Phycological Research

Phycological Research 2021; **69:** 12–30 doi: 10.1111/pre.12395

REVIEW

Japan's nationwide long-term monitoring survey of seaweed communities known as the "*Monitoring Sites 1000*": Ten-year overview and future perspectives

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SUMMARY

"*Monitoring Sites 1000*" – Japan's long-term monitoring survey was established in 2003, based on the Japanese Government policy for the conservation of biodiversity. Ecological surveys have been conducted on various types of ecosystems at approximately 1000 sites in Japan for 15 years now and are planned to be carried out for 100 years. Since 2008, seaweed communities had been monitored at six sites, featuring the kelp (e.g. *Saccharina* and *Ecklonia*; Laminariales) and *Sargassum* (Fucales) communities in the subarctic and temperate regions of Japan. Annual surveys were carried out during the season when these canopy-forming seaweeds are most abundant. A non-destructive quadrat sampling method, with permanent quadrats placed along transects perpendicular to the shoreline, was used to determine species composition, coverage, and vertical distribution of seaweeds at these sites; while destructive sampling was done every 5 years to determine biomass. The occurrence of canopy-forming species *Saccharina japonica* (var. *japonica*) and *Ecklonia cava* have appeared to be stable at the Muroran (southwestern part of Hokkaido Island) and Shimoda (Pacific coast of middle Honshu Island) sites, respectively; whereas the coverage of *Ecklonia radicosa* (= *Eckloniopsis radicosa*) at the Satsuma-Nagashima site in southern part of Kyushu Island was highly variable until its sudden disappearance from the habitat in 2016. Thalli of *E. radicosa* lost most of their blades through browsing by herbivorous fish, and thus, this may be one of the causes of the decline. A shift in the community structure related to environmental changes had also been observed at some other sites. Pre- and post-disaster data revealed the impact of the 2011 earthquake and *tsunami* disasters, including a shift in the vertical distribution of *Ecklonia bicyclis* (= *Eisenia bicyclis*) to shallower depths at the Shizugawa site in the Pacific coast of northern Honshu Island, due to seafloor subsidence.

Key words: algae, climate change, community structure, *Ecklonia*, gap dynamics, kelp forest, *Saccharina*, *Sargassum*, subsidence, succession.

INTRODUCTION

Japan is the largest island country in East Asia, comprising over 6000 islands extending along the Pacific coast. It lies between latitudes of 24° and 46°N, with its islands characterized by subtropical, temperate and subarctic climates (Geospatial Information Authority of Japan 2018). The country has the sixth longest coastline in the world that stretches around 30 000 km (Central Intelligence Agency 2018). Coastal habitats include coral reefs, seagrass meadows, algal forests, intertidal mudflats, and rocky/sandy shores. The geography of Japan and the flow directions of the ocean currents along this coastal region allow the development and persistence of several temperate and subarctic seaweeds, such as *Sargassum patens* C. Agardh (Fucales); *Ecklonia cava* Kjellman and *Saccharina japonica* (Areschoug) Lane *et al.* (Laminariales; Yoshida 1998; Yoshida *et al.* 2001). These seaweed communities are of great ecological importance within the coastal ecosystem, serving as food, habitat, and nursery for many associated biological organisms (Mukai

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Communicating editor: Kazuhiro Kogame
Received 27 December 2018; accepted 29 April 2019.

1971; Edgar & Aoki 1993; Steneck *et al*. 2002; Graham 2004; Christie *et al*. 2009; Harley *et al*. 2012; Raybaud *et al*. 2013; Teagle *et al*. 2017). Some species of seaweeds have also been harvested by local inhabitants for direct human consumption (Ohno & Largo 1998; Zemke-White & Ohno 1999).

In 2001, Ministry of the Environment, Government of Japan (MEGJ) listed 500 important wetlands (MEGJ 2001), as candidate sites in the Ramsar List of wetlands of international importance; and field surveys were undertaken to assess the flora and distribution of seaweed communities at 129 of these sites in the early 2000s (The 7th National Survey on the Natural Environment [Seaweed communities], MEGJ 2008). While data from a single-year survey revealed the current status of seaweed and/or seagrass communities in this region, long-term monitoring is necessary to identify the changes in these communities, especially in relation to the effects of exploitation and climate change. Hence, the "*Monitoring Sites 1000*" was launched in 2003. It is a project sponsored by MEGJ to continuously conduct ecological surveys in terrestrial (alpine zones, forests, grasslands) and aquatic ecosystems including seaweed and/or seagrass communities at approximately 1000 sites throughout Japan (MEGJ 2003). It was also one of the proposals outlined in the Second National Biodiversity Strategy of Japan in 2002. The project was founded on the basic premise that long-term datasets are essential to detect trends in the abundance and distribution of 'structuring' organisms, and to monitor possible alterations of natural communities in the face of climate change. This long-term project is planned to be carried out for 100 years, in close cooperation with scientists in research and academic institutions as well as non-profit and non-governmental organizations (MEGJ 2003). It will likewise promote widespread information sharing by extending its research activity and its international scientific networks. The data gathered from this project is relevant to the development of regulations and directives to ensure biodiversity conservation and environmental sustainability.

Annual monitoring of rocky shores, estuaries, seagrass beds, and seaweed communities commenced in 2008, after the establishment of a standard methodology that can be applied to all these coastal habitats in 2007. Quantitative description of communities, in terms of species composition, percentage cover, and vertical distribution of foundation species were obtained at various sites across Japan.

In fact, the degradation of natural coastal areas (e.g. land reclamation and urbanization of coastal areas) has led to the loss of much natural habitat. It has been estimated that the aggregate area of seaweed/seagrass communities in Japan has decreased from 200 000 to 125 000 ha between 1978 and 2007 (Fisheries Agency of Japan 2011). The loss of these communities has become a serious problem for local fisherman and the local economy (e.g. Dotsu *et al*. 1999; Serisawa *et al*. 2000; Hasegawa *et al*. 2003). Massive decline of the seaweed vegetation including algal forests has also become a worldwide concern, in relation to seawater temperature rise driven by global warming (Wernberg *et al*. 2011, 2013, 2016; Harley *et al*. 2012; Raybaud *et al*. 2013; Voerman *et al*. 2013; Vergés *et al*. 2014, 2016, 2019; Filbee-Dexter & Wernberg 2018). In Japan, shifts in abundance and distribution of subtropical and temperate species of *Sargassum* have been reported (Tanaka *et al*. 2012, 2013; Kumagai *et al*. 2018); these changes are generally most evident near their northern or southern limits of distribution (Nakashima *et al*. 2013; Watanabe *et al*. 2014; Terada *et al*. 2016). Moreover, the 2011 Great East Japan Earthquake (GEJE) and *tsunami* disaster in the Sanriku coast, northeastern part of Honshu Island facing the Pacific Ocean, resulted in the loss of its marine vegetation. Pre- and post-disaster data in this affected area revealed the significant impact on the coastal biological communities (Seike *et al*. 2013; Takami *et al*. 2013; Noda *et al*. 2016; Muraoka *et al*. 2017; Nakaoka *et al*. 2017; Suzuki *et al*. 2017; Sakanishi *et al*. 2018).

In this paper, we summarize the results of the 10-year monitoring of seaweed communities, including the characteristic distribution of canopy-forming species at various sites in Japan. It is expected that the information, knowledge and insights provided by this report will be able to assist the government and other interested parties design policies that relate to conservation and sustainable use of these coastal habitats.

METHODS

Monitoring sites

Japan is surrounded by four bodies of water: the Sea of Okhotsk in the north, the Pacific Ocean in the east and south, the East China Sea in the southwest, and the Sea of Japan in the west. Its coastline is also influenced by the warm *Kuroshio* and cold *Oyashio* currents (also known as the Japan Current and Kurile Current, respectively; Hydrographic and Oceanographic Department, Japan Coast Gard [HOC-JCG] 2018). Based on these factors that influence the coastal environment, Japan's coast was divided into six regions by the coastal working group of the current project (Fig. 1).

Region #1 is located in the east coast of Hokkaido and the northeastern coast of Honshu (the Pacific coast of Tohoku region) islands, and is influenced by the cold *Oyashio* current. Despite the relatively low latitude in the northern hemisphere, the *Oyashio* current facilitates the growth of cold-water kelps like *Saccharina* (= *Laminaria auctorum japonicorum*, Lane *et al*. 2006), *Alaria*, and *Costaria* (Laminariales) in this region (Kawashima 1989, 2012; Borlongan *et al*. 2018, 2019a). Region #2 is located along the coast of Sea of Japan in Honshu and the west coast of Hokkaido, and is mainly influenced by the warm *Tsushima* current (a branch of the *Kuroshio* that flows north through the Sea of Japan). In this region, temperate kelps (e.g. *Ecklonia* [*sensu lato*; including *Eisenia* and *Eckloniopsis*, Rothman *et al*. 2015], Laminariales) and *Sargassum* (Fucales) are found, in addition to the cold-water kelps that dominate the coast of Hokkaido. Region #3 is located in the semi-enclosed Seto Inland Sea that is surrounded by three major islands of Japan (Honshu, Shikoku and Kyushu). *Ecklonia* and *Sargassum* are the abundant canopy-forming seaweeds in this region. Due to its semi-enclosed environment, the influence of the major ocean current (i.e. *Kuroshio*) is somewhat limited. However, nutrient loading into the coastal water favors the growth of seaweed communities (Yoshida *et al*. 2001). Regions #4 and #5 are located in the Pacific coast of middle Honshu (#4), and of

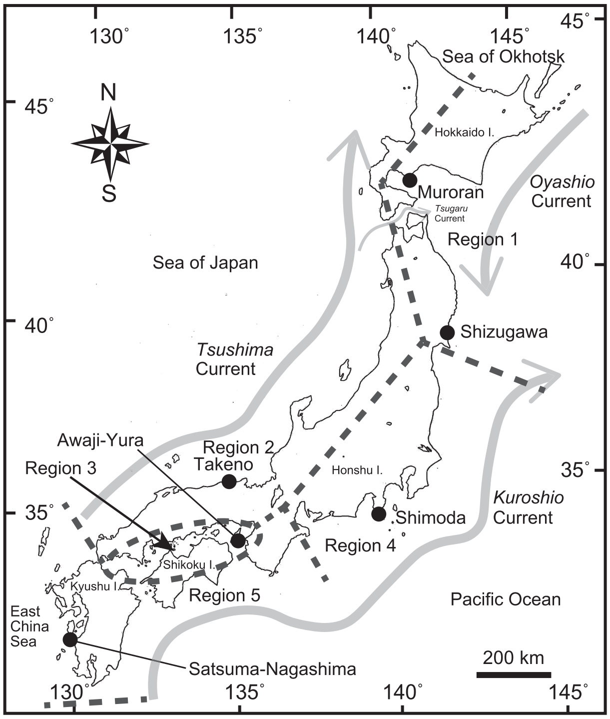

Fig. 1. Map of Japan showing the location of six monitoring sites and the ocean currents in the offshore of Japan. Based on the factors ocean currents that influence the coastal environment, Japan's coast could be divided into six regions. The regions 1–5 are located in four major islands in Japan proper. The sixth region is located in the Ryukyu Islands; however, it was removed from the map due to the absence of a monitoring site.

southern Honshu, Shikoku and Kyushu islands (#5), respectively. These areas are particularly influenced by the warm *Kuroshio* current, and are characterized by *Ecklonia* and *Sargassum*-dominated communities. Subtropical seaweeds (e.g. *Sargassum ilicifolium* (Turner) C. Agardh, *Sargassum alternato-pinnatum* Yamada; Shimabukuro *et al.* 2007; Tsuchiya *et al.* 2011) also occur in southern Kyushu (Region #5), thereby suggesting this region as an ecotone for temperate and subtropical seaweed communities. Region #6 is located in the Ryukyu archipelago. It is strongly influenced by the warm *Kuroshio* current, which is the primary factor producing the high species richness of the Japanese coral fauna (Spalding *et al.* 2001). Northward reductions in coral biodiversity through the Ryukyu Islands with disappearance of low-latitude species along the Pacific coast of the Japanese mainland also indicates the northern latitudinal limit for coral reefs in this region (Yamano *et al.* 2001, 2011, 2012). Tropical and subtropical seaweeds can also be found in the coral lagoons.

