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Seaweed community structures in the temperate zooxanthellate scleractinian coral *Alveopora japonica* bed in the western Seto Inland Sea, Japan

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Abstract : The zooxanthellate scleractinian coral *Alveopora japonica* is endemic to the northwestern Pacific, ranging from Taiwan to Korea and Japan. This coral has recently expanded into seaweed beds in the temperate waters of these regions, as the seawater temperature increased. The largest known bed of *A. japonica* (1940 m^2) was found in 2012 at Yashiro Island, in the Seto Inland Sea in the temperate region of Japan, where the minimum seawater temperature is the lowest among the regions inhabited by this coral. We surveyed the coverage of seaweeds and *A. japonica* in this coral bed during the seaweed-abundant and seaweed-sparse seasons in 2014. Throughout the year, the coverage of *Ecklonia kurome* and sargassaceous plants was low in places where the coverage of *A. japonica* was high. The maximum seawater temperature was within the optimal range for the growth of these seaweeds, indicating that the increasing temperature did not adversely affect seaweed growth. Evidently, a local environmental stress rather than the increase in seawater temperature caused the decline of the canopy-forming seaweeds that, in turn, allowed the coral bed to expand. Our research provides baseline data to compare with and analyze future changes at the edge of *A. japonica* distribution.

Keywords : *Alveopora japonica; Ecklonia kurome*; climate change; Sargassaceous plants; Seawater temperature increase

Introduction

Recently, degradation of seaweed bed ecosystems and poleward shifts in the distribution of subtropical or tropical seaweeds and hermatypic corals have been occurring along the Japanese coasts, at the same time that the coastal water temperatures have been rising (Sugihara et al. 2009; Yamano et al. 2011; Tanaka et al. 2012; Fisheries Agency of Japan 2015). Average sea surface temperatures around Japan rose by 1.09℃ between 1915 and 2015 (Japan Meteorological Agency 2016).

The temperate zooxanthellate scleractinian coral *Alveopora japonica* Eguchi 1968 is distributed from Taiwan to the temperate coasts of Korea and Japan. The largest known bed of *A. japonica* (1940 m^2) was found in 2012 at Yashiro Island (hereafter Yashiro Is.), located in the western part of the Seto Inland Sea in Japan (Fig. 1). A Marine Park (Jikamuro Marine Park), part of the Seto Inland Sea National Park, was

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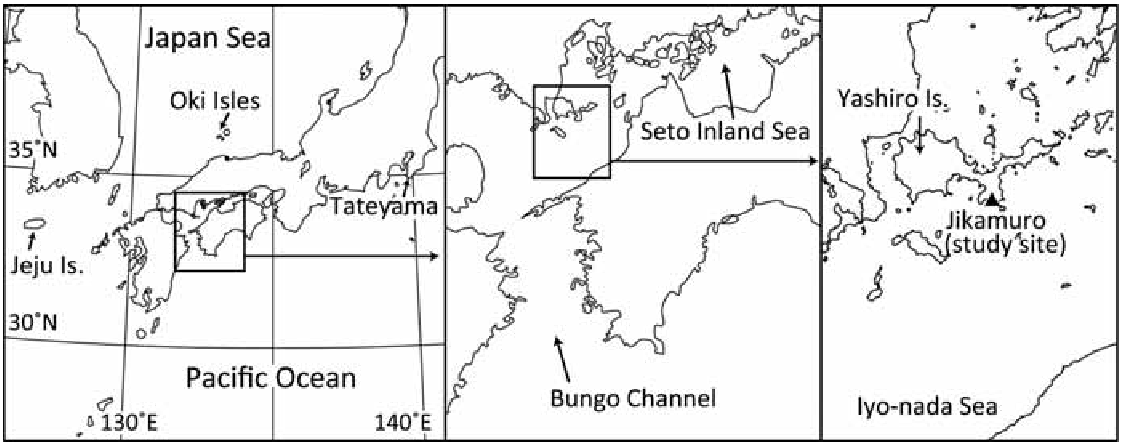

Fig. 1. Site of the *Alveopora japonica* bed at Yashiro Island in the western Seto Inland Sea in Japan.

designated at Yashiro Is. in 2013 to preserve the high diversity of flora and fauna that are supported by flourishing seaweed beds (Ministry of the Environment of Japan 2013). The existence of the large bed of *A. japonica* is an important characteristic of this Marine Park (Ministry of the Environment of Japan 2012a). Unsubstantiated observations suggest that the *A. japonica* bed at Yashiro Is., which lies within a seaweed bed, has grown to its current size in the last two decades. According to an analysis of seawater temperatures in the Seto Inland Sea from 1973 to 2003, after 1989–1990, the temperature remained at a higher level than that recorded in the 1980s (Tarutani 2007). However, the winter mean temperature in the Iyo-nada Sea (10 ℃ from 1996 to 2003, Wanishi 2005), the part of the Seto Inland Sea that Yashiro Is. faces, is near that of the northern limits of *A. japonica* (10–13 ℃, Harii et al. 2001; Japan Oceanographic Data Center 2012). Therefore, the water temperature at Yashiro Is. appears unsuitable for *A. japonica* to thrive.

