

Ecology of seagrasses *Zostera* spp. (Zosteraceae) in Japanese waters: A review

Masahiro Nakaoka* and Keiko Aioi

Ocean Research Institute, the University of Tokyo, Minamidai, Nakano, Tokyo 164–8639, Japan

*E-mail: nakaoka@ori.u-tokyo.ac.jp

The seagrass flora of Japan is characterized by the occurrence of several species of the family Zosteraceae, including some endemic and threatened species such as *Z. asiatica* and *Z. caulescens*. In this paper, we review ecological studies reporting distribution, abundance, productivity and life history of *Zostera* spp. in natural seagrass meadows along Japanese coasts. Among five species of *Zostera*, *Z. marina* and *Z. japonica* have wide distribution, occurring from northernmost to southernmost parts of the Japanese main islands, whereas live populations of *Z. asiatica*, *Z. caespitosa* and *Z. caulescens* are currently known only at limited localities in the northern half of the main islands. In multispecific seagrass beds where two or more species of *Zostera* co-occur, *Z. marina* is generally found in shallow subtidal bottoms (between 1 and 5 m deep), *Z. japonica* in shallower intertidal habitats, and other three species (*Z. asiatica*, *Z. caespitosa* and *Z. caulescens*) in deeper parts of the beds. Possible factors affecting the pattern of depth distribution contain light condition, bottom disturbance and interspecific interactions. Biomass, shoot density, growth and productivity vary greatly among and within populations of each species, and among sympatric species. Due to such multiple sources of variation, it is difficult to find general patterns of regional and latitudinal trends in these parameters. Phenology and life history traits of these seagrasses also show large regional and interspecific variation. Within the same species, southern populations initiate flowering and fruiting earlier than northern populations. It is also found that flowering and fruiting seasons of *Z. caespitosa* are 1–2 months earlier than sympatric *Z. marina*. Based on the available knowledge on ecology of these *Zostera* species, we address some perspectives for future research, especially for conservation of endemic species.

Key words: *Zostera* seagrasses, Japan, distribution, biomass and production, life history

INTRODUCTION

Seagrasses are marine angiosperms that form extensive meadows (seagrass beds) on shallow bottoms. (Den Hartog 1970, Larkum et al. 1989, Vermaat et al. 1997). Seagrass beds support a high primary production (Duarte 1989, Hilman et al. 1989, Duarte and Chiscano 1999), and host a wide variety of associated fauna including commercially important fishes and endangered marine mammals such as dugongs and manatees (Heinssohn et al. 1977, Kikuchi and Peres 1977, Bell and Pollard 1989, Mazzella et al. 1992, Jernakoff et al. 1996). These features of seagrass beds make themselves known as one of the most important components in coastal ecosystems (Duarte and Chiscano 1999).

Among some sixty species of seagrasses in the world, 16 species have been recorded from Japanese waters (Table 1; Aioi 1998). One of the prominent characters of Japanese seagrass flora is that it contains several species of the family Zosteraceae that are considered to be endemic to the northwestern Pacific (Japanese, Korean and southeast Russian waters), namely, *Zostera asiatica*, *Z. caespitosa*, *Z. caulescens*, *Phyllospadix iwatensis* and *P. japonicus* (Omori 1993, Aioi 1998). Despite such high species diversity, only little attention has been given to ecological studies of these species. After pioneer studies by Makino (1897, 1899, 1910, 1931) and Miki (1932, 1933, 1934a, b) who described these endemic species, studies on these seagrasses were rarely conducted in Japan until the early 1970's, except some works by Arasaki (1950a, b) and Tanaka et al. (1962a, b). Since then, studies on seagrasses increased in number, although most of them were descriptive reports

published in local journals and periodicals in the Japanese language. Especially for the endemic *Zostera* species, information on their distribution and ecology was not available until recently after their first description by Miki, partly due to their occurrence in deeper parts of seagrass beds.

Despite their importance in coastal ecosystems, most seagrass beds in the world suffered rapid decline during the last century due to direct and indirect effects of human activities (Orth and Moore 1983, Fortes 1988, Shorts and Wyllie-Echeverria 1996). This is also true for seagrass beds in Japan. For eelgrass, *Z. marina*, the area of its vegetation decreased more than 20 km², i.e., 4% of total estimated area of seagrass beds in Japan, during the period between 1978 and 1991 (Environment Agency of Japan 1994). In particular, >30% of eelgrass beds disappeared in localities such as Ariake Sea, Kagoshima Bay and Hyuga-nada in Kyushu during this period (Environment Agency of Japan 1994). In Seto Inland Sea, more than 70% of eelgrass beds have been lost since 1977, which seriously affected coastal fisheries (Komatsu 1997, Aioi 1998). For endemic species of *Zostera*, the situation may be more serious because live populations are now known only in a few localities around Japan. In fact, *Z. asiatica* and *Z. caulescens* are now listed in the Red Data Book of threatened Japanese plant species (Environment Agency of Japan 2000). Basic information on distribution and ecology is urgently required for promoting effective and efficient conservation of these seagrasses.

This paper reviews ecological studies of seagrasses belonging to the genus *Zostera* in Japanese waters. We primarily focused on previous studies reporting distribution, biomass, population dynamics, productivity and life history

of *Zostera* spp. in natural seagrass meadows. By reviewing these data, we provide our perspectives for future studies on seagrass ecology and its application for conservation and management of seagrass beds that are now rapidly declining from Japanese coastal waters.

GENERAL PROPERTIES OF OCEANOGRAPHICAL CONDITIONS AND SEAGRASS FLORA IN JAPANESE COASTAL WATERS

Japan consists of four main islands, i.e., Hokkaido, Honshu, Shikoku and Kyushu (Fig. 1), and many small islands surrounding them, such as Ryukyu Islands, southeast of Kyushu. The climate varies greatly with latitude: subtropic in Ryukyu Islands, temperate in Kyushu, Shikoku and Honshu, and boreal in Hokkaido. The coastal areas are affected by several warm and cold currents. The warm Kuroshio runs along the western coast of the Pacific from the Ryukyu Islands, Kyushu, Shikoku to central Honshu. A branch of Kuroshio (Tsushima warm current) runs through the East China Sea to the Japan Sea. The cold Oyashio runs along the eastern coast of Hokkaido to the northeastern coast of Honshu. See references such as Kawai (1972) and Sugimoto (1990) for more information on physical and hydrodynamic properties around the Japanese coast.

Among the 16 species of seagrasses in Japan (Table 1), nine species belonging to the family Hydrocharitaceae and Cymodoceaceae are commonly found in tropical and subtropical areas of the Indo-west Pacific region (Den Hartog 1970). In Japan, their distribution is restricted to the southwestern islands (Ryukyu and Amami Islands), except for *Halophila ovalis* that has been found in the southern half of Honshu. In contrast, the distribution of all the species of Zosteraceae is limited to the main islands except for *Z. japonica* that also occurs in Ryukyu Islands (Toma 1999). Thus, the seagrass flora in Japan shows distinct separation between the subtropical southwestern islands and the temperate coasts of the main islands.

We have collected 50 papers reporting the ecology of *Zostera* spp. from various parts of Japanese coasts (Table 2). Location of study sites tended to center on some specific regions (Fig. 1). In this paper, we classify regions of the study sites into the following six units: (1) eastern Hokkaido, (2) northeastern Honshu, (3) the Pacific coasts of central Honshu, (4) the Japan Sea coasts of Honshu, (5) Seto Inland Sea, and (6) western Kyushu (Fig. 1, Table 2). The former two regions are characterized by low water temperature (annual range of 5–20°C or lower), and the latter four by high water temperature (annual range of 10–25°C or higher) under the influence of the cold and the warm currents, respectively.

GEOGRAPHICAL DISTRIBUTION OF *Zostera* spp. AROUND JAPAN

The seagrasses belonging to the genus *Zostera* have a bipolar distribution. Some species (such as *Z. capricorni*, *Z. mucronata* and *Z. muelleri*) occur in the temperate Southern Hemisphere, whereas others (such as *Z. marina*, *Z. noltii* and *Z. japonica*) in the Northern Hemisphere (Den Hartog 1970, Aioi 2000). Among six species in the Northern Hemisphere, all the species except *Z. noltii* occur around Japan (Miki 1933, Aioi et al. 1998).

Table 1. List of seagrass species recorded in Japanese waters.

