Marine Ecology. ISSN 0173-9565

ORIGINAL ARTICLE

Seagrasses from the Nansei Islands, Southern Japanese Archipelago: species composition, distribution and biogeography

John Kuo[1], Ziyusei Kanamoto[2], Hitoshi Iizumi[3], Keiko Aioi[4] & Hiroshi Mukai[5]

1 Centre for Microscopy and Microanalysis, The University of Western Australia, Crawley, WA 6009, Australia
2 Center for Marine Environmental Studies, Division of Aquatic Biology and Ecology, Ehime University, Ehime, Japan
3 Japan Sea National Fisheries Research Institute, Fisheries Research Agency, Niigata, Japan
4 22413-105, Hounan, Suginami, Tokyo, 168-0062, Japan
5 Akkeshi Marine Station, Field Science Center for Northern Biosphere, Hokkaido University, Akkeshi, Hokkaido, Japan

Keywords
Biogeography; Nansei Islands; northern distributional limit; seagrasses.

Correspondence
John Kuo, Centre for Microscopy and Microanalysis, The University of Western Australia 35 Stirling Highway, Crawley, WA 6009, Australia.
E-mail: jjskuo@cyllene.uwa.edu.au

Accepted: 12 July 2006

doi:10.1111/j.1439-0485.2006.00098.x

Abstract

The Nansei Islands in the southern Japanese Archipelago have 15 taxa of seagrasses from seven genera within three families. Seagrasses in this region grow on coral sands or coral debris in shallow reefs and on sandy or muddy substrata in the shallow areas of bays and inlets. Certain *Halophila* species grow in deep water off some islands. *Enhalus acoroides* only reaches to Ishigaki I. with winter sea water temperature (WST) at 23 °C, while Okinawa I. (WST at 21.6 °C) is the northern biogeographic limit for *Halophila decipiens*, *H. okinawensis*, *H. major* and *H. gaudichaudii*. Amami-oshima I. (WST at 20.7 °C) is the northern border for *Thalassia hemprichii*, *H. minor*, *H. ovalis*, *Cymodocea serrulata*, *Cymodocea rotundata*, *Syringodium isoetifolium*, *Halodule uninervis* and *Halodule pinifolia*. *Halophila mikii* the sole seagrass collected from Yakushima I. (WST at 19.3 °C), is of volcanic origin. The distribution of tropical seagrasses in the Nansei Islands is clearly associated with the warm Kuroshio Current, WST and habitat availability. *Zostera japonica* is the only temperate species occurring in the region. Meadows of *Z. japonica*, *H. ovalis* and *Halodule pinifolia* have disappeared from certain localities in the Archipelago, due probably to human activities and natural siltation.

Problem

The rich diversity of seagrass species in Japan has drawn marine researchers to explore its biogeographical significance (Miki 1934a,b; Aioi & Nakaoka 2003; Kuo *et al.* 2006). In particular, the Nansei Islands are the most prolific region in Japan with the most substantial diversified seagrasses (Miki 1934a,b). Miki (1932, 1933, 1934a) discussed nine species, *viz. Enhalus acoroides*, *Thalassia hemprichii*, *Syringodium isoetifolium*, *Cymodocea rotundata*, *C. serrulata*, *Halodule uninervis*, *Halodule pinifolia*, *Zostera japonica* and *Halophila ovalis* from the Ryukyu Islands relating sea water temperature and currents to their habitat. The same seagrass species were later mentioned by Tsuda & Kamura (1990) and by Toma (1999). Kuo *et al.* (1995) added *H. decipiens* to this list. Kuo *et al.* (2006) further pointed out that four more *Halophila* species occur in the region.

The Nansei Islands or Nansei-Shoto (the South-West Islands, as directly translated from Japanese) consist of a string of about 70 islands and islets, and extend southwest from the southern tip of Kyushu Islands to Yonaguni I. for more than 1100 km, just over 100 km from the east coast of Taiwan (Fig. 1). They represent a natural