Seaweeds and *A. japonica* have a competitive relationship in their shared habitats at Yashiro Is., although the seaweeds generally show a clear seasonal fluctuation, with most species more abundant from winter to spring than from late summer to autumn (e. g., Kato and Jonai 2016). However, until recently, only one detailed survey of the *A. japonica* bed at Yashiro Is. had been conducted, in September 2011 (Ministry of the Environment of Japan 2012b).

Jeju Island (hereafter Jeju Is.), Korea, also has an *A. japonica* bed, which recently expanded to cover more than 1 ha and thrives alongside *Ecklonia cava* Kjellman 1885 (Denis et al. 2013). Jeju Is. and Yashiro Is. lie on the same latitude (33°N). However, the process of *A. japonica* expansion at Jeju Is. is thought to have included a shift from seaweed forest to coral meadow, passing through a phase of barren ground during which seaweeds declined and coralline algae covered the sea bottom (Vieira et al. 2016). This process seems to be different from the process at Yashiro Is., where there are rich seaweed beds alongside the *A. japonica* bed. Jeju Is. is directly affected by the distributary Tsushima Current, which is part of the warm Kuroshio Current, whereas Yashiro Is. is located in a sheltered inland sea where the warm current seldom reaches, which affects the characteristics of the seaweed and coral communities. In general, community structures of seaweeds and corals in the temperate to warm temperate regions are less investigated than those of the tropical regions (Denis et al. 2015; Wernberg et al. 2016).

Assessing and understanding current community structures and species diversity of major benthic organisms such as seaweeds and corals are important parts of documenting changes in and conserving coastal ecosystems in temperate regions. Seawater temperatures are predicted to increase 2 ℃ in the top 100 m depth by 2100, according to the worst-case scenario model, which assumes a constant increase in greenhouse gas emissions (Pachauri et al. 2014). Because Yashiro Is. is at the edge of the known range of *A. japonica*, it is an appropriate place to detect changes caused by climate change. The present study aimed to provide baseline data on the seaweed flora, including seasonal changes in the seaweed community structure, for the *A. japonica* bed at Yashiro Is.

Methods

The study site was the *A. japonica* bed at Jikamuro Marine Park (33°51′N, 132°21′E), located on the southern coast of Yashiro Is., in Suo-Oshima town, Yamaguchi Prefecture, Japan (Fig. 1). Surveys of seaweed community structure were conducted by scuba diving in 2014. Two transect lines (Fig. 2) were selected to represent seaweed community structures based on descriptions of 66 quadrats (1 m^2) of 11 transect lines (40–75 m, mean 54 m) in a previous survey (Ministry of the Environment of Japan 2012b). These two lines were similar in topography and substrata and therefore they were chosen to infer environmental factors affecting the seaweed community structure. The transects were set on the slopes of the southern and northern sides of a submerged rocky reef. The southern side of the reef faces the open Iyo-nada Sea, whereas the northern side is more sheltered, facing toward Yashiro Is. According to Ministry of the Environment of Japan (2012b), along the southern transect line, *A. japonica* coverage was up to 10% and canopy-forming brown algae grew thickly (up to 100%); along the northern line, *A. japonica* coverage was up to 70% and canopy-forming brown algae grew sparsely. The origins of the transect lines were placed on the shoreline sides with the transect lines extending toward the open sea, along the sea bottom. The southern line was 45 or 50 m long, and the northern line was 40 m long. The lengths of the transect lines and intervals between quadrats were based on a preliminary survey conducted in February 2014. Depths and substratum types were recorded for every quadrat. Measured depths were calculated to the datum level. Substratum type was categorized by sediment type according to Bain et al. (1985).

Surveys were conducted at the northern line in April and October 2014 and the southern line in May and September 2014. The surveys recorded *A. japonica* and all algal species found in each 1 m^2 quadrat, which were placed at 5 m intervals (intervals of less than 5 m were used when the substrata or seaweed community drastically changed within the interval). Identification of seaweed species found in quadrats and around transect lines were based on field observation or microscopic observations of specimens collected when it was difficult to identify species by field observation alone. We treated the temperate kelp *Ecklonia kurome* Okamura 1927 as an independent species due to differences in morphological features and distribution in Japan, although this species is generally regarded as a taxonomic synonym of *E. cava*, with no known genetic difference between the species (Tanaka et al. 2007).

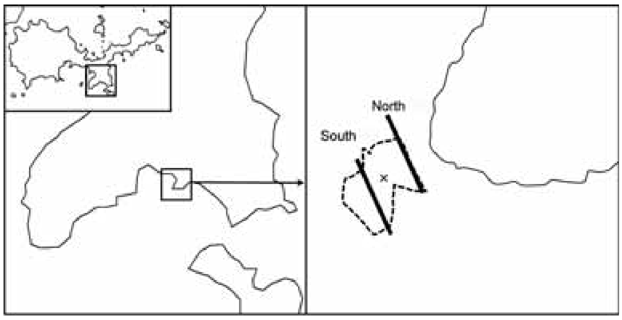

Fig. 2. The detailed location of the transect lines at the Jikamuro Marine Park in Yashiro Island, Japan. The dotted line indicates the *A. japonica* bed on a submerged rocky reef. Thick lines indicate transect lines. The × indicates the top of the submerged rocky reef, where it is emergent at low tide.

