

Distribution, productivity, life history and biodiversity of seagrass community along Sanriku Coast: A review

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Received: 21 January 2003

Accepted: 1 March 2003

The seagrass flora in Japan is characterized by the occurrence of several species of Zosteraceae that are considered to be endemic to the northwestern Pacific. In seagrass beds along Sanriku Coast, northeastern Honshu Island of Japan, the endemic *Zostera* spp. generally occur at subtidal soft bottom, usually forming multispecific seagrass beds with the cosmopolitan eelgrass *Z. marina*. This paper reviews some of the recent studies on ecology of the seagrass community conducted at Otsuchi Bay, Funakoshi Bay and Yamada Bay along Sanriku Coast of Iwate Prefecture. We specially focus on following subjects; (1) spatial distribution of *Z. caespitosa* in Yamada Bay surveyed using eco-sounding techniques, (2) comparative studies on morphological and life history traits of *Zostera* spp., (3) quantitative estimation on shoot dynamics, growth and primary production of *Z. caulescens*, (4) ecology of epifaunal community on the aboveground parts of seagrasses, and (5) population genetic structure and gene flow among populations of *Z. caespitosa* analyzed using molecular data. The results of these studies showed that the seagrass community along Sanriku Coast is one of the most productive parts of the coastal ecosystem, and that various environmental and biological factors are involved in a complex manner to produce observed patterns of population structure and dynamics of the seagrass community.

Key words: biodiversity, epifauna, population structure, Sanriku Coast, *Zostera* seagrass

INTRODUCTION

The seagrass flora in Japan is characterized by the occurrence of 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*. Among them, *Zostera* spp. generally occur at subtidal soft bottom in northern Japan, usually forming multispecific seagrass beds with the cosmopolitan eelgrass *Z. marina*. Some of these species are now known only in a few localities around Japan and considered to be in the risk of extinction (Nakaoka and Aioi 2001). Basic information on distribution and quantitative aspect of their ecology and population genetic structure is urgently required for promoting effective and efficient conservation of these seagrasses.

Multispecific seagrass beds are among the most conspicuous components of coastal ecosystems along Sanriku Coast, northeastern Honshu Island of Japan. Three species of *Zostera* have been known to inhabit at subtidal seagrass beds at the inner parts of Otsuchi Bay, Funakoshi Bay and Yamada Bay that locate in the middle parts along Sanriku Coast of Iwate Prefecture (Fig. 1). *Zostera marina* occurs in all the three bays, *Z. caulescens* in Otsuchi Bay and Funakoshi Bay, and *Z. caespitosa* in Otsuchi Bay and Yamada Bay. In addition, *Z. asiatica* was recently discovered in Funakoshi Bay and reported as a first record in

Honshu Island (Aioi et al. 2000). Therefore, shallow subtidal bottoms along Sanriku Coast can be regarded as a 'hot spot' of seagrass floral diversity in the temperate Pacific region. Due to its ecological significance, the seagrass beds in the three bays were recently listed among the 500 most valuable wetlands in Japan.

To understand structures and dynamics of seagrass populations and communities along Sanriku Coast, intensive field surveys focusing on various aspects of seagrass ecology have been ongoing at the multispecific seagrass beds at Otsuchi Bay, Funakoshi Bay and Yamada Bay. In the present paper, we review results of these studies that specially focusing on the following subjects. (1) Estimation on spatial distribution and abundance of *Z. caespitosa* in a seagrass bed in Yamada Bay. (2) Comparative studies on morphological and life history traits of *Zostera* spp. (3) Quantitative studies on population structure, growth and productivity of *Z. caulescens*. (4) Ecology of epifaunal community on aboveground parts of seagrasses, with special reference to sessile epifauna. (5) Molecular analyses of population genetic structure and gene flow among populations of *Z. caespitosa*. Based on these studies, we discuss functional roles of the multispecific seagrass beds on the coastal ecosystems along Sanriku Coast.

DEPTH DISTRIBUTION AND ABUNDANCE OF *Zostera caespitosa* IN YAMADA BAY

Methods for monitoring and mapping subtidal seagrass

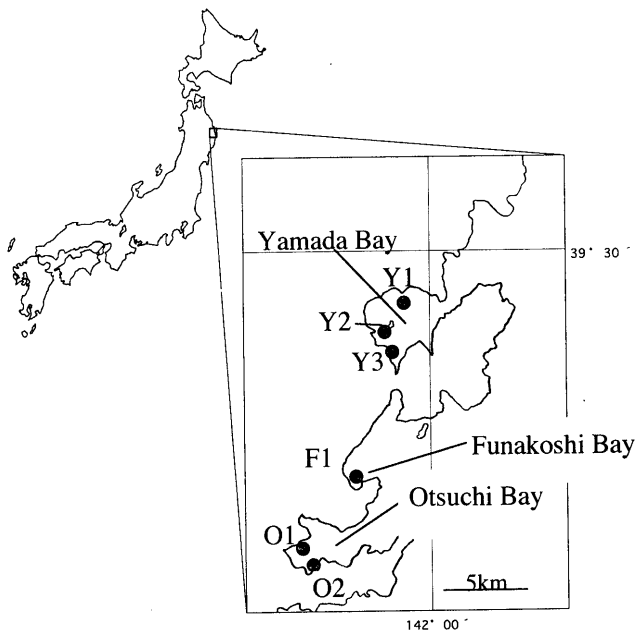


Fig. 1. A map showing study sites for seagrasses along Sanriku Coast (Otsuchi Bay, Funakoshi Bay and Yamada Bay). Closed circles show location of seagrass beds reviewed in the present paper.

beds over large spatial scales have advanced recently with the development of acoustic surveying devices (Komatsu et al., in press). See Tatsukawa et al. (1996), Sultana and Komatsu (2002) and Komatsu et al. (2003, this volume) for its application to *Z. caulescens* population in a seagrass bed of Funakoshi Bay. This section reviews the results of our survey conducted for a *Z. caespitosa* population in Yamada Bay to estimate spatial distribution, depth distribution and abundance.

