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Seasonal dynamics of *Zostera caulescens*: relative importance of flowering shoots to net production

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Abstract

Zostera caulescens occurs only in limited localities around Japan and Korea, and is listed as a threatened plant species in Japan. We present the first quantitative data on seasonal dynamics of *Z. caulescens* based on a 13-month field study of a subtidal seagrass bed (4–6 m deep) in Funakoshi Bay, northeastern Japan. We investigated the relative importance of flowering shoots on total net production: these flowering shoots form a canopy structure several meters above the sea bottom. Flowering shoots were observed throughout the year but showed large seasonal variation in density, with a maximum in spring to summer (>30 shoots m^{-2}) and a minimum in winter (3 shoots m^{-2}). The density of vegetative shoots fluctuated between 120 and 238 shoots m^{-2}, but did not show a significant seasonal variation. Age distribution of both flowering and vegetative shoots showed marked seasonal variation, with the peak in recruitment observed during winter to early spring. Leaf plastochrone intervals were 2- to 3-fold shorter in summer than in winter, with an annual average of 15.3 and 18.1 days for flowering and vegetative shoots, respectively. On the basis of these data, the absolute age of the oldest flowering shoot was estimated at 13 months. Biomass and net production of *Z. caulescens* were highest in summer and lowest in winter. During spring to autumn, flowering shoots constituted more than 70% of both biomass and production, while the contribution of vegetative shoots dominated during winter, when the density of flowering shoots was low. Annual net production was estimated to be 292 and 134 g DW m^{-2} per year for the aboveground parts of flowering and vegetative shoots, respectively, and 47 g DW m^{-2} per year for the belowground parts, giving a total of 473 g DW m^{-2} per year. These findings demonstrated that the flowering shoots of *Z. caulescens* are important not only for seed production, but also as major photosynthetic parts of the population, helping to achieve high primary production despite their distribution at the deeper parts of the multispecific seagrass bed.

Keywords: Seagrass; Shoot dynamics; Production; Seasonal variation; *Zostera caulescens*; Northeastern Japan

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1. Introduction

The seagrass flora of Japan is characterized by the occurrence of several species of 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. japonica* (Omori, 1993; Aioi et al., 1998). Among them, *Zostera* spp. generally occur on subtidal soft bottoms in northern Japan, usually forming multispecific seagrass beds with the cosmopolitan eelgrass *Z. marina* (Nakaoka and Aioi, 2001). Some of these species are now known only in a few localities around Japan and are thus considered to be at risk of extinction in Japan. In fact, *Z. asiatica* and *Z. caulescens* are listed in the Red Data Book of threatened Japanese plant species (Environment Agency of Japan, 2000). Basic information on these species' distribution and the quantitative aspect of their ecology is urgently required for promoting an effective and efficient conservation of these seagrasses.

Z. caulescens Miki is found in northern to central parts of Honshu, the largest island of Japan (Nakaoka and Aioi, 2001), and in some locations along the Korean coast (Shin and Choi, 1998). The most remarkable characteristic of this species is that it develops extraordinarily long flowering shoots (erect shoots) that end with several (4–8) large blades, forming a canopy structure several meters above the sea bottom (Omori, 1991; Aioi et al., 1998; Kouchi and Nakaoka, 2000). A maximum shoot height of 5.3 m is reported in Odawa Bay, on the Pacific coast of central Honshu (Kudo, 1999), and 6.8 m in Funakoshi Bay, northeastern Honshu, considered to be a record length among seagrasses (Aioi et al., 1998). Concerning ecology of this species, some previous studies reported depth distribution, seasonal and regional variation in morphology, phenology and reproductive traits (Omori, 1989, 1992, 1994, 1995; Tatsukawa et al., 1996; Aioi et al., 1998; Omori and Aioi, 2000). However, quantitative aspects of its population dynamics, such as spatial and temporal variation in biomass, growth and productivity, have not been investigated.

The aim of the present paper is to present the first quantitative data on shoot dynamics, growth and productivity of *Z. caulescens* based on fieldwork conducted over 13 months. For a population in Funakoshi Bay, we examined seasonal changes in shoot density, biomass and shoot age–size structure by monthly census and collection. We also measured variation in leaf plastochrone intervals, growth and net production using a leaf-marking method. On the basis of these data, we estimated annual production of the population, focusing on the relative importance of flowering and vegetative shoots on total net production.

2. Materials and methods

2.1. Study site

The research was conducted in Funakoshi Bay, northeastern Honshu, Japan, at a seagrass bed located in the protected sandy bottom in the southwestern part (Kirikiri) of the bay (39°22.3′N; 141°57.1′E). Tatsukawa et al. (1996) estimated that the area of the seagrass bed is 0.5 km^2, covering the bottom of 2–17 m depth. The seagrass bed consists of three *Zostera* species: *Z. caulescens* is dominant and found throughout the seagrass bed; *Z. marina* occurs only in the shallower parts of the bed (2–5 m; Nakaoka, unpublished data); and *Z. asiatica* occurs sporadically at a depth of about 5 m (Aioi et al., 2000).

2.2. Quantitative estimation of shoot density, shoot height and shoot age structure

Fieldwork using SCUBA was carried out monthly from April 1999 through May 2000. A research site was established at the inner part of the seagrass bed between depths of 4 and 6 m. Each month, we haphazardly placed 10 square quadrats of 0.04 m^2 area within the *Z. caulescens* vegetation, and counted the number of flowering shoots and vegetative shoots. We also measured the height of flowering and vegetative shoots using a meter stick.

Flowering shoots of *Z. caulescens* are transformed from vegetative plants by producing upright vertical stems, whereas new vegetative shoots are produced by side-branching of rhizomes (Omori, 1991, 1992, 1995). Thus, the number of internodes on the vertical stem and the rhizome represents a relative measure of age for flowering and vegetative shoots, respectively. To estimate the age structure of the two types of shoots, we collected 20–50 flowering shoots and 30–100 vegetative shoots of *Z. caulescens* haphazardly from the research site, and counted the number of internodes on the vertical stem and the rhizome for each flowering and vegetative shoot, respectively.

