

Changes in shoot density, biomass and leaf area of *Zostera caulescens* Miki from Summer to Autumn in Funakoshi Bay of the Sanriku Coast, Japan

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The world's longest seagrass, *Zostera caulescens* Miki, is found in Funakoshi Bay along the Sanriku Coast of Honshu Island, Japan. Our study describes the changes in vertical distribution of shoot density, leaf area index (LAI) and biomass of *Z. caulescens* from summer (flowering season) to autumn (preparing for overwintering) in Funakoshi Bay. The samples were collected from a 0.5×0.5 m quadrat at depths of 4.4 m, 10.9 m, 13.3 m, 14.3 m and 15.3 m in July, and, for October, at 5.4 m, 7.4 m, 9.2 m, 12.9 m, and 15.7 m. Above- and below-ground biomass, and flowering and vegetative shoot densities decreased with increasing bottom depth in both summer and autumn seasons except at the shallowest sampling depth, while the maximum above-ground biomass in both seasons was 187.3 g DW/m² at the depth of 7.4 m and 213.5 g DW/m² at the depth of 10.9 m, respectively. Densities of vegetative shoots were greater than those of flowering shoots at each sampling depth in both seasons except a bottom depth of 15.3 m in July. The maximum length of flowering shoots in autumn (737 cm) was greater than in summer (546 cm), and the range of shoot lengths in autumn was wider than in summer. Biomass and densities of vegetative shoots at different depths in autumn were higher than those in summer, and Leaf Area Indices (LAI) of flowering and vegetative shoots at different depths in summer were higher than those in autumn. In addition, the mean LAIs of individual flowering and vegetative shoots in summer were greater than those in autumn as well. These results suggest that *Z. caulescens* has a higher LAI in summer when there is low seawater transparency and after ripening from summer to autumn, it also makes vegetative shoots in preparation for growth during the next spring.

Key words: seagrass, *Zostera caulescens*, shoot, biomass, leaf area, Sanriku

INTRODUCTION

Protecting seagrass involves not just managing the marine environment but also land-based activities. Farmers and developers inadvertently contribute to soil erosion, killing the seagrass with river-borne sediments and nutrients that screen the light the seagrass needs to survive (Finkel 1997). Seagrass is known as the canary of the sea for its ability to signal changes in the marine environment, and it is disappearing due to the activities of farmers and developers in many areas (Finkel 1997). They also are vulnerable to physical perturbations caused by severe climatic conditions or human activities (e.g. eutrophication) and therefore vary in aerial cover due to shoot mortality (Shepherd et al. 1989). Recent die-offs occurring throughout the world have caused concern (Robblee et al. 1991, Quammen and Onuf 1993).

Seagrass are known as prominent components of coastal ecosystems, where they sustain high primary production (den Hartog 1979, Duarte 1989, Hilman et al. 1989, Duarte and Chiscano 1999, Vermaat et al. 1995, Agawin et al. 1996), and host a wide variety of associated fauna including commercially important fishes and endangered marine mammals such as dugongs and manatees (Heinsohn et al. 1977, Bell and Pollard 1989). They provide nursery habitats for fishes (Orth et al. 1984), and seagrass beds also contribute to marine environments by stabilizing bottom sedi-

ments and helping to maintain coastal water quality and clarity (Ward et al. 1984).

In Japan, 16 species of seagrass have been recorded from different areas (Aioi 1998). Among them, eelgrass *Zostera marina* L. is one of the most important due to its distribution area. However, in the Seto Inland Sea, more than 70% of *Z. marina* beds have been lost since 1977, which seriously affected coastal fisheries (Komatsu 1997, Aioi 1998). The decreases in eelgrass beds in Japan are due to environmental destruction, particularly by reclamation projects and by water pollution near inlets (Numata and Furota 1997, Hayashida 2000). For example, *Z. marina* and *Z. caulescens* have also disappeared from the bay head of Tokyo Bay (Aioi 1989). In Odawa Bay near Tokyo, the distribution of subtidal seagrass has changed, because compared with 1977, a remarkable decline and disappearance of *Z. marina* has been observed while *Z. caulescens* has increased in a limited area (Kudo 1999). However the cause of this change is still unclear because the ecology of the latter species isn't well known.

Zostera caulescens Miki is an endemic species of north-east Asia and is distributed in Funakoshi Bay along the Sanriku Coast of Honshu, adjacent to the western North Pacific. It grows up to 7 m long and is reported to be the longest seagrass in the world (Aioi et al. 1998). This species is distributed from a depth of 4 m to 16 m (Sultana and Komatsu 2002, Tatsukawa et al. 1996). The biomass of

the above-ground part of *Z. caulescens* in Funakoshi Bay was greatest in summer and minimal in winter (Nakaoka et al. 2000). Flowering (erect) shoots had fallen in winter and vegetative shoots grew up in the next spring (Nakaoka et al. 2000). However, differences of both flowering and vegetative shoots at different depths along the bottom between summer and autumn have not been examined. Not only to conserve the seagrass, but also to understand its change in distribution, it is necessary to know its biological and ecological characteristics. This study attempted to clarify the changes in the vertical distribution of biomass, shoot density and leaf area index (LAI) of *Z. caulescens* from summer to autumn.