The biology and ecology of *Z. caespitosa* remained largely unknown until recently due to its presence in the deep subtidal bottom, and possible decline of its distribution with environmental deterioration. Recently, this species was reported to occur in Yamada Bay and Otsuchi Bay along Sanriku Coast (Omori et al. 1996, Omori and Aioi 1998), although quantitative aspect of their distribution, such as depth distribution and biomass, was not examined previously.

A series of field surveys were carried out at a subtidal seagrass bed of Yamada Bay (Y2 in Fig. 1) where Omori et al. (1996) reported the existence of a large seagrass bed consisting mainly of *Z. caespitosa*. A preliminary survey was undertaken in June 1997 to examine the morphological feature of echograms taken for *Z. caespitosa*. Quantitative census of the seagrass beds using the acoustic sounding system was conducted in June 1998 and 1999 by setting a research plot of 160 m × 120 m area within the seagrass bed. Four parallel transect lines of each 160 m long was set in north-south direction at the interval of 40 m. The bottom topography and the seagrass vegetation were scanned along the lines using an acoustic echosounder (Kaijo Denki Co. Ltd., Model PS-11E, 200 kHz). To estimate abundance of *Z. caespitosa*, the area of echogram showing the seagrass vegetation was calculated for 20 m distance around each point set at the interval of 40 m along each transect line (a total of 20 points). The average of 5 individual traces of echogram

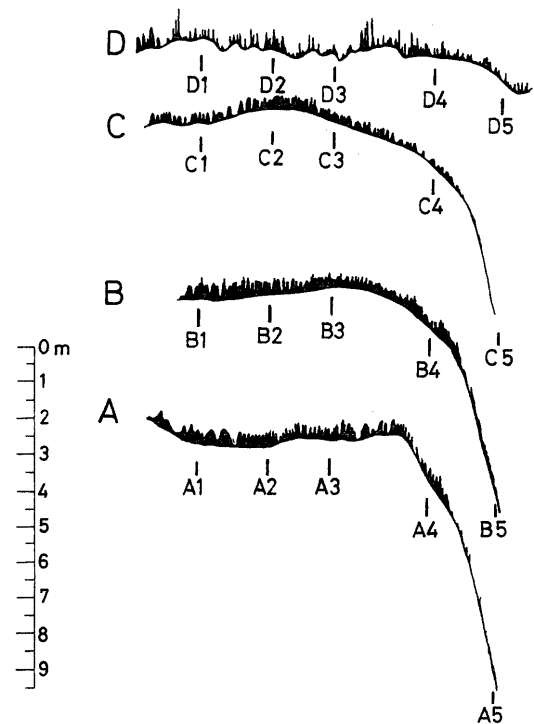


Fig. 2. Echograms showing vegetation of *Zostera caespitosa* along the four transect lines set at a seagrass bed (Y2 in Fig. 1) in Yamada Bay.

for each point was used as the index of seagrass biomass to examine its spatial variation in seagrass vegetation.

The presence or absence of *Z. caespitosa* in the seagrass bed was clearly distinguished by the acoustic echogram (Fig. 2). The echograms of *Z. caespitosa* showed different morphological feature from that of other seagrasses, because this species has tufted rhizome systems and makes clumps (see below). The average shoot height of *Z. caespitosa*, measured from the echograms was 30–75 cm with the maximum shoot height of 1 m, the latter corresponded to the height of flowering shoots.

The depth of the research area ranged between 2.5 m and 9.5 m, within which *Z. caespitosa* was found to occur at the depth between 2.5 m and 9 m (Fig. 2). The index of seagrass biomass estimated from the echogram was generally higher at the shallower stations (Fig. 2). The biomass was negatively correlated with the bottom depth ($r = -0.622$, $p = 0.003$). It is likely that the light availability is one of the major factors determining the depth limit of *Z. caespitosa* in the seagrass bed.

MORPHOLOGICAL AND LIFE HISTORY TRAITS OF *Zostera* spp.

All the Japanese endemic species of *Zostera* grow in slightly deeper site of sea bottom than *Z. marina* (Nakaoka and Aioi 2001). Their morphological features are so similar to each other that they had not been distinguished from *Z. marina* before Miki's detailed descriptions (Miki 1932). *Zostera asiatica* is characterized by the largest leaves and reproductive organs among them, but its growth form is similar to that of *Z. marina* (Omori 1989, 1994). *Zostera caespitosa* does not have creeping but sub-erect rhizomes, and *Z. caulescens* has very long erect reproductive shoots with large leaves on the top (Miki 1932, 1933). The mor-

phological characteristics and the growth form of the four species of *Zostera* are summarized in this section.