Mean current velocity (water speed) was estimated using plaster balls (gypsum blocks), following the methods of Kawamata (2001), from December 2013 to November 2014. Gypsum blocks were placed at four points that differed in coverage of canopy-forming seaweeds and *A. japonica* near the transect lines. The gypsum blocks were replaced every 2 months. Water temperature data loggers (UTBI-001 or UA-002-64, Onset Computer Corporation, Bourne, MA, USA) were installed at the same places from March 2014 to January 2015, and water temperature was measured at 1-hour intervals for comparison of temperature variation among locations.

The seasonal difference in coverage of canopy-forming seaweeds at each line was analyzed using the Wilcoxon rank-sum test because the distribution of the coverage of *E. kurome* and sargassaceous plants was not normal. These coverage differences were not significant, and therefore spring and autumn data were combined to analyze the differences between the northern and southern lines. The line-based differences in coverage of *A. japonica*, *E. kurome*, and sargassaceous plants were also analyzed using a Wilcoxon rank-sum test. Correlations among coverage of *E. kurome*, sargassaceous plants, and *A. japonica* and depth were calculated with the Spearman rank correlation coefficient (ρ). We used JMP statistical software (version 10, SAS Institute Inc., Cary, NC, USA) for all statistical analyses.

Results

During the survey on and around the two transect lines, a total of 69 macroalgae species were identified: 7 species of Chlorophyceae, 30 species of Phaeophyceae, and 32 species of Rhodophyceae (Table 1). The most commonly observed canopy-forming seaweeds were the temperate kelp *E. kurome* and the sargassa-

Table 1. List of seaweeds in the *Alveopora japonica* bed at Yashiro Island, Japan. Asterisks indicate voucher specimens that are stored at Takehara Fisheries Research Station, Hiroshima University, Japan.

Class	Scientific name
Chlorophyceae	*Ulva intestinalis* Linnaeus
	Ulva pertusa Kjellman
	Ulva prolifera Müller
	Codium arabicum Kützing*
	Codium contractum Kjellman*
	Codium fragile (Suringer) Hariot
	Codium spongiosum Harvey
Phaeophyceae	*Ralfsia* sp.
	Dictyopteris latiuscula (Okamura) Okamura*
	Dictyopteris prolifera (Okamura) Okamura
	Dictyopteris undulata Holmes
	Dictyota dichotoma (Hudson) Lamouroux
	Distromium decumbens (Okamura) Levring*
	Pachydictyon coriaceum (Holmes) Okamura*
	Padina arborescens Holmes*
	Ruglopteryx okamurae (Dawson) Hwang, W.J. Lee et Kim*
	Sphaerotrichia divaricata (C. Agardh) Kylin
	Tinocladia crassa (Suringar) Kylin
	Punctaria latifolia Greville*
	Colpomenia bullosa (Saunders) Yamada
	Colpomenia sinuosa (Mertens ex Roth) Derbès et Solier
	Hydroclathrus clathratus (C. Agardh) Howe
	Cutleria multifida (Turner) Greville*
	Carpomitra costata (Stackhouse) Batters*
	Desmarestia dudresnayi Lamouroux ex Leman subsp. *tabacoides* (Okamura) Peters et al.
	Desmarestia viridis (O.F. Müller) Lamouroux*
	Undaria pinnatifida (Harvey) Suringar*

Class	Scientific name
Phaeophyceae	*Chorda asiatica* Sasaki et Kawai*
	Ecklonia kurome Okamura*
	Myagropsis myagroides (Mertens ex Turner) Fensholt*
	Sargassum fulvellum (Turner) C. Agardh*
	Sargassum fusiforme (Harvey) Setchell*
	Sargassum horneri (Turner) C. Agardh*
	Sargassum macrocarpum C. Agardh*
	Sargassum siliquastrum (Turner) C. Agardh*
	Sargassum yamamotoi Yoshida*
	Sargassum yendoi Okamura et Yamada*
Rhodophyceae	*Dichotomaria apiculata* (Kjellman) Kurihara et Masuda*
	Nemalion vermiculare Suringar
	Amphiroa anceps (Lamarck) Decaisne*
	Amphiroa beauvoisii Lamouroux
	Corallina crassissima (Yendo) Hind et Saunders*
	Corallina pilulifera Postels et Ruprecht*
	Jania adhaerens Lamouroux*
	Lithophyllum okamurae Foslie
	Mesophyllum nitidum (Foslie) Adey*
	Synarthrophyton chejuensis Kim et al.*
	Sporolithon durum (Foslie) Townsend et Woelkerling*
	Gelidium elegans Kützing*
	Ptilophora subcostata (Okamura) Norris*
	Asparagopsis taxiformis (Delile) Trevisan
	Bonnemaisonia hamifera Hariot*
	Dudresnaya japonica Okamura*
	Halarachnion latissimum Okamura*
	Chondrus ocellatus Holmes
	Grateloupia turuturu Yamada
	Hypnea flexicaulis Yamagishi et Masuda
	Callophyllis japonica Okamura*
	Kallymenia sp.*
	Peyssonnelia sp.*
	Peyssonnelia caulifera Okamura*
	Plocamium cartilagineum (Linnaeus) Dixon*
	Plocamium telfairiae (Hooker et Harvey) Harvey*
	Gracilaria incurvata Okamura
	Champia bifida Okamura
	Champia parvula (C. Agardh) Harvey
	Pterothamnion intermedium (Tokida) Athanasiadis et Kraft*
	Plumariella yoshikawae Okamura*
	Dasya sp.*

ceous plants *Sargassum macrocarpum* C. Agardh 1820, *Myagropsis myagroides* (Mertens ex Turner) Fensholt 1955, *S. horneri* (Turner) C. Agardh 1820, *S. yamamotoi* Yoshida 1983, and *S. fulvellum* (Turner) C. Agardh 1820. The most common understory species were articulated coralline species *Amphiroa anceps* (Lamarck) Decaisne 1842 and *Corallina crassissima* (Yendo) Hind et Saunders 2013 and crustose coralline species *Mesophyllum nitidum* (Foslie) Adey 1970. *Alveopora japonica* was the only zooxanthellate scleractinian coral found at Yashiro Is.