From these six regions, six study sites were selected for monitoring (Fig. 1). Two sites belong to Region #1: the Muroran site in Hokkaido Island, and the Shizugawa site in Miyagi Prefecture facing the Pacific Ocean. These sites were chosen, since the degree of influence of the cold *Oyashio* current on the two coastlines was found to be different (Kawashima 1989; Suzuki *et al.* 2015; HOC-JCG 2018; Sakanishi *et al.* 2018). The Takeno site in the northern coast of Hyogo Prefecture represents Region #2, while the Awaji-Yura site is in the Seto Inland Sea (Region #3). The Shimoda site in Shizuoka Prefecture and Satsuma-Nagashima site in Kagoshima Prefecture represent Regions #4 and #5, respectively. No study site was assigned in the Ryukyu Islands (Region #6), since the survey was limited to canopy-forming seaweed communities. Nevertheless, turf-forming seaweeds (e.g. *Turbinaria ornata* (Turner) J. Agardh; Fucales), corals and seagrasses constitute the benthic marine communities in this region (Nishihara & Terada 2011; Toma 2012).

Monitoring protocols

A standard methodology for monitoring seaweed communities at all sites was established. Annual surveys have been conducted during the highest abundance of the dominant species; the spatial changes in macroalgal assemblage composition at each site are characterized. Monitoring methods include: 1) line transect survey, 2) permanent quadrat sampling for estimation of species abundance (in terms of percent cover), and 3) destructive sampling (conducted every 5 years) for estimation of macroalgal composition and biomass (excluded from this review; MEGJ 2019). Measurements of seawater temperature were optionally and partly carried out at the actual depth of seaweed communities at the study sites using data-loggers (e.g. TidbiT v2 or HOBO UA-002-64, Onset Computer Corporation, MA, USA; Fig. 2). The seawater temperature in Figure 2 was derived from the following periods at each site: 1) Muroran site (January to December 2015); 2) Shizugawa site (2012–2017); 3) Takeno and Awaji-Yura sites (May 2017 to May 2018); and 4) Shimoda site (2011–2017); and 5) Nagashima site (July 2013 to July 2014).

A 100–130 m transect line was positioned perpendicular to the shoreline to reveal species composition and vertical distribution of the community at each site (Fig. 3). The percentage cover of canopy-forming and understory species (the latter was excluded from this review) was estimated 0.5 m × 0.5 m quadrats (0.25 m^2) placed every 10 m along the transect. For the safety of the divers during SCUBA, the surveys were conducted within the depth of 10m, and the number of transect replicates (i.e. transect line and quadrats at 10 m interval) was limited to one. Nevertheless, the same sites (as closely as could be determined with GPS coordinates taken during the initial survey) were re-surveyed every year. Furthermore, up to six 2 m × 2 m permanent quadrats (4 m^2) were also set up in the seaweed community to estimate species abundance. Based on the zonation of canopy-forming species, they were placed along the transect line; the layout of the permanent quadrats may vary depending on the topography of the study sites.

In the destructive sampling, two 0.5 m × 0.5 m quadrats (0.25 m^2) were placed assigned according to the density of cover at the canopy-forming species along the line transect, and the seaweeds were collected (excluded from this review). Biomass was calculated from the dry weight of each species collected in each quadrat; the species were identified based on morphology and for some, by molecular phylogenetic analyses. Herbarium specimens have been deposited in the Biodiversity Center of Japan (BIODIC), MEGJ, and the National

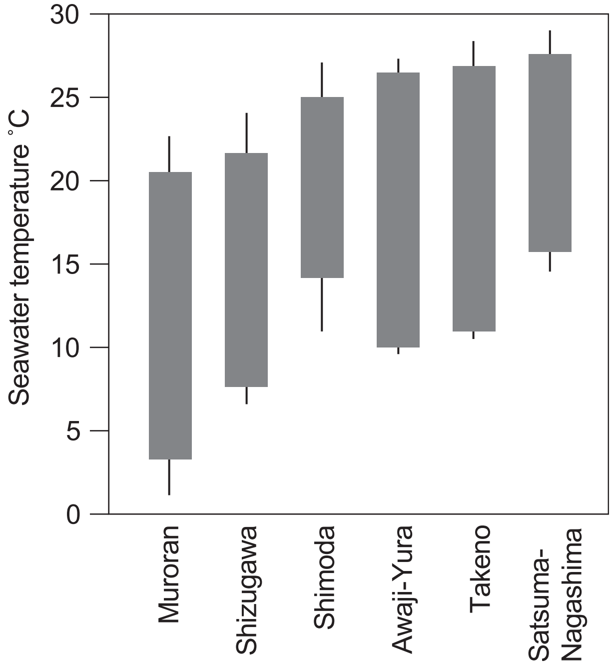

Fig. 2. Seawater temperature at the six monitoring sites. Bars indicate the range of monthly mean temperatures (highest: August; lowest: February), and the lines indicate the range of actual highest and lowest temperatures observed from daily measurements. The temperature at the Muroran site was derived from the dataset in 2015; those at the Shizugawa site was derived from the dataset in 2012–2017; those at the Awaji-Yura and Takeno sites were derived from dataset between May 2017 and May 2018; those at the Shimoda site was derived from the dataset in 2011–2017; and the seawater temperature at the Nagashima site was derived from the dataset between July 2013 and July 2014.

Museum of Nature and Science, Tokyo. Biomass surveys are carried out every 5 years (excluded from this review; MEGJ 2019).

All data and annual report (in Japanese) are available at the BIODIC-MEGJ website (Biodiversity Center of Japan, Ministry of the Environment, Government of Japan 2019; http://www.biodic.go.jp/moni1000/index.html) and at the Ocean Biogeographic Information System (OBIS) website (Ocean Biogeographic Information System 2018; http://www.iobis.org/) as the supplementary data. It may also soon be accessed from the Global Biodiversity Information Facility (GBIF) website (Global Biodiversity Information Facility 2018; https://www.gbif.org/) via OBIS.

OVERVIEW

Distribution of major canopy-forming species in Japan

Based on records of the current project and the 7th National Survey on the Natural Environment (2008), as well as on herbarium specimens deposited in the Hokkaido University Museum (SAP) and the Herbarium Department of Botany, National Museum of Nature and Science, Tokyo (TNS), the regional distributions of the 10 major canopy-forming species in Japan are shown in Figure 4. The subarctic kelp *Saccharina japonica* (*S. japonica sensu stricto* = *S. japonica* var. *japonica*; Note: we use the name "*S. japonica*" as the *S. japonica* var. *japonica* in this article; Yotsukura *et al*. 2008) is distributed in the southeastern coast of Hokkaido and northeastern part of Tohoku region facing the Pacific Ocean and the Tsugaru Strait (Fig. 4a). The distribution of *Alaria crassifolia* Kjellman is also somewhat the same as that of *S. japonica* (Fig. 4b), with their southern distributional limit in north Honshu (Borlongan *et al*. 2019a). Indeed, these two cold-water adapted kelps have been observed at the Muroran and Shizugawa sites (Table 1). Meanwhile, the temperate annual kelp *Undaria pinnatifida* (Harvey) Suringar (Laminariales) is widely distributed along the coast of all four major islands of Japan (Fig. 4c); populations of this alga have been observed at all monitoring sites. However, its distribution in Hokkaido is restricted to the northwestern coast which is influenced by the warm *Tsushima* and *Tsugaru* currents; the northern boundary population of *U. pinnatifida* on the Pacific side are found at near the Muroran site (Kawashima 1989, 2012).

As for *Ecklonia* species, their regional distributions in Japan are limited to Honshu, Shikoku and Kyushu islands, and also tend to overlap (Fig. 4d–g). *Ecklonia bicyclis* Kjellman (= *Eisenia bicyclis* (Kjellman) Setchell; Rothman *et al*. 2015) has been observed at the Shizugawa and Shimoda sites; *E. cava* at both Shimoda and Awaji-Yura sites; *Ecklonia kurome* Okamura at the Takeno site; and *Ecklonia radicosa* (Kjellman) Okamura (= *Eckloniopsis radicosa* (Kjellman) Okamura; Rothman *et al*. 2015) at the Satsuma-Nagashima site (Table 1). Among these four naturally-occurring species of *Ecklonia* (*sensu lato*) in Japan, *E. radicosa* is found in the lowest latitude of the western Pacific (Fig. 4g; Komazawa *et al*. 2015; Terada *et al*. 2016). *Sargassum macrocarpum* C. Agardh, *S. patens*, and *Sargassum siliquastrum* (Mertens ex Turner) C. Agardh occur widely in temperate waters of Honshu, Shikoku and Kyushu islands (Fig. 4h–j); dense populations of these species have been observed particularly at the Awaji-Yura and Takeno sites (Table 1).

Ten-year status of seaweed communities at each monitoring site

Muroran site (Region #1)

The Muroran site is located at Charatsunai Beach, facing Uchiura Bay (42°19′20″ N, 140°59′20″ E), Muroran City, Hokkaido Island (Fig. 1). This coastline is primarily influenced by the cold *Oyashio* current flowing down from the east coast of Hokkaido, and also affected by the warm *Tsugaru* current, a branch of the *Tsushima* current that flows through the Tsugaru Strait and passes along the eastern coast of Honshu (Ohtani 1971; Ohtani *et al*. 1971). The presence of both warm and cold currents in the current-systems along the coast result in a diverse assemblage of kelp species, predominantly of the cold water-adapted *S. japonica, A. crassifolia* and *Costaria costata* (C. Agardh) Saunders, as well as the temperate *U. pinnatifida* (Fig. 5).