MATERIALS AND METHODS

Sampling area

The present study was performed in Funakoshi Bay (39°22.5'N, 141°57'E) along the Sanriku Coast of Honshu, Japan, in the western North Pacific (Fig. 1) during summer and autumn, which are the seasons of maximal biomass of the above-ground part of *Z. caulescens* in Funakoshi Bay (Nakaoka et al. 2000). We studied the shoot density and biomass of this seagrass and their relationship to bottom depth by sampling the plants in quadrats by SCUBA diving at depths (datum level: lowest low water based on tide tables (Anon 2000, 2001) of 4.4 m, 10.9 m, 13.3 m, 14.3 m, and 15.3 m in Funakoshi Bay in summer 2000 and at depths of 5.4 m, 7.4 m, 9.2 m, 12.9 m and 15.7 m in autumn 2001. Destructive plant density determinations were adapted according to techniques proposed by Dennison (1990) using a 0.5 m×0.5 m quadrat, each sampling time. Bottom depths of sampling stations were measured by a depth gauge for diving.

Sample collection and sorting

The seagrass samples were stored in 5% formalin in plastic bags. Plant material was rinsed in fresh water and cleaned of sand and shells in the laboratory. Samples were also sorted into above- and below-ground parts. Leaves and stems that were encrusted by epiphytes were soaked in 4% acetic acid for two hours (Mazzella and Ott 1984) to dissolve the calcareous crusts.

Shoot density and leaf area index (LAI)

Both the shoot density and length of foliar portions were measured. Shoot density refers only to the above-ground foliar portions of the plant and is expressed as the number of seagrass shoots per unit area (hereafter, we use shoots/m²). Shoot length (i.e. length from the bottom end of shoot to the top of the blade) was measured by a centimeter scale. Leaf length and width were measured by a millimeter scale to calculate leaf area index (LAI). LAI is expressed as one-sided leaf area per unit ground area (hereafter, we use m²/m²).

Biomass

The dry weight of every shoot and root of the samples were measured after drying them at 60°C for 48 h in a hot air oven (DX300, Yamato Scientific Co. Ltd.) to obtain above- and below-ground biomass. Biomass is expressed as dry weight (g) in unit area (hereafter, we use g DW/m²),

which is the most widely used expression for biomass.

RESULTS

The size of the shoots of *Z. caulescens* varied widely during both seasons and the shoots with lengths greater than 80 cm were classified as flowering shoots. In summer, the shoot lengths ranged from 4–546 cm (a depth of 13.3 m) at the five different sampling depths (Fig. 1a). The number of shoots was the greatest in the size class of shoot lengths less than 40 cm at all depths except at a depth of 14.3 m, where the class between 40 and 80 cm was the greatest. In autumn, the shoot lengths ranged from 2–737 cm (a depth of 9.2 m) at all depths, and the number of shoots was greatest at shoot lengths less than 40 cm at all depths (Fig. 1b). Nakaoka et al. (2000) examined the lengths of flowering and vegetative shoots in Funakoshi Bay in July and August, and they reported that the length range of vegetative shoots and flowering shoots were 19–98 cm and 96–445 cm in July and 24–87 cm and 84–471 cm in August, respectively. According to Fig. 1 and the observations by Nakaoka et al.