Species	Distribution in Japan
HYDROCHARITACEAE	
<i>Enhalus acoroides</i>	Ryukyu Islands
<i>Thalassia hemprichii</i>	Ryukyu Islands to Amami Islands
<i>Halophila decipiens</i>	Ryukyu Islands
<i>Halophila ovalis</i>	Ryukyu Islands to central Honshu
CYMODOCEACEAE	
<i>Cymodocea rotundata</i>	Ryukyu Islands to Amami Islands
<i>Cymodocea serrulata</i>	Ryukyu Islands to Amami Islands
<i>Halodule pinifolia</i>	Ryukyu Islands to Amami Islands
<i>Halodule uninervis</i>	Ryukyu Islands to Amami Islands
<i>Syringodium isoetifolium</i>	Ryukyu Islands to Amami Islands
ZOSTERACEAE	
<i>Phyllospadix iwataensis</i>	northern Honshu to Hokkaido
<i>Phyllospadix japonicus</i>	central Honshu
<i>Zostera asiatica</i>	northern Honshu to Hokkaido
<i>Zostera caespitosa</i>	northern Honshu to Hokkaido
<i>Zostera caulescens</i>	central to northern Honshu
<i>Zostera japonica</i>	Ryukyu Islands to Hokkaido
<i>Zostera marina</i>	Kyushu to Hokkaido

Eelgrass *Zostera marina* L. is a cosmopolitan species commonly found in temperate to subarctic coasts of the Northern Hemisphere (Den Hartog 1970). It is a perennial plant that increases its population size by clonal propagation of rhizomes and by seed production, although the annual form is sometimes found (Keddy and Patriquin 1978, Imao and Fushimi 1985, van Lent and Verschuure 1995). In Japan, eelgrass occurs in numerous localities along the coastlines of the main islands (Aioi 1998). The northernmost population of eelgrass in Japan is known near Cape Soya, Hokkaido (45°30'N; Omori 1992), and the southernmost population in Satsuma Peninsula, Kyushu (31°10'N; Environmental Agency of Japan 1994).

Zostera japonica Ascherson & Graebner is a small-sized species that generally inhabits intertidal and shallow sandy or muddy bottom. It is found along the coast of East Asia, from Vietnam to Sakhalin and Kamchatka, Russia (Den Hartog 1970, Shin and Choi 1998). It also occurs from the central coast of western North America, but is considered to be introduced from Japan (Harrison and Bigley 1982). In Japan, *Z. japonica* is observed in localities such as Notsuke Bay, eastern Hokkaido (Mizushima 1985), Toyama Bay in the Japan Sea (Tsutsui and Sano 1996, Fujita and Takayama 1999, Higashide et al. 1999), Sagami Bay, the Pacific coast of central Honshu (Kudo 1999), and Ryukyu Islands, southwestern part of Japan (Kanamoto and Watanabe 1981, Tsuda and Kamura 1990, Toma 1999).

Zostera asiatica Miki was originally recorded from southern Sakhalin, northeastern and southern parts of Hokkaido, the central part of Honshu facing the Japan Sea, and the eastern coast of Korean Peninsula (Miki 1933). This species is distinguishable from *Z. marina* by its broad leaf width (Aioi et al. 2000). In Japan, live populations are currently known only in Hamanaka Bay and Akkeshi Bay, Hokkaido (Omori 1993), and in Funakoshi Bay, northeastern coast of Honshu (Aioi et al. 2000). In addition to this,

Table 2. List of localities and types of ecological information on seagrasses cited in this paper. Numbers in locality correspond to the positions in the map (Fig. 1).

Locality (Prefecture)	Depth distribution	Seasonal variation in biomass and density	Population size/age structure and dynamics	Growth and production	Phenology and reproductive traits	Reference number
North to east Hokkaido						
1: Soya (Hokkaido)	—	—	—	—	+	1)
2: Beniya (Hokkaido)	—	—	—	—	+	1)
3: Notoro-ko (Hokkaido)	+	+	—	+	+	2)
4: Notsuke Bay (Hokkaido)	+	+	+	+	+	3)
5: Akkeshi Bay (Hokkaido)	+	—	—	+	+	1), 4), 5)
Northeastern Honshu						
6: Asamushi (Aomori)	—	—	—	—	+	1)
7: Moura (Aomori)	—	—	—	—	+	1)
8: Noheji (Aomori)	—	—	—	—	+	1)
9: Yamada Bay (Iwate)	+	—	+	—	—	6–8)
10: Funakoshi Bay (Iwate)	+	—	+	+	—	1), 9–12)
11: Otsuchi Bay (Iwate)	+	+	—	+	+	13–15)
Pacific coast of central Honshu						
12: Takeoka (Chiba)	+	—	—	—	—	16)
13: Odawa Bay (Kanagawa)	+	+	+	+	+	1), 17–25)
14: Moroiso Bay (Kanagawa)	—	+	—	—	—	26)
15: Nabeta Bay (Shizuoka)	—	—	—	+	+	27), 28)
16: Hamana-ko (Shizuoka)	+	+	—	—	+	29)
17: Mikawa Bay (Aichi)	+	+	—	—	+	30–31)
Japan Sea coast of central Honshu						
18: Nanao South Bay (Ishikawa)	+	—	—	—	—	32)
19: Nanao North Bay (Ishikawa)	+	—	—	—	—	32)
20: Uchiura (Ishikawa)	+	—	—	—	—	32)
21: Iida Bay (Ishikawa)	+	+	+	—	+	33)
22: Obama Bay (Fukui)	—	—	—	—	+	34)
23: Takahama (Fukui)	—	—	—	—	+	1)
24: Maizuru Bay (Kyoto)	+	+	+	—	+	35–36)
25: Miyazu Bay (Kyoto)	+	—	—	—	—	37)
Seto Inland Sea						
26: Tsuda Bay (Kagawa)	—	+	—	—	—	38)
27: Ushimado (Okayama)	+	+	+	—	+	39–42)
28: Ajino Bay (Okayama)	+	—	—	—	—	43)
29: Hosonosu (Hiroshima)	+	+	—	—	—	44)
30: Yanai Bay (Yamaguchi)	+	+	—	+	+	45–47)
31: Beppu Bay (Oita)	—	—	—	—	+	48)
Western Kyushu						
32: Tomioka Bay (Kyushu)	+	+	—	—	—	49–50)

References: 1) Omori 1992; 2) Hokkaido Abashiri Fisheries Experimental Station 1997; 3) Mizushima 1985; 4) Lee et al. 1999; 5) Watanabe et al. 2000; 6) Omori 1996; 7) Omori et al. 1996; 8) Omori and Aioi 1998; 9) Tatsukawa et al. 1996; 10) Aioi et al. 1998; 11) Aioi et al. 2000; 12) Nakaoka et al. 2000; 13) Iizumi 1996; 14) Aioi and Komatsu 1996; 15) Omori and Aioi 2000; 16) Nakase 2000; 17) Mukai et al. 1980; 18) Aioi 1980; 19) Aioi 1981; 20) Terawaki et al. 1984; 21) Kawasaki et al. 1988a; 22) Omori 1989; 23) Omori 1994; 24) Omori 1995; 25) Kudo 1999; 26) Horinouchi et al. 1999; 27) Mukai et al. 1979; 28) Aioi et al. 1981; 29) Imao and Fushimi 1985; 30) Arasaki 1950a; 31) Arasaki 1950b; 32) Tajima and Sano 1978; 33) Taniguchi and Yamada 1979; 34) Miki 1933; 35) Douke et al. 2000a; 36) Douke et al. 2000b; 37) Douke et al. 1995; 38) Yamaga et al. 1996; 39) Azuma and Harada 1969; 40) Fukuda and Yasuie 1980; 41) Yasuie and Fukuda 1980; 42) Fukuda and Tsuchiya 1987; 43) Komatsu and Tatsukawa 1998; 44) Tsukidate and Takamori 1978; 45) Kawabata et al. 1990; 46) Kawabata et al. 1993a; 47) Kawabata et al. 1993b; 48) Hatate et al. 1974; 49) Kikuchi 1966; 50) Kikuchi 1973

some stranded dead plants were collected at several beaches in Hokkaido and one site in Toyama Bay (Omori 1993, Higashide et al. 1999). In Korea, several live populations were recently found along the east coast (Shin and Choi

1998, Lee et al. 1999). This species has also been recorded along the coast of California, U.S.A. (Phillips and Echeverria 1990). It is thus possible that *Z. asiatica* is a pan-pacific species with wider distribution range than pre-