Typical substrate types in the site include bedrock, boulder, and cobble; the sea bottom is gently sloped, and approximately 3 m in depth at a distance of 100 m from the shoreline. *S. japonica* dominates the upper subtidal zone

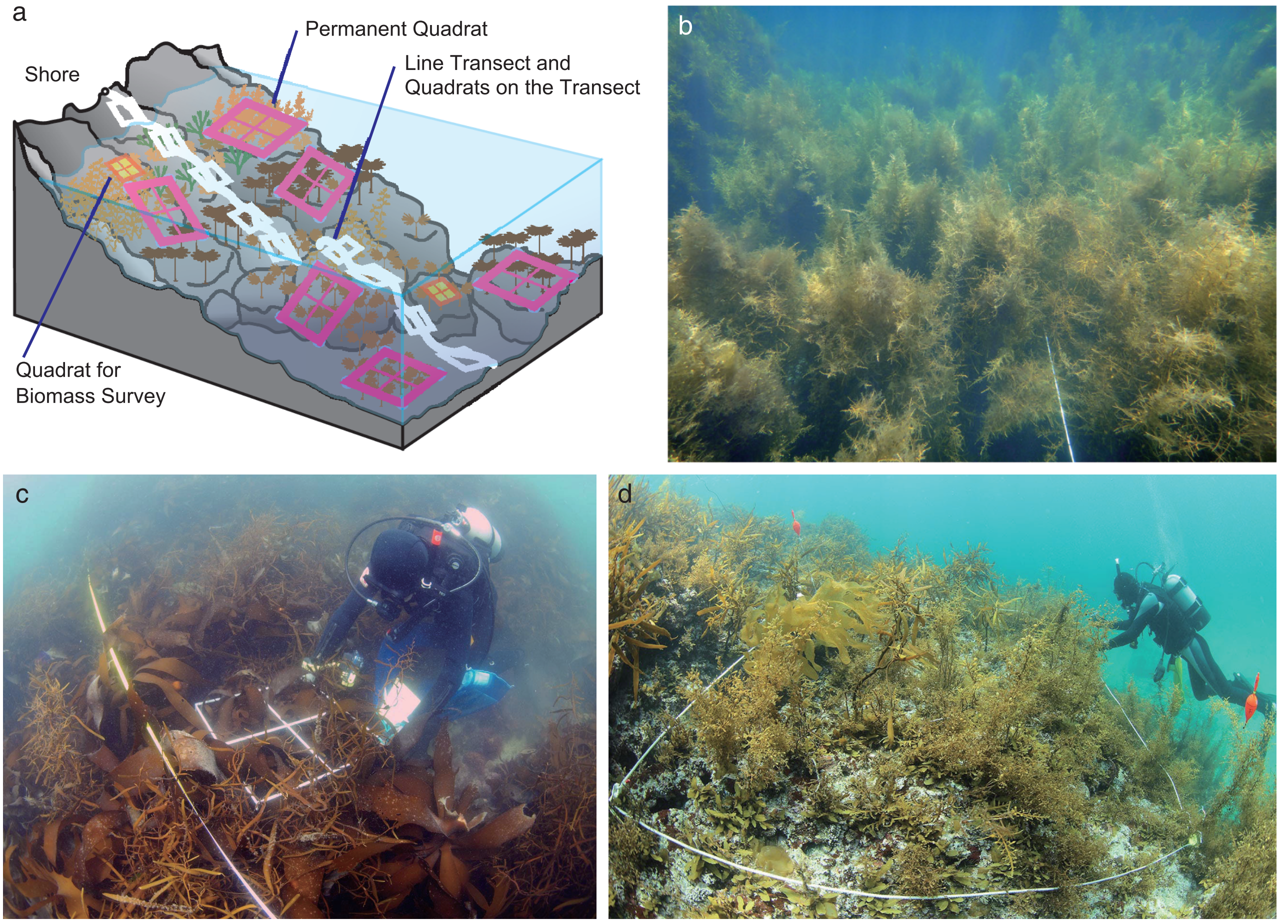

Fig. 3. Schematic diagram of the seaweed community and the photos of the survey showing the layout (a) of the permanent quadrats (big rectangles) and the line transect (white line) with the quadrats (small rectangles). (b) The transect line and *Sargassum* communities at the Takeno site. (c) Observation of the quadrat on the transect line at the Awaji-Yura site. (d) Observation of the permanent quadrat at the Takeno site. [Color figure can be viewed at wileyonlinelibrary.com]

from 1 to 4 m in depth, with up to 100% coverage (Table 2). *C. costata*, *A. crassifolia* and *U. pinnatifida* likewise occur at these depths, forming populations between 1 and 3 m; *A. crassifolia* are commonly found in areas exposed to heavy waves. *Agarum clathratum* Dumortier occur at greater depths (> 4 m). Apart from kelps, the red alga *Odonthalia corymbifera* (Gmelin) Greville (Ceramiales) has been found at depths between 1 and 5 m. Crustose coralline algae *Corallina officinalis* Linnaeus (formerly as *Bossiella cretacea* (Postels et Ruprecht) Johansen) and *Lithophyllum yessoense* Fosile (Corallinales) have also been observed on the substrata under kelp canopies. Meanwhile, temperate/cold-water seagrass *Phyllospadix iwatensis* Makino (Zosteraceae) grows patchily among other species from 2 to 3 m in depth.

Annual surveys at this site are carried out between July and September, during the peak of growth and reproductive maturation of *S. japonica* and other cold-water kelp species. Throughout the monitoring from 2011 to 2017, the occurrence of these canopy-forming kelps in all six permanent quadrats seemed stable, with *S. japonica* as the most abundant alga (Fig. 5). However, decline in species cover and changes in species composition were also observed in some quadrats, related to succession or gap dynamics of seaweed vegetation (Saito *et al*. 1976; Maegawa & Kida 1989; Murase *et al*. 2000). For instance, populations of *S. japonica* in quadrat F declined by 40–70% in 2013 and 2014. They were then partly replaced by *C. costata* and *U. pinnatifida* in 2016 and 2017 (Fig. 5). Abundance of *A. crassifolia* in quadrat E was also variable throughout the 7-year monitoring; their low percentage cover in 2013 and 2014 may have been due to the delayed surveys carried out in September, during which this species had already decreased from the habitat after maturation. Nonetheless, the rise in seawater temperature in the summer may limit the persistence of the subarctic kelp communities in this region (Borlongan *et al*. 2018, 2019a, b); while the rise in seawater temperature in the winter may be advantageous for the temperate *U. pinnatifida.* Diligent monitoring is essential to detect further changes in their distribution and population size.

Surface seawater temperatures at the site from 40 years ago up to the present range between 3°C in the winter and 20°C in the summer (Muroran Marine Station website: Muroran Marine Station 2018; http://www.fsc.hokudai.ac.jp/muroran/kaisuion.pdf; Fig. 2 in 2015); however, records of the highest and lowest temperatures vary every year. For instance, the highest mean temperature in September 2012

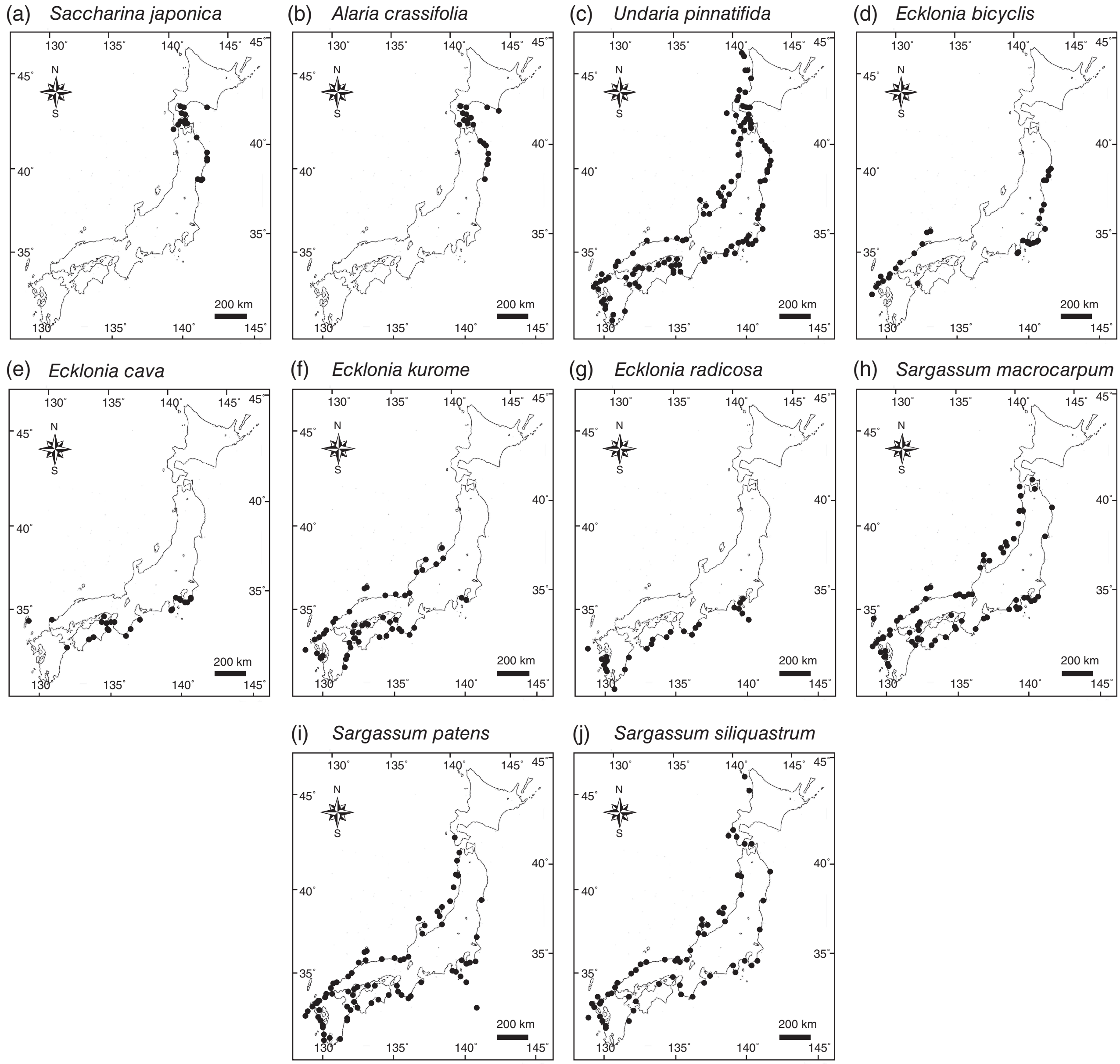

Fig. 4. Map of Japan showing the distribution of major canopy-forming species of seaweeds that have been surveyed by the long-term monitoring survey, “Monitoring Sites 1000”. Dots indicate the sites from which the different seaweeds were collected. (a) *Saccharina japonica* (var. *japonica*); (b) *Alaria crassifolia*; (c) *Undaria pinnatifida*; (d) *Ecklonia bicyclis*; (e) *Ecklonia cava*; (f) *Ecklonia kurome*; (g) *Ecklonia radicosa*; (h) *Sargassum macrocarpum*; (i) *Sargassum patens*; (j) *Sargassum siliquastrum.*

Table 1. Major kelp species that are monitored in the nationwide long-term monitoring survey, “Monitoring Site 1000”

Species	Muroran	Shizugawa	Izu-Shimoda	Awaji-Yura	Takeno	Satsuma-Nagashima
Alaria crassifolia	++					
Saccharina japonica[‡]	++	+				
Ecklonia bicyclis		++	++			
Ecklonia cava			++	++		
Ecklonia kurome					++	
Ecklonia radicosa						++

[++]Found in the study site.
[‡]*Saccharina japonica sensu stricto* (= *S. japonica* var. *japonica*).
[+]Not found in the study site, but found in its vicinity.