2.3. Measurements of growth and productivity

We estimated the growth rate of *Z. caulescens* by marking leaf blades monthly from April 1999 through May 2000. Each month, 10–25 flowering shoots plus 10–25 vegetative shoots were selected, and their blades were punched with a pin at 1 cm above the sheath. The flowering shoots were randomly selected each month, whereas only vegetative shoots larger than 20 cm in height were marked because it was difficult to punch the narrow blade of shorter shoots without damaging them. We harvested the marked shoots 17–42 days later and counted the number of new leaves produced since marking. The shoots were collected by digging sediments carefully by hands, so that belowground parts, including root materials, were not lost upon collection. For flowering shoots and some old vegetative shoots, however, it was difficult to dig out the entire parts of the rhizomes without cutting them, which may influence the estimation of belowground biomass and production (see below). For each marked shoot, we measured length and width of sheath, leaf blade and vertical stem, and the length of each rhizome internode. The shoots were then separated into rhizome (plus roots), stem, sheath and blade; further, new growth was separated for each part. The plants were dried in an oven at 60 °C for >48 h to a constant weight and weighed on an electronic balance to the nearest 0.1 mg.

2.4. Data analysis

In the present study, the age of flowering shoot was defined as the time since it transformed from vegetative plants, and the age of vegetative shoot as the time since it branched from a parent rhizome. Age structure of flowering and vegetative shoots was examined by constructing frequency histograms for each month using the number of internodes as a relative measure of age.

We estimated leaf plastochrone intervals PI (days) separately for flowering shoots and vegetative shoots using the following equation:

$$\mathrm{PI} = \frac{mt}{n}$$

where m is number of marked shoots, t is the time interval between the marking and the retrieval (days), and n is the total number of new leaves produced during the experimental period. Average leaf turnover period (days) for each month was calculated by multiplying PI by the average number of leaves in that month.

Absolute age of flowering and vegetative shoots was estimated by calculating the average number of internodes produced between two successive months ($\mathrm{IN}_{i,i+1}$) as follows:

$$\mathrm{IN}_{i,i+1} = \frac{d}{\mathrm{PI}_{i,i+1}}$$

where $\mathrm{PI}_{i,i+1}$ is the leaf plastochrone interval between months i and $i+1$, and d is the period (days) during the successive months. Then the recruitment month of each flowering and vegetative shoot was back-calculated by subtracting $\mathrm{IN}_{i,i+1}$ from the number of internodes until it became zero.

Aboveground biomass of flowering shoots of *Z. caulescens* for each month was determined by multiplying average biomass of marked shoots by the shoot density estimated by the monthly census. For vegetative shoots, however, this method may lead to overestimation because only shoots larger than 20 cm in shoot height were marked and measured. We obtained size-adjusted estimates of aboveground biomass of vegetative shoots (AB_v) using an allometric equation relating shoot biomass (SB) and shoot height (SH) by linear regression analysis ($\mathrm{SB} = a\mathrm{SH}^b$, where a and b are constants) for each month, and applying the equation to data on size frequency distribution measured by the monthly census as follows:

$$\mathrm{AB}_v = \mathrm{SD}\sum_i p_i \mathrm{SB}_i = \mathrm{SD}\sum_i p_i a \mathrm{SH}_i^b$$

where SD is the shoot density, p_i is the frequency of shoots with biomass of SB_i and height of SH_i (heights classified in 10 cm intervals). The density of vegetative shoots was assumed to be constant throughout the year (169 shoots m^{-2}) because we were unable to detect significant monthly variation in its density (see Section 3).

Belowground biomass of flowering and vegetative shoots per unit area (m^2) was estimated by multiplying average dry weight of belowground parts (rhizome and root) by the density for each shoot type. For most flowering shoots, however, it was difficult to dig out entire rhizomes without cutting them. Because the average number of rhizome internodes of flowering shoots collected undamaged was nine, we used data only from shoots with no fewer than eight rhizome internodes, and calculated belowground biomass for the last nine nodes by multiplying the dry weight of the entire belowground plant parts with the ratio of the length of the nine last rhizome internodes to the total length of collected rhizome.

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. The belowground production of vegetative shoots was obtained by measuring the dry weight of newly produced rhizome internodes (with root materials), whose number corresponded to the number of new leaf blades that emerged during the marking period because leaf plastochrone intervals were equal to rhizome internode plastochrone intervals in *Zostera* species (Short and Duarte, 2001).

To estimate net production per area, the average daily net production per flowering shoot was multiplied by the average flowering shoot density during the two successive months before and after the marking experiment. For the vegetative shoots, aboveground net production calculated by this method may have been overestimated because we did not mark shoots shorter than 20 cm. To obtain size-adjusted estimates of net production, we first examined the relationship between shoot height and aboveground production using linear regression analysis, and then applied the regression equations to monthly data on size distribution using the same method as for estimating size-adjusted aboveground biomass of vegetative shoots (see above). For estimation of monthly belowground production per area, we multiplied the average belowground production per vegetative shoot by the annual mean shoot density.

3. Results

3.1. Seasonal changes in environmental parameters

Water temperature and salinity in the seagrass bed were measured monthly by STD (Alec Electroniks, model AST-1000s). The temperature varied seasonally between a maximum of 22.1 °C in September and a minimum of 7.3 °C in March, whereas the salinity remained almost constant during the study period. Solar insolation, measured at the adjacent Otsuchi Bay (4 km from the study site) varied seasonally, with a maximum of 227 W m^{-2} in early August and a minimum of 44 W m^{-2} in early January.

3.2. Seasonal changes in shoot density and height

Shoot density of *Z. caulescens* was greater for vegetative shoots than flowering shoots in all months (Fig. 1A). The average density of vegetative shoots fluctuated between a minimum of 120 shoots m^{-2} in June 1999 and a maximum of 238 shoots m^{-2} in May 2000, but showed no apparent seasonal cycle (Fig. 1A). Vegetative shoot density did not vary significantly among months (ANOVA, $F = 1.106$, d.f. $= 13$, $P = 0.360$). In contrast, flowering shoots showed clear seasonal variation in their density, which was high (>30 shoots m^{-2}) from April to August 1999, decreased to a minimum of 3 shoots m^{-2} in November and December 1999, and increased again from winter to spring (Fig. 1A). Monthly variation in flowering shoot density was statistically significant (ANOVA, $F = 6.651$, d.f. $= 13$, $P < 0.001$).

Vegetative shoot height was mostly lower than 1 m throughout the year; average height varied between 19 cm (in March and April 2000) and 35 cm (in July 1999). Seasonal trends in height of vegetative shoots were not obvious (Fig. 1B). Flowering shoot height varied greatly among months (Fig. 1B). Average height of flowering shoots increased from ca. 150 cm in spring to >200 cm in summer to autumn, then decreased from winter to early spring to a minimum of 76 cm in April 2000. The tallest flowering shoot (530 cm) was recorded in August 1999.