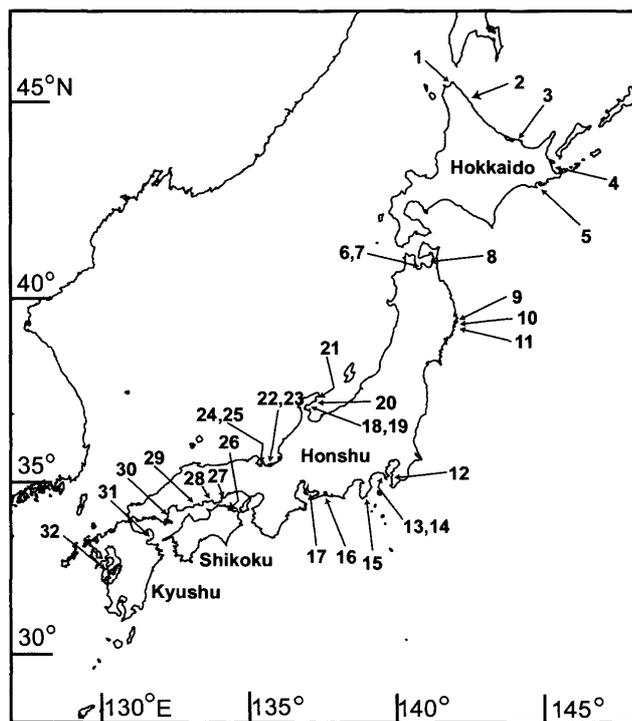


Fig. 1. Map showing main islands of Japan. The numerals and arrows denote locations of the seagrass beds where ecological studies were conducted (listed in Table 2).

viously thought.

Zostera caespitosa Miki was reported to occur in Hokkaido, northern half of Honshu and east Korea (Miki 1933). An unique character of this species is that it forms a shrub-like clump consisting of many shoots with numerous old leaf sheaths that remain after the detachment of each leaf blade (Omori 1996, Omori et al. 1996, Omori and Aioi 1998). Unlike other *Zostera* species whose rhizomes grow horizontally in the sediment, the rhizome of *Z. caespitosa* grow vertically or obliquely with short internodes (Omori 1996). The live populations of this species were recently reported from Notoro-ko and Notsuke Bay in Hokkaido (Mizushima 1985, Hokkaido Abashiri Fisheries Experimental Station 1997), Mutsu Bay, northern Honshu (Omori 1993), Yamada Bay and Otsuchi Bay, northeastern Honshu (Omori et al. 1996, Omori and Aioi 1998), and Toyama Bay, the Japan Sea (Higashide et al. 1999).

Zostera caulescens Miki was known from limited localities along the central to northern coast of Honshu and southern coast of Korean Peninsula when Miki first described this species (Miki 1932, 1933). The most remarkable character of this species is that it develops extraordinarily long flowering shoots (erect shoots) which end with several (4–8) large blades (Omori 1991, Aioi et al. 1998). It thus forms a high canopy structure several meters above the sea bottom (Kouchi and Nakaoka 2000, Nakaoka et al. 2000). The maximum shoot height of 5.3 m is reported in Odawa Bay, the Pacific coast of central Honshu (Kudo 1999) and 6.8 m in Funakoshi Bay (Aioi et al. 1998). In Funakoshi Bay, we recently found a flowering shoot of 7.8 m in length, which is considered to be the world's tallest record in all seagrasses (Nakaoka et al., unpublished data). In Japan, some recent papers reported the existence of live populations in Mutsu Bay, northern Honshu (Omori 1993),

Funakoshi Bay and Otsuchi Bay (Omori 1993, Aioi et al. 1998, Omori and Aioi 2000), Tokyo Bay and Sagami Bay, the Pacific coast of central Honshu (Nozawa 1974, Omori 1991, 1994, Kudo 1999, Nakase 2000), and Toyama Bay (Higashide et al. 1999). In Korea, it occurs along the East Sea to the South and West Sea (Shin 1998, Shin and Choi 1998).

The geographical distribution of these *Zostera* species overlaps widely in the northern parts of Japan, and they sometimes co-occur within a single bed. For example, four seagrass species (*Z. marina*, *Z. japonica*, *Z. caulescens* and *H. ovalis*) co-occur in Odawa Bay (Kudo 1999), three species in Otsuchi Bay (*Z. marina*, *Z. caespitosa* and *Z. caulescens*) and Funakoshi Bay (*Z. marina*, *Z. asiatica* and *Z. caulescens*) (Aioi and Komatsu 1996, Aioi et al. 2000).

DEPTH DISTRIBUTION

The depth range of seagrass beds has been reported from many localities in Japan (Fig. 2). Most of the data came from multispecific seagrass beds where two or more species co-occur in a single bed. Generally, each species in the multispecific beds shows a different depth distribution, forming some patterns of zonation along the depth gradient (Fig. 2).

Earliest attempts at describing zonation of *Zostera* spp. were made by Miki (1933) and Tanaka et al. (1962a) who indicated the depth distribution from shallow to deep habitats in the order of *Z. japonica*, *Z. marina*, *Z. caespitosa*, *Z. asiatica* and *Z. caulescens*, although quantitative data were not presented in their papers to support this hypothesis. Among recent reports on depth distribution in multispecific seagrass beds, *Z. japonica* is always found in the uppermost parts, at the depth shallower than 1 m and at the intertidal zones (Fig. 2), except for a population in Iida Bay, Noto Peninsula where it occurs at the depth of 1–4 m (Taniguchi and Yamada 1979). *Zostera marina* occurs in shallow parts of the subtidal bottom, mostly at 1–5 m deep (Fig. 2), but down to 10 m deep in some areas such as Mikawa Bay (Arasaki 1950a, b) and Iida Bay (Taniguchi and Yamada 1979).

The other three species generally occur in deeper habitats than *Z. marina*: *Z. asiatica* from the intertidal to 5 m deep, *Z. caespitosa* between 1 and 20 m, and *Z. caulescens* between 3 and 17 m (Fig 2). Their depth range normally overlaps to some degree with *Z. marina* which grows in shallower bottom. Among three deep-living seagrasses (*Z. asiatica*, *Z. caespitosa*, and *Z. caulescens*), their zonation pattern was not clear because they rarely occur together (reported only in Funakoshi Bay and Otsuchi Bay; Aioi and Komatsu 1996, Aioi et al. 2000).

The depth range of *Z. asiatica* in Akkeshi Bay and Otsuchi Bay is no deeper than 5 m (Fig. 2). In Akkeshi Bay, it is also found at an intertidal beach (Watanabe et al. 2000). Interestingly, populations outside of Japan are found in much deeper habitats: between 8 and 15 m in four populations in Korea (Lee et al. 1999), and between 5–14 m in five populations along the west coast of North America (Phillips and Echeverria 1990). No accounts have been available to explain the difference.

These *Zostera* species living in deep habitats have morphological characters that appear to be adaptive to low light conditions. For example, wide and long leaves of *Z. asiatica*

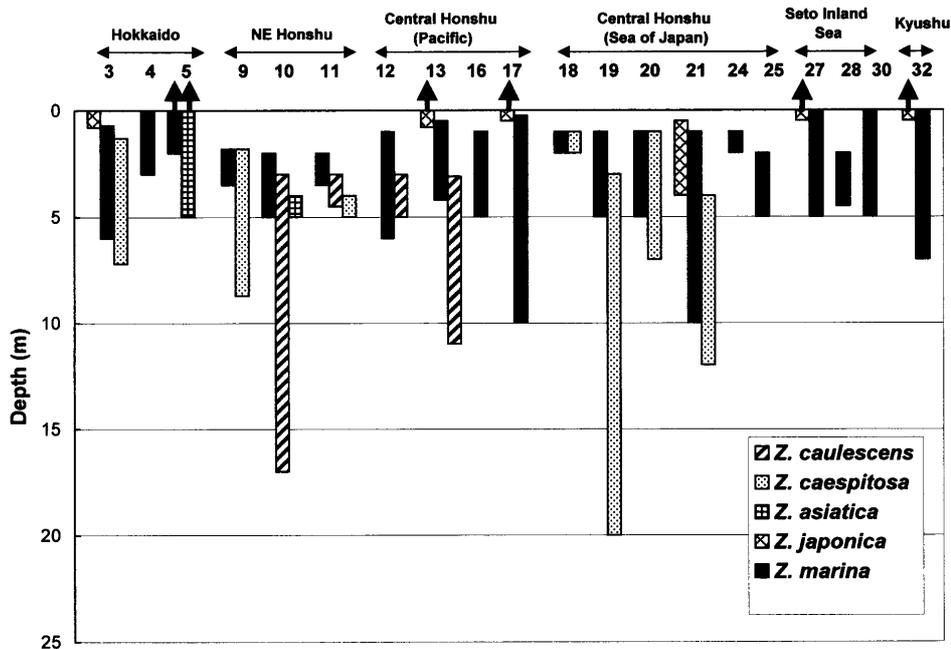


Fig. 2. *Zostera* spp. Depth distribution of seagrasses in major seagrass beds around Japanese coast. The arrows indicate the occurrence of seagrass at intertidal areas. The numerals denote the locality of study sites shown in Fig. 1 and Table 2.