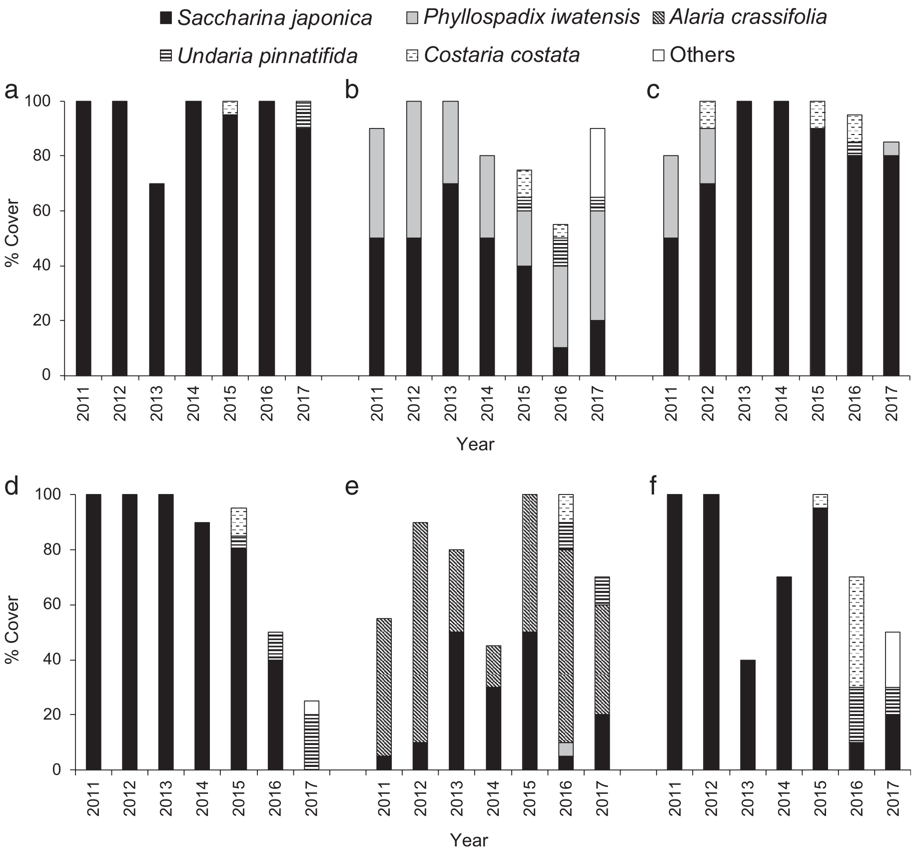

Fig. 5. Yearly change in the percentage cover of the canopy-forming species in six permanent quadrats (a) – (f) at the Muroran site, Hokkaido, Japan. *Saccharina japonica* indicates *S. japonica sensu stricto* (= *S. japonica* var. *japonica*).

Table 2. Vertical and horizontal distribution of the % cover† of canopy-forming species in the seaweed communities in 2015 at the Muroran Site, Hokkaido, Japan

July 7, 2015	Distance (m) from the shore	10	20	30	40	50	60	70	80	90	100
	Depth (m) from the datum	–	+0.7	0.9	1.2	2.0	2.8	3.0	3.5	3.8	4.5
	Substratum	BU	BU	BU	BU, C	BR, BU	BU	C	BU	BU, C	BU
	Saccharina japonica§			90	70	80	30	50	90	100	90
	Costaria costata			10	20	10	10	40	5	+	+
	Undaria pinnatifida			+		+	5	5	+	+	
	Alaria crassifolia				+						
	Phyllospadix iwatensis						40	+			
	Agarum clathratum									+	+

†Values for each species indicate the coverage of the quadrat (50 cm × 50 cm).
+Indicates the coverage less than 5%.
§*Saccharina japonica sensu stricto* (= *S. japonica* var. *japonica*).
BR, Bedrock; BU, Boulders; C, Cobbles.

was 22.6°C, but 18.8°C in August 2008. Meanwhile, the lowest mean temperature in February 2018 was 1.8°C, but 4.3°C in February 2008 (Muroran Marine Station website). These variations in seawater temperature can be related to the degree of influence of the cold and warm currents flowing through the study site, and which may be due to climate change. Indeed, highest seawater temperature in the summer was generally less than 20°C between 1978 and 2009; however, it has reached to more than 20°C in 2010 (Muroran Marine Station website).

Shizugawa site (Region #1)

Most results of the monitoring survey at the Shizugawa site have already been reported in Sakanishi *et al.* (2018). The site is located in a rocky subtidal zone at the east coast of Tsubaki-shima Island (38°39′04″ N, 141°29′31″ E) in Shizugawa Bay, the Sanriku Coast, Miyagi Prefecture, Honshu (Fig. 1). Monthly mean seawater temperature at the study site in summer (August) and winter (February) during 2012 trough 2017 was 21.7°C and 7.8°C, respectively (Fig. 2). The study site was divided into three different algal zones, characterized by one or a few visually dominant taxa that occurred along a water depth gradient: 1) the *Sargassum* zone (1–2.5 m below chart datum level before the GEJE), which is mostly composed of *Sargassum yezoense* (Yamada) Yoshida et Konno and sometimes *Sargassum confusum* C. Agardh; 2) the kelp zone (2–4 m) of *E. bicyclis*; and 3) the crustose coralline algal zone (>4 m) of *L. yessoense* (Table 3). The bottom substrate

Table 3. Vertical and horizontal distribution of the % cover† of canopy-forming species in the seaweed communities during the long-term monitoring survey between 2008 and 2017 at the Shizugawa Site, Miyagi Prefecture, Japan

July 23, 2008	Distance (m) from the shore	15	25	35	45	55	65	75	85	95	105
	Depth (m) from the datum	0.8	1.9	2.1	3.0	3.1	3.6	3.4	3.7	3.8	4.2
	Substratum	BR	BR	BR	BR	BR, BU	BR	BR	BR	BR	BR, BU
	Sargassum yezoense	100	5	60							
	Sargassum confusum		5	5						5	
	Ecklonia bicyclis		90	10	90	90	100	80	5	+	
	Sargassum micracanthum									+	10
June 13, 2009	Depth (m) from the datum	0.5	1.3	2.9	2.4	2.7	3.7	3.7	3.4	4.0	4.7
	Sargassum yezoense	100	100								
	Ecklonia bicyclis			80	100	100	100	100	80	10	
June 15, 2010	Depth (m) from the datum	1.4	1.3	2.7	3	2.7	3.5	3.3	3.5	3.9	4.5
	Sargassum yezoense	0	100	100							
	Ecklonia bicyclis				100	100	100	100	90		
	Sargassum micracanthum									+	
Post Disaster after March 11, 2011											
June 20, 2011	Depth (m) from the datum	2.0	2.2	3.5	3.0	3.3	3.9	4.1	4.2	4.9	4.9
	Sargassum yezoense	100	100	100	90						
	Ecklonia bicyclis					80	80	30	90		
June 28, 2012	Depth (m) from the datum	1.2	2.3	3.1	3.8	3.1	4.3	4.4	4.5	4.3	4.5
	Sargassum yezoense	5	40	5							
	Undaria pinnatifida	95	60		5	40	+				
	Ecklonia bicyclis			80	40		30	50			
	Sargassum confusum				20						+
	Sargassum micracanthum									+	
June 19, 2013	Depth (m) from the datum	2.0	2.6	3.3	3.9	4.1	4.4	4.3	4.8	4.9	4.7
	Sargassum yezoense	95	50	80							
	Ecklonia bicyclis	5	50	10	5	70	40				
	Sargassum micracanthum									5	5
July 2, 2014	Depth (m) from the datum	1.0	2.3	3.1	3.3	3.2	3.8	3.8	4.0	4.0	4.6
	Sargassum yezoense	60	5	+							
	Ecklonia bicyclis	40	95	90	15	20					
	Sargassum micracanthum										+
June 26, 2015	Depth (m) from the datum	0.5	2.0	1.9	2.5	2.4	3.4	3.2	3.5	3.7	3.8
	Sargassum yezoense	10		5	5						
	Ecklonia bicyclis		100	95	50	100					
	Sargassum micracanthum									5	
July 1, 2016	Depth (m) from the datum	1.7	2.7	2.7	3.5	3.3	4.1	4.3	4.4	4.4	4.1
	Ecklonia bicyclis	100	20	100	20						
	Sargassum yezoense		20		5						
July 6, 2017	Depth (m) from the datum	1.3	2.7	3.3	3.6	3.1	4.2	4.2	4.3	4.6	4.7
	Undaria pinnatifida	+									
	Sargassum yezoense	+	5	5	+						
	Ecklonia bicyclis	80			70	40					
	Sargassum confusum		40	50							

†Values for each species indicate the coverage of the quadrat (50 cm × 50 cm).
+Indicates the coverage less than 5%.
BR, Bedrock; BU, Boulders.
Gray highlighted: *Ecklonia bicyclis* communities.