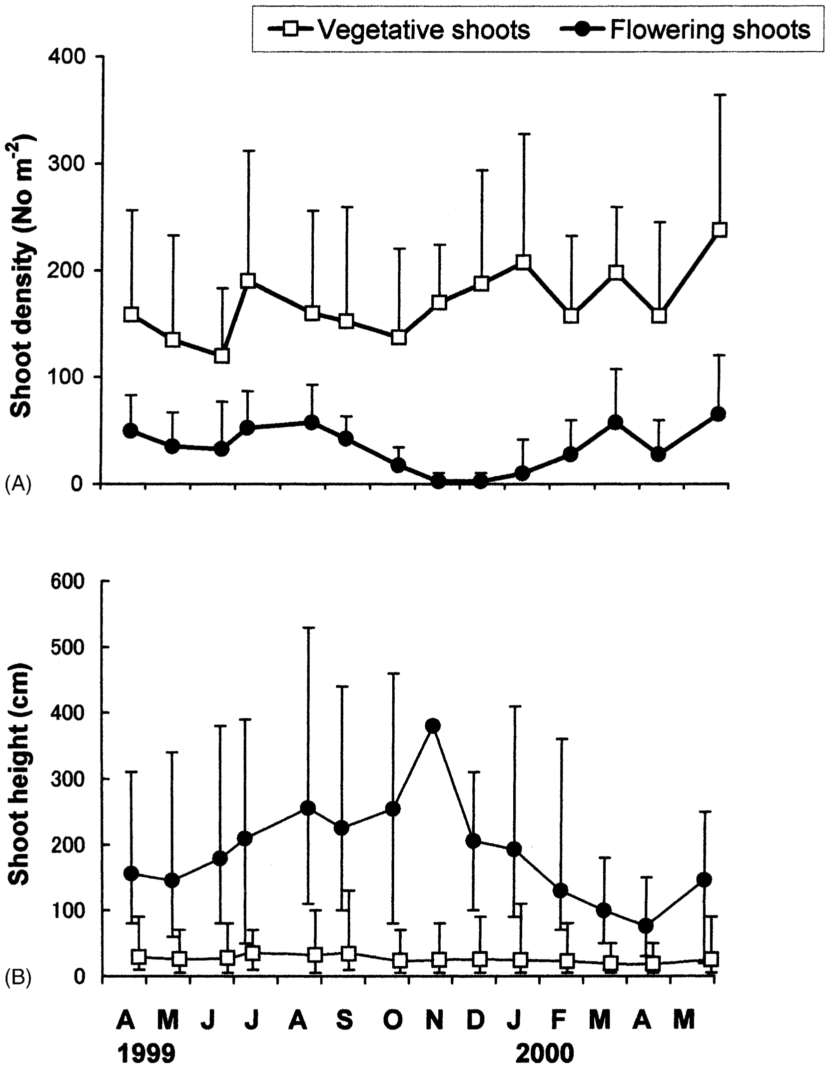

Fig. 1. Seasonal changes in (A) shoot density and (B) shoot height of *Zostera caulescens* in Funakoshi Bay. The data on vegetative shoots and flowering shoots are presented separately. Bars denote standard deviation in (A) and the range of height distribution in (B).

3.3. Shoot age structure

Age structure of flowering shoots, represented by the frequency histogram of the number of internodes on its vertical stem, showed marked variation with seasons (Fig. 2). In April, flowering shoots were mostly composed of young shoots with no more than six internodes. The mode and the oldest shoots increased from spring to summer. Between September and November, there was a wide range of ages (between 6 and 24 internodes). The youngest

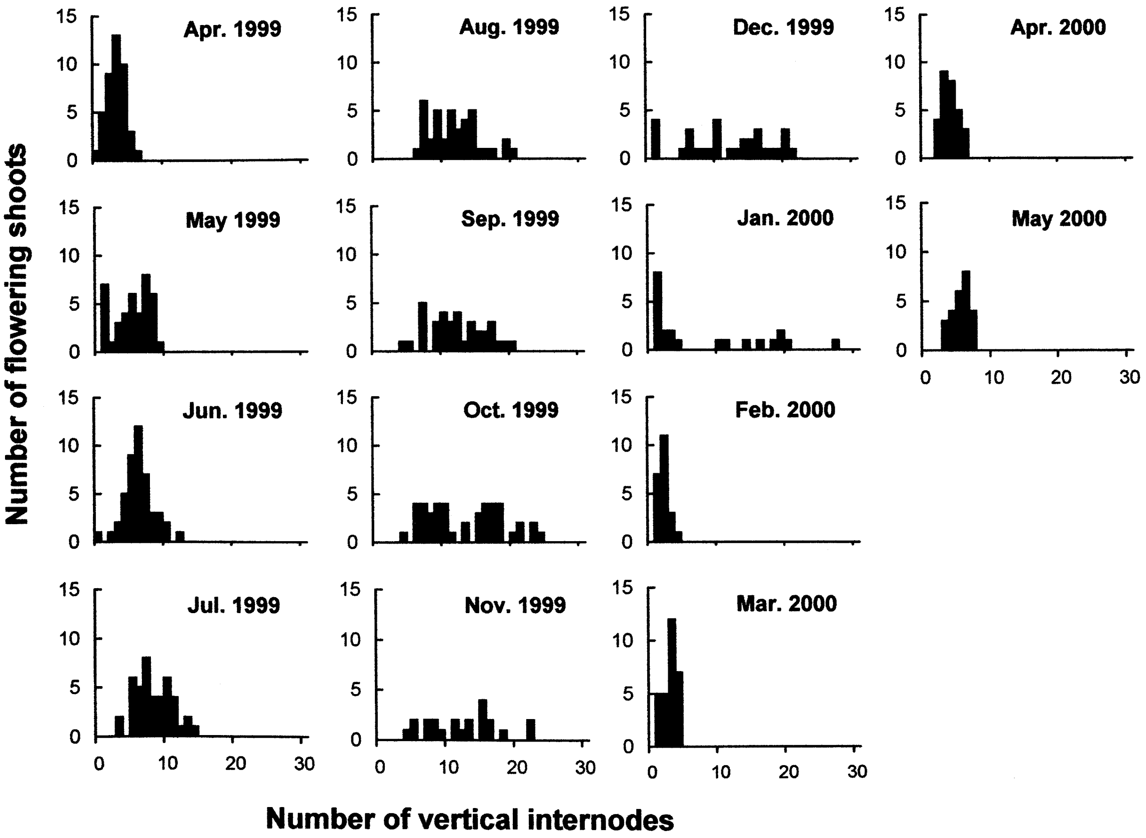

Fig. 2. Frequency histograms of the number of vertical internodes on stems of flowering shoots of *Zostera caulescens* in Funakoshi Bay.