Inflorescence, flower and seed. The inflorescence and flowers of *Zostera* species are different from each other in size and proportion. *Zostera asiatica* has the broadest spathe (70–90 mm in length and 8–10 mm in width), *Z. caulescens* has the longest one (70–120 mm in length and 7–8 mm in width), and *Z. caespitosa* has the smallest one (50–65 mm in length and 4–4.5 mm in width). The spathe of *Z. marina* shows wide variation both in the length (35–100 mm) and the width (3–6 mm) (Omori 1992).

The seed and seed coat morphology provide us more distinguishable and useful characteristics than that of the flowers. *Zostera asiatica* and *Z. caulescens* have long ellipsoid seeds with smooth and striped seed coat. *Zostera marina* has cylindrical seeds with ridged but smooth seed coat, and *Z. caespitosa* has ovoid seeds with ridged and granular seed coat (Omori 1994).

Growth form. The *Zostera* species have either sub-erect rhizomes (*Z. caespitosa*) or creeping rhizomes (other species). Every top of the rhizome has a bunch of leaves but each leaf dies and falls off as the internodes grow. Therefore, the leaves of *Zostera* are only located at the top of each rhizome. On the other hand, the leaves of most of other seagrasses are seen at both the tops and the nodes of rhizome because their rhizomes have short shoots at the rhizome nodes.

Some of the rhizome tops of *Zostera* species differentiate into erect reproductive shoots in winter. The erect shoots produce inflorescences as lateral branches in spring. The erect shoots are monopodially branched in *Z. caulescens* but are sympodially branched in the other species. Two characteristics of growth form, i.e., the extremely long erect shoots of *Z. caulescens* and the sub-erect rhizomes of *Z. caespitosa*, are remarkable among *Zostera* species and have been comparatively studied as follows.

The most prominent characteristic of *Z. caulescens* is the longest erect shoots among seagrasses (ca. 7 m) with the long and broad leaves at the top that differ from the leaves attached to rhizome in shape and size. It is inferred that the erect shoots of *Z. caulescens* play a more important role than those of other *Zostera* species in productivity (see below). Just after branching, each top of the rhizomes is differentiated into an erect reproductive shoot in early winter, long before anthesis. The earliest differentiation from horizontal to erect shoot in *Z. caulescens* leads to its extremely long shoot. The vegetative shoot differentiates into erect reproductive shoot after supplying one or two branches of rhizomes from the main apex. The erect shoots die and are removed from the rhizome after fruition in warmer sea areas (e.g., Sagami Bay), or before differentiation of new erect shoots in cooler sea areas (e.g., Sanriku Coast). According to the differences in the length of growing period, the erect shoots elongate only to 5.6 m in Sagami Bay, whereas they reach at the maximum of 7 m in Sanriku Coast (Aioi et al. 1998).

Zostera asiatica, *Z. caulescens* and *Z. marina* have slightly compressed cylindrical rhizomes that creep horizontally and have regular long internodes. On the other hand, *Z. caespitosa* has compressed rhizomes that grow sub-erectly and densely to make a stock with many tightly

grown leaves and old leaf sheaths. The rhizome has short and dense internodes (1.4–1.7 mm in length), and long and sparse ones (5–35 mm in length) that are arranged alternately. It seems that the reproductive shoots of *Z. caespitosa* and *Z. asiatica* are differentiated from the apex of the newest lateral shoot of rhizome branching, whereas those of *Z. caulescens* and *Z. marina* develop from the rhizome apex.

The diversity of the growth form among *Zostera* species is considered to be related to their adaptation to depth, sediment structure, flow velocity and temperature. More detailed analyses are necessary for understanding adaptive significance of morphological and life historical variation among species and among populations of each species.

SHOOT DYNAMICS, GROWTH AND PRODUCTIVITY OF *Zostera caulescens*

Among five *Zostera* species inhabiting northeastern coast of Japan, *Z. caulescens* is prominent in developing extraordinarily long flowering shoots (erect shoots) with a canopy structure of vegetative leaves on apex (Omori 1994, Aioi et al. 1998, see above section). In Funakoshi Bay, northeastern Japan, the flowering shoots stand up to 7 m from the bottom with a typical length of 4.8 m, making this species known as the world's longest seagrass (Aioi et al. 1998). Quantitative analyses on growth and shoot dynamics are necessary to understand how the *Z. caulescens* population develops and maintains its high canopy structure, and how its presence affect overall productivity and energy flow in the coastal ecosystem.

In this section, we review studies on clonal growth and shoot dynamics of *Z. caulescens* in Funakoshi Bay, based mostly on Nakaoka et al. (2000) with some additional data taken thereafter. In these studies, seasonal variation in shoot age structure, recruitment and growth of vegetative and flowering shoots of *Z. caulescens* was measured by monthly quantitative census and collection, and annual productivity was estimated based on these data.