Coverage of seaweeds and *A. japonica* on the two examined transect lines of this coral bed at Yashiro Is. is shown in Figures 3 and 4. There were only small differences in coverage between spring (Fig. 3) and autumn (Fig. 4) among canopy species. In both lines, canopy-forming

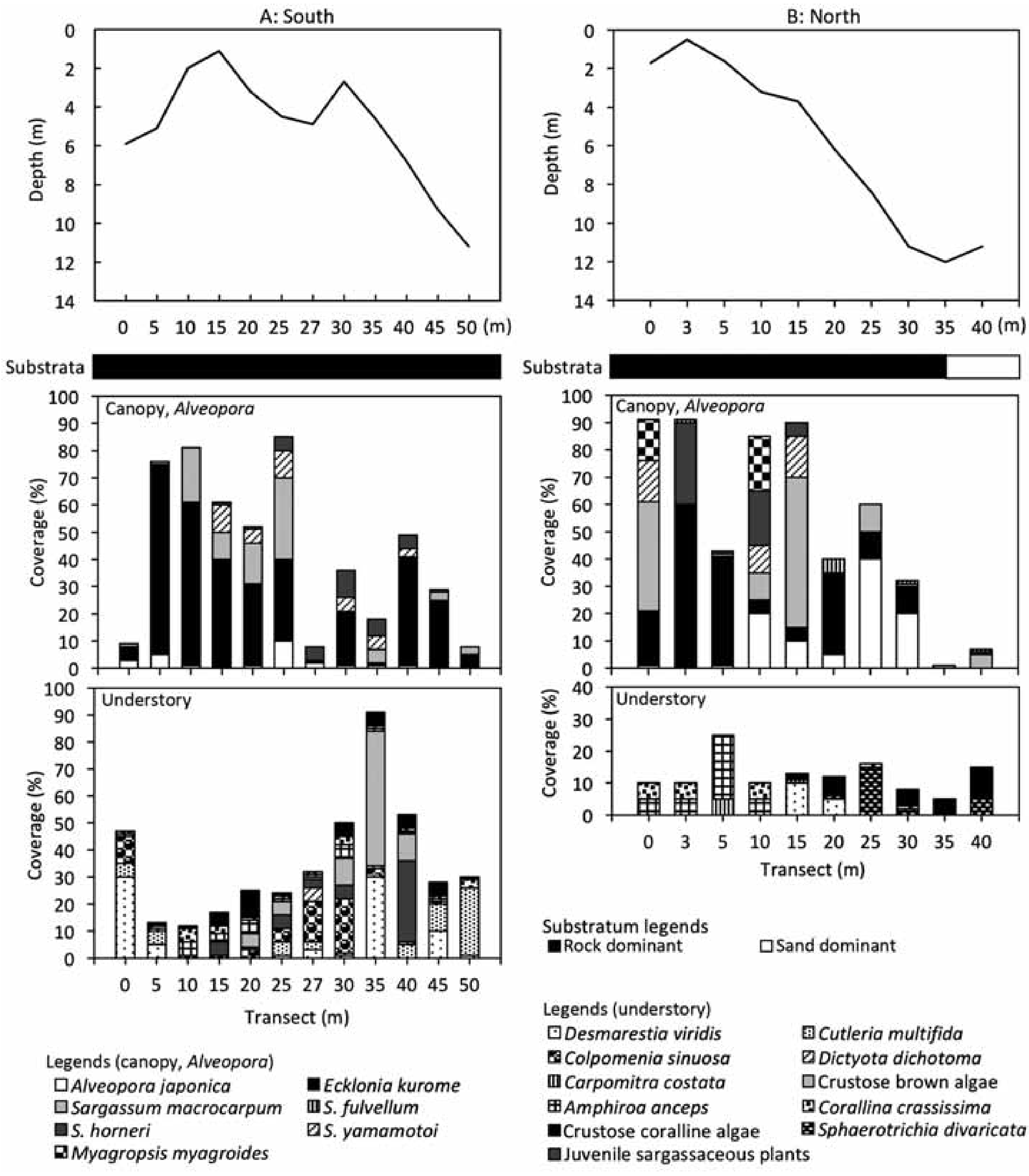

Fig. 3. Diagrams of vertical topography (solid lines), dominant substrata (horizontal bars), and coverage (vertical bars) by *Alveopora japonica* and seaweeds forming the canopy and understory on the (A) southern and (B) northern transect lines surveyed in spring at Yashiro Island, Japan.