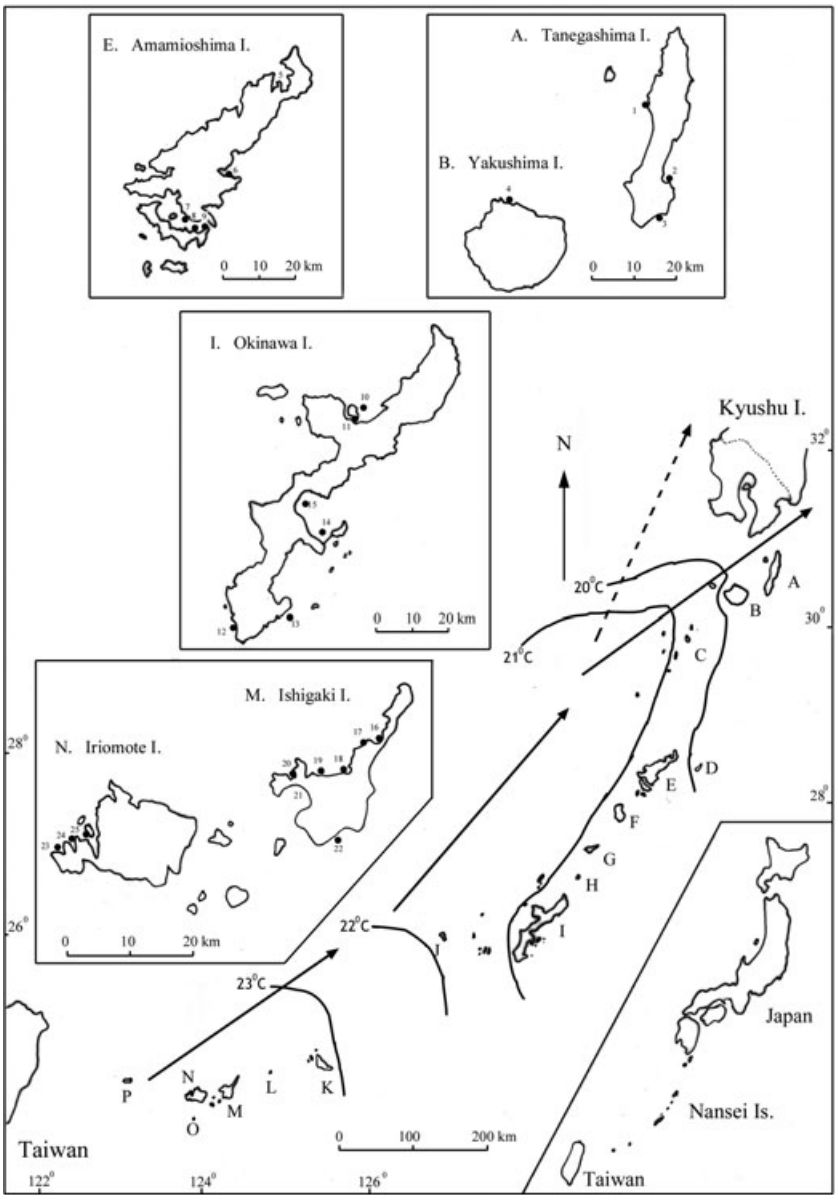

Fig. 1. (A) Map of major collecting sites of seagrasses in the Nansei Islands, Japan. Tanegashima I.: site 1 Sumiyoshi, site 2 Kumano, site 3 Takezaki. (B) Yakushima I.: site 4 Motoura. (C) Tokara Is. (D) Kikaijima I. (E) Amami-oshima: site 5 Maehida, site 6 Yamama, site 7 Atetsu, site 8 Doren, site 9 Ankyaba. (F) Tokunoshima I. (G) Okino-erabujima I. (H) Yoron I. (I) Okinawa I.: site 10 Sumoide, site 11 Yagachi, site 12 Itoman, site 13 Chinen, sites 14–15 Kin Bay. (J) Kumeshima I. (K) Miyako I. (L) Taramashima I. (M) Ishigaki I.: site 16 Ibaruma Bay, site 17 Fukido River mouth, site 18 Tomino, site 19 Yonehara, site 20 Sakieda Bay, site 21 Nagura Bay, site 22 Ohama. (N) Iriomote I.: site 23 Sakiyama Bay, site 24 Amitori Bay, site 25 Shirahama. (O) Hateruma I. (P) Yonaguni I. Lines in the Map show surface water temperature in winter (February). Arrows show the warm Kuroshio Current (solid arrows) and the warm Tsushima Current (dotted arrow). (Information from The Geographical Survey Institute, Ministry of Construction, Hydrographic Department, Japan).

wide latitudinal gradient from 25° N to 31° N providing various geophysical environments and habitats. In addition, the warm Kuroshio current that passes through the region may play an important role in explaining how the tropical species from the Indo-Pacific region have spread into the Nansei Islands (Mukai 1993).

To further investigate the reasons for the diversified seagrass distribution in the Nansei Islands, this study intends to update the current available species distributional information through two substantial field surveys conducted in 1996 and 1999. In addition, two previously surveyed transit sites Iriomote I. (Habe *et al.* 1984) and Okinawa I. (Tr. I., Fig. 8, Toma 1993) were re-examined in 1999 to note the seagrass meadow changes over 10–15 years.

Based on extensive field surveys in the region, a thorough examination of herbarium material and a comprehensive review of the Japanese literature, this paper discusses seagrass species, their composition and distributional changes in relation to biogeographic features, such as the current regime, winter sea water temperature (WST) and habitat availability.

Material and Methods

The northern half of the Nansei Islands (Fig. 1) belongs to the Kagoshima Prefecture and is known as Satsunan Is including Osumi Is, Tokara Is, and Amami Is. The southern half of the Nansei Islands is under the Okinawa

Prefecture and is known as Ryukyu Is comprising Okinawa I. in the north, the largest island in the archipelago, and Sakishima Is to the south which includes Miyako Is and Yaeyama Is (Fig. 1; Table 1).