ca may be more advantageous than *Z. marina* to get more light under dim conditions (Watanabe et al. 2000). This species also shows intraspecific variation in morphology within the population by producing thinner and larger leaves at deeper bottoms with lower light condition, as in some shade-tolerant species in terrestrial plants (Watanabe et al. 2000). In *Z. caulescens*, large leaf blades attached at the apex of long flowering shoots obviously benefit them by reaching better light conditions in deeper water (Omori 1989, 1994, 1995). In fact, the flowering shoots of *Z. caulescens* also function as the main photosynthetic parts (Omori 1991, 1995, Nakaoka et al. 2000), yielding higher annual primary production than vegetative shoots (Nakaoka, unpublished data). Nevertheless, actual mechanisms causing the zonation patterns among *Zostera* spp. in multispecific meadows are not elucidated at the present stage. Aioi (2000) compared photosynthesis-irradiance curves of *Z. marina* and *Z. caulescens* in Otsuchi Bay, but the critical differences were not found in parameters such as the light compensation point and the maximum photosynthetic rate.

Concerning latitudinal and regional differences in depth distribution of seagrasses, Tanaka et al. (1962a) speculated that the temperate species of seagrasses occur in deeper habitats at lower latitudes. However, no clear patterns of latitudinal variation are discerned for eelgrass from 20 localities ranging from Hokkaido to Kyushu (Fig. 2). It should be noted, however, that the depth limit of eelgrass was deepest (10 m) in the central parts of the Pacific and the Japan Sea coasts of Honshu where coastal water is warmer and generally more transparent than in Hokkaido and northeastern Honshu where the cold and nutrient-rich Oyashio predominates.

FACTORS AFFECTING DEPTH DISTRIBUTION

A variety of factors have been considered to be responsible for determining depth range of seagrasses, including

light, temperature, physical disturbance, desiccation and interspecific interactions with other seagrasses, algae and animals (Fonseca et al. 1983, Howard and Short 1986, Duarte 1991, Yabe et al. 1995, 1996). Examining all these possible factors by citing papers from all over the world is far beyond the focus of this review. Instead, we introduce some literature investigating these factors for local seagrass populations in Japan.

It is widely acknowledged that light availability limits distribution of seagrasses, especially at the deeper margin of seagrass beds (e.g., Backman and Barilotti 1976, Dennison and Alberte 1985, Dennison 1987, Duarte 1991). Based on field measurements of light intensity and an outdoor tank experiment manipulating light intensity, Kawasaki et al. (1990) estimated that minimum average light intensity for the survival of eelgrass in Odawa Bay is $3 \text{ E m}^{-2} \text{ d}^{-1}$. The similar conclusion was obtained in other eelgrass beds in Ushimado and Yanai Bay, both in Seto Inland Sea (Ishikawa et al. 1988, Kawabata et al. 1990). The minimum required light level ($3 \text{ E m}^{-2} \text{ d}^{-1}$) corresponds to 10–20% of surface irradiance level in Odawa Bay (Mukai et al. 1980, Kudo 1999), which agrees with the general prediction on seagrass depth limit (at the depth with 11% of surface irradiance level) by Duarte (1991).

To test the hypothesis that light availability limits the depth distribution of eelgrass, Iizumi (1996) examined seasonal and spatial variation in leaf growth and aboveground production of eelgrass growing at different depths (2–5 m) in Otsuchi Bay. As expected from seasonal variation in irradiance, leaf growth and production were maximum in June–July, and the lowest in winter. Among different depths, however, leaf growth and production did not show so large a difference as that of irradiance. Iizumi (1996) considered that the depth limit of eelgrass was not determined by average irradiance level, but by incidental events of extremely low irradiance occurring in winter, such as the occurrence of turbid water in relation to disturbance by storms.

The depth limit of seagrass beds is not always determined by light conditions. In Maizuru Bay, the Japan Sea, the eelgrass bed is confined to sand bottoms no deeper than 2 m (Douke 2000a, b). Douke et al. (2000b) found that massive amounts of drifting algae accumulated in the deeper edge of the eelgrass bed. It is likely that competition for light with drifting algae determines the depth limit for this population. For eelgrass, competition for light with other deep-living *Zostera* species (*Z. asiatica*, *Z. caespitosa* and *Z. caulescens*) may be responsible for setting its depth limit in multispecific beds, although no data are available hitherto that support or reject this hypothesis.

Temperature can also affect distribution of seagrass by changing productivity, survivorship, seed production rates and seed germination rates of eelgrass (Marsh et al. 1986, Bulthuis 1987, Short and Neckless 1999). Kawasaki et al. (1986a, b, 1990) demonstrated by a series of laboratory experiments that survivorship of eelgrass is highly dependent on temperature. For seedlings, survivorship did not differ largely at temperatures between 5 to 25°C, but it decreased rapidly with higher temperatures, and all the seedlings died out at 30°C (Kawasaki et al. 1986a). The high temperature (30°C) also decreased survivorship of established populations (average survival period of 4 weeks at 30°C; Kawasaki et al. 1986b). Furthermore, seed germination and formation of flowering shoots were suppressed in temperatures 3–6°C higher than the natural condition (Kawasaki 1987). Based on these results, it is predicted that the eelgrass bed in Odawa Bay would decrease if water temperature becomes higher than the present (Kawasaki 1987).

Water and sediment movements are other major factors affecting the distribution of eelgrass (Fonseca et al. 1983, Fonseca and Bell 1998). A transplantation experiment revealed that shoot number of transplanted eelgrass rapidly decreased at the site where the bottom level fluctuated more than 10 cm over a short period, whereas they could successfully establish where the bottom was more stable (Kawasaki et al. 1988a). Douke et al. (2000b) considered that the upper limit of eelgrass distribution in Maizuru Bay is determined by the sediment movement, because no seedling recruitment was observed at the shallower limit of the eelgrass bed where sediment movement rate was high. In contrast, many seedlings were observed in the middle and deeper parts of the bed where sediment was more stable. Effects of sand movement on eelgrass bed developments were further investigated using simulation models. Maruyama et al. (1987) and Nakase (2000) analyzed the relationship between seagrass distribution and sediment stability using a parameter Shields number (Ψ) that quantitatively expresses degree of sediment movements. The shallower limit of eelgrass distribution in Odawa Bay is restricted by the sediment movement rate of $\Psi < 0.08$ in normal sea condition (Maruyama et al. 1987), whereas in Takeoka, Tokyo Bay, eelgrass was found in area of $0.2 \leq \Psi \leq 0.5$ under stormy conditions (Nakase 2000). At Naruto, an eastern entrance of Seto Inland Sea, an extensive eelgrass bed was found inside the breakwater of the fishery port (Dan et al. 1998). It was considered that disturbance of sand bottom by strong waves in winter limits distribution of the eelgrass bed (Dan et al. 1998).

BIOMASS AND SHOOT DENSITY

Quantitative studies on biomass and shoot density have been conducted in several eelgrass beds in Japan, ranging from northeastern Hokkaido to southwestern Kyushu (Table 3). The direct comparisons of these studies, however, should be made with caution because each study differs in research intensity, duration and methodology. For example, some studies estimated only aboveground biomass of seagrasses, whereas others reported total biomass without giving information on relative proportion of above- and below-ground biomass.