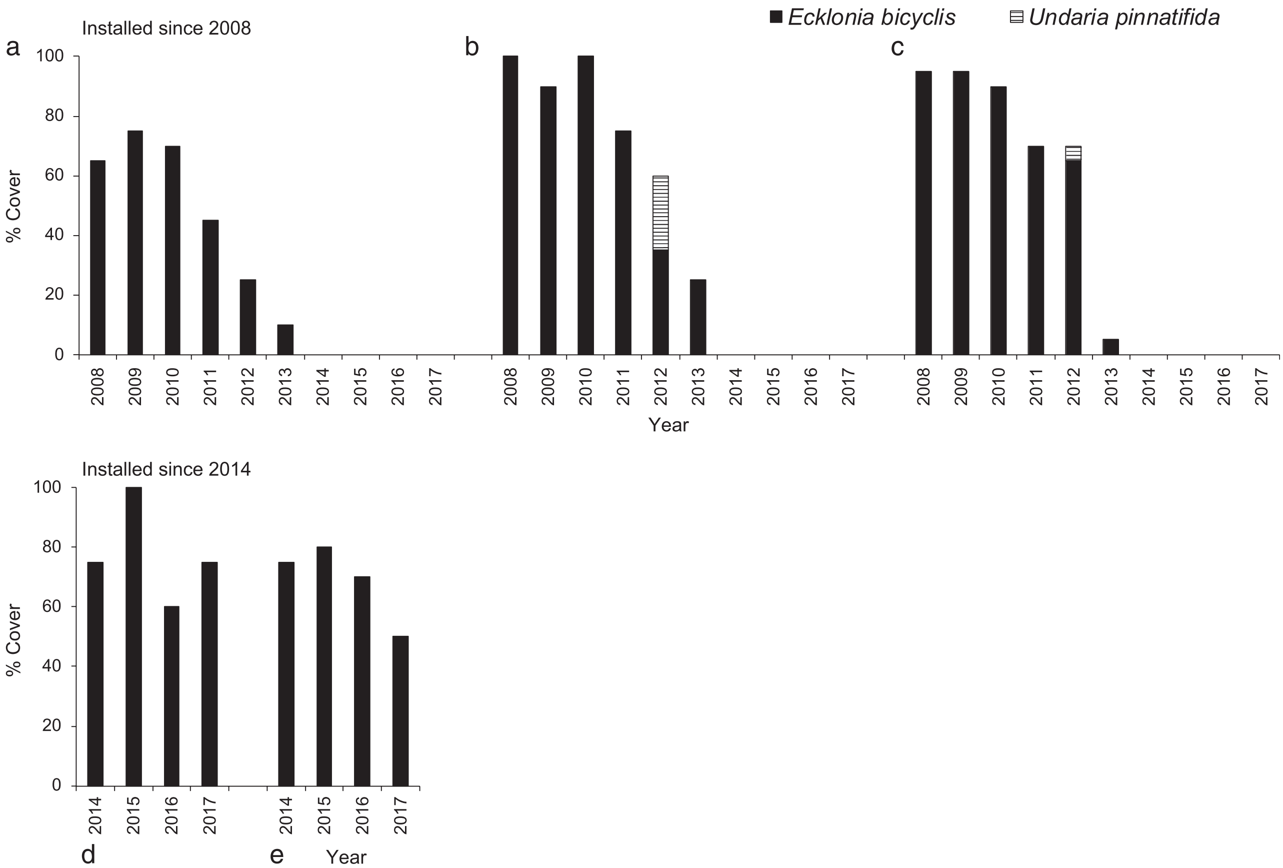

Fig. 6. Yearly change in in the percentage cover of the canopy-forming species in five permanent quadrats (a) – (e) at the Shizugawa site, Miyagi Prefecture, Japan. There was a negative relationship between the percent cover and monitoring year in (a) (r = –0.95, $P < 0.01$), (b) (r = –0.95, $P < 0.01$) and (c) (r = –0.93, $P < 0.01$) that were installed near the vertical limit of the *Ecklonia* community before the 2011 disaster, while there was no change trend in (d) and (e) that were installed in the *Ecklonia* community after the disaster.

along the 105 m transect line was mostly bed rock, with isolated rock and cobbles. The site was directly affected by wave impact because there are no islands or reefs offshore of the site. Algal bed monitoring survey was carried out from July 2008. During the survey period, the 2011 GEJE, which induced huge *tsunami* waves and seafloor subsidence, occurred and greatly affected the coastal ecosystems in Shizugawa Bay. Pre- and post-earthquake water depths revealed a vertical subsidence of the seafloor by 0.8 m (Sakanishi *et al*. 2018). This seafloor subsidence probably was the cause of the post-earthquake gradual decline and subsequent complete disappearance of the *Ecklonia* community near the deep edge of the kelp bed (Table 3). The change in abundance of the canopy-forming kelp *E. bicyclis* was assessed based on the percentage cover of this species in five permanent quadrats; three quadrats (A, B and C) were initially installed near the vertical limit of the kelp zone (based on the pre-disaster depth level; 60 m offshore) in July 2008 (pre-disaster), and two additional quadrats (D and E) were installed in the kelp zone (40 m offshore; 3 m in depth) in July 2014 (post-disaster). The coverage of *E. bicyclis* in quadrats A, B and C were consistently high (> 70%) from 2008 to 2010 (Fig. 6, Table 3). However, it declined to 45–70% in June 2011 (3 months after the earthquake), then continued to decrease, and finally reached zero in 2014. As for quadrats D and E, kelp cover was variable throughout the monitoring period. The deep (offshore) edge of the *Ecklonia* bed also showed an upward (shoreward) shift (Fig. 6, Table 3), perhaps in consequence to decreased incident irradiance at the subsided depth zone.

The post-earthquake/tsunami *Ecklonia* community showed a slow and prolonged change, with over 2 years of recovery process of the subsided deep edge of the kelp bed to the pre-earthquake growing depth zone (Sakanishi *et al*. 2018). Such observations are different from previous reports (Chavanich *et al*. 2005; Castilla *et al*. 2010; Whanpetch *et al*. 2010; Takami *et al*. 2013), wherein huge *tsunami* waves instantly destroyed the coastal habitats.

Takeno site (Region #2)

The Takeno site is located in Oh-ura Cove, Takeno (Toyooka City, Hyogo Prefecture; 35°39′49″ N, 134°44′43″ E), facing the Sea of Japan (Fig. 1), and is part of the Sanin Kaigan National Park. It is partially enclosed by a rocky cliff (Hirai-jima, 5.1 m high and approximately 1300 m^2), and has rocky and sandy substrata with scattered rock boulders.

The macroalgal community in the study area is dominated by *Sargassum* species (Table 4; e.g. *S. autumnale* Yoshida, *S. confusum*, *S. fulvellum* (Turner) C. Agardh, *S. fusiforme* (Harvey) Setchell, *S. hemiphyllum* (Turner) C. Agardh,

Table 4. Vertical and horizontal distribution of the % cover[†] of canopy-forming species in the seaweed communities in 2015 at the Takeno Site, Hyogo Prefecture, Japan

May 9, 2013	Distance (m) from the shore	7	10	20	30	40	50	60	70	80	90	100
	Depth (m) from the datum	0.3	1.2	1.3	3.3	3.4	3.3	3.4	3.6	2.7	2.45	2.56
	Substratum	BR	BR	BR	BU, C	BU, C	BU, C	BU, C	BU, C	BU, C	BU	BU
	Sargassum nigrifolium	80										
	Undaria pinnatifida		5									
	Ecklonia kurome		10									
	Sargassum ringgoldianum subsp. *coreanum*		30	10								
	Sargassum patens		10	30	10	10	50	10	10	60	20	30
	Sargassum siliquastrum			30	40	80	30	50	60	10	10	60
	Sargassum confusum			20			20	20	10		+	10
	Sargassum piluliferum			+			+		10	10	60	
	Sargassum macrocarpum							10		10		
	Myagropsis myagroides										10	

[†]Values for each species indicate the coverage of the quadrat (50 cm × 50 cm).
[+]Indicates the coverage less than 5%.
BR, Bedrock; BU, Boulders; C, Cobbles; P, Pebbles; S, Sand.

S. horneri (Turner) C. Agardh, *S. macrocarpum*, *S. micracanthum* (Kützing) Endlicher, *S. muticum* (Yendo) Fenshold, *S. nigrifolium* Yendo, *S. patens*, *S. piluliferum* (Turner) C. Agardh, *S. ringgoldianum* Harvey subsp. *coreanum* (J. Agardh) Yoshida (= *S. coreanum* J. Agardh), *S. serratifolium* (C. Agardh) C. Agardh, *S. siliquastrum*, *S. yendoi* Okamura et Yamada, and *S. yezoense*), but is also comprised of two kelp species (*E. kurome* and *U. pinnatifida*).

Six permanent quadrats were installed at 2.5–5 m in depths. Quadrats A and B were initially characterized by the dominant *E. kurome,* with 60–70% and 30–40% coverage in 2009 and 2010, respectively (Fig. 7). However, populations of this species in quadrat A and B decreased in abundance, and no longer returned to its initial coverage until 2017. Quadrats C–F are characterized by a mixture of several *Sargassum* species, or sometimes dominated by a single species (e.g. *S. ringgoldianum* subsp. *coreanum* in quadrat C, and *S. siliquastrum* in quadrat F). Relative abundances of other *Sargassum* species in quadrats D and E were variable throughout the monitoring survey.

Monthly average seawater temperatures at the Takeno site between May 2017 and May 2018 range from 10.0°C (February) to 29.5°C (August; Fig. 2). The yearly maximum and minimum water temperatures differed by about 2°C depending on the years. The summer maximum was relatively high in 2011 and 2012, exceeding 29°C, but it was lower than 28°C in 2013–2015 (Kawai unpublished data). Yearly differences in the minimum temperatures were less conspicuous than maximum temperatures. The minimum seawater temperature was 11–12°C in 2012, 2015 and 2016, and was 10°C or lower in 2013 and 2014.

Awaji-Yura site (Region #3)

The Awaji-Yura site is located in Oishi-zaki, Yura, Awaji-shima Island (Sumoto City, Hyogo Prefecture; 34°16′22″ N, 134°57′15″ E). It faces the Kitan Strait, which connects to the Pacific Ocean at the southern end of Osaka Bay (Fig. 1). Macroalgal vegetation is relatively sparse, and the species diversity is low in the northeastern side of Osaka Bay; but is abundant and high in species diversity along the southern shores of Awaji-shima Island, due to a well-preserved natural coastline and frequent water exchange.

The sea bottom of the study site is gently sloped (4 m in depth at 100 m from the shoreline; Table 5). The intertidal zone (10–20 m from the shore line) consists of rocky outcrops and boulders; while the substrate in the zone of 20 to 100 m from the shoreline is a solid bedrock of 2–4 m in depths. The zone beyond 100 m has a sandy bottom mixed with rock outcrops. Inshore from the monitoring site is a steep hill and there are no houses in the area.

The site is characterized by mixed communities of the perennial species *S. fusiforme*, *S. ringgoldianum* subsp. *coreanum* and *E. cava*, and the annual species *U. pinnatifida* and *S. horneri* (Fig. 8, Table 5). Other *Sargassum* species observed in the site include: *S. confusum*, *S. fulvellum*, *S. hemiphyllum*, *S. micracanthum*, *S. muticum*, *S. thunbergii* (Mertens ex Roth) Kuntze and *S. yamamotoi* Yoshida. The change in abundance of the two-dominant species (*E. cava* and *S. ringgoldianum* subsp. *coreanum*) over time was assessed at six quadrats at 2–3 m depth.

In 2008, *E. cava* and *S. ringgoldianum* subsp. *coreanum* were dominant in all of the permanent quadrats, and populations of these two species were more or less stable until 2011 with coverages above 60% (Fig. 8). However, *E. cava* cover declined considerably in 2012. It recovered a little in 2013 and 2014, and yet again declined in 2015. *S. ringgoldianum* subsp. *coreanum* cover likewise declined in 2015. *U. pinnatifida* then increased considerably in the gaps left by the decrease of these two taxa, and had the highest percentage cover in almost all quadrats in 2015–2017. The overall decrease in abundance of the seaweeds in 2015 may be attributed to the destruction by the Category five typhoon *Vongfong* in October 2014 that passed near Awaji-shima Island, and brought intense waves, which caused abrasion and breakage of thalli. The seaweeds recovered to some extent in the following years, with 80–100% coverage in 2017. At the study site, warm-water taxa such as *Umbraulva japonica* (Holmes) Bae et I. K. Lee (Ulvales), *Dudresnaya japonica* Okamura (Gigartinales) and *Scinaia japonica* Setchell (Nemaliales), which had not been observed before, have been patchily but frequently recorded since 2015 within the permanent quadrats.