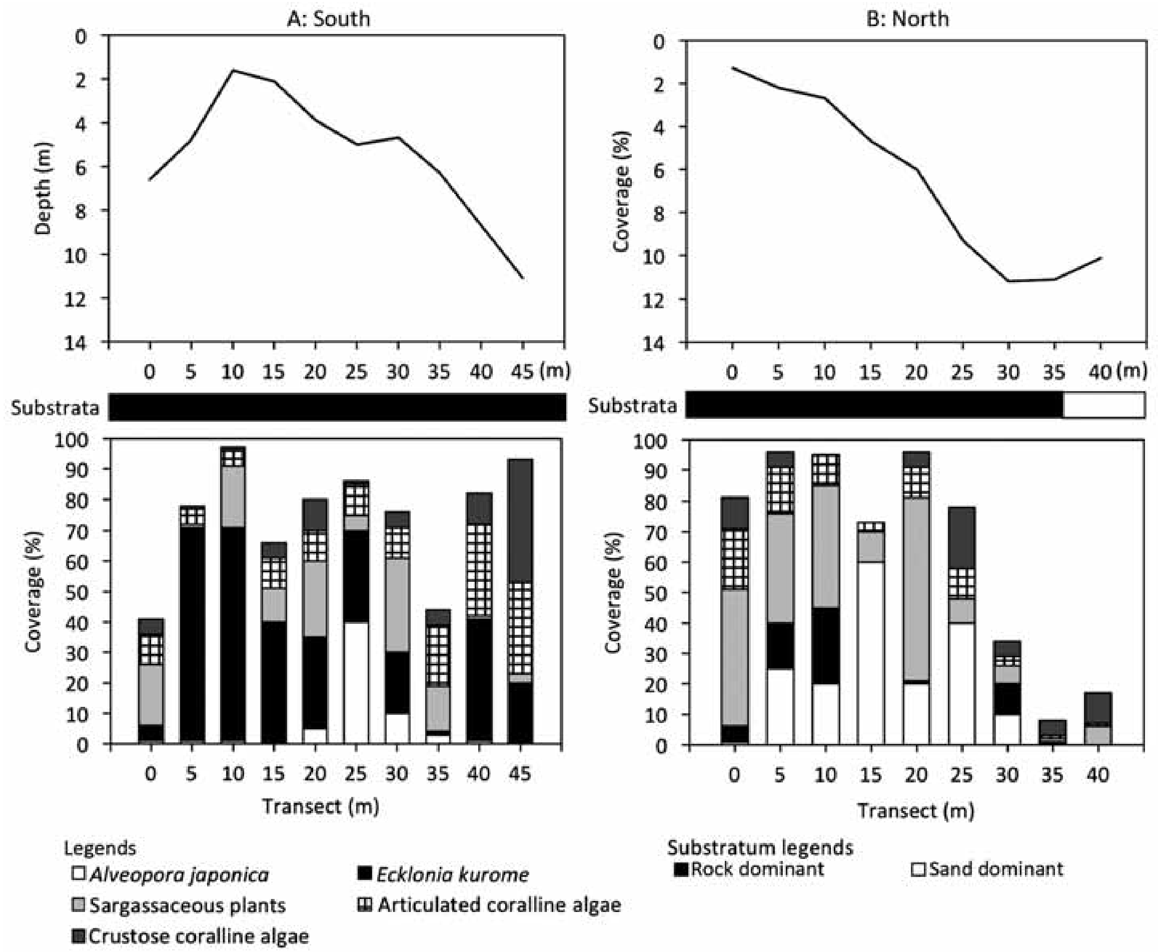

Fig. 4. Diagrams of vertical topography (solid lines), dominant substrata (horizontal bars), and coverage (vertical bars) by *Alveopora japonica* and seaweeds forming the canopy and understory on the (A) southern and (B) northern transect lines surveyed in autumn at Yashiro Island, Japan.

seaweeds (*E. kurome* and sargassaceous plants) had more than 60% coverage at depths of 1–6 m. *Alveopora japonica* was dominant (40–60% coverage) in deeper water (5–9 m) along the northern line. However, even at *A. japonica*-dominated depths, *E. kurome* and sargassaceous plants covered 8–35% of each quadrat. Understory species that had high coverage (15–30%) in spring were *Colpomenia sinuosa* (Mertens ex Roth) Derbès et Solier 1851, *Cutleria multifida* (Turner) Greville 1830, *Desmarestia viridis* (O. F. Müller) Lamouroux 1813, and *Sphaerotrichia divaricata* (C. Agardh) Kylin 1940, although these species were not found in autumn. There was no barren ground where seaweeds had declined and coralline algae covered the sea bottom at either transect line at either sampling date.

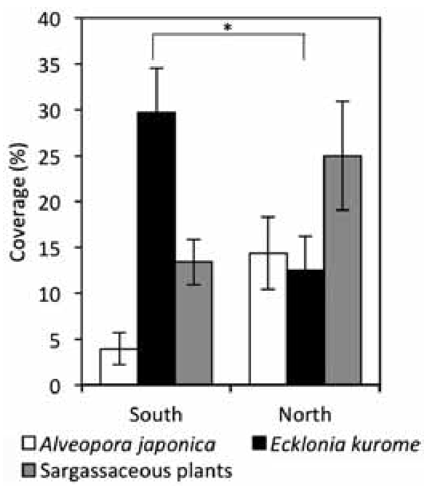

Fig. 5. Coverage of *Alveopora japonica, Ecklonia kurome*, and sargassaceous plants on the transect lines at Yashiro Island, Japan. An asterisk indicates a statistically significant difference ($p<0.05$) between two lines.