For eelgrass, biomass and shoot density showed large variation among and within populations (Table 3). Within a population, biomass and shoot density sometimes varied more than 2-fold among stations at different depths (Table 3). Biomass tended to be greater in shallower parts of the bed, but no consistent tendency is observed for the relationship between shoot density and depth. Among populations, aboveground biomass as high as 500 g dry weight m^{-2} was recorded in some areas such as Notsuke Bay, Otsuchi Bay, Maizuru Bay and Ushimado, whereas maximum biomass was less than 200 dry weight m^{-2} for populations in Odawa Bay, Iida Bay and Yanai Bay (Table 3). No distinct relationship was observed between the maximum biomass and latitude or geographical location of the eelgrass populations.

For seasonal variation, highest values for biomass and shoot density were generally observed in spring and summer, and the lowest between autumn and winter (Table 3), as in eelgrass populations in other regions (Sand-Jensen 1975, Jacobs 1979, Wium-Andersen and Borum 1984, Olsen and Sand-Jensen 1994). Peak biomass tended to be found earlier in the southern eelgrass populations, whereas it is not clear whether the seasons for the maximum and minimum shoot density vary with latitude and water temperature (Table 3). Patterns of seasonal variation in shoot density also varied greatly within each site. In Odawa Bay, for example, Kawasaki et al. (1988a) reported that seasons of maximum shoot density varied between January and July among different parts of the eelgrass bed.

Quantitative information on spatial and seasonal variation in biomass and shoot density is sparse for other species of *Zostera*. Biomass of *Z. japonica* at Mikawa Bay varied greatly with seasons, with maximum biomass of 270 g dry weight m^{-2} recorded in July and a minimum of 30 g during December to January (Arasaki 1950a). For *Z. caespitosa*, maximum aboveground biomass of 60 g dry weight m^{-2} was recorded at the depth of 8 m (in its depth range of 4–12 m) in Iida Bay, Ishikawa Prefecture, which was about the same level as that of *Z. marina* inhabiting the same depth (Taniguchi and Yamada 1979). At Uchiura, another site of Ishikawa Prefecture, the shoot density of *Z. caespitosa* was maximum at the depth of 10 m (440 shoots m^{-2}) within its depth range of 3–20 m (Tajima and Sano 1978). For *Z. asiatica* at Akkeshi Bay, Hokkaido, the biomass (427 g dry weight m^{-2}) was twice that of *Z. marina* (221 g dry weight m^{-2}), whereas the shoot density (134 shoots m^{-2}) was nearly half that of *Z. marina* (229 shoots m^{-2}) when comparing monospecific stands at the same depth, reflecting larger shoot size of the former (Watanabe et al. 2000).

Table 3. *Zostera marina*. Regional comparisons of biomass, shoot density and their seasonal variation. Numbers in locality correspond to the positions in the map (Fig. 1).

Station	Depth (m)	Aboveground biomass (g dry wt. m ⁻²)		Shoot density (m ⁻²)		Remarks			
		maximum	(month)	minimum	(month)	maximum	(month)	minimum	(month)
3: Notoro-ko (Hokkaido Abashiri Fisheries Experimental Station 1997)								No data during Jan.–Mar.	
A	1	500	Jul.	150	Dec.	600	Jul. & Nov.	300	Aug.
4: Notsuke Bay (Mizushima 1985)								No data during Jan.–Apr.	
1	1–2	400	Aug.	150	Dec. & May	276	Jul.	150	Oct.
2	1–2	550	Jul.	150	Dec.	330	May	180	Oct.
3	1–2	250	Jul.	80	May	248	Jul.	150	Oct.
4	1–2	380	Jul.	180	May	380	May	170	Dec.
11: Otsuchi Bay (Iizumi et al. 1996)									
SE	2	450	Aug.	80	Jan.	300	Mar.	90	Sep.
MD	3	620	Jun.	50	Jan.	300	Mar.	140	Jan.
DE	4	300	Aug.	20	Jan.	220	Jun.	40	Jan.
DP	5	370	Jun.	30	Jan.	200	Mar.–Jun.	50	Jan.
12: Odawa Bay (Aioi 1980)									
1	5	91	May	4	Dec.	427	Mar.	213	Dec.
2	3	174	May	13	Dec.	379	Apr.	85	Dec.
3	3	193	May	11	Dec.	501	Apr.	149	Dec.
7	2	138	Apr.	21	Dec.	171	Mar.	59	Oct.
12: Odawa Bay (Kawasaki et al. 1988a)									
A1	1.3	—	—	—	—	190	Mar.	50	Sep.
A2	2.1	—	—	—	—	70	Apr.	30	Nov.
A3	3.0	—	—	—	—	50	Jul.	20	Nov.
B1	1.0	—	—	—	—	540	Jan.	200	Jul.
B2	2.1	—	—	—	—	540	Feb.	150	Sep.
B3	3.6	—	—	—	—	270	Jan.	50	Jul.
13: Moroiso Bay (Horinouchi et al. 1999)								No data during Sep.–Nov.	
	1.5–2.0	—	—	—	—	200	Apr.	120	Jul.–Aug. and Dec.–Jan.
16: Hamana-ko (Imao and Fushimi 1985)									
A	3.5	100	May	0	Jul.–Sep.	—	—	—	Annual population
B	3.0	160	Apr.	0	Jul.–Nov.	—	—	—	Annual population
C	3.0	180	May	0	Jun.–Oct.	—	—	—	Annual population
D	1.5	260	Apr.	10	Oct.	—	—	—	Perennial population
17: Mikawa Bay (Arasaki 1950a, b)									
	0.3–1.8	260	May	100	Oct.	—	—	—	Aboveground biomass estimated from total biomass and weight ratio of aboveground and belowground parts
21: Iida Bay (Taniguchi and Yamada 1979)									
	4–6	170	Jul.	20–30	Nov.	347	Jun.	100	Nov.
24: Maizuru Bay (Douke et al. 2000a, b)									
	1.5	678	Jun.	70	Sep.	462	Jun.	140	Sep.
26: Tsuda Bay (Yamaga et al. 1996)									
Shallow	2.0	—	—	—	—	85	Jun.–Jul.	10	Dec.
Deep	3.5	—	—	—	—	115	Jul.	30	Nov.
27: Ushimado (Azuma and Harada 1969)									
Z1	<2	500	Jun.	20	Nov.	—	—	—	—
Z2	<2	500	Jun.	0	Jan.	—	—	—	—
Z5	<2	500	Jun.	0	Dec.–Jan.	—	—	—	—
Z6	<2	330	Jun.	0	Nov.–Jan.	—	—	—	—
29: Hosonosu (Tsukidate and Takamori 1978)									
	Intertidal	200	Jun.	64	Dec.	240	Mar.	120	Oct.
30: Yanai Bay (Kawabata et al. 1990)									
	0–1	140	Aug.	50	Nov. & Feb.	—	—	—	—
32: Tomioka Bay (Kikuchi 1973)									
Inner part	0–5	330	May	70	Dec.	—	—	—	—
Outer part	0–5	420	Jun.	40	Dec.–Jan.	—	—	—	—

At a larger spatial scale, some studies estimated overall distribution and areal biomass of entire seagrass beds using eco-sounder and Global Positioning System. Komatsu and Tatsukawa (1998) estimated that the total area of eelgrass beds in Ajino Bay, Seto Inland Sea was 6.5 km². They also estimated that the total aboveground biomass of the eelgrass bed was 594.1 tons dry weight based on a relationship between the density of an eelgrass echo trace and aboveground biomass obtained by quadrat samplings (Komatsu and Tatsukawa 1998). Tatsukawa et al. (1996) applied the same method to estimate a spatial distribution of a multi-specific bed in Funakoshi Bay, northeastern Honshu consisting of *Z. marina* and *Z. caulescens*. The total area of the seagrass bed was 0.5 km², and it covered a depth range of 2–17 m. From an echo trace, they also estimated changes in the canopy height of the flowering shoots of *Z. caulescens* with the depth gradient (Tatsukawa et al. 1996).

POPULATION STRUCTURE AND SHOOT DYNAMICS

Studies on population structures and dynamics of seagrasses have made a remarkable progress in recent years by the development of demographic analyses using age markers in rhizomes, such as the lepidochronological analysis for *Posidonia oceanica* (Pergent 1990) and the reconstruction techniques for long-lived tropical seagrass species (Duarte et al. 1994). For *Zostera* spp., these techniques are not fully applicable because of the short life span of rhizomes, but can be used for estimating seasonal variation in recruitment, growth, production and survivorship (Olsen and Sand-Jensen 1994). In Japan, however, very few studies have quantitatively analyzed shoot dynamics of seagrasses using this type of analysis.