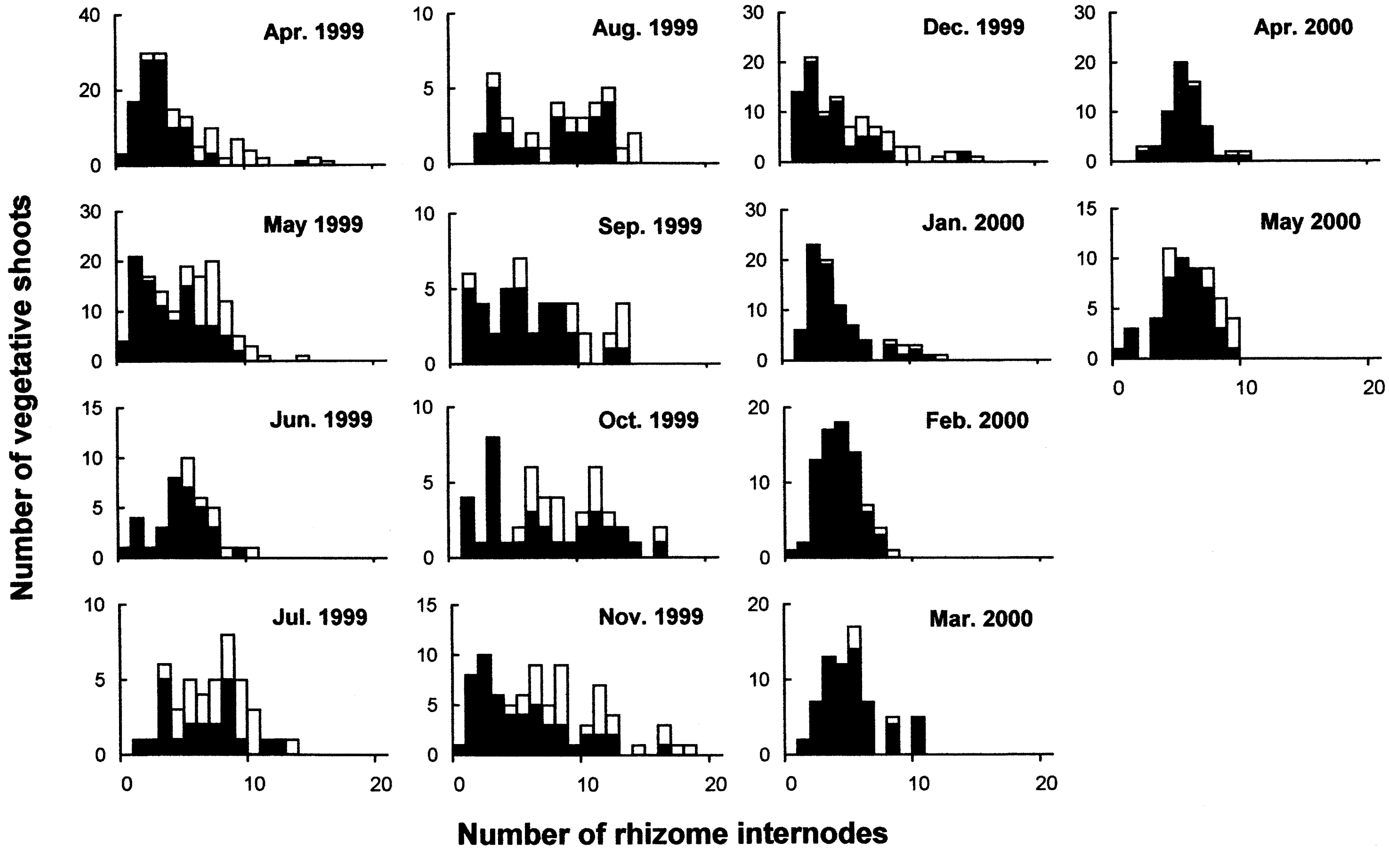

Fig. 3. Frequency histograms of the number of internodes on rhizomes of vegetative shoots of *Zostera caulescens* in Funakoshi Bay. The solid columns denote the data taken from branched rhizomes and the open columns from rhizomes cut or degraded at the end for which the relative age may be underestimated.

shoots (one internode) appeared in December and the relative abundance of the young recruits increased from December through January, whereas the relative abundance of the older shoots (>5 internodes) decreased and then totally disappeared by February. The modal age of the recruits increased gradually from January to May 2000 (Fig. 2). The recruitment of flowering shoots thus occurred mostly in winter (between December and March).

The age structure of vegetative shoots, represented by the frequency histogram of the number of internodes on the rhizome, also showed large variation from month to month (Fig. 3). Its seasonal pattern, however, was less apparent than that of the flowering shoots, partly due to the occurrence of shoots with degraded or broken rhizomes with which the age could not be determined. Most of the shoots with intact rhizomes had less than five internodes in April 1999. The age distribution expanded toward older age classes from May to November. Unlike flowering shoots, young vegetative shoots appeared even in these seasons. The relative abundance of old shoots (>10 internodes) decreased from November to January; vegetative shoots consisted exclusively of younger classes (<10 internodes) in February. Their modal age increased from February to May 2000 (Fig. 3).

3.4. Leaf plastochrone intervals and estimation of absolute age

Leaf plastochrone intervals of flowering and vegetative shoots varied seasonally with an annual average of 15.3 and 18.1 days, respectively (Table 1). They were short in summer to early autumn and long from winter to early spring, varying 2- to 3-fold between these seasons. Comparing the flowering and vegetative shoots in the same month, plastochrone interval was shorter for flowering shoots in most months (Table 1). Leaf turnover period, or average lifespan of an individual leaf, showed similar seasonal variation, varying 2- to 3-fold (Table 1).

The absolute age of flowering and vegetative shoots, estimated using the data on internode number and leaf plastochrone intervals, showed large monthly variation in both mean age and maximum age (Table 2). The mean age of flowering shoots increased from April to August, and it was 4–5 months between August and January. It then suddenly dropped to a minimum of one month in February 2000, and increased again till May 2000. Seasonal variation in maximum age followed a similar pattern (Table 2). A maximum lifespan of 13 months was estimated for a flowering shoot collected in January 2000. The seasonal change in mean and maximum age of vegetative shoots was not obvious, but the youngest mean age (two months) was recorded in December and January (Table 2). A maximum age of 9 months was estimated for vegetative shoots, although underestimation was likely because most of the old vegetative shoots had rhizomes with degraded ends (Fig. 3). Within a given month, average age of flowering shoots was 1–2 months younger than vegetative shoots between February and July, whereas it was 1–3 months older between August and January (Table 2).