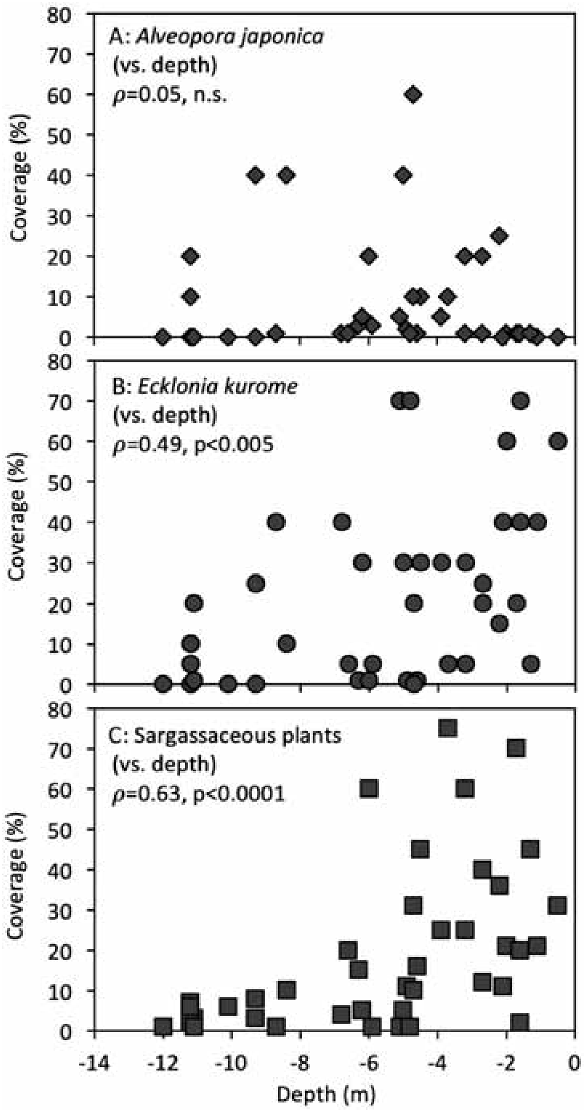

Fig. 6. Relationships (scatter plots) between depth and coverage of (A) *Alveopora japonica*, (B) *Ecklonia kurome*, and (C) sargassaceous plants on the transect lines. Correlation coefficients and p-values (n.s. = not significant) are also shown.

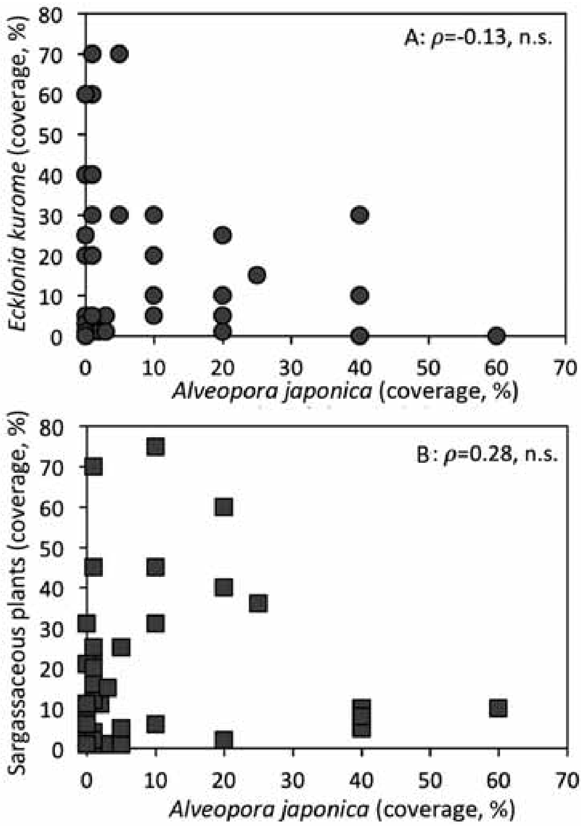

Fig. 7. Relationships (scatter plots) between coverage of *Alveopora japonica* and that of (A) *Ecklonia kurome* and (B) sargassaceous plants of the transect lines. Correlation coefficients and p-values (n.s. = not significant) are also shown.

The between-line coverage difference was significant for *E. kurome*, but not for sargassaceous plants or *A. japonica* (Fig. 5; *E. kurome*: $z = -2.75$, $p < 0.01$; *A. japonica*: $z = 1.59$; sargassaceous plants: $z = 0.97$). Correlations between coverage and depth (Fig. 6) were observed for *E. kurome* ($\rho = 0.49$, $p < 0.005$) and sargassaceous plants ($\rho = 0.63$, $p < 0.0001$) but not for *A. japonica* ($\rho = 0.05$). However, there were no correlations between the coverage of *A. japonica* and the canopy-forming seaweeds (Fig. 7; *E. kurome*: $\rho = -0.13$; sargassaceous plants: $\rho = 0.28$). The substrata of the sea bottom along the southern line were primarily composed of bedrock with a few larger boulders. The coverage of fine sediment settled onto the 1 m^2 quadrats was below 5% at depths shallower than 3 m but 5–90% at depths deeper than 3 m.