The census and collection of *Z. caulescens* was carried out between February 1999 and January 2000, at a subtidal seagrass bed (4 to 6 m deep) of Kirikiri, Funakoshi Bay (F1 in Fig. 1). Each month, >10 flowering shoots and >10 vegetative shoots were randomly harvested for morphological measurements. The growth rate of *Z. caulescens* was estimated monthly by marking leaf blades of flowering and vegetative shoots (Nakaoka et al. 2000). Seasonal variation in the shoot age structure of vegetative shoots was analyzed by determining their relative age as the number of horizontal rhizome internodes present since they have branched from parent rhizomes. Similarly, the relative age of flowering shoots was determined as the number of vertical internodes of upright stems. Each month, recruitment rate of flowering and vegetative shoots was estimated as the proportion of shoots with ≤ 2 vertical and horizontal internodes among all the collected flowering and vegetative shoots, respectively. Daily net production of aboveground parts of flowering and vegetative shoots was determined by dividing the dry weight of newly-produced leaf blades, sheaths and stems by the marking period. See Nakaoka et al. (2000) for detailed information on the methods of measurements and estimation of the above population parame-

Table 1. *Zostera caulescens*. Parameters on size, age structure, growth and productivity of flowering and vegetative shoots.

Date	Shoot height (cm)		Aboveground production (g DW d ⁻¹ shoot ⁻¹)	Recruitment rate (%)	Cohort	Relative shoot age (the number of internodes per shoot)	
	mean	range	mean			mean	range
Flowering shoots							
Feb. 17, 1999	327	120–560	—	57	young	2.1	1–3
Mar. 24	152	80–370	—	94	old	18.9	11–25
					young	1.7	1–5
Apr. 19	154	60–300	—	32	old	14.0	13–15
					young	3.0	1–6
May 17	187	40–340	27.4	20		5.0	1–9
Jun. 17	206	70–440	37.1	2		6.0	2–12
Jul. 11	248	100–450	30.6	0		8.0	3–14
Aug. 19	272	80–470	38.9	0		11.5	6–20
Sep. 13	254	60–490	27.6	0		11.9	4–20
Oct. 13	242	50–500	15.1	0		13.1	4–24
Nov. 15	169	110–230	11.0	0		12.1	4–22
Dec. 14	206	100–310	11.8	13	young	1.0	1–1
					old	13.1	5–21
Jan. 12, 2000	193	90–410	8.3	45	young	1.7	1–4
					old	17.1	10–27
Vegetative shoots							
Feb. 17, 1999	27	20–40	—	33		2.7	1–7
Mar. 24	31	10–80	—	53		2.2	0–7
Apr. 19	22	20–30	—	34		2.9	0–14
May 17	38	20–60	3.4	28		3.6	0–9
Jun. 17	36	20–70	3.2	15		4.3	0–9
Jul. 11	47	20–100	4.9	5		5.9	1–12
Aug. 19	51	20–90	7.1	5		7.2	2–12
Sep. 13	43	20–80	3.5	20		5.1	1–13
Oct. 13	35	20–60	4.1	10		6.7	1–16
Nov. 15	43	20–60	4.3	24		4.8	0–16
Dec. 14	26	5–90	4.0	35		3.5	1–14
Jan. 12, 2000	24	5–110	2.5	35		3.6	1–11

ters.

Average shoot height was always greater for flowering shoots than vegetative shoots (Table 1). Average height of flowering shoots was at a maximum in February and a minimum in March, increased thereafter through August, and dropped again in autumn. In contrast, height of vegetative shoots was consistently low throughout the year.

Examination of shoot age structures revealed that the flowering shoots consisted of two distinct cohorts from February to March 1999, and from December 1999 to January 2000, in which the young cohort consisted of shoots with <5 vertical internodes on the stems, and the old cohort with ≥5 internodes (Table 1). One continuous cohort was discerned in other months. New recruits of flowering shoots were found from February to June and from December to January with a peak in March, and that of vegetative shoots mostly from February to May, and from November to January with a peak in March (Table 1).

Growth rate and aboveground net production per shoot were much greater for the flowering shoots than the vegetative shoots (Table 1). This contrasts with other *Zostera* species for which flowering shoots consist mostly of non-photosynthetic tissues such as spadices, sheaths and stems. With better light availability at higher positions in the water

column, flowering shoots of this species play a major role in primary production.

Annual aboveground net production of *Z. caulescens* per area is estimated to be 426 g DW m⁻² y⁻¹ (Nakaoka, unpublished data). This estimate was similar to those estimated for other *Zostera* species that live at intertidal and subtidal beds shallower than 1 m deep (Cebrián et al. 1997, Duarte and Chiscano 1999). Thus, the productivity of *Z. caulescens* is quite high despite its distribution in deep water (4–6 m) with poor light conditions. These findings suggest that *Z. caulescens* population in Funakoshi Bay contributes greatly to achieving high primary production at the deeper parts of the subtidal bottoms along Sanriku Coast.

