr, i.e. since the beginning of intensive trading in the 1960s.

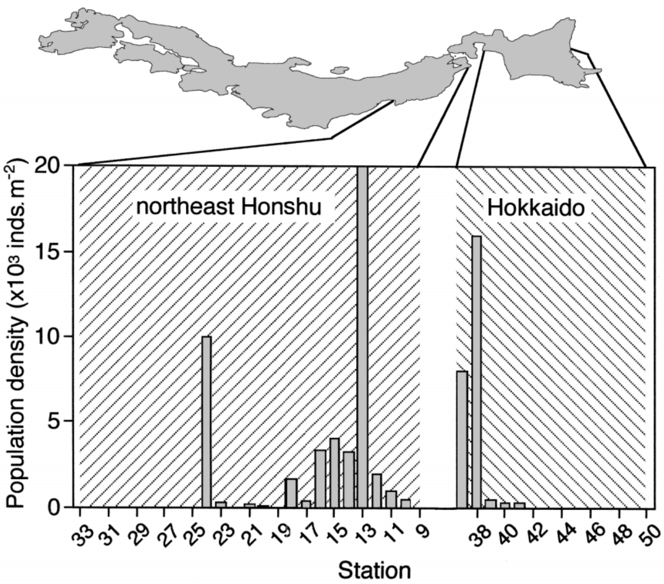

Fig. 6. *Balanus glandula.* Maximum population density at stations surveyed on Pacific coast of northern Japan. Station numbers as in Table 1 & Fig. 2

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