The annual mean current velocity (December 2013 to November 2014) was 5.8 ± 1.7 cm/s at the point of high seaweed coverage on the southern line (3 m depth), which was higher than at the three other measurement points (3.3 ± 0.6 to 3.8 ± 0.8 cm/s) on the southern and northern lines (6–7.5 m depth). The range of monthly mean water temperature (March 2014 to January 2015) was 10.9℃ (March 2014) to 23.7℃ (September 2014) at the 3–7.5 m depth. There were no significant differences among the water temperatures recorded at the four points of the two transect lines.

Discussion

This is the first detailed study of the community structures of seaweed and coral in the zooxanthellate coral *A. japonica* bed at Yashiro Is., Japan. Our data show that *A. japonica* exists in this temperate seaweed bed in both seaweed-abundant and seaweed-sparse seasons. The 69 species of macroalgae identified at the study site were temperate species, most of which have previously been reported in the western Seto Inland Sea (Murase et al. 1993; Kato and Jonai 2016). In particular, the presence of *E. kurome* and eight sargassaceous species indicates that the diversity of canopy-forming species common to temperate seaweed beds also appears in the *A. japonica* bed at Yashiro Is. Mean coverage (maximum coverage) values were 23.9% (70%) for *E. kurome*, 19.3% (75%) for sargassaceous plants, and 12.0% (60%) for *A. japonica*, which largely agreed with the previous survey's values: 28.1% (80%), 12.9% (61%), and 5.2% (70%), respectively (Ministry of the Environment of Japan 2012b). At Jeju Is., Korea, *E. cava* covered approximately 4% and the total seaweed community covered less than 20% of the area (Denis et al. 2013, 2015), a coverage that is less than half that at Yashiro Is. However, the mean coverage of *A. japonica* at Jeju Is. (more than 60%; Denis et al. 2013, 2015) is much higher than that at Yashiro Is. The difference in the benthic community structure between Yashiro Is. and Jeju Is. may be attributed to seawater temperatures, because the range of the typical monthly seawater temperature at Jeju Is. (13.3–26.1℃, Denis et al. 2015) is greater than that around Yashiro Is. (10–26℃ at 0-m depth in the Iyo-nada Sea from 1996 to 2003, Wanishi 2005). The *A. japonica* bed at Yashiro Is. experiences a more temperate environment than that at Jeju Is.

Seawater temperature increases lead to a decline in temperate canopy-forming seaweeds and their replacement by subtropical or tropical species of seaweeds and corals (e.g., Wernberg et al. 2016). *Alveopora japonica* is a hermaphroditic brooding coral that releases planula larvae instead of gametes into the water column; it has the advantage of rapid colonization (Harii et al. 2001). Therefore, the recent temperature increase in the Seto Inland Sea (Tarutani 2007) may have contributed to expansion of this coral bed by reducing the early settlement mortality of *A. japonica* larvae and extending the growth period of this coral; in Japan, the larvae are released in September and October (Harii et al. 2001).

However, the reasons for the expansion of *A. japonica* are not limited to the seawater temperature increase. The lowest monthly mean temperature at our study site at Yashiro Is. (10.9℃) is similar to that of the Iyo-nada Sea (10℃, Wanishi 2005), and to those at the northern limits of *A. japonica*'s distribution in Japan: 13℃ in Tateyama from 1994 to 1995 (Harii et al. 2001) and 10.6℃ in Oki Islands from 2002 to 2009 (Japan Oceanographic Data Center 2012). Bungo Channel is located 50 km south of Yashiro Is. and is connected to the Kuroshio Current. Along the 100 km of Bungo Channel, where seawater temperature ranges from 11–17℃ from north to south in winter, there is a clear gradient from luxuriant underwater forests with many temperate kelp and sargassaceous plants to barren ground with coralline algae, sea urchins, and zooxanthellate corals (Yoshida et al. 2011). However, large populations of *A. japonica* have never been found in Bungo Channel (Ministry of the Environment of Japan 2011).

When seawater temperatures exceed the optimal temperatures for growth of seaweeds, photosynthesis, growth rate, or both can decline, which can lead to a decrease in seaweed coverage (Serisawa et al. 2001; Haraguchi et al. 2005). The maximum seawater temperature recorded during the present study was 24.4℃ (September 5, 2014). This temperature is within the optimal temperature ranges for growth of the perennial canopy-forming seaweeds common to Yashiro Is.: 22–25℃ for gametophytes of *E. kurome* (Tanaka et al. 2008), 25–27℃ for sporophytes of *E. cava* (Serisawa et al. 2001), and 10–25℃ for sargassaceous species (*M. myagroides, S. fulvellum*, and *S. macrocarpum*) (Haraguchi et al. 2005). Therefore, the seawater temperature at Yashiro Is. was not a critical factor in the decline of canopy-forming seaweeds. In fact, along the southern coast of Yashiro Is. where *A.*

japonica does not grow, there is more than 60% coverage of *E. kurome* at depths of up to 12 m, whereas at the *A. japonica* bed at Yashiro Is., such coverage existed only up to depths of 6 m (Ministry of the Environment of Japan 2012b; Yoshida et al. 2014; this study). Seawater temperature is an important factor in determining the biogeographic distribution of *A. japonica* and temperate seaweeds. However, the distribution of these species within the small scale of the *A. japonica* bed at Yashiro Is. seem to be influenced by local environmental factors.