DISTRIBUTION AND ABUNDANCE OF SESSILE EPIFAUNA ON *Zostera caulescens*

Seagrass bed is one of the productive ecosystems in coastal area, and seagrasses support diverse associated organisms by providing their habitats (Hemminga and Duarte 2000). Epiphytal invertebrate animals inhabiting aboveground parts of seagrasses are among the major components in seagrass communities. They are classified into two major groups, i.e., mobile and sessile epifauna. Mobile epi-

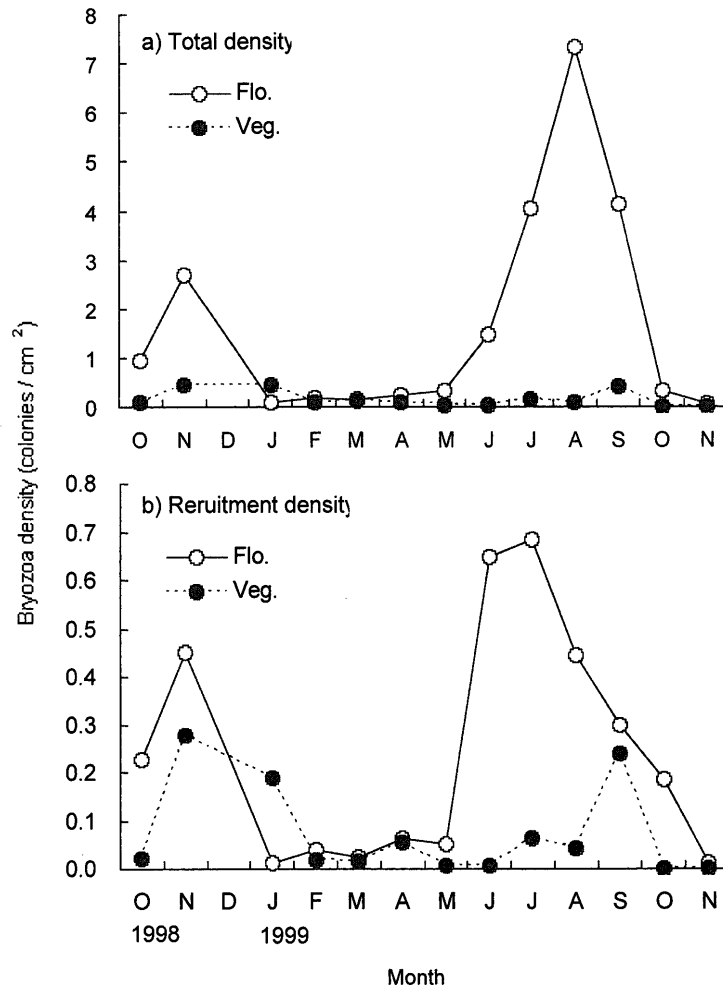


Fig. 3. Seasonal change in the density of *Microporella trigonellata* on *Zostera caulescens* in Kirikiri, Funakoshi Bay, Japan. a) Total density and b) recruitment density.

fauna include gastropods, crustaceans and errantry polychaetes, and sessile epifauna contain ascidians, bryozoans and sedentary polychaetes. Studies on mobile epifauna in seagrass beds along Sanriku Coast have been conducted in Otsuchi Bay (Toyohara 1997, Toyohara et al. 1999, 2001, Nakaoka et al. 2001, Nakaoka 2002), and were reviewed by Toyohara et al. (2000). In this section, we review recent findings on ecology of sessile epifauna on *Z. caulescens* in Funakoshi Bay, based on studies by Kouchi et al. (2000) and Kouchi (2001), with some additional data taken thereafter.

As shown in the previous two sections, *Z. caulescens* in Funakoshi Bay has high canopy structure reaching up to 7 m high from the sea bottom. Thus, *Z. caulescens* provides habitats for sessile epifauna within wide range of height. To provide a first step for understanding the effects of seagrass structure and dynamics on sessile epifauna, seasonal variation was described for *Microporella trigonellata*, an encrusting bryozoan species that is the most dominant sessile animal on the leaf surface of *Z. caulescens* in Funakoshi Bay.

A fieldwork was carried out at a seagrass bed of Kirikiri, Funakoshi Bay (F1 in Fig. 1). Ten flowering shoots and vegetative shoots of *Z. caulescens* were collected haphazardly at monthly intervals from October 1998 to November 1999 by SCUBA. After the measurements of size of leaves

(sheath and blades) and stems, the blades were cut at the base, divided into 5 cm segments from base to tip. The number of *M. trigonellata* colonies on the leaf surface was counted for each segment. Colonies with ≤ 2 zooids was defined as early recruits (settled within 2 weeks) and their number was also counted. The densities of whole *M. trigonellata* colonies and those of the recruits were calculated for each shoot type and for each month.

An average bryozoan density per shoot fluctuated widely on flowering shoots than on vegetative shoots (Fig. 3a). In flowering shoots, density was high in November, decreased to the lowest in January and remained low until May. It increased from June to the maximum density in August, and decreased steeply to October. In contrast, the bryozoan density on vegetative shoots was consistently lower than on flowering shoots except in January 1999. Seasonal variation in the density of early recruited colonies agreed well with that of all colonies (Fig. 3b), suggesting that the recruitment process is one of important factors for determining seasonal dynamics of *M. trigonellata*.

The bryozoan density increased greatly in summer when most of them were found on flowering shoots. This finding showed that the flowering shoot is important as a primary habitat for *M. trigonellata*. However, most of the flowering shoots fell down and disappeared in autumn through winter (see above). The bryozoan population could have not sur-

vived through winter if they only inhabited flowering shoots. The bryozoan density was higher on vegetative shoot than flowering shoot in January 1999 (Fig. 3). The vegetative shoots in this season grew and became flowering shoots from spring to summer. Therefore, the vegetative shoots provide important habitat for the bryozoan population from winter to spring. Ongoing demographic and experimental studies on the dynamics of this species will provide more information about responses of epifauna to seasonal and spatial dynamics of *Z. caulescens*.