3.5. Biomass and productivity

Biomass of *Z. caulescens* fluctuated greatly for both aboveground and belowground parts (Fig. 4). Aboveground biomass was high from May to September with a maximum in August (173 g DW m^{-2}). It decreased rapidly during autumn to a minimum in November (24 g) and

Table 1
Number of leaves (mean ± S.D., with sample sizes in parentheses), leaf plastochrone intervals (PI) and leaf turnover period of flowering and vegetative shoots of *Zostera caulescens* in Funakoshi Bay

Period	Marking period (days)	Flowering shoots			Vegetative shoots		
		Leaf number	PI (days)	Leaf turnover period (days)	Leaf number	PI (days)	Leaf turnover period (days)
April–May 1999	28	5.1 ± 1.1 (7)	14.0	71.4	4.2 ± 0.6 (10)	21.0	88.2
May–June 1999	29	5.3 ± 1.0 (25)	11.2	59.4	4.2 ± 0.8 (25)	15.4	64.7
June–July 1999	20	5.7 ± 1.0 (22)	10.7	61.0	4.0 ± 0.8 (22)	14.5	58.0
July–August 1999	42	5.1 ± 0.8 (15)	10.7	54.6	4.6 ± 0.5 (8)	12.2	56.1
August–September 1999	20	4.8 ± 0.9 (16)	9.7	46.6	2.8 ± 0.8 (18)	16.0	44.8
September–October 1999	27	3.8 ± 1.4 (13)	13.0	49.4	3.8 ± 0.6 (19)	10.5	39.9
October–November 1999	28	4.0 (2)	11.2	44.8	3.3 ± 0.5 (12)	12.9	42.6
November–December 1999	25	4.1 ± 1.6 (7)	15.6	64.0	3.8 ± 0.9 (22)	18.3	69.5
December 1999–January 2000	29	3.8 ± 0.8 (6)	21.8	82.8	3.5 ± 0.9 (19)	25.2	88.2
January–February 2000	30	4.3 ± 0.7 (8)	20.9	89.9	3.7 ± 0.8 (17)	20.7	76.6
February–March 2000	27	4.6 ± 0.7 (18)	21.8	100.3	3.8 ± 0.6 (17)	19.6	74.5
March–April 2000	25	4.4 ± 0.8 (24)	23.1	101.6	4.0 ± 0.5 (22)	30.6	122.4
April–May 2000	37	5.2 ± 0.7 (14)	17.9	93.1	4.1 ± 0.7 (16)	20.4	83.6

Table 2
Estimation of absolute age (in months) of flowering and vegetative shoots of *Zostera caulescens* with average and maximum number of internodes

Month	Absolute age (months)			
	Flowering shoots		Vegetative shoots	
	Mean	Maximum	Mean	Maximum
April 1999	2	4	3	9
May 1999	3	6	4	8
June 1999	3	7	3	7
July 1999	3	7	4	8
August 1999	5	10	4	9
September 1999	4	10	3	7
October 1999	5	10	3	9
November 1999	4	9	3	9
December 1999	5	8	2	7
January 2000	4	13	2	6
February 2000	1	3	3	5
March 2000	2	3	3	6
April 2000	3	4	4	6
May 2000	4	5	4	6

steadily increased from winter through spring. Biomass of flowering shoots was higher than that for vegetative shoots in all months, except from November to January. Flowering shoot biomass contributed more than 70% of the total aboveground biomass between May and September 1999, and between March and May 2000.

Belowground biomass was much smaller than aboveground biomass throughout the year (Fig. 4). Belowground biomass was less than 18% of total biomass, except between October and December, when it represented 24–38% of the total biomass. It showed a similar seasonal pattern to that of aboveground biomass: high in summer and low in winter. Vegetative shoots had more belowground biomass than flowering shoots in all months except March 2000.

Annual mean aboveground and belowground biomass estimated for the period between April 1999 and April 2000 was 50.1 and 2.9 g DW m^{-2}, respectively, for flowering shoots, and 24.1 and 9.8 g DW m^{-2} for vegetative shoots.

Aboveground net production was 3- to 12-fold greater for flowering shoots than for vegetative shoots when compared on a per-shoot basis (Fig. 5). For vegetative shoots, belowground production per shoot was 10–30% of aboveground production. Aboveground production of flowering and vegetative shoots as well as belowground production of vegetative shoots all showed marked seasonal variation (Fig. 5). They were generally higher in summer and lower in winter.

Net production per area also showed large seasonal fluctuations, with maximum total production (3.1 g DW m^{-2} per day) in August 1999 and minimum (0.3 g DW m^{-2} per day) in January 2000 (Fig. 6). Aboveground production was 4- to 14-fold higher than belowground production. Flowering shoots contributed 70–80% of aboveground production between April and September 1999, and between March and May 2000. In contrast, vegetative shoots were the main source of aboveground production between October 1999 and January 2000, contributing ca. 80–90%.