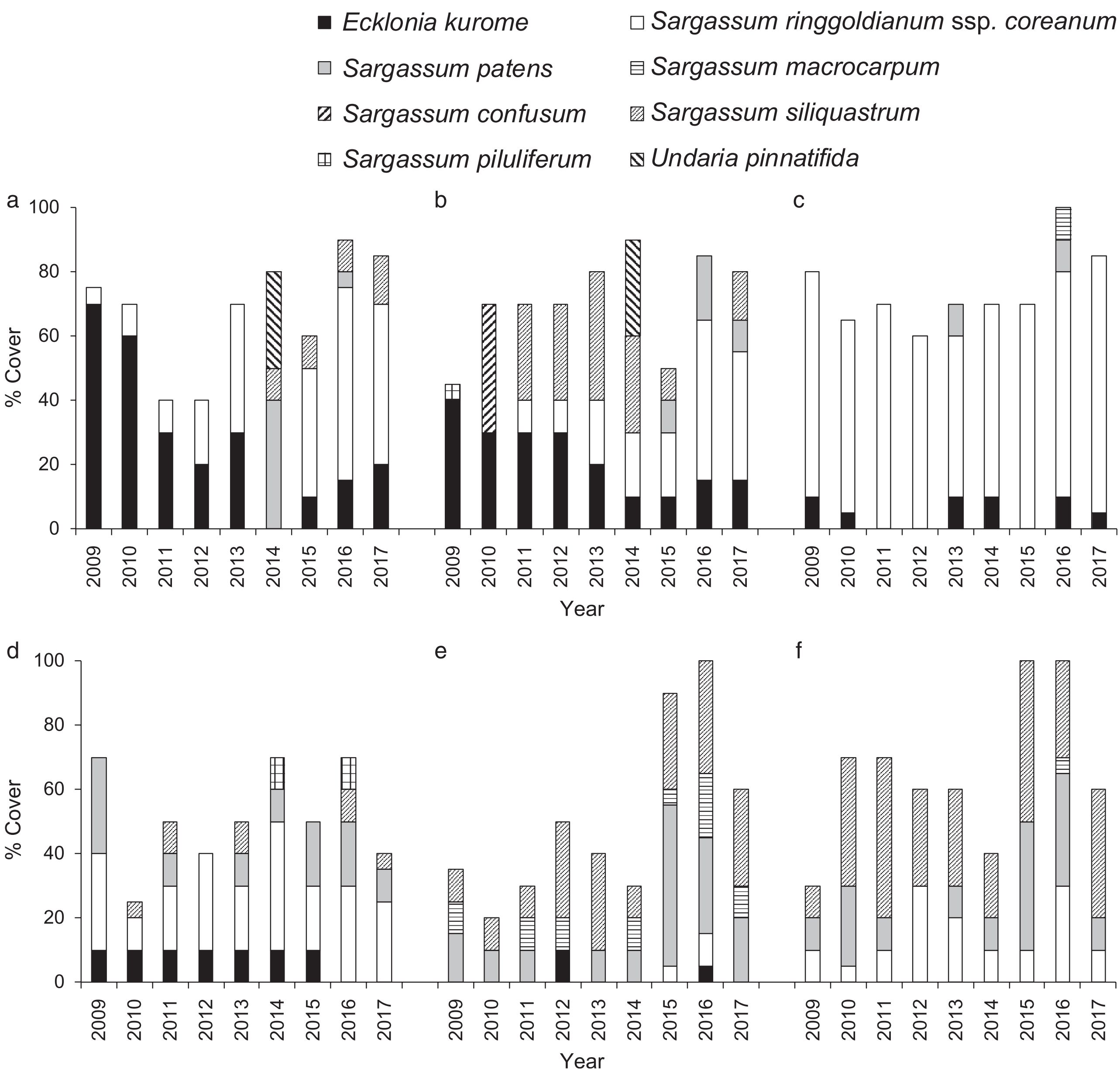

Fig. 7. Yearly change in the percentage cover of the canopy-forming species in six permanent quadrats (a) – (f) at the Takeno site, Hyogo Prefecture, Japan.

Monthly mean seawater temperatures in the site between May 2017 and May 2018 were in the range of 9.5–27.5°C (Fig. 2). The yearly maximum and minimum water temperatures differed by about 2°C, depending on the year. The highest summer temperature was relatively high in 2011, 2012 and 2014 reaching 26.5–27°C, but was about 25°C in 2013 and 2015 (Kawai unpublished data). The periods reaching 27°C were relatively long in 2012. The minimum water temperature was 11–12°C in 2015 and 2016, but was lower than 10°C in 2012–2014.

Shimoda site (Region #4)

The Shimoda site is located in Shidagaura Bay, Shimoda, at the southeastern part of Izu Peninsula, Shizuoka Prefecture, central Japan (34°39′58″ N, 138°56′32″ E; Fig. 1). In this site, which is moderately exposed to wave action, the perennial brown algae *E. cava* and *E. bicyclis* form dense underwater forests, along with other *Sargassum* species (Table 6). *E. bicyclis* and *S. ringgoldianum* subsp. *ringgoldianum* occur at a depth range of 3–4 m, while *E. cava* occupies deeper water of 3 m or more. *Sargassum spathulophyllum* J. Tanaka, Murakami et Arai, which is believed to be endemic to Japan, was also recorded from the site. In addition to these canopy-forming seaweeds, *Gelidium elegans* Kützing (Gelidiales) and articulated coralline algae (*Corallina aberrans* (Yendo) Hind et Saunders, *Corallina crassissima* (Yendo) Hind et Saunders; Corallinales) have been found on the substrata under kelp canopies. The bottom substrata are mainly composed of rocks and boulders.

Table 5. Vertical and horizontal distribution of the % cover[†] of canopy-forming species in the seaweed communities in 2013 at the Awajishima-Yura Site, Hyogo Prefecture, Japan

May 8, 2013											
	Distance (m) from the shore	10	20	30	40	50	60	70	80	90	100
	Depth (m) from the datum	+0.4	0.4	0.8	0.2	0.7	2.0	2.3	1.9	3.1	3.7
	Substratum	BR, BU, C	BR, BU, C, S	BR	BR	BR	BR, BU, C, P	BR, BU, C, S	BR	BR	BR
	Sargassum fusiforme	50									
	Undaria pinnatifida		10			10		5	10		
	Sargassum horneri					50			20		
	Sargassum ringgoldianum subsp. *coreanum*					10	90	10			
	Ecklonia cava					20		80	70	100	

[†]Values for each species indicate the coverage of the quadrat (50 cm × 50 cm).
BR, Bedrock; BU, Boulders; C, Cobbles; P, Pebbles; S, Sand.

Three permanent quadrats in *Ecklonia* communities were positioned at a depth of approximately 4 m to observe the change in abundance of the canopy species throughout the monitoring period (Fig. 9). Although *E. cava* was dominant in all quadrats, its coverage gradually decreased from 2009 to 2015. The coverage of *E. cava* was 75–95% in

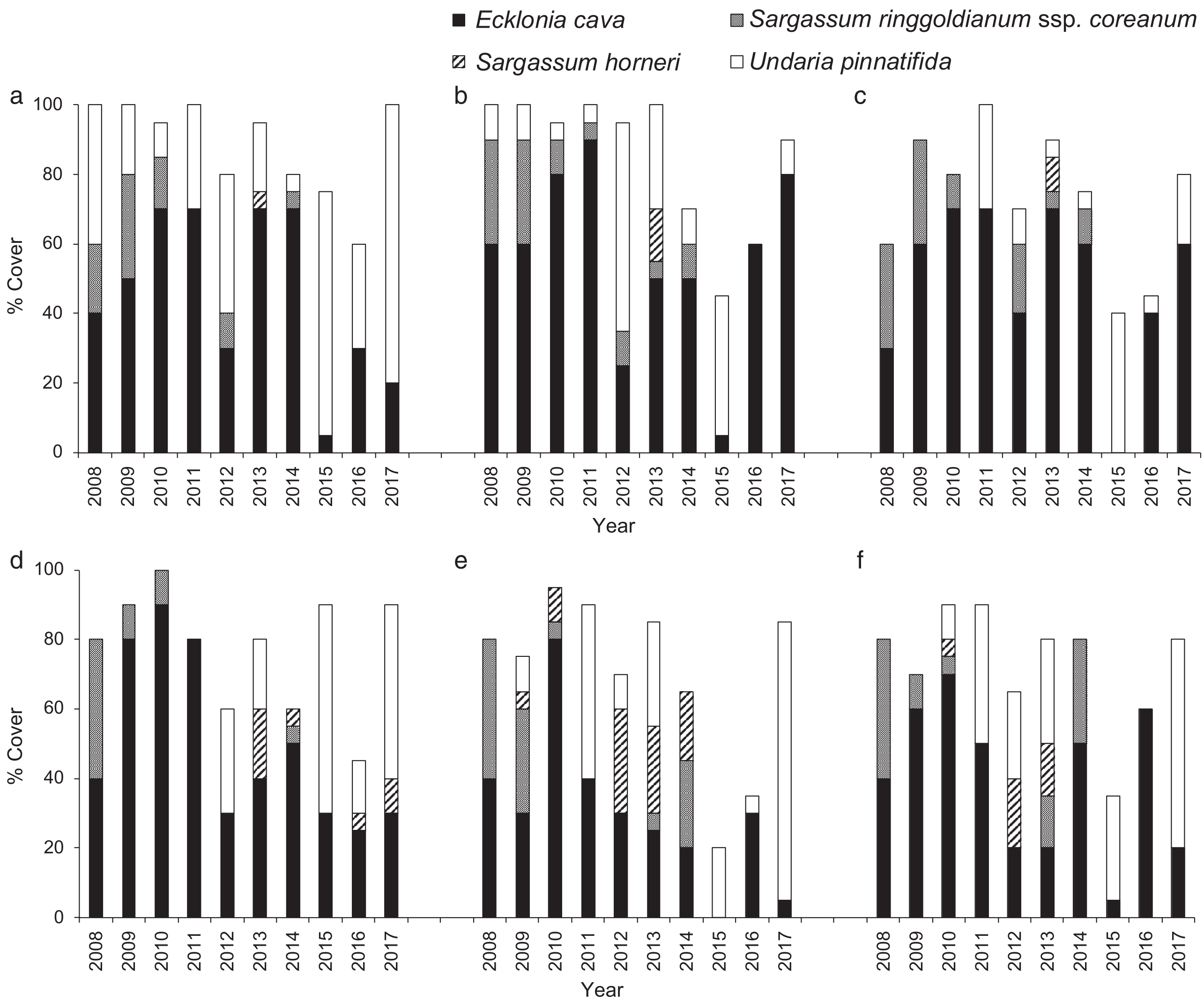

Fig. 8. Yearly change in the percentage cover of the canopy-forming species in six permanent quadrats (a) – (f) at the Awaji-Yura site, Hyogo Prefecture, Japan.