POPULATION GENETIC STRUCTURE AND GENE FLOW AMONG POPULATIONS OF *Zostera caespitosa*

In seagrasses (marine angiosperms), pollen and seeds are dispersed on the water surface or in the water (Den Hartog 1970). Therefore, gene flow among populations is probably influenced by environmental parameters, such as the movement of water (sea currents and so on), that differ from those affecting terrestrial plants. However, general patterns of gene flow of seagrasses was not characterized in previous studies (Alberte et al. 1994, Waycott et al. 1997, Ruckelshaus 1998, Schlueter and Guttman 1998). The nature of gene flow likely differs according to each species and its environment.

This section reviews genetic variation within and among populations of seagrass along Sanriku Coast, based on the study of *Z. caespitosa* by Tanaka et al. (2002). Many seagrasses develop creeping rhizomes in all directions and form dense beds (Den Hartog 1970). Distinguishing individual plants in a population is difficult for these species and it may impede sampling for population genetic analysis. For *Z. caespitosa*, however, its rhizomes grow diagonally and do not creep (see above), which makes it easy to distinguish individuals. Therefore, *Z. caespitosa* is suitable for population genetic analysis.

Representative samples from about 20 plants were collected from each of the six populations of *Z. caespitosa* investigated, resulting in a total of 260 individual samples. Of the six populations, two were located in Otsuchi Bay (O1 and O2 in Fig. 1), three in Yamada Bay (Y1, Y2 and Y3 in Fig. 1), and one was in Mutsu Bay. Mutsu Bay is in Aomori Prefecture, northern Japan and is used to compare with Sanriku Coast. See Tanaka et al. (2002) for detailed information on the methods of DNA extraction, RAPD amplification, and statistical analyses.

The results of the AMOVA analysis (Excoffier et al. 1992, Huff et al. 1993) showed that 60% of the total genetic variation was maintained among populations, and the remaining variation was maintained within populations. Excluding the population in Mutsu Bay, which is located at a distance from the other populations, 45% of the total variation was maintained among populations, and the remaining variation was maintained within populations. Two-level variance partitioning of the total variation between these five populations showed that the variance between Otsuchi Bay and Yamada Bay was small (3.53%).

The observed genetic variation among and within populations of *Z. caespitosa* was generally closer to that of inbreeding species than of outcrossing species (Hamrick and Godt 1990, Bussell 1999). This shows that gene flow

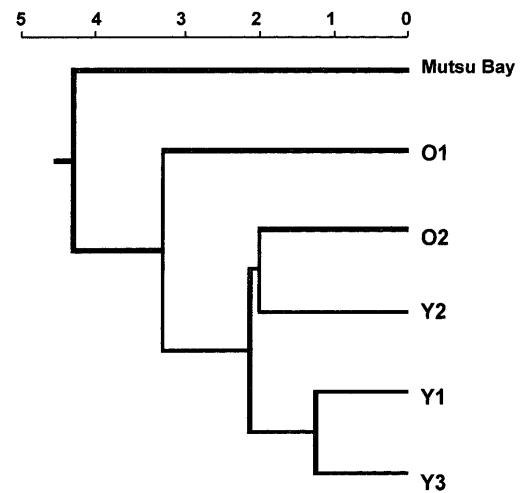


Fig. 4. UPGMA dendrogram of six population of *Zostera caespitosa* based on average number of Euclidian distance between populations. Location of populations are shown in Fig. 1. Redrawn from Tanaka et al. (2002).

among the populations is restricted and differentiation is promoted among the populations. According to overviews of the genetic variation within and among plant populations, high interpopulation variation is found in selfing breeding systems and in systems with limited seed dispersal (Loveless and Hamrick 1984, Hamrick and Godt 1990). For the *Z. caespitosa* population, however, the precise reasons for the low gene flow remain to be investigated.

A UPGMA dendrogram based on Euclidian distances between populations (Fig. 4) showed that the five populations (O1, O2, Y1, Y2, Y3) in Otsuchi Bay and Yamada Bay formed a cluster, but the two populations from Otsuchi Bay (O1, O2) did not form a single cluster, nor did the three populations from Yamada Bay (Y1, Y2, Y3). The results shows that only population O1 was dissimilar, while the other four populations in Otsuchi Bay and Yamada Bay were similar. It is clear that gene flow between populations in Otsuchi Bay is very restricted, while more gene flow takes place in Yamada Bay. A phylogenetic study including information on more populations in and around the region is necessary to clarify the causes of different modes of gene flow in *Z. caespitosa* between Otsuchi Bay and Yamada Bay.

CONCLUSION

The results of our research focusing on several different aspects of ecology of the multispecific seagrass beds along Sanriku Coast have revealed that these seagrass communities are remarkable and important in the coastal ecosystems with respect to the following points. First, it is a major physical structure in the soft bottoms at inner part of the bays along Sanriku Coast. Second, the endemic seagrass species in the multispecific beds have unique morphological and life history characters compared to cosmopolitan eelgrass (*Z. marina*), which may play important roles for the coexistence of several different seagrass species in a single bed. Third, the endemic seagrasses show very high productivity despite its distribution in relatively deep subtidal areas, which contributes to enhanced primary productivity in the coastal ecosystem along Sanriku Coast. Fourth,

the seagrass beds host diverse fauna that live in association with seagrasses, and their population dynamics are tightly associated with temporal and spatial dynamics of seagrasses. And finally, molecular genetic analysis of the seagrasses has revealed that their population genetic structures are not uniform but different among populations in different bays, possibly reflecting different patterns of gene flow among bays along Sanriku Coast.