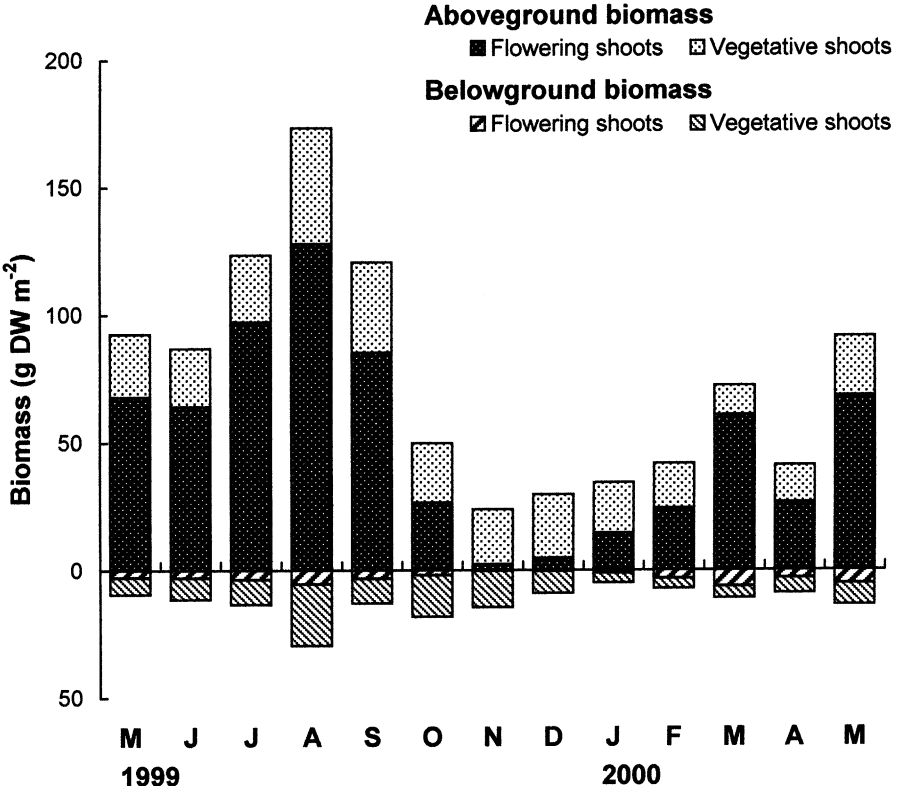

Fig. 4. Seasonal changes in aboveground and belowground biomass of *Zostera caulescens* in Funakoshi Bay. The data on flowering and vegetative shoots are presented separately.

Annual net production, estimated by average monthly data for the period between April 1999 and April 2000, was 292 and 134 g DW m^{-2} per year for aboveground parts of flowering and vegetative shoots, respectively, and 47 g DW m^{-2} per year for belowground parts. Summing these data, total annual net production of *Z. caulescens* was estimated to be 473 g DW m^{-2} per year with an aboveground-to-belowground ratio of 9.1. The production/biomass ratio was calculated to be 5.4 using the data of annual mean biomass (see above).

4. Discussion

The present study provides the first quantitative data on seasonal dynamics of shoot age structure, growth and net production of *Z. caulescens*, a seagrass endemic to the Japan and Korea region (Nakaoka and Aioi, 2001). The results contrast greatly with previous studies of other species of *Zostera* (mainly the cosmopolitan *Z. marina*), particularly with reference to the role and dynamics of its unique flowering shoots.

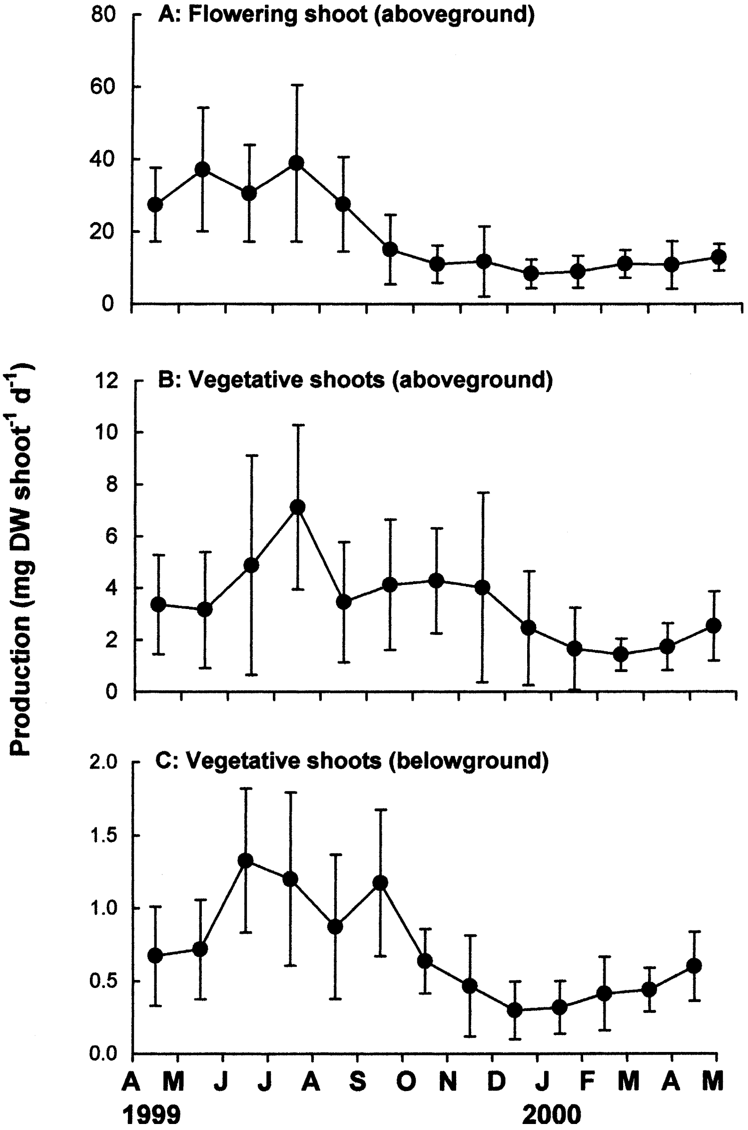

Fig. 5. Seasonal changes in aboveground net production of flowering shoots (A) and vegetative shoots (B), and belowground net production of vegetative shoots (C) per shoot of *Zostera caulescens* in Funakoshi Bay. Bars denote standard deviation.

Flowering shoots of *Z. caulescens* are greater than its vegetative shoots not only in shoot height but also in aboveground biomass, mostly due to the presence of several large leaf blades (maximum length of >100 cm and width of >15 mm, Nakaoka et al., 2000) on the apex of the flowering shoots (Omori, 1994, 1995; Aioi et al., 1998). This morphological character is different from other *Zostera* species, in which flowering shoots consist mostly of

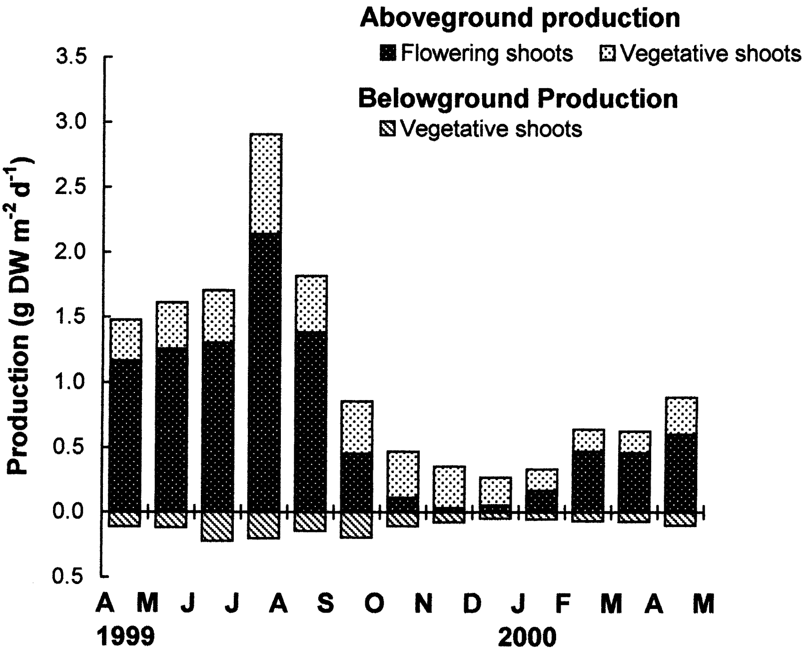

Fig. 6. Seasonal changes in aboveground and belowground net production per area of *Zostera caulescens* in Funakoshi Bay. The data on flowering and vegetative shoots are presented separately.