For eelgrass, Taniguchi and Yamada (1979) analyzed seasonal changes in shoot size structure for a population in Iida Bay, the Japan Sea, and found that shoot recruitment by rhizome branching and seed germination mostly occurs in January and February. Massive recruitment of new shoots by rhizome branching was observed during October to February in Odawa Bay, the Pacific coast of central Honshu (Terawaki et al. 1984). For a northern population in Notsuke Bay, Mizushima (1985) showed that the shoot recruitment of eelgrass occurs during October to April. Thus, shoot recruitment mostly occurs in winter in Japanese populations of eelgrass.

Nakaoka et al. (2000) examined the shoot age structure of *Z. caulescens* in Funakoshi Bay. The recruitment of both the flowering shoots (transformation from vegetative shoots by developing an upright stem) and the vegetative shoots (side-branching of the rhizomes) mostly occurred from February to April, and the mean age of the flowering and vegetative shoots increased from spring to summer as they grew. Age of the longest flowering shoot in the population (6.8 m, collected in September; Aioi et al. 1998) was estimated to be approximately 400 d, confirming the previous account by Aioi et al. (1998) that the high canopy of *Z. caulescens* is attained by overwintering flowering shoots (Nakaoka et al. 2000).

A unique growth form of *Z. caespitosa*, i.e., upright growth of rhizome and the resultant shrub-like structure, makes it possible to distinguish each individual (genet)

from others (Omori 1996). In Yamada Bay, Omori (1996) found that the rhizome of *Z. caespitosa* has a specific internode pattern in which 6–7 short internodes (each 1 mm in length) and 1–2 long internodes (each 10–20 mm) are arranged alternately. The change in internode length is probably caused by seasonal changes in environmental factors such as temperature (Omori and Aioi 1998). The number of internodes in this unit (a combination of several short and a few long internodes) agrees with that formed annually (Omori and Aioi 1998). Thus, this internode pattern of *Z. caespitosa* can be used as an age marker as in other seagrass species such as *Cymodocea nodosa* (Duarte and Sand-Jensen 1990) and *Z. marina* (Olsen and Sand-Jensen 1994). Using this method, Omori and Aioi (1998) estimated that the maximum age of the largest individual is 7–8 years.

For the dynamics of clonal plant populations, the relative importance of clonal propagation (by rhizome branching) and sexual reproduction (by seed production and subsequent seedling establishment) varies with different environmental conditions (Cook 1985, Watson 1990). In an annual population of eelgrass in Ushimado, Fukuda and Tsuchiya (1987) found positive correlation between shoot density and seed density, suggesting that the distribution of seeds is important for the maintenance of the eelgrass bed. Seed production and subsequent seed germination are also important in the dynamics of perennial seagrass populations subject to frequent disturbance such as storms and heavy grazing by herbivores (Preen et al. 1995, Peterken and Conacher 1997). Aioi and Komatsu (1996) observed for eelgrass in Otsuchi Bay that the number of seedlings was extremely higher ($\geq 300 \text{ m}^{-2}$) in a year following heavy winter storms than in normal years ($< 20 \text{ m}^{-2}$). Thus, seedlings play an important role in recovery processes of eelgrass after disturbance of this population.

GROWTH AND PRODUCTIVITY

Growth and productivity of *Zostera* spp. have been measured and reported from various parts of the world (see reviews in Duarte 1989, Cebrián et al. 1997, Duarte and Chiscano 1999). As a cosmopolitan species, eelgrass *Z. marina* was most studied, followed by *Z. capricorni* in Australia and *Z. noltii* in Europe (Duarte and Chiscano 1999).

Mukai et al. (1979) and Aioi et al. (1981) measured growth and productivity of eelgrass in Nabeta Bay, the Pacific coast of central Honshu, by a culture experiment in an outdoor aquarium. Growth and production varied greatly between seasons. Between April and June, the mean life span of leaves was 43.6 d (plastochrone interval of 8 d), and net production of aboveground and belowground parts was 5.2 and 2.0 g dry weight $\text{m}^{-2} \text{d}^{-1}$, respectively (Mukai et al. 1979). In contrast, the plastochrone interval was 13 d, and net production was 0.8 and 0.7 g dry weight $\text{m}^{-2} \text{d}^{-1}$ for aboveground and belowground parts, respectively, between December and February (Aioi et al. 1981). Aioi (1981) used these data for estimating primary productivity of eelgrass in Odawa Bay, and yielded annual estimates of primary production of 470–1020 g dry weight $\text{m}^{-2} \text{yr}^{-1}$ (data for four stations with different depth). Estimation of primary production by *in situ* leaf and rhizome markings was carried out for an eelgrass population in Yanai Bay, Seto

Inland Sea (Kawabata et al. 1990, 1993a, b). They estimated aboveground and belowground production of 2.3 and 0.4 g dry weight $m^{-2}d^{-1}$, respectively, in the intertidal zone, and 7.4 and 2.7 g dry weight $m^{-2}d^{-1}$ for the subtidal zone for the period from April to July. Plastochrone interval was 10.8–13.9 d, and the rhizome elongation rate was 19 $mm d^{-1}$ in mid May and 3 $mm d^{-1}$ in mid July. Iizumi (1996) measured aboveground production of eelgrass in Otsuchi Bay, northeastern Honshu by leaf marking, and found that it varied between $<1 g dry weight m^{-2}d^{-1}$ in January and 5–13 g dry weight $m^{-2}d^{-1}$ in June, giving annual estimates of 1100–2400 g dry weight $m^{-2}yr^{-1}$.

For eelgrass in Notsuke Bay, Hokkaido, Mizushima (1985) estimated that aboveground production of eelgrass was 34 g dry weight m^{-2} for new recruits and 233 g dry weight m^{-2} for older shoots for the period of May to December, giving daily estimates of 1.3 g dry weight $m^{-2}d^{-1}$. For another population in Notoro-ko, aboveground production was 235 g dry weight m^{-2} for new recruits and 371 g dry weight m^{-2} for older shoots for the period of April to December, giving daily estimates of 2.5 g dry weight $m^{-2}d^{-1}$ (Hokkaido Abashiri Fisheries Experimental Station 1997). However, underestimation is likely in these two studies because their estimates are based on seasonal changes in leaf number per area and weight per leaf, instead of direct measurements of leaf growth and leaf turnover rates. Using leaf marking methods, Watanabe et al. (2000) estimated aboveground net production of 3.4 g dry weight $m^{-2}d^{-1}$ and plastochrone intervals of 18 d for eelgrass in Akkeshi Bay during the period between July and August.

These estimates of production of eelgrass in Japanese waters are within a range of those reported from other parts of the world (annual aboveground production of 100–2600 g dry weight $m^{-2}yr^{-1}$, and daily aboveground production of 0–13 g dry weight $m^{-2}d^{-1}$; Cebrián et al. 1997, Duarte and Chiscano 1999). Direct comparisons among studies are, however, difficult due to variation in methods and research periods.

For other species of *Zostera*, only a few fragmental data are available that quantitatively measured growth and productivity. For *Z. asiatica* in Akkeshi Bay, Watanabe et al. (2000) estimated that plastochrone intervals was 25 and 34 d, and aboveground net production was 5.2 and 3.2 g dry weight $m^{-2}d^{-1}$ for shallow site (1.5 m) and deep site (3 m) of the seagrass bed, respectively, in summer. The longer plastochrone interval of *Z. asiatica* than *Z. marina* is compensated by higher leaf growth rates, resulting in a similar level of production between the two species in the same bed.

Nakaoka et al. (2000) measured growth rates of *Z. caulescens* by leaf marking, and estimated that the plastochrone interval of vegetative shoots was 9.7–14.0 d for the flowering shoots and 10.5–21.0 d for the vegetative shoots. It was estimated that the tall flowering shoots grow at the rate of 1.5 cm/d, reaching average canopy height of 5 m in 280 days and the maximum height of 7 m in approximately 400 days. An ongoing study on primary productivity suggests that annual production of *Z. caulescens* growing at the depth of 4–5 m is comparable to that of *Z. marina* inhabiting shallower waters (Nakaoka et al., unpublished data).