Physical features and oceanographic conditions, obtained from the Geographical Survey Institute, Ministry of Construction, Hydrographic Department, Japan (Fig. 1, Table 1), provide essential information for a better understanding of the distribution of seagrasses in this region and are reported below.

Island origins

There are three different origins among the 70 islands of the Nansei Islands, although each original type may not be restricted to a specific geographic distribution. Tanegashima I. (A, Fig. 1) is the only island of continental origin, while Yakushima I. (B, Fig. 1), Tokara Is (C, Fig. 1) and Kumeshima I. (J, Fig. 1) are volcanic islands. The remaining islands of the Nansei Islands are of coral origin.

Currents

The warm Kuroshio Current, which originates from the equator, flows all the year round, and northward along the east coasts of the Philippines and Taiwan; and then passes the west coast of the Ryukyu Islands. It divides into two branches north of Amami-oshima I. (E, Fig. 1). The main, eastern branch flows around Tanegashima I. and Yakushima I., continues northwards along the southern Shikoku Islands, and then reaches the eastern Honshu Islands. The western branch, also known as the warm Tsushima Current, flows northward along the west coast of the Kyushu and Honshu Islands.

Table 1. Physical features and habitat conditions in the Nansei Islands, Japan (The Geographical Survey Institute, Ministry of Construction, Hydrographic Department, Japan).

		sea water temperature [°C]					
islands	locality	February	August	areas [km]	coastlines [km^2]	substratum type	seagrass
Kyushu Island							
Kagoshima	31°53′ N, 130°12′ E	17.4	27.9			muddy sands	3[a]
Nansei Islands							
Satsunan Is							
Osumi Is							2
Tanegashima I.	30°35′ N, 131°00′ E	19.5	28.4	445.0	165	muddy sands	2
Yakushima I.	30°20′ N, 130°30′ E			504.9	132	gravel sands	1
Tokara Is							0
Suwanosejima I.	29°38′ N, 129°42′ E	21.3	28.7	22.3	27	gravel sands	0
Nakanoshima I.	29°50′ N, 129°45′ E			35	20		
Amami Is							9
Amami-oshima I.	28°20′ N, 129°25′ E	20.7	28.7	712.2	426	coral sands	9
Kikaijima I.	28°19′ N, 129°58′ E			56.9	48.6		2
Tokunoshima I.	27°40′ N, 128°55′ E			247.8	94		3
Plomp-erabujima I.	27°25′ N, 128°30′ E			93.6	57		1
Yoron I.	27°02′ N, 128°25′ E			20.5	23.7		9
Ryukyu Is							
Okinawa Is							13
Okinawa I.	26°12′ N, 128°00′ E	21.3	28.7	1202.3	476	reef platform	13
Kumeshima I.	26°20′ N, 126°45′ E			58.8	48	sandy, sandy gravel	9
Sakishima Is							
Miyako Is							10
Miyako I.	24°47′ N, 124°10′ E	23.6	28.7	158.7	114	coral sand	10
Taramashima I.	24°38′ N, 124°40′ E			24	15		7
Yaeyama Is							13
Ishigaki I.	24°30′ N, 139°22′ E	23.2	29.3	222.5	138		10
Taketomishima I.	24°20′ N, 129°15′ E			5.5	8.5		3
Iriomote I.	24°20′ N, 122°99′ E			289.3	129		13
Yonaguni I.	24°27′ N, 129°54′ E			29.5	13.7		9
Hateruma I.	24°04′ N, 139°22′ E			14.8	18.9		8

I, single island; Is, island groups.

[a]*Zostera marina*, *Zostera japonica*, *Halophila nipponica*.

Tides

There are two tides a day with a range of <1 m throughout the year.

Sea water temperature

The surface temperature of the sea water is in the subtropical range and remains constant at 26 °C in the summer months for the whole region. However, there is about a 3° difference in the winter months between the southern islands, *e.g.* Ishigaki I., Iriomote I. and the northern islands, *e.g.* Tanegashima I. and Yakushima I. (Table 1).

Salinity

The salinity of sea water in the region is constant at 34 psu all the year round. The salinity at river mouths or estuaries varies according to time and location but was not considered in the present study.

Seagrass field surveys were conducted at Okinawa I. (I, Fig. 1) and Ishigaki I. (M, Fig. 1) in May 1996, and at Tanegashima I. (A, Fig. 1), Yakushima I. (B, Fig. 1), Amami-oshima I. (E. Fig. 1), Okinawa I., Ishigaki I., and Iriomote I. (N, Fig. 1) in May–June 1999. Surveys were conducted by direct observations at low tide or using scuba and snorkeling. Representative specimens were collected at each site and seagrass species identification was based on Kuo & den Hartog (2001). The habitats and reproductive status of each seagrass species at each site were noted. This survey did not measure shoot density, growth rate or other biological factors. However, seagrass transects previously studied by Habe *et al.* (1984) and Toma (1993) were re-investigated and compared in June 1999.