The present study also highlights that processes and mechanisms maintaining population and community structures are not simple, but that they are affected by a network of complex interactions of various factors, such as hydrodynamics and transportations of organisms, physical oceanographic processes, chemical and biological processes such as recruitment, photosynthesis and nutrient uptake. Future researches including large-scale mapping of seagrass beds and other oceanographic factors using GIS, ecophysiological studies using *in situ* measurement of photosynthetic ability of seagrasses, experimental analyses manipulating species interactions among major components of seagrass communities, and genetic studies using molecular markers such as microsatellite DNA are worthwhile to deepen our understanding of dynamics and ecological functions of the multispecific seagrass communities.

The current knowledge on the ecology of the multispecific seagrass beds in northern Japan mostly comes from some intensive works in the limited localities reviewed here (Otsuchi Bay, Funakoshi Bay and Yamada Bay). However, it is not clear the results shown here can be applicable to other seagrass beds along Sanriku Coast and other parts of Japan where multispecific beds are also observed (Nakaoka and Aioi 2001). More extensive studies comparing regional variation in distribution, morphology, population and community dynamics, and genetic diversity of seagrasses are promising to answer this question.

ACKNOWLEDGEMENTS

The authors wish to thank the staff of the Otsuchi Marine Research Center, Ocean Research Institute, University of Tokyo, for facilitation of our research. We are also grateful to T. Kobayashi, T. Komatsu, J. Michimata, A. Moriyama, S. Tamura, T. Toyohara and M. Watanabe for field assistance. This earlier version of paper was presented at UNU-Iwate-UNESCO Joint International Conference entitled "Man and the Ocean: Conserving Our Coastal Environment (Section of Marine Ecology and Environment)" on July 10, 2002, at Tokyo.

LITERATURE CITED

- Aioi, K., Komatsu, T. and Morita, T. 1998. The world's longest seagrass, *Zostera caulescens* from northern Japan. *Aquat. Bot.* 61: 87–93.
- Aioi, K., Nakaoka, M., Kouchi, N. and Omori, Y. 2000. A new record of *Zostera asiatica* Miki (Zosteraceae) in Funakoshi Bay, Iwate Prefecture. *Otsuchi Mar. Sci.* 25: 23–26.
- Alberte, R. S., Suba, G. K. and Zimmerman, R. C. 1994. Assessment of genetic diversity of seagrass populations using DNA fingerprinting: Implications for population stability and management. *Proc. Natl. Acad. Sci. USA* 91: 1049–1053.
- Bussell, J. D. 1999. The distribution of random amplified polymorphic DNA (RAPD) diversity amongst populations of *Isotoma petraea* (Lobeliaceae). *Mol. Ecol.* 8: 775–789.
- Cebrián, J., Duarte, C. M., Marbà, N. and Enríquez, S. 1997. Magnitude and fate of the production of four co-occurring Western Mediterranean seagrass species. *Mar. Ecol. Prog. Ser.* 155: 29–44.
- Den Hartog, C. 1970. *The sea-grasses of the world*. North Holland Publishing Company, Amsterdam.
- Duarte, C. M. and Chiscano, C. L. 1999. Seagrass biomass and production: a reassessment. *Aquat. Bot.* 65: 159–174.
- Excoffier, L., Smouse, P. E. and Quattro, J. M. 1992. Analysis of molecular variance inferred from metric distances among DNA haplotypes: Application to human mitochondrial DNA. *Genet. Soc. Amer.* 131: 479–491.
- Hamrick, J. L. and Godt, M. J. W. 1990. Allozyme diversity in plant species. In *Plant Population Genetics, Breeding, and Genetic Resources*. Brown, A. H. D., Clegg, M. T., Kahler, A. L. and Weir, B. S. (eds.), pp. 43–63, Sinauer, Sunderland.
- Hemminga, M. A. and Duarte, C. M. 2000. *Seagrass Ecology*. Cambridge University Press.
- Huff, D. R., Peakall, R. and Smouse, P. E. 1993. RAPD variation within and among natural populations of outcrossing buffalograss [*Buchnoe dactyloides* (Nutt.) Engelm.]. *Theor. Appl. Genet.* 86: 927–934.
- Komatsu, T., Igarashi, C., Tatsukawa, K., Nakaoka, M. and Taira, A. 2003. Mapping of seagrass and seaweed beds using hydro-acoustic methods. *Fish. Sci.* (in press)
- Komatsu, T., Mikami, A., Sultana, S., Ishida, K., Hiraishi, T. and Tatsukawa, K. 2003. Hydro-acoustic methods as a practical tool for cartography of seagrass beds. *Otsuchi Mar. Sci.* 28: 72–79.
- Kouchi, N. 2001. Population dynamics of epifaunal bryozoa on seagrass. Master thesis, Graduate School of Science, University of Tokyo.
- Kouchi, N. and Nakaoka, M. 2000. Distribution of encrusting bryozoa on *Zostera caulescens* in Funakoshi Bay, Japan: effects of seagrass vertical structure on epifauna. *Biol. Mar. Mediterranea* 7: 247–250.
- Loveless, M. D. and Hamrick, J. L. 1984. Ecological determinants of genetic structure in plant populations. *Ann. Rev. Ecol. Syst.* 15: 65–95.
- Miki, S. 1932. On sea-grasses new to Japan. *Bot. Mag. 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. *Bot. Mag. Tokyo* 47: 842–862.
- Nakaoka, M. 2002. Predation on seeds of seagrasses *Zostera marina* and *Zostera caulescens* by a tanaid crustacean *Zeuxo* sp. *Aquat. Bot.* 72: 99–106.
- Nakaoka, M. and Aioi, K. 2001. Ecology of seagrasses *Zostera* spp. (Zosteraceae) in Japanese waters: A review. *Otsuchi Mar. Sci.* 26: 7–22.
- Nakaoka, M., Kouchi, N. and Aioi, K. 2000. Growth and shoot dynamics of *Zostera caulescens* Miki in Funakoshi Bay, Japan: how does it maintain high canopy structure? *Biol. Mar. Mediterranea* 7: 103–106.
- Nakaoka, M., Toyohara, T. and Matsumasa, M. 2001. Seasonal and between-substrate variation in mobile epifaunal community in a multispecific seagrass bed of Otsuchi Bay, Japan. *P. S. Z. N. Mar. Ecol.* 22: 379–395.
- Omori, Y. 1989. Morphology of the flowering shoot and the leaf of *Zostera caulescens* Miki and *Z. asiatica* Miki (Zosteraceae). *Sci. Rept. Yokosuka City Mus.* 37: 55–59 (in Japanese with English abstract).
- Omori, Y. 1992. Geographical variation of the size of spadix and spathe and the number of flowers among the four species of the subgenus *Zostera* (Zosteraceae). *Sci. Rept. Yokosuka City Mus.* 40: 69–74 (in Japanese with English abstract).
- Omori, Y. 1994. Seasonal changes of the reproductive shoot of *Zostera caulescens* (Zosteraceae) in Sagami Bay, central Japan.