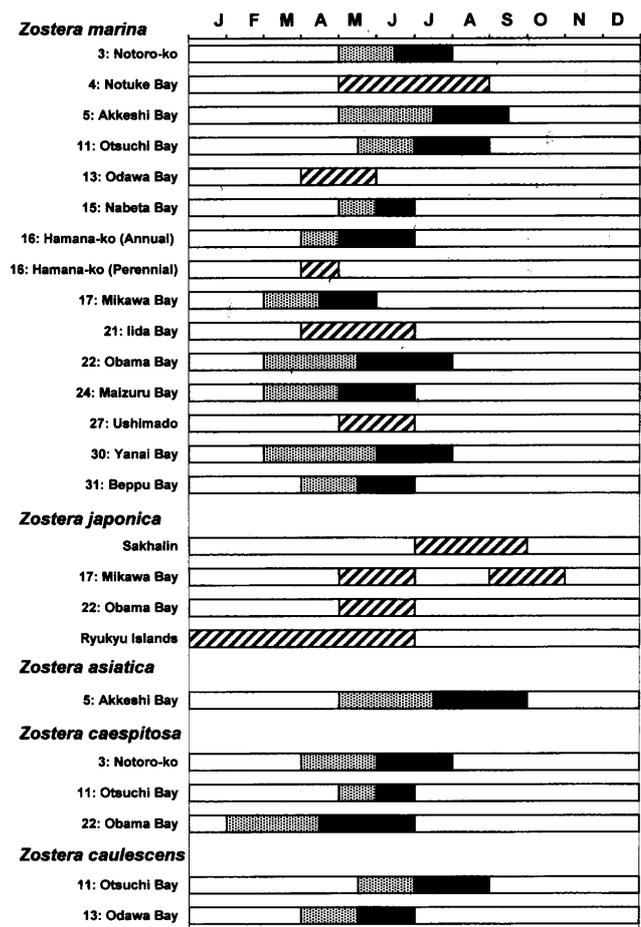


Fig. 3. *Zostera* spp. Phenology of seagrasses in major habitats around Japanese coast. Shaded columns show the flowering season and filled columns the fruiting seasons. The striped columns indicate flowering and fruiting seasons that were not distinguished in the literature. The numerals in front of the locality name denote the position in the map of Fig. 1. See Table 2 for the references except for data on *Z. japonica* in Sakhalin (Den Hartog 1970) and Ryukyu Islands (Toma 1999).

For the purpose of understanding optimal conditions for transplantation and restoration of eelgrass beds, Kawasaki and his colleagues conducted a series of intensive laboratory experiments and transplantation experiments and measured growth rates of eelgrass under various environmental conditions (Kawasaki et al. 1988a, b, 1990, and references therein). The maximum growth rate of transplanted eelgrass was obtained under the following conditions; (1) water temperature of 15–20°C, (2) salinity between 17–34 psu, (3) average irradiance level of $\geq 3 E m^{-2}d^{-1}$, (4) water current of $\leq 15 cm/sec$, and (5) ammonium addition of 5,000 μM to the sediment.

PHENOLOGY

Information on flowering and fruiting seasons of eelgrass and other *Zostera* species is available from some localities in Japan (Fig. 3). In *Z. marina*, seasons for flowering and fruiting vary 2–3 months among different regions. For the northern populations in Hokkaido and northeastern Honshu, flowering starts in May and seeds are produced through summer. In the southern populations, flowering generally begins earlier (March to April), and they fruit be-

tween April and July. Earlier reproduction in lower latitudes is also observed along the Pacific and the Atlantic coasts of North America, and thus seems a general phenomenon for eelgrass (Phillips et al. 1983b). Germination of seeds was generally observed during winter for populations in warm areas, such as Mikawa Bay (Arasaki 1950b), the Seto Inland Sea (Hatate et al. 1974, Fukuda and Yasuie 1980, Yasuie and Fukuda 1980, Kawabata et al. 1990), and along the Japan Sea coast (Miki 1933, Taniguchi and Yamada 1979, Douke et al. 2000a, b).

The greater variation in flowering season was observed for *Z. japonica* that has a wider geographical distribution than *Z. marina* (Fig. 3). In subtropical areas such as Ryukyu Islands, the flowering shoots were observed between January and July (Toma 1999), whereas they were found between July and September in a northern population at Sakhalin (Den Hartog 1970). Interestingly, a population in Mikawa Bay has biannual flowering seasons (April-June and September-October; Arasaki 1950b). Heat stress possibly inhibits their reproductive activity in summer months (Arasaki 1950b).

For other *Zostera* species, flowering and fruiting seasons have been reported only from limited localities. *Zostera asiatica* in Akkeshi Bay starts flowering in May and produces mature seeds from August to early September (Watanabe and Nakaoka, unpublished data). Thus, its phenology is almost synchronous with that of the co-occurring *Z. marina* (Fig. 3). Flowering and fruiting seasons of *Z. caespitosa* vary greatly among three localities in different regions (Hokkaido, northeastern Honshu and the Japan Sea coast, Fig. 3). It is notable that at each site, *Z. caespitosa* flowers and fruits about one month earlier than the sympatric *Z. marina* (Fig. 3).

For *Z. caulescens*, seasonal variation in their flowering and fruiting, as well as the dynamics of its characteristic flowering shoots were compared between populations in Otsuchi Bay and Odawa Bay (Omori 1994, 1995, Omori and Aioi 2000, Nakaoka et al. 2000). At Odawa Bay, the differentiation of lateral bud to inflorescence begins in December and stems of flowering shoots appear in February. It flowers in April to May and fruits in May to June. After fruiting, all the flowering shoots immediately fall down between July and early September (Omori 1994, 1995). In Otsuchi Bay, the formation of flowering shoots occurs at about the same season as in Odawa Bay (January to March), and they have flowers and fruit about 1–2 months later (Fig. 3). After fruiting in August, most of the flowering shoots continue growing until late autumn to early winter, and then they fall down (Omori 1995, Nakaoka et al. 2000). The difference in life span of the flowering shoots between the two populations is possibly related to the differences in temperature (Omori and Aioi 2000).

REPRODUCTIVE AND LIFE HISTORY TRAITS

Relative proportions of flowering shoots, and the average number of the spathes per flowering shoot in the peak reproductive season vary greatly among and within populations of eelgrass (Table 4). On an average, flowering shoots are less than 15% of the shoot density, except for the populations at Hamana-ko and Maizuru Bay. In an annual population in Hamana-ko, vegetative shoots were very rarely ob-

served in the flowering season (Imao and Fushimi 1985). For other *Zostera* species, the data are available for three populations of *Z. caespitosa* (Table 4). Comparisons with sympatric *Z. marina* in Notoro-ko revealed that the relative abundance of flowering shoots was higher for *Z. caespitosa*, whereas the number of spathes per shoot was higher for *Z. marina* (Hokkaido Abashiri Fisheries Experimental Station 1997).

The number of seeds per spathe also varies among populations of seagrasses. For eelgrass, Omori (1992) found that average number of seeds per spathe varied more than 2-fold among eight populations in northern Japan. In *Z. asiatica*, the number of seeds in Akkeshi Bay (12–17 seeds per spathe) was greater than that of four populations in Korea (8–12 seeds per spathe; Lee et al. 1999). The factors causing such variation remain unknown. In contrast, no large variation was found in the average number of seeds per spathe for two populations of *Z. caespitosa* (7.3 and 8.5) and among three populations of *Z. caulescens* (between 12 and 18) (Table 4).

It has been argued that environmental and genetic variations are both important in determining annual versus perennial life cycles of eelgrass (Keddy and Patriquin 1978, Gagnon et al. 1980, Phillips et al. 1983a, van Lent and Verschure 1995). In Japanese eelgrass, Imao and Fushimi (1985) found both annual and perennial forms of eelgrass in Hamana-ko, and considered that low salinity level and higher maximum temperature are key factors for the occurrence of the annual form in the inner part of the lagoon. Kikuchi et al. (1987) cultured annual and perennial populations of eelgrasses from their seeds under the same conditions in a laboratory aquarium and found that all the seeds from annual population produced flowers and seeds within a year, whereas those from perennial population did not. They also showed that the second generation of the annual population kept in the aquarium also showed high flowering and fruiting rates under conditions similar to the perennial habitat. Based on these data, Kikuchi et al. (1987) considered that the formation of flowering shoots in the annual population is determined genetically, but not by short-term phenotypic responses to environmental conditions.