The seagrass information for some smaller islands, *e.g.* Kikaijima I. (D, Fig. 1), Tokunoshima I. (F, Fig. 1), Okino-erabujima I. (G, Fig. 1), Yoron I. (H, Fig. 1), Miyako I. (K, Fig. 1), and Yonaguni I. (P, Fig. 1) was based on examinations of herbarium collections from Kyoto University, The University of Tokyo, The Tokyo Metropolitan University, and The National Science Museum, Tsukuba.

Results

In all 15 seagrass species from seven genera, within three families have been found in the Nansei Islands. Table 2 provides information on all seagrass species growing at each major island in the region. Most of these species mainly grow in two shallow water habitats: coral reefs (reef platforms, dead coral debris and coral sand) and sheltered bays (inlets and river mouths with sandy or muddy sand substrata). In addition, certain species grow sparsely at more than 20 m depth on coarse coral and shell debris sand at Okinawa I. and Iriomote I. The majority of seagrasses grow as patches of mixed species and very rarely as pure stands. The intertidal species are exposed to the air for a few hours each day.

Zostera japonica Aschers. & Graneb.

This seagrass is the only temperate species occurring in the region and in Japan, and it has been collected in all the major islands (Table 2), including at Takezaki (site 3, Fig. 1), and except at Kumano, Tanegashima I (site 2, Fig. 1) as reported by Miki (1933). This species prefers muddy sand in shallow water and has two distinct morpho-types and ecological forms (J. Kuo & Z. Kanamoto, unpublished data). The intertidal form normally grows near the mouth of rivers to form patches or meadows and in extreme low water pools; it is exposed to the air occasionally. The subtidal form usually grows among other tropical seagrass species, such as *Halodule*, *Thalassia* and *Cymodocea*, and neither forms meadows nor is exposed to the air. Flowering of this species was recorded in March. Patches of intertidal meadows in association with mangroves were found near the river mouth at Yamama, Sumiyo Bay on the east coast of Amami-oshima I. (site 6, Fig. 1). Toma (1993) reported large meadows of *Z. japonica* and *H. ovalis* along a 1-km transect, on the southern shore of Yagagi Is, Hagegi Inland Sea in Okinawa I. (Tr. I, Fig. 8 by Toma 1993) (site 11, Fig. 1). However, only several small patches about 3×3 m of *Z. japonica* were observed growing among the planted mangrove seedlings from the same transect in 1999. In addition, meadows of this species together with *Halodule pinifolia* were not observed in 1999 from the transect site near the mouth of the Udara River at the base of Amitori Bay (site 24, Fig. 1) as reported previously (Habe *et al.* 1984).

Enhalus acoroides (L. *f.*) Royle

The species only occurs at Ishigaki I., Iriomote I., and Hateruma I. (O, Fig. 1) in the Yaeyama Is. Vast, pure or mixed meadows of *Enhalus* with numerous plants at different flowering and fruiting stages, and numerous seedlings <50 cm in height, were observed in Amitori and Sakiyama Bays and other locations at Iriomote I. (sites 23–25, Fig. 1). On the other hand, only about 20 shoots of this species without reproductive material were found in a 30 m^2 area at the Fukido River mouth, Ishigaki I. (site 17, Fig. 1). Flowering in this species was observed from September to January, and fruiting occurs all the year round, except in July and August at Amitori Bay, Iriomote I. (Table 2).

Table 2. Seagrass species from the Nansei Islands, Japan.

	seagrass species															
locality	*Si*	*Cr*	*Cs*	*Hp*	*Hu*	*Zj*	*Ea*	*Th*	*Hd*	*Ho*	*Hao*	*Hm*	*Ham*	*Hv*	*Hj*	total
Satsunan Is																
Osumi Is																
Tanegashima I.						C					H					2
Yakushima I.											C					1
Tokara Is																
Suwanosejima I.																0
Amami Is																
Kikaijima I.		L	H													2
Amami-oshima I.	C	C	C	C	C	C		C		C		C				9
Tokunoshima I.					H			H		H						3
Okino-erabujima I.									H							1
Yoron I.	C	H	H	H	H	H		H		H		H				9
Ryukyu Is																
Okinawa Is																
Okinawa I.	C	C	C	C	C	C		C	C	C		C	C	C	C	12
Kumeshima I.	L	L	L	L	L	L	L[a]	L		L						9
Sakishima Is																
Miyako Is																
Miyako I.	H	H	L	L	H	H		H	H	C		C				10
Taramashima I.		L	L	L	L			L	L	L						7
Yaeyama Is																
Ishigaki I.	C	C	C	C	C	C	C	C		C		C				10
Iriomote I.	C	C	C	C	C	C	C	C	C	C		C		C	C	13
Hateruma I.	L	H	L	L	H		L	H	H	H						9
Yonaguni I.	H	L	L	H	H			H	H	H						8

I, single island; Is, island groups.