Table 6. Vertical and horizontal distribution of the % cover† of canopy-forming species in the seaweed communities in 2011 at the Izu-Shimoda Site, Shizuoka Prefecture, Japan

October 5, 2011	Distance (m) from the shore	0	10	20	30	40	50	60	70	80	90
	Depth (m) from the datum	+0.7	0.6	0.6	1.6	1.9	1.9	3.0	3.1	4.1	4.7
	Substratum	BR	BR	BR	BR	BR, C	BU	BU	BR	BR	C, P, S
	Sargassum fusiforme	10									
	Sargassum hemiphyllum	80									
	Sargassum ringgoldianum subsp. *ringgoldianum*		10	40		10					
	Ecklonia bicyclis		80	50	80			30			
	Ecklonia cava						90	30	90	80	

†Values for each species indicate the coverage of the quadrat (50 cm × 50 cm).
BR, Bedrock; BU, Boulders; C, Cobbles; P, Pebbles; S, Sand.

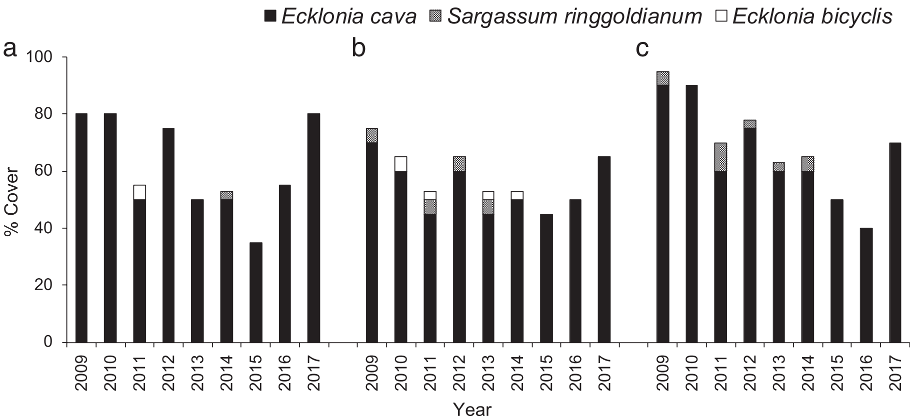

Fig. 9. Yearly change in the percentage cover of the canopy-forming species including *Ecklonia cava* in three permanent quadrats (a) – (c) at the Shimoda site, Shizuoka Prefecture, Japan. *Sargassum ringgoldianum* indicates *S. ringgoldianum seunsu stricto* (= *S. ringgoldianum* subsp. *ringgoldianum*).

2009; it declined to 35–50% in 2015, and recovered to 65–80% in 2017. Abundances of other canopy species (*E. bicyclis* and *S. ringgoldianum* subsp. *ringgoldianum*) were relatively low.

Monthly average seawater temperatures at the Shimoda site in 2011–2017 ranged between 14.5°C (February) and 24.7°C (August; Fig. 2). The annual average water temperature throughout the 7-year monitoring period (2011–2017) ranged from 18.4 to 19.6°C. A maximum temperature of 27.3°C was recorded in August 2012 and 2013, and a minimum temperature of 11.2°C was recorded in February 2013. No clear trend in temperature changes was observed.

Satsuma-Nagashima site (Region #5)

The Satsuma-Nagashima Site is located at Dozaki, Nagashima Island, facing the East China Sea (Nagashima Town, Kagoshima Prefecture, Japan; 32°8′39″ N, 130°6′46″ E; Fig. 1). Along the coast of Nagashima Island and the western coast of Satsuma Peninsula, Kyushu Island, dense populations of temperate kelp *E. radicosa* are found (Terada *et al*. 2016). Among the six species of Japanese *Ecklonia*, *E. radicosa* occurs in the lowest latitudes of Japan (31°N–35°N), with Kagoshima Prefecture being the southernmost distributional limit. In Japan, Kagoshima is considered to be a boundary region between temperate and tropical marine algae, and also represents the southern limit of distribution for many temperate marine algae (e.g. *U. pinnatifida*, Watanabe *et al*. 2014). Indeed, *E. radicosa* in this study site is close to its distributional limit in the western coast of Satsuma Peninsula, with the distance of 50 km north from the actual limit (Terada *et al*. 2016).

The subtidal slope of the coast is usually gentle (up to 10 m in depth at a distance of 130 m from the shoreline), and is largely comprised of bedrock, boulder and cobble. The site is sometimes affected by the warm water mass from the branch current of the *Kuroshio*; hence the occurrence of both temperate and subtropical seaweeds in this area. Various small red algae including *Meristotheca papulosa* (Montagne) J. Agardh (Gigartinales), *Delisea japonica* Okamura (Bonnemaisoniales) and *Chondria ryukyuensis* Yamada (Ceramiales) were also found adjacent to the *E. radicosa* community.

Since 2010, six permanent quadrats were set on *E. radicosa* communities; three quadrats (A, B, C) were positioned at a depth of 3 m, and another three quadrats (D, E, F) at 10 m deep. A 130-m line transect survey has also been conducted to reveal the vertical distribution of algae. Annual monitoring is usually conducted in July, as the most abundant and maturation period of *E. radicosa.* Along the transect line, *E. radicosa* continuously occur on the bedrock and boulders at depths between 3 and 10 m, with up to 100% coverage in 2014 and 2015 (Table 7).

Unlike other species of Japanese *Ecklonia*, *E. radicosa* is an annual species, observed only in winter through early summer (Terada *et al*. 2016). After zoospore release in the summer, the sporophytes disappear from the habitat by autumn. The *E. radicosa* community has been unstable during the monitoring from 2010 to 2015, because all individuals that compose the community rely on the recruits from the fertilized egg of the microscopic stage (gametophyte). More importantly, *E. radicosa* communities have suddenly disappeared

Table 7. Vertical and horizontal distribution of the % cover† of canopy-forming species in the seaweed communities during the long-term monitoring survey between 2014 and 2017 at the Satsuma-Nagashima Site, Kagoshima Prefecture, Japan

June 19, 2014	Distance (m) from the shore	10	20	30	40	50	60	70	80	90	100	110	120	130
	Depth (m) from the datum	1.5	3.5	4.4	6.2	6.9	7.5	6.9	8.1	8.5	8.9	10.0	9.8	10.0
	Substratum	BR	BR	BR	BR	BR	BU	BU	BU	BU	BR, C	BR, C	BU	BR, C
	Ecklonia radicosa	60	90	90	90	100	90	5	90	80	90	90	90	90
July 10, 2015	Depth (m) from the datum	2.5	4.1	4.9	5.7	6.5	7.7	7.7	8.3	8.5	8.3	9.0	9.4	10.2
	Ecklonia radicosa	80	100	80	80	80	80	100	100	100	100	80	100	90
July 6, 2016	Depth (m) from the datum	2.6	4.4	4.9	5.7	6.5	7.3	7.6	8.4	9.0	9.3	9.1	9.2	9.9
	Ecklonia radicosa			+	+	+		+			+	+		+
July 13, 2017	Depth (m) from the datum	1.2	3.7	4.9	6.6	7.0	8.0	8.2	6.7	7.5	9.0	8.4	9.5	10.1
	Ecklonia radicosa													

†Values for each species indicate the coverage of the quadrat (50 cm × 50 cm).
+Indicates the coverage less than 5%.
BR, Bedrock; BU, Boulders; C, Cobbles.
Gray highlighted: *Ecklonia radicosa* communities.

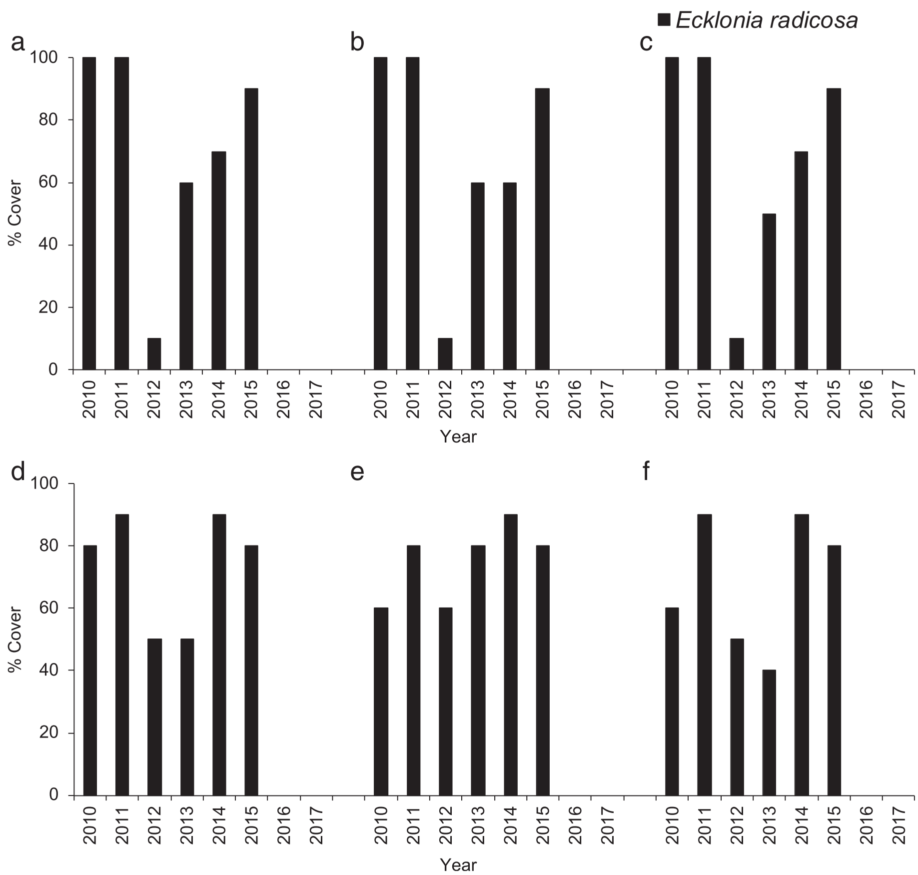

Fig. 10. Yearly change in the percentage cover of *Ecklonia radicosa* at the Satsuma-Nagashima site, Kagoshima Prefecture, Japan.

from the substrata since 2016 (Fig. 10; Table 7). Disappearance of *E. radicosa* communities has occurred widely, on the west coast of Nagashima Island as well as the Satsuma Peninsula both facing the East China Sea (Terada unpublished data). In contrast, *E. radicosa* communities are still present at the opposite side (east coast) of Nagashima Island facing the semi-enclosed Yatsushiro Bay, suggesting that it has disappeared only at the sites that are affected by the warm water mass from the branch current of *Kuroshio* including the vicinity of its southern distributional limit. Blades of *E. radicosa* were lost frequently by browsing by herbivorous fish, and this could be contributing to its decline (Fig. 10).

Seawater temperature is also considered one of the important factors that limit the abundance or decline of the *E. radicosa* community. In fact, monthly mean seawater temperature at the study site during July 2013 through June 2014 ranged between 15.4°C in winter (February) and 27.4°C in summer (August; Fig. 2), and has always been 1–2°C higher than in the opposite side of the island facing semi-enclosed Yatsushiro Bay (13.7–26.8°C; Terada *et al*. 2016). This difference is due to the influence of the warm water mass from the branch of *Kuroshio* that flows through the study site. Moreover, coastal mean seawater temperature has been reported to have increased by 1–2°C in the past four decades in Kagoshima (Shimabukuro *et al*. 2007; Tsuchiya *et al*. 2011), suggesting the impact of increasing summertime seawater temperature to the thermal inhibition of temperate algae (Tanaka *et al*. 2012; Watanabe *et al*. 2014).