PERSPECTIVE FOR FUTURE RESEARCH

In this review, we examined intraspecific and interspecific variation in quantitative parameters describing the ecology of *Zostera* spp. in Japan. Large variations were found in these parameters among populations in different localities, and among different species in the same seagrass bed. We found some general patterns by comparisons of studies conducted at different localities around Japan, such as earlier start of flowering and fruiting in southern populations, and deeper depth distribution of endemic *Zostera* species than *Z. marina*. For quantitative parameters such as biomass, growth and productivity, however, it is difficult to find general large-scale patterns such as latitudinal gradient because many other factors, e.g., local variation in depth and other environmental factors, and variation in research intensity, duration and methodology among studies, are confounded with geographical variation. For species other than eelgrass, only a few studies have quantitatively examined ecological parameters in natural vegetation. For a better understanding

Table 4. *Zostera* spp. Comparisons of reproductive traits among populations and species. Locality of each study site is shown in Fig. 1 by numbers. See Table 1 for the reference number.

Locality	Percentage of flowering shoots (%)	Number of spathes per shoot	Number of seeds per spathe	Reference number
<i>Zostera marina</i>				
1: Soya	—	—	6.3	1)
2: Beniya	—	—	13.3	1)
3: Notoro-ko	11.2–14.5	9–11	—	2)
4: Notsuke Bay	0–28 (average 10)	—	—	3)
5: Akkeshi Bay	—	—	13.7	1)
6: Asamushi	—	—	12.6	1)
7: Moura	—	—	10.8	1)
11: Otsuchi Bay	—	—	12.2	1)
13: Odawa Bay	2–14	20	11.3	1), 18), 21–22)
16: Hamana-ko				
Annual population	ca. 100	—	—	29)
Perennial population	20	—	—	29)
17: Mikawa Bay	—	7–16	3–11	30–31)
23: Takahama	—	—	12.1	1)
24: Maizuru Bay	2–31	15.2	8.6	35–36)
30: Yanai Bay	—	15	10–13	45)
<i>Zostera japonica</i>				
13: Odawa Bay	—	5–10	—	22)
17: Mikawa Bay	—	3–5	1–5	30–31)
<i>Zostera asiatica</i>				
5: Akkeshi Bay	—	—	12–17	1), 4)
<i>Zostera caespitosa</i>				
3: Notoro-ko	14.2–27.4	4–6	—	2)
6: Asamushi	—	—	7.3	1)
8: Noheji	—	—	8.5	1)
9: Yamada Bay	13–29	7–11	—	7–8)
11: Otsuchi Bay	13–44	5–7	—	8)
<i>Zostera caulescens</i>				
7: Moura	—	—	14	1)
11: Otsuchi Bay	—	—	11.8	1)
13: Odawa Bay	—	10–20	14–18	1), 22–24)

on the ecology of *Zostera* species and for its effective application to conservation, here we address some remarks for future research on seagrasses in Japan.

First of all, we need to gain more precise information on distribution of each species of seagrasses all around Japanese coast. Most of the studies on seagrass ecology have been centered on some specific areas, such as northeastern Honshu, central parts of Honshu and Seto Inland Sea, whereas very few data are available from areas such as western Hokkaido, the Japan Sea coast of north Honshu, and around Kyushu area (Fig. 1). It would be interesting to compare data from western Hokkaido to eastern Hokkaido, and those from the western coast of north Honshu to northeast Honshu, because water temperature differs greatly among these pairs of sites that are located at the same latitude. It would then give us a good opportunity to examine regional variations in seagrass ecology by separating effects of latitude (i.e., photoperiod) and temperature. For the Kyushu area, ecological information of eelgrass is urgently needed, because it is the area where eelgrass beds are decreasing most rapidly (Environmental Agency of Japan 1994). For other *Zostera* species, it is necessary to know the exact distribution of vegetation and its areal extent. Especially for *Z. asiatica*, in addition to a few live popula-

tions that are now known to exist in eastern Hokkaido and northeast Honshu, some stranded plants were collected at other beaches in southern Hokkaido and Toyama Bay, which indicates existence of live populations nearby (Omori 1992, Higashide et al. 1999). With quantitative information on distribution, it is possible to evaluate current risk of extinction for threatened species such as *Z. asiatica* and *Z. caulescens* (Environmental Agency of Japan 2000).

Secondly, we should take more comparative and experimental approaches to elucidate factors causing interspecific and intraspecific variation in ecology of seagrasses. For the depth distribution in multispecific meadows, for example, we now know that *Z. asiatica*, *Z. caespitosa* and *Z. caulescens* tend to occur in deeper habitats than *Z. marina* (Fig. 2). However, we do not yet know about the critical factors responsible for their different depth distribution. Possible factors contain not only the light requirement, but also the nutrient requirement, tolerance to stress and disturbance, and interspecific interactions among seagrasses such as competition and facilitation. Factorial experiments manipulating orthogonally two or more factors would be effective to detect interacting effects of these factors on seagrass distribution and production. Such kinds of analyses will help us to understand the mechanisms of their coexistence

in a single seagrass bed.

Thirdly, we should promote systematic approaches integrating field studies of population and community processes of seagrasses with other aspects of seagrass biology, such as physiology, genetics and mathematical biology. In physiological aspects of seagrasses, *in situ* measurement of photosynthetic activity is now possible for submerged populations using an underwater pulse-amplitude modulated chlorophyll fluorometer (Diving-PAM; Beer et al. 1998, Ralph et al. 1998). The use of such new technology in combination with field measurements of productivity would be effective for elucidating different light responses of *Zostera* spp. along the depth gradient. Studies on genetic variation of seagrasses using molecular markers such as microsatellite DNA have been given increasing attention (Reusch 2001). Information on genetic diversity is important especially for endemic and threatened species such as *Z. asiatica* and *Z. caulescens*, because loss of genetic diversity is likely in small and isolated populations and it may accelerate their decline by genetic deterioration such as inbreeding depression. Mathematical modeling and numerical simulations using quantitative data on growth, survivorship, reproduction, and their spatial and temporal variation would be useful to predict changes in distribution, biomass and species composition of seagrass beds with environmental modification. Using these data, it is also possible to undertake population viability analyses to estimate extinction probability for threatened seagrass populations.

Finally, we should organize large-scale, long-term research programs to monitor changes in distribution, biomass and productivity of seagrass beds according to local and global environmental changes. In the cases of multispecific seagrass meadows, changes in environmental conditions caused by humans may influence not only overall distribution and total abundance, but also species composition of seagrass beds. In Odawa Bay, for example, reduced light conditions due to eutrophication during the past 20 years resulted in the decline of eelgrass in shallow habitats, but it might have favored deeper-living *Z. caulescens* to expand its population to the shallower depth (Kudo 1999). However, due to lack of species-by-species data in the past literature, we were unable to test that *Z. caulescens* truly increased with light reduction. Long-term field surveys of seagrass beds using unified approaches is thus necessary to monitor future changes in seagrasses in relation to local changes in environmental conditions, and to larger-scale environmental changes such as global warming that are likely to alter seagrass distribution and productivity worldwide (Short and Neckless 1999).

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日本沿岸におけるアマモ属（アマモ科）海草類の生態学（総説）

仲岡 雅裕・相生 啓子

東京大学海洋研究所
〒164-8639 東京都中野区南台1-15-1

日本沿岸の海草藻場は、地域固有種を含む複数のアマモ科の種が出現することが特徴的である。本総説では日本におけるアマモ属 (*Zostera*) の生態学的研究について、これまでの成果を概説すると共に、今後の研究の方向性について展望する。日本に出現するアマモ属5種のうち、アマモ (*Z. marina*) とコアマモ (*Z. japonica*) は北海道から九州にかけて広く分布するが、他の3種（オオアマモ *Z. asiatica*, スゲアマモ *Z. caespitosa*, タチアマモ *Z. caulescens*) の分布は本州中部以北に限られる。複数の種が共存する藻場では、コアマモが潮間帯に、アマモが潮下帯浅部に、他3種が最も深いところに生息する。現存量・株密度・成長量・生産量には、水深間・地域間および種間に大きな変異が認められた。しかし、これら多種の変異が複合的に作用しているため、緯度勾配に伴った一般的な傾向は不明であった。開花・結実期についても大きな地域間および種間変異が認められた。同種内では、緯度が低い地域ほど開花・結実期が早いこと、また同所的に生息するアマモとスゲアマモでは、スゲアマモのほうが早く開花・結実することが示された。

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