Si = *Syringodium isoetifolium*; *Cr* = *Cymodocea rotundata*; *Cs* = *Cymodocea serrulata*; *Hp* = *Halodule pinifolia*; *Hu* = *Halodule uninervis*; *Zj* = *Zostera japonica*; *Ea* = *Enhalus acoroides*; *Th* = *Thalassia hemprichii*; *Hd* = *Halophila decipiens*; *Ho* = *Halophila ovalis*; *Hao* = *Halophila mikii*; *Hm* = *Halophila minor*; *Ham* = *Halophila okinawensis*; *Hv* = *Halophila gaudichaudii*; *Hj* = *Halophila major*.

C, H, L indicate collected, herbarium specimens and literature information, respectively. The published literature did not separate *H. minor* and *H. major* from *H. ovalis*.

[a]Doubtful literature record.

Thalassia hemprichii (Ehrenh.) Aschers.

This is the dominant species in reef-associated habitats and occurs at all islands from Amami-oshima I. southward. It can form large meadows mixed with other species. Together with *H. ovalis*, it is the most widely distributed seagrass in the region. Fruiting of this species occurs all the year round, except in July and August in the Nansei Islands.

Halophila decipiens Ostenf.

In addition to Okinawa I. (Kuo *et al.* 1995), this species was collected at 38 m depth in Amitori Bay, Iriomote I. (site 24, Fig. 1). It grows sparsely and sometimes is associated with *H. okinawensis* and *H. gaudichaudii* in clear deep water, but with other tropical seagrasses in shallower water at 5 m depth. This species is the only annual monoecious *Halophila* in Japan. The plant appears in spring; flowers and settled seeds are found in summer and disappear in winter (Kuo *et al.* 1995).

Halophila minor (Zoll.) Hartog

Halophila minor was previously identified as *H. ovalis* or *H. ovata* in the Nansei Islands by Tsuda & Kamura (1990) and Toma (1999). This species is found at all major islands south of the Amami Is in the region, including sites 5 and 7–9 in Fig. 1. *Halophila minor* normally grows on coral sand and muddy sand together with *H. ovalis* and with other tropical seagrasses in shallow water. It also extends into deeper water, down to 7 m, where it forms sparse patches or mixed with other species such as *H. okinawensis* and *Halodule pinifolia*. Flowering of this species is from June to September and fruiting is in August and September.

***Halophila okinawensis* J. Kuo**

This taxon has only been collected between 5 and 24 m depth at several localities at Okinawa I. (sites 12, 14 and 15, Fig. 1). Tsuda & Kamura (1990) noted that this taxon has a slender leaf blade with fewer cross veins than those in normal *H. minor* and is considered to resemble to *H. ovalis* ssp. *linearis* (Hartog). Flowering of this taxon was observed in April-May.

Halophila ovalis* (R. Br.) Hook. *f.

This species commonly grows from MLW, to about 15 m deep in this region. It does not form large meadows, but is usually associated with other species on the reef, *i.e.* sites 16, 18 and 19–22 at Isigaki I. and may also grow in small patches in deeper water. Isolated patches were found in a submarine hot spring at 15 m depth off Taketomi Island near Ishigaki I. (Kuo *et al.* 2001). During an extremely low tide in June 1999, only a single patch of *H. ovalis* was observed in the same transect recorded previously (Tr. 1, Fig. 8, Toma 1993) (site 11, Fig. 1). In contrast, up to eight healthy seagrass species co-existed on the ocean side of the Hanegi Island Sea (site 10, Fig. 1).

***Halophila mikii* J. Kuo**

Miki (1934a) treated this taxon, collected from Sumiyoshi, Tanegashima I. (site 1, Fig. 1) as 'an intermediate form' of the Japanese *H. ovalis*. This taxon was not found in Tanegashima I. during our survey in June 1999; however, a small population without reproductive organs discovered in adjacent Yakushima I. (site 4, Fig. 1) making it the first seagrass recorded from this island. Flowering and fruiting, observed only from herbarium material, may take place from August to October.

***Halophila gaudichaudii* J. Kuo**

This species previously known as *H. ovata* Gaud. (Kuo 2000; Kuo *et al.* 2006), commonly grows in Micronesia and the Philippines, but grows in a few localities at Iriomote I. and Okinawa I. It grows sparsely with *H. ovalis*, *H. minor* and *Halodule pinifolia* in shallow water (5–7 m) or with *H. decipiens* and *H. okinawensis* in clear deeper water (24 m). The flowers of *H. gaudichaudii* have been collected in late May.

***Halophila major* (Zoll.) Miq.**

Den Hartog (1970) considered that *H. ovalis* contained several synonyms including *H. major* and *H. euphlebia* Makino. Based on morphological and molecular studies, Uchimura *et al.* (2006) suggested that *H. euphlebia* has a distinct species status, while Kuo *et al.* (2006) recommended that *H. euphlebia* should be treated as a synonym of *H. major*. The species is widely distributed in the Micronesia and West Pacific regions, and was found at some larger islands in the Nansei Islands. *Halophila major* grows as small patches or mixed with *H. ovalis* and/or *H. minor*, and other tropical seagrasses such as *Halodule* spp., *Cymodocea* spp., *Syringodium isoetifolium* or *T. hemprichii* in the shallow water of coral sands. Flowering is from June to September and fruiting is in August and September.