In the present study, the coverage of the canopy-forming seaweeds was affected by depth, but *A. japonica* coverage was not significantly affected by either depth or seaweed coverage. However, *A. japonica* coverage tended to decrease where the coverage of canopy-forming seaweeds was high (Figs 3, 4, 7). These results suggest that *A. japonica* cannot win in competition with seaweeds. One local environmental factor that may be associated with the decline of canopy-forming seaweeds is the fine sediments that are suspended in the water column and settle at the sea bottom. The suspended sediments generally consist of mineral and organic matter such as silt and decomposed organisms; they make the water muddy and cover substrate and seaweed surfaces (Fig. 8A). This prevents the settlement and germination of seaweed spores and also inhibits photosynthesis of seaweeds by blocking the light, thus preventing these species from growing (Hiraoka et al. 2001; Fisheries Agency of Japan 2015). *Alveopora japonica* can survive not only in turbid and shallow habitats inside bays (1–3 m depth), but also at sites deeper than 15 m, in locations facing the Pacific Ocean or the Japan Sea (Sugihara et al. 2009; telephone interviews of local SCUBA diving shops in Japan). At Yashiro Is., this coral was found at depths of 1–15 m (Ministry of the Environment of Japan 2012b; this study). However, the tolerance of *A. japonica* to the suspended sediments may not be higher than that of seaweeds. The upper surface of some *A. japonica* colonies had died and their skeletons were exposed at Yashiro Is. (Fig. 8B). This may have happened because sediment deposits on the corals prevented them from feeding or engaging in photosynthesis (Rogers 1990; Erftemeijer et al. 2012). Therefore, we hypothesize that the decrease in the seaweed coverage due to sediments or other environmental factors provides open spaces in which the coral may grow. In open spaces near the seaweeds where *A. japonica* grows, the effects of sediment deposits may be mitigated, and there may be enough light intensity for *A. japonica* to engage in photosynthesis. Further research is needed to clarify the optimal environmental conditions for *A. japonica* growth, including water quality and current velocity. Our data showed that *E. kurome* coverage was higher at a relatively high current velocity than at a lower current velocity, which may indicate that

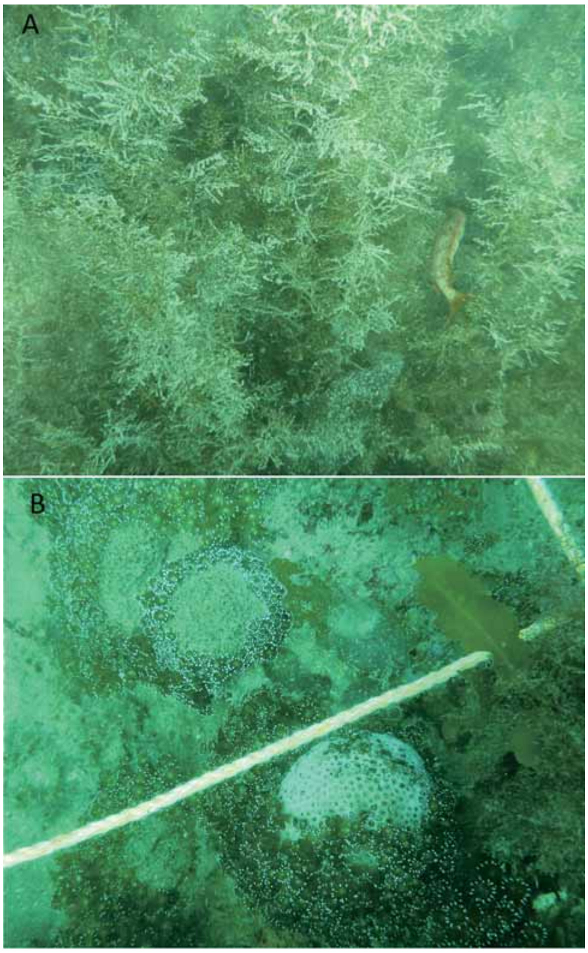

Fig. 8. Seaweeds and *Alveopora japonica* at the coral bed in Yashiro Island, Japan (Photographs taken on October 24, 2014). (A) Sargassaceous plants covered by fine sediments. (B) *A. japonica* colonies of which the upper surface died and skeletons were exposed.

current velocity has an effect on seaweed growth and sediment deposits.

In conclusion, the *A. japonica* bed at Yashiro Is., Japan, showed a community structure more like a temperate one than that observed at Jeju Is., Korea. It has expanded within a flourishing temperate seaweed bed without transitioning through seaweed bed to barren ground. This *A. japonica* expansion, in the lowest temperature region within its distribution range, was probably influenced by both a seawater temperature increase and other local environmental conditions. Furthermore, net photosynthesis of *Ecklonia* species is adversely affected by high water temperature and low irradiance (Kurashima et al. 1996); thus, as global warming progresses, juvenile *Ecklonia* under the adult canopy may suffer from the negative effects of both high temperature and low irradiance. A seawater temperature increase may also indirectly affect seaweeds by enabling prolonged grazing by herbivorous fish (Takao et al. 2015). Constant assessments of seaweed and *A. japonica* community structures at this coral bed at Yashiro Is. are necessary to clarify their dynamics and develop plans for conservation.

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