spadices, sheaths and stems, but do not have major leaves (Den Hartog, 1970). With better light availability at high positions in the water column, flowering shoots of this species may play a major role in primary production (Omori, 1995; Omori and Aioi, 2000). The present study quantitatively demonstrates that the contribution of flowering shoots to net production is larger than that of vegetative shoots, especially during spring to autumn when the seagrass is most productive. *Zostera caulescens* mostly occurs in deep water within multispecific seagrass beds around northern Japan (Nakaoka and Aioi, 2001). Structural characters of flowering shoots are thus well adapted to acquire more light in deep habitats, which results in its high productivity. In contrast, the smaller contribution of vegetative shoots implies that primary production (photosynthesis) may not be their major function. The horizontal expansion of the beds by clonal propagation seems to be the major function of vegetative shoots.Previous studies on the growth pattern of *Z. caulescens* revealed that flowering shoots are transformed from vegetative plants in winter by differentiation of some rhizome tops that produce upright vertical stems (Omori, 1991, 1992, 1995). The decrease in oldest vegetative shoots during winter is thus partly due to their transformation to flowering shoots. Each vegetative shoot supplies one or two branches of rhizomes from the main apex by side-branching just prior to the differentiation (Omori, Y., unpublished data). This accounts for the fact that major recruitment was observed simultaneously between February and May for both flowering and vegetative shoots, although seasonal variation was less obvious for vegetative shoots due to the addition of new shoots throughout the year.

Analyses on shoot age structure revealed that the lifespan of flowering shoots of *Z. caulescens* is quite long: their mean age exceeds that of vegetative shoots in most seasons, with an estimated maximum age of 13 months. In other *Zostera* species, flowering shoots generally emerge just before the flowering season and immediately drop off after seed production (Arasaki, 1950; Aioi, 1980; Olsen and Sand-Jensen, 1994; Laugier et al., 1999). The 13-month maximum lifespan of flowering shoots we found is longer than that of the same species in Sagami Bay, where flowering shoots annually develop from January to August, but die off in September (Omori, 1994). The flowering and fruiting seasons of *Z. caulescens* at our study site are May–June and July–August, respectively (Nakaoka and Aioi, 2001). Thus, the flowering shoots continue to grow for a few months after seed production. The longevity of these flowering shoots suggests that their major functional role may shift from seed production to photosynthesis.

Biomass, growth and production all showed large seasonal variation. The leaf plastochrone interval was more than 2-fold shorter in summer–autumn than in winter–spring, as was the leaf turnover period. Similar large seasonal fluctuations in the leaf plastochrone intervals were observed for *Z. marina* (Sand-Jensen, 1975; Jacobs, 1979; Mukai et al., 1979; Aioi et al., 1981). Growth of shoots and rhizomes of *Z. caulescens* (measured as aboveground and belowground net production per shoot, respectively) and production per area also varied more than 5-fold among seasons, with seasonal patterns (maximum in summer and minimum in winter to early spring) similar to those of *Z. marina* in adjacent Otsuchi Bay (Iizumi, 1996), and those generally reported for temperate seagrass species (Duarte, 1989). In previous studies, seasonal variation in seagrass productivity was explained mostly in relation to variation in light intensity and temperature (Dennison, 1987; Marbà et al., 1996; Laugier et al., 1999). At our study site, peak light availability and temperature occur in the same season (around August), while the lowest temperatures (between March and April) occur ca. 3 months later than lowest light availability (between December and January). Production of aboveground and belowground parts of *Z. caulescens*, both in terms of per shoot and per area, did not increase rapidly after the minimum in winter, but remained at low levels until May. It is likely that the low temperature during early spring may cause the lower growth rate of *Z. caulescens* in this season even though light availability is quite high.

Net production of *Z. caulescens* was slightly lower than most estimates for *Z. marina* but similar to or larger than those for *Z. noltii* and *Z. capricornii* (see Cebrián et al., 1997; Duarte and Chiscano, 1999; for a review). Most of the data for other *Zostera* species were taken from populations at intertidal and shallow subtidal beds (<1 m deep). Thus, the productivity of *Z. caulescens* is quite high despite its distribution in deep water (4–6 m) with low light availability. Aboveground-to-belowground ratio of both biomass and production was much higher than those for other *Zostera* species (Duarte and Chiscano, 1999), due to the presence of large flowering shoots throughout the year.

The annual productivity of *Z. caulescens* at our study site is ca. $190\,\mathrm{g\,C\,m^{-2}}$ (using a conversion equation of $1\,\mathrm{g\,DW} = 0.4\,\mathrm{g\,C}$; Cebrián et al., 1997). Primary productivity of phytoplankton in this area was estimated to be $200\,\mathrm{g\,C\,m^{-2}}$ during February and April (Takahashi, 1991) when the annual primary productivity in the water column is highest due to the occurrence of phytoplankton blooms (Iizumi et al., 1990; Furuya et al., 1993). We conclude that the seagrass bed composed of *Z. caulescens* is one of the major sources of primary production in Funakoshi Bay. The area of the seagrass bed in Funakoshi Bay is estimated to be ca. 0.5 km^2 (Tatsukawa et al., 1996), mostly consisting of *Z. caulescens* (Nakaoka, unpublished data). Assuming constant primary production over the area, the total net annual primary production of the bed is calculated to be 9.5×10^7 g C. *Z. caulescens* thus contributes greatly to primary productivity in the coastal area, without which very low primary productivity is predicted on the deep subtidal bottom with low light conditions.

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References

Aioi, K., 1980. Seasonal change in the standing crop of eelgrass (*Zostera marina* L.) in Odawa Bay, central Japan. Aquat. Bot. 8, 343–354.

Aioi, K., Mukai, H., Koike, I., Ohtsu, M., Hattori, A., 1981. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan. II. Growth analysis in winter. Aquat. Bot. 10, 175–182.