***Cymodocea rotundata* Ehrenb. & Hempr. ex Aschers.**

This species was recorded from most of the major southern islands up to Amami-oshima I. in the north. It commonly grows at 2–5 m depth and often extends into bare sand areas and frequently with other tropical species, such as *Thalassia*, *Halodule* and *Syringodium*. Flowers of this species were observed once in November 2005 (Z. Kanamoto, unpublished data), while fruits were never recorded from the Nansei Islands.

***Cymodocea serrulata* (R. Br.) Aschers.**

Makino (1912) described a new seagrass species of *Cymodocea*, as *C. asiatica*, based on a specimen collected from Naha, Okinawa I. This species was subsequently considered as a synonym of *C. serrulata* (Miki 1932) and recorded from various islands in the region north to Amami-oshima I. It always occurs mixed with other species, primarily on a coral substratum. Male flowers had been observed from October to February in Okinawa I., while there is no record of female flowers or fruits in the area.

***Halodule pinifolia* (Miki) Hartog**

Miki (1932) described this species as *Diplanthea pinifolia* based on specimens collected from Okinawa I. and Taiwan. This species is widely distributed in the Archipelago from Amami-oshima I. southward and grows in the intertidal and subtidal sites. At the intertidal sites, it may grow in river mouths as pure patches or mixed with other intertidal species such as *Z. japonica*, or with *Halophila* in bays and on reef platforms. The subtidal populations always grow with other tropical species, in particular *Thalassia*, *Cymodocea* spp., *Halodule uninervis*, *H. ovalis* and *H. minor* at several sites in Okinawa I. (*e.g.* sites 12 and 13, Fig. 1). Flowering and fruiting of this species occur all year round, except from December to February. *Halodule pinifolia* was not observed in 1999 from the same transect site at the base of the Amitori Bay, Iriomote I. (site 24, Fig. 1) as reported previously by Habe *et al.* (1984).

Halodule uninervis (Forssk.) Aschers.

This species with two morphological forms (narrow and wide leaved) is widely distributed in the Western Pacific and Indian Oceans (Kuo & den Hartog 2001) and only the wide-leaved form extends to Amami-oshima I. The species normally forms mono-specific meadows but sometimes it is mixed with other tropical species on reef platforms, river mouths or sheltered bays down to 5 m depth. Flowering has been observed once in August 2001 (Z. Kanamoto, unpublished data).

Syringodium isoetifolium (Aschers.) Dandy

This species is widely distributed in the region from Amami-oshima I. southward. It is commonly found to be sparsely mixed among other reef-associated species, such as *Thalassia*, *Cymodocea* spp. and *Halodule* and grows down to about 5 m depth but is not exposed to air during low tide. Kanamoto (2001) noted that the density of *Syringodium* appeared to have increased in the outer part of Nagusu Bay at Ishigaki I. during the last 20 years. Flowering of this species has been observed from July to September in the region.

Discussion

In total, 15 seagrass species belonging to six genera and three families are found in the southern Japanese Archipelago, the Nansei Islands, and among them, *Halophila decipiens*, *H. minor*, *H. major*, *H. okinawensis*, *H. gaudichaudii* and *H. mikii* are new additions to those reported earlier for the region (Tsuda & Kamura 1990; Toma 1999). The seagrass species composition of the southern Japanese Archipelago is comparable with that of the tropical neighboring countries such as the Philippines (Meñez *et al.* 1983), Thailand (Supanwanid & Lewmanomont 2003) and Indonesia (Kuriandewa *et al.* 2003). There is little doubt that the warm Kuroshio Current plays an important role in the dispersal of the seagrasses northward from the equator to the Nansei Islands (Miki 1933; Mukai 1993). However, it is worth emphasizing that certain tropical species including *H. spinulosa* (R.Br.) Aschers., *H. beccarii* Aschers., and *Thalassodendron ciliatum* (Forsk.) den Hartog are absent from the Nansei Islands. The northern distributional limit for *Thalassia ciliatum* in the West Pacific Ocean is Palawan (10°00′ N; 119°30′ E), while the northern border for *H. spinulosa* is southern Luzon Island, the Philippines (14°30′ N; 121°30′ E) (Meñez *et al.* 1983). It is possible that temperature may impede the growth of these two tropical species in the Nansei Islands. In addition, *H. beccarii*, which usually occurs in association with mangrove communities on muddy substrates, extends northwards only to Budai in south-western Taiwan (23°20′ N; 120°10′ E) in the western Pacific region (Lin 2000). Although there are abundant mangroves in the southern Nansei Islands, they normally grow on coral sand substrate and are rarely associated with muddy tidal flats; thus, it is most likely that the lack of suitable habitat may preclude *H. beccarii* from occurring in the Nansei Islands.