- Sci. Rept. Yokosuka City Mus. 42: 65–69 (in Japanese with English abstract).
- Omori, Y. and Aioi, K. 1998. Rhizome morphology and branching pattern in *Zostera caespitosa* Miki (Zosteraceae). Otsuchi Mar. Res. Cent. Rep. 23: 49–55 (in Japanese).
- Omori, Y., Aioi, K. and Morita, K. 1996. A new record of *Zostera caespitosa* Miki (Zosteraceae): Its distribution in Yamada Bay, Iwate Prefecture, Japan. Otsuchi Mar. Res. Cent. Rep. 21: 32–37 (in Japanese).
- Ruckelshaus, M. H. 1998. Spatial scale of genetic structure and an indirect estimate of gene flow in eelgrass, *Zostera marina*. Evolution 52: 330–333.
- Schlueter, M. A. and Guttman, S. I. 1998. Gene flow and genetic diversity of turtle grass, *Thalassia testudinum*, Banks ex König, in the lower Florida Keys. Aquat. Bot. 61: 147–164.
- Sultana, S. and Komatsu, T. 2002. Preliminary study on shoot density and biomass of seagrass, *Zostera caulescens*, in Funakoshi Bay off Sanriku Coast, Japan. Otsuchi Mar. Sci. 27: 23–27.
- Tanaka, N., Omori, Y., Nakaoka, M. and Aioi, K. 2002. Gene flow among populations of *Zostera caespitosa* Miki (Zosteraceae) in Sanriku Coast, Japan. Otsuchi Mar. Sci. 27: 17–22.
- Tatsukawa K., Komatsu, T., Aioi, K. and Morita, K. 1996. Distribution of seagrasses off Kirikiri in Funakoshi bay, Iwate Prefecture, Japan. Otsuchi Mar. Res. Cent. Rep. 21: 38–47.
- Toyohara, T. 1997. Population dynamics and reproductive traits of phytal gastropods, *Lirularia iridescens* and *Hilota tristis*, inhabiting subtidal seagrass bed in Otsuchi Bay, Northeastern Japan. Master thesis, Graduate School of Science, University of Tokyo.
- Toyohara, T., Nakaoka, M. and Aioi, K. 1999. Population dynamics and reproductive traits of phytal gastropods in seagrass bed in Otsuchi Bay, northeastern Japan. P. S. Z. N. Mar. Ecol. 20: 273–290.
- Toyohara, T., Kouchi, N. and Nakaoka, M. 2000. Ecology of epiphytic animals in seagrass beds. Aquabiology 22: 557–565 (in Japanese).
- Toyohara, T., Nakaoka, M. and Tsuchida, E. 2001. Population dynamics and life history traits of *Siphonacmea oblongata* Yokohama on seagrass leaf in Otsuchi Bay (Siphonariidae, Pulmonata). Venus (Jap. J. Malacol.) 60: 27–36.
- Waycott, M., James, S. H. and Walker, D. I. 1997. Genetic variation within and between populations of *Posidonia australis*, a hydrophilous, clonal seagrass. Heredity 79: 408–417.