Aioi, K., Komatsu, T., Morita, K., 1998. The world's longest seagrass, *Zostera caulescens* from northern Japan. Aquat. Bot. 61, 87–93.

Aioi, K., Nakaoka, M., Kouchi, N., Omori, Y., 2000. A new record of *Zostera asiatica* Miki (Zosteraceae) in Funakoshi Bay, Iwate Prefecture. Otsuchi Mar. Sci. 25, 23–26.

Arasaki, S., 1950. Studies on the ecology of *Zostera marina* and *Zostera nana* (2). Bull. Jpn. Soc. Sci. Fish. 16, 70–76 (in Japanese with English abstract).

Cebrián, J., Duarte, C.M., Marbà, N., 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 Grass of the World. North Holland Publishing Company, Amsterdam, p. 275.

Dennison, W.C., 1987. Effects of light on seagrass photosynthesis, growth and depth distribution. Aquat. Bot. 27, 15–26.

Duarte, C.M., 1989. Temporal biomass variability and production/biomass relationships of seagrass communities. Mar. Ecol. Prog. Ser. 51, 269–276.

Duarte, C.M., Chiscano, C.L., 1999. Seagrass biomass and production: a reassessment. Aquat. Bot. 65, 159–174.

Environment Agency of Japan, 2000. Threatened Wildlife of Japan: Red Data Book, second ed., vol. 8: Vascular Plants (in Japanese). Japan Wildlife Research Center, Tokyo, p. 660.

Furuya, K., Takahashi, K., Iizumi, H., 1993. Wind-dependent formation of phytoplankton spring bloom in Otsuchi Bay, a ria in Sanriku, Japan. J. Oceanogr. 49, 459–475.

Iizumi, H., 1996. Temporal and spatial variability of leaf production of *Zostera marina* L. at Otsuchi Bay, northern Japan. In: Kuo, J., Phillips, R.C., Walker, D.I., Kirkman, H. (Eds.), Seagrass Biology: Proceedings of an International Workshop, Rottenest Island, Western Australia, 25–29 January 1996. Faculty of Science, The University of Western Australia, Nedlands, pp. 143–148.

Iizumi, H., Furuya, K., Takeuchi, I., Kutsuwada, K., Tada, A., Kawaguchi, K., 1990. Dynamics of nutrients and chlorophyll *a* at Otsuchi Bay: analyses of the data of monthly observation. Otsuchi Mar. Res. Centre Rep. 16, 63–65 (in Japanese).

Jacobs, R.P.W.M., 1979. Distribution and aspects of the production and biomass of eelgrass, *Zostera marina* L., at Roscoff, France. Aquat. Bot. 7, 151–172.

Kouchi, N., Nakaoka, M., 2000. Distribution of encrusting bryozoa on *Zostera caulescens* in Funakoshi Bay, Japan: effects of seagrass vertical structure on epifauna. Biol. Mar. Medit. 7, 247–250.

Kudo, T., 1999. Distribution of seagrasses in Odawa Bay, Central Japan. Bull. Kanagawa Pref. Fish. Exp. Station 4, 51–60 (in Japanese with English abstract).

Laugier, T., Rigollet, V., de Casabianca, M.L., 1999. Seasonal dynamics in mixed eelgrass beds, *Zostera marina* L. and *Z. noltii* Hornem., in a Mediterranean coastal lagoon (Thau lagoon, France). Aquat. Bot. 63, 51–69.

Marbà, N., Cebrián, J., Enríquez, S., Duarte, C.M., 1996. Growth patterns of Western Mediterranean seagrasses: species-specific responses to seasonal forcing. Mar. Ecol. Prog. Ser. 133, 203–215.

Mukai, H., Aioi, K., Koike, I., Iizumi, H., Ohtsu, M., Hattori, A., 1979. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific coast of Japan. I. Growth analysis in spring–summer. Aquat. Bot. 7, 47–56.

Nakaoka, M., Aioi, K., 2001. Ecology of seagrasses *Zostera* spp. (Zosteraceae) in Japanese waters: a review. Otsuchi Mar. Sci. 26, 7–22.

Nakaoka, M., Kouchi, N., Aioi, K., 2000. Growth and shoot dynamics of *Zostera caulescens* Miki in Funakoshi Bay, Japan: how does it maintain high canopy structure? Biol. Mar. Medit. 7, 103–106.

Olsen, B., Sand-Jensen, K., 1994. Demography of shallow eelgrass (*Zostera marina*) populations—shoot dynamics and biomass development. J. Ecol. 82, 379–390.

Omori, Y., 1989. Morphology of the flowering shoot and the leaf of *Zostera caulescens* Miki and *Z. asiatica* Miki (Zosteraceae) (in Japanese with English abstract). Sci. Rep. Yokosuka City Mus. 37, 55–59.

Omori, Y., 1991. Peculiarity of the flowering shoot of *Zostera caulescens* (Zosteraceae). Sci. Rep. Yokosuka City Mus. 39, 45–50 (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., 1993. Zosteraceous species endemic to Japan. Bull. Water Plant Soc. Jpn. 51, 19–25 (in Japanese).

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., 1995. Observations on the growth of erect shoots in *Zostera caulescens* Miki (Zosteraceae). Sci. Rept. Yokosuka City Mus. 43, 41–45 (in Japanese with English abstract).

Omori, Y., Aioi, K., 2000. Seasonal changes of the erect shoot of *Zostera caulescens* Miki (Zosteraceae) in Sanriku Kaigan, northern Honshu. Sci. Rept. Yokosuka City Mus. 47, 67–72 (in Japanese with English abstract).

Sand-Jensen, K., 1975. Biomass, net production and growth dynamics in an eelgrass (*Zostera marina* L.) population in Vellerup Vig, Denmark. Ophelia 14, 185–201.

Shin, H., Choi, H.-K., 1998. Taxonomy and distribution of *Zostera* (Zosteraceae) in eastern Asia, with special reference to Korea. Aquat. Bot. 60, 49–66.

Short, F.T., Duarte C.M., 2001. Methods for the measurement of seagrass growth and production. In: Short, F.T., Coles, R.G. (Eds.), Global Seagrass Research Methods. Elsevier, Amsterdam, pp. 155–182.

Tatsukawa, K., Komatsu, T., Aioi, K., Morita, K., 1996. Distribution of seagrasses off Kirikiri in Funakoshi Bay, Iwate Prefecture, Japan. Otsuchi Mar. Res. Cent. Rep. 21, 38–47 (in Japanese).

Takahashi, K., 1991. Studies on primary production during spring blooms in coastal seas. Masters thesis, Mie University, p. 35.