Tsuda & Kamura (1990) found that the seagrass flora in the Ryukyu Islands and Micronesia are very similar, with the exception that *T. ciliatum* occurs in Guam, Micronesia while *Zostera japonica* is present in the Ryukyu Is. Guam (13°30′ N, 144°45′ E) is located south-east of the Nansei Islands. This further confirmed that the warm sea water from the Kuroshio Current is one of the most important determining factors for the distribution of seagrass species. On the other hand, it is interesting to note that Taiwan, the closest neighbor to the southernmost Japanese Archipelago, with the Kuroshio Current flowing along the east coast, is rather poor in tropical seagrasses (Yang 2000). This could be because Taiwan is of continental origin with very limited coral to support reef-dependent tropical seagrass species.

The Nansei Islands are the northern boundary for most of the tropical seagrass species in the western Pacific region. Ishigaki I. with a winter water temperature of 23 °C is the northern distributional limit for *E. acoroides* while Okinawa I. (21.6 °C) is the border for *H. decipiens*, *H. major*, *H. gaudichaudii* and *H. okinawensis*. Amami-oshima I. (20.7 °C) is the northern limit for *T. hemprichii*, *H. ovalis*, *H. minor*, *Cymodocea rotundata*, *C. serrulata*, *Halodule pinifolia*, *Halodule uninervis* and *Syringodium isoetifolium*. None of the above mentioned species are present at Tanegashima I. and Yakushima I. of the northern Nansei Islands, where the WST falls below 19.3–19.7 °C (Table 1). However, an abrupt reduction of the species richness from nine at Amami-oshima I. to one or two species in Tanegashima I./Yakushima I. may not only be the results of cooler WST (Miki 1934b; Nozawa 1981) or current flow direction (Mukai 1993). It was found that in the Nansei Islands, if tropical coral reefs are present, then most of the tropical seagrass species occur. It should be noted that tropical coral reefs reach only the south of Tokara Is. (C, Fig. 1) (Yamaguchi 1985). Thus, reef-dependent tropical seagrass species, which normally grow on dead reef platforms, coral debris or coral sands, are absent from Yakushima I. and Tanegashima I. These two islands have continental and volcanic origins without tropical coral associations and support only species that prefer muddy sand as substratum, such as *H. mikii* and *Z. japonica*. A lack of suitable habitats, because of the

absence of corals seems to play an important role in seagrass distribution in this region.

Yokochi (1999) reported that the meadows of eight tropical seagrasses in Sakiyama Bay and Amitormi Bay, Iriomote I. apparently had not changed between 1977 and 1997. Our observations on the decline of *Z. japonica* and *Halodule pinifolia* from the river mouths in these two bays could be associated with natural siltation, as these remote bays had little human activities, while the meadow reduction of *Z. japonica* and *H. ovalis* at the Hanegi Inland Sea, Okinawa I. appears to be influenced by human activities such as the construction of roads and port facilities that increase sediment siltation in the area. Furthermore, the loss of *H. mikii* at Tanegashima I., during the present study, was more likely to be associated with run-off from agricultural practices. With the evidences from this study of disappearing seagrass meadows from certain areas within the region, special attention towards environmental protection measures is warranted.

Acknowledgements

Dr Lucia Mazzella had been fascinated by the diversity and biogeography of the tropical and temperate species of seagrasses in Japan and Australia. Lucia attended the first International Seagrass Workshop (ISBW) in Tokyo (1993) and served as one of the Organizing Committee members. She also participated in the second ISBW in Perth (1996). However, she had the opportunity to observe only the temperate and not the tropical seagrasses in these countries. We gathered enormous knowledge on the various aspects of seagrass biology, particularly the species diversity and the distribution of the seagrasses, through our constant communications with Lucia. For this reason, we would like to dedicate this paper to our good friend, Lucia.

We would like to thank Dr Hugh Kirkman, Dr Marion Cambridge and anonymous reviewers for constructive comments on this manuscript and to Lih-yuh Kuo for making Fig. 1. Special thanks to M. Nishihira, H. Yokochi, T. Shibuno, and many others for their help in collecting samples and providing literature. We wish to extend our gratitude to the curators and staff of the various herbaria for allowing us to study their collections. This project was supported by the Heiwa Nakajima Foundation and Japan Society for the Promotion of Science (JSPS).

References

Aioi K., Nakaoka M. (2003) The seagrasses of Japan. In: Green E.P., Short F.S. (Eds), *World Atlas of Seagrasses*. University of California Press, Berkeley, CA: 185–192.

Den Hartog C. (1970) *Sea-Grasses of the World*. North-Holland, Amsterdam.

Habe T., Yokochi H., Kawakami A., Monji N., Uryu T. (1984) Seasonal variation of the animal fauna on the seagrass bed in the Amitori Bay, Iriomote Island. *Bulletin Institute Oceanic Research & Development, Tokai University*, **6**, 17–27 (in Japanese with English Abstract).