DISCUSSION

Based on the 10-year monitoring survey, seaweed communities at the six sites along the Japanese coast are dominated by *Saccharina*, *Ecklonia* and *Sargassum* species. Temporal and spatial variability in the structure and dynamics of climatic and oceanographic processes are major driving factors in the distribution of these canopy-forming species in the region. Fluctuations in the abundance of canopy-forming species observed at all sites throughout the monitoring period are indicators of the changes in their respective community structure and species distributions, as a result of both natural (e.g. seawater temperature rise, grazing, destruction by typhoon or earthquake) and human-induced (e.g. overfishing in kelp forests, coastal urbanization) disturbances (e.g. Dayton 1972; Graham *et al*. 1997; Thibaut *et al*. 2005; Prathep *et al*. 2008; Foster & Schiel 2010; Wernberg *et al*. 2011, 2013, 2016; Tanaka *et al*. 2012; Raybaud *et al*. 2013; Voerman *et al*. 2013; Filbee-Dexter & Scheibling 2014; Vergés *et al*. 2014, 2016, 2019; Ling *et al*. 2015; Filbee-Dexter & Wernberg 2018).

Saccharina-dominated communities seemed to be stable at the Muroran site, subarctic Hokkaido Island. However, decline in their species cover of the perennial species of *S. japonica* and associated replacement by the annual species of *Costaria costata* and *Undaria pinnatifida* were observed in the permanent quadrat survey. Similar replacement by *U. pinnatifida* was also observed in the *Ecklonia cava* communities at the Awaji-Yura site in between Honshu and Shikoku Islands. Sufficient breaks in the canopy may have facilitated such replacement by the annual species (Endo *et al*. 2019). Although there were declines in abundance of *Ecklonia* spp. at the Shimoda and Shizugawa sites due to some physical disturbance (as in the case at the Shizugawa site), they were not replaced by other species (Sakanishi *et al*. 2018). Locally, kelp forests are established and maintained by successful settlement of zygotes (Steneck *et al*. 2002). Kelp recruitment and growth is regulated by light available through breaks in the kelp canopy, but the kelp species that grow to dominance will depend upon nutrient conditions (Mizuta *et al*. 1994, 1998, 2007; Tegner *et al*. 1997; Nimura *et al*. 2002). It is also possible for a range of abiotic and biotic factors to come into play and to be influencing the recruitment and growth. Nonetheless, the rise in seawater temperature as well as low nutrient availability in the summer limit the persistence of the subarctic kelp communities in the Pacific side of Hokkaido and northern Honshu islands (Gao *et al*. 2015, 2017; Borlongan *et al*. 2018, 2019a, b), while the rise in seawater temperature in the winter may allow the expansion of the temperate *U. pinnatifida* (Endo *et al*. 2017). Alternatively, inter-populational differences may also occur in various developmental stages of perennial species (e.g. *E. cava* and *E. bicyclis*; Maegawa & Kida 1989) associated with local environmental conditions, which 'opens' the kelp canopy for the annual *U. pinnatifida.*

Yearly changes of the canopy-forming species were observed among the species of *Ecklonia* and *Sargassum* in the temperate region of the Awaji-Yura and Takeno sites, which may also be associated with the succession or gap dynamics of seaweed vegetation (Graham *et al*. 1997; Murase *et al*. 2000; Endo *et al*. 2019). Perhaps differences in life cycles, influenced by variable environmental factors, enabled the growth of different species in the gap. Indeed, the occurrence of the annual *Sargassum* species (e.g. *S. horneri*) was shown to have a negative effect on the growth and colonization of the perennial *Sargassum* species (e.g. *S. patens*) in the first year of colonization, probably because of its overgrowth. However, the occurrence of the annual *Sargassum* species seems to have little effect on the dominance of the perennial *Sargassum* species in the second and the following years (Endo *et al*. 2019). Following an intense storm that thinned kelp canopies at the Awaji-Yura site, recruitment was successful but the species that grow to dominate was *U. pinnatifida.* The replacement of canopy-forming species in the seaweed communities is a consequence of succession and gap dynamics (Saito *et al*. 1976; Maegawa & Kida 1989; Graham *et al*. 1997; Murase *et al*. 2000; Endo *et al*. 2019).

Disturbances like typhoons and mega-earthquake disasters cause destructive impacts to the seaweed communities. At the Awaji-Yura site, the heavy waves associated with the category five typhoon (*Vongfong*) in October 2014 reduced *Ecklonia/Sargassum* cover in 2015; but recovery was rapid due to high recruitment into the breaks in the canopy. The 2011 earthquake that induced huge *tsunami* waves and seafloor subsidence likewise affected the coastal communities at the Shizugawa site (Sakanishi *et al*. 2018). However, the direct impact of *tsunami* waves to the seaweed communities was somewhat limited, as *Ecklonia*/*Sargassum* communities were still present just after the disaster; hence suggesting the resilience of these species against the waves (Muraoka *et al*. 2017). *Tsunami* waves instantly transported various benthic organisms including sea urchins away from habitats (Seike *et al*. 2013; Takami *et al*. 2013). Resultant seafloor subsidence may have been the cause of the gradual decline of *E. bicyclis* near the lower limit of vertical distribution and the shoreward shift of the forest (Suzuki *et al*. 2017; Sakanishi *et al*. 2018), perhaps in relation to the possibility of decreased incident irradiance and/or increased grazing of sea urchins at the subsided depth zone. However, our long-term survey is essential to reveal the actual factor of the shoreward shift of the forest (Suzuki *et al*. 2017; Sakanishi *et al*. 2018). Indeed, such change in the post-earthquake/tsunami *Ecklonia* community was rather slow including the time-lagged effects, with over 2 years for recovery of the subsided deep edge of the kelp bed to the pre-earthquake growing depth zone (Sakanishi *et al*. 2018). The result of this vertical shift of the seaweed community might be a good case study to consider, in relation to sea level rise.

The sudden disappearance of *E. radicosa* communities has been observed at the Satsuma-Nagashima Site, Kyushu island, since 2016. *E. radicosa* occurs in the lowest latitude of Japan (31°N – 35°N). This species was previously found in Mageshima Island of northern Ryukyu Islands (30°N) more than 70 years ago, but has disappeared in the past two decades (Fig. 4g; Tanaka 1950; Terada *et al*. 2016), suggesting the northward shift of its southern distributional limit in the western Pacific. It has been generally assumed that the global warming would cause a shift in the distributional boundaries of seaweed species (Wernberg *et al*. 2011, 2013, 2016; Tanaka *et al*. 2012; Kumagai *et al*. 2018; Filbee-Dexter & Wernberg 2018). Indeed, coastal mean seawater temperature has been reported to increase by around 1–2°C in the past four decades in Kagoshima (Shimabukuro *et al*. 2007; Tsuchiya *et al*. 2011). Increasing summertime seawater temperatures in this region resulted to the thermal inhibition of temperate algae, particularly *E. radicosa* (Watanabe *et al*. 2014, Kokubu *et al*. 2015; Terada *et al*. 2016), thereby limiting the growth of gametophytes and juvenile sporophytes. Likewise, other temperate kelp, *E. cava* and *E. kurome* along the coast of Shikoku and southern part of Kyushu islands facing the Pacific Ocean widely disappeared in the late 1990s and 2000s, along with the shift to the subtropical species of *Sargassum* (Serisawa *et al*. 2004; Tanaka *et al*. 2012). The disappearance of these species at Shikoku and southern Kyushu islands may lead to their fragmented distributions in the near future, similar to the characteristic distribution of *E. bicyclis* at the western and eastern part of Honshu Island. *S. patens*, *S. macrocarpum* and *S. siliquastrum* are widely distributed in the temperate region of Japan; however, the shift to the subtropical species of *Sargassum* may become a future concern especially at the southern boundary of each temperate species (Terada *et al*. 2018).

Furthermore, browsing on the seaweed communities by herbivorous fish (e.g. rabbitfishes, *Siganus fuscescens* (Houttuyn, 1782), *Kyphosus bigibbus* Lacepeède, 1802; Perciformes) has also been a serious concern in warm temperate regions of Japan since 2000s (Kiriyama *et al*. 2001, 2002; Kawamata & Hasegawa 2006; Nimura *et al*. 2007; Noda *et al*. 2014; Vergés *et al*. 2014, 2016, 2019). Browsing pressure by these two fish species was reported to decline if the temperature was less than 20°C and 16–17°C, respectively (Kawamata & Hasegawa 2006; Yamaguchi *et al*. 2006); therefore, the rise of seawater temperature in the autumn and early winter has led to increased grazing on juvenile sporophytes of *Ecklonia* spp., and subsequent reduction of these species (Harley *et al*. 2012). Moreover, at the vicinity of the study site, occurrence of the corals has also been reported (Nakashima *et al*. 2013; Kumagai *et al*. 2018); competition for space among these corals and marine algae may also be a serious concern in near future.

This monitoring survey has provided a decade-long perspective of how the distributions of various foundation species in seaweed communities across Japan have changed and possibly where they are headed in the future. Long-term survey data are essential for the early recognition and evaluation of the direct or indirect impacts on seaweed ecosystems of global warming as well as degradation of coastal environments. For the last 10 years, a total of 468 individuals including phycologists, students and volunteers have contributed to the annual survey at six sites. A shortage of contributors for the survey is a serious concern, especially for future generations, reinforcing the importance of education and understanding of the biodiversity of coastal ecosystem.

ACKNOWLEDGMENTS

We thank the total of 468 contributors for their active involvement and support during the survey. We are also grateful to all staff members of the Muroran Marine Station, Field Science center for Northern Biosphere, Hokkaido University (Muroran Site), Shizugawa Nature Center, Minamisanriku Town (Shizugawa Site), Takeno Snorkeling Center (Takeno Site), Marine Site, Kobe University Research Center for Inland Seas (Awaji-Yura Site), Shimoda Marine Research Center, University of Tsukuba (Shimoda Site), and Azumacho Station, Education and Research Center for Marine Resources and Environment, Faculty of Fisheries, Kagoshima University (Satsuma-Nagashima Site) for their kind arrangements of our fieldwork in each study site. Cordial thanks are due to Dr. Tsuyoshi Abe, Hokkaido University Museum, and Dr. Taiju Kitayama, National Museum of Nature and Science, Tokyo, for their kind arrangements of our herbarium-specimen survey in the present study. This long-term survey has been supported by the BIODIC-MEGJ, and conducted by the management of a non-profit organization, the Wetlands International Japan (WIJ). This study was also supported in part by the Grant-in-Aid for Scientific Research (16H02939; RT) from Japan Society for the Promotion of Science (JSPS). All authors have provided consent and are arranged alphabetically except for the first and last authors.

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