Kanamoto Z. (2001) Spatial distributions of seagrass and their seasonal change in Nagura Bay, Ishigaki Island, Okinawa. *Otsuchi Marine Science*, **26**, 28–39 (in Japanese with English abstract).

Kuo J. (2000) Taxonomic notes on *Halophila minor* and *Halophila ovata*. *Biologia Marina Mediterranea*, **7**(2), 79–82.

Kuo J., den Hartog C. (2001) Seagrass taxonomy and identification key. In: Short F.S., Coles R.G. (Eds), *Global Seagrass Research Methods*. Elsevier, Amsterdam: 31–58.

Kuo J., Kanamoto Z., Toma T., Nishihira M. (1995) Occurrence of *Halophila decipiens* Ostenfeld (Hydrocharitaceae) in Okinawa Island, Japan. *Aquatic Botany*, **51**, 329–334.

Kuo J., Shibuno T., Kanamoto Z., Noro T. (2001) *Halophila ovalis* (Br.) Hook. (Hydrocharitaceae) from a submarine hot spring in Southern Japan. *Aquatic Botany*, **70**, 329–335.

Kuo J., Kanamoto Z., H. Iizumi, H. Mukai (2006) Seagrasses of the genus *Halophila* Thouars (Hydrocharitaceae) from Japan. *Acta Phytotaxonomica et Geobotanica*, **57**(2), 127–154.

Kuriandewa T.E., Kiswara W., Humoto M., Soemodihardjo S. (2003) The seagrasses of Indonesia. In: Green E.P., Short F.S. (Eds), *World Atlas of Seagrasses*. University of California Press, Berkeley, CA: 171–182.

Lin C.-C. (2000) *Aquatic Plants of Taiwan. I. Illustrations of Natural Observations.* Tein-Ya Field Imaging Publisher, Taipei (in Chinese).

Makino T. (1912) Observations on the flora of Japan. *Botanic Magazine Tokyo*, **26**, 208–210.

Meñez E.G., Phillips R.C., Calumpong H.P. (1983) *Seagrasses from the Philippines. Smithsonian Contribution to Marine Sciences* Number 21. Smithsonian Institution Press, Washington, DC.

Miki S. (1932) On the sea-grasses new to Japan. *Botanic Magazine Tokyo*, **46**, 774–788.

Miki S. (1933) On the sea-grasses in Japan (I). *Zostera* and *Phyllospadix*, with special reference to morphological and ecological characters. *Botanic Magazine Tokyo*, **47**, 842–862.

Miki S. (1934a) On the sea-grasses in Japan (II). Cymodoceaceae and marine Hydrocharitaceae. *Botanic Magazine Tokyo*, **48**, 131–142.

Miki S. (1934b) On the sea-grasses in Japan (III). General consideration on the Japanese sea-grasses. *Botanic Magazine Tokyo*, **48**, 171–178.

Mukai H. (1993) Biogeography of the tropical seagrasses in the western Pacific. *Australian Journal Marine & Freshwater Research*, **44**, 1–17.

Nozawa K. (1981) The distribution of sea-grass in Japan. *Plants & Nature*, **15**(13), 15–19 (in Japanese).

Supanwanid C., Lewmanomont K. (2003). The seagrasses of Thailand. In: Green E.P., Short F.S. (Eds), *World Atlas of Seagrasses*. University of California Press, Berkeley, CA: 144–151.

Toma T. (1993) Biomass of sea-grasses (1977–1978) in Okinawa Island from the three sites suffering from land pollution. *Annual Report of Okinawa Prefecture Fisheries Experimental Station* March 2003, 135–141 (in Japanese).

Toma T. (1999) Seagrasses from the Ryukyu Islands. I. Species and distribution. *Biological Magazine Okinawa*, **37**, 75–92 (in Japanese with English abstract).

Tsuda R.T., Kamura S. (1990) Comparative review on the floristics, phytogeography, seasonal aspects and assemblage patterns of the seagrass flora in Micronesia and the Ryukyu Islands. *Galaxea*, **9**, 77–93.

Uchimura M., Faye E.J., Shimada S., Arai S., Inoue T., Nakamura Y. (2006) A re-evaluation of the taxonomic status of *Halophila euphlebia* Makino (Hydrocharitaceae) based on morphological features and ITS sequence data. *Botanica Marina*, **49**, 111–121.

Yamaguchi M. (1985) Tropical and subtropical zones in marine biogeography. *Aquabiology*, **7**, 410–416 (in Japanese).

Yang Y.P. (2000) Hydrocharitaceae, Zannichelliaceae, and Zosteraceae. In: The Editorial Committee (Ed.) *The Flora of Taiwan*, 2nd edn, Volume V, Angiosperms-Monocotyledons. Department of Botany, National Taiwan University, Taipei: 11–19, 28–30.

Yokochi H. (1999) State of Sakiyama Bay Nature Conservation Area, Okinawa, Japan. Nature Conservation Bureau, Environment Agency, Japan: 81–92.