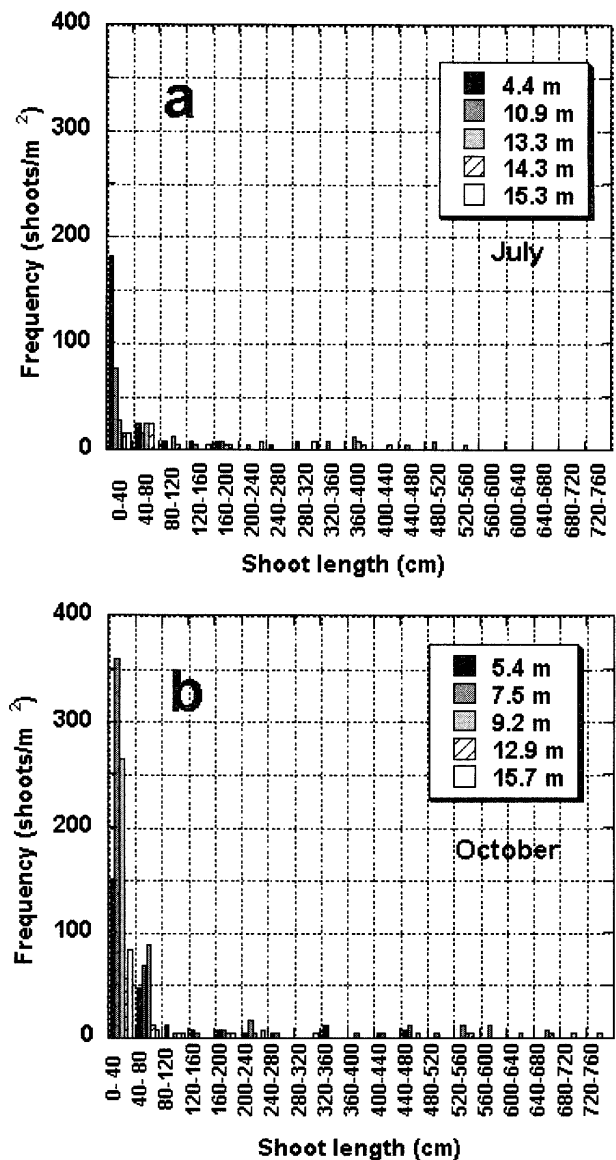


Fig. 1. Shoot length frequency of *Zostera caulescens* at five different bottom depths in Funakoshi Bay in July (a) and in October (b).

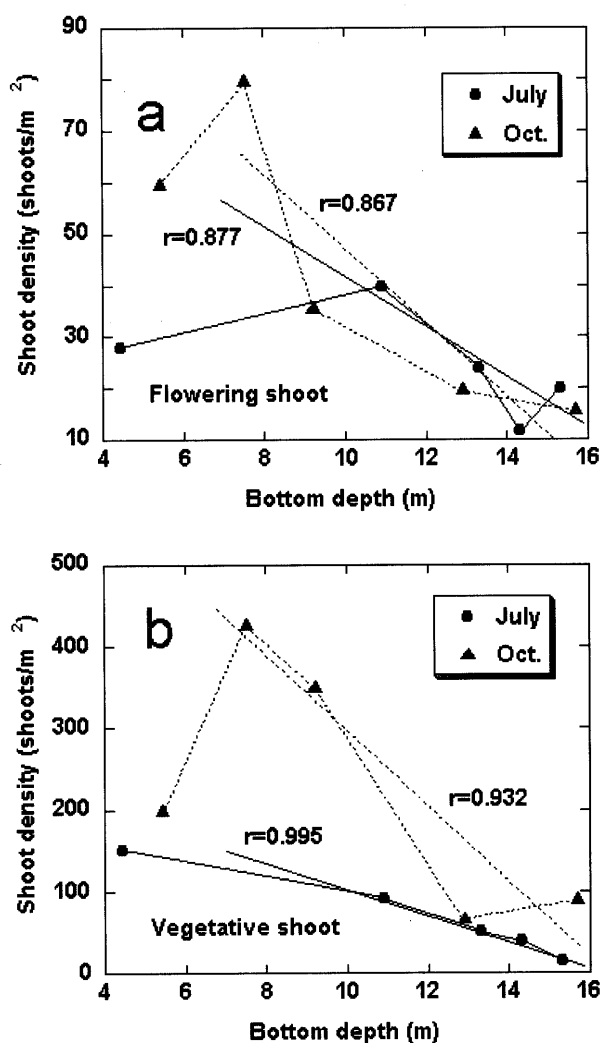


Fig. 2. Shoot densities of *Zostera caulescens* per m² at five different bottom depths in July (closed circles) and in October (closed triangles). The upper panel (a) and lower panel (b) correspond to flowering shoot densities (>80 cm) and vegetative shoot densities (≤80 cm). Regression lines showing the relationship between shoot densities and bottom depths except at the shallowest bottom depths in July and in October are represented with solid and dotted lines, respectively.

(2000), we grouped shoots into two categories with lengths above and below 80 cm for further analysis. We assumed that these two sizes roughly correspond to vegetative and flowering shoots, and therefore it was clear that the number of vegetative shoots less than 80 cm increased from summer to autumn at all depths.

Shoot density

The shoot density of *Z. caulescens* including flowering and vegetative shoots at each station in summer and in autumn ranged between 36 (a depth of 15.3 m) and 180 shoots/m² (a depth of 4.4 m), and 88 (a depth of 12.9 m) and 508 shoots/m² (a depth of 7.5 m), respectively. The densities of vegetative shoots were greater than those of flowering shoots at each station in both seasons except at a bottom depth of 15.3 m in July (Fig. 2).

In summer, the vegetative shoot density decreased from the shallowest bottom depth of 4.4 m (152 shoots/m²), to the deepest bottom depth of 15.3 m (16 shoots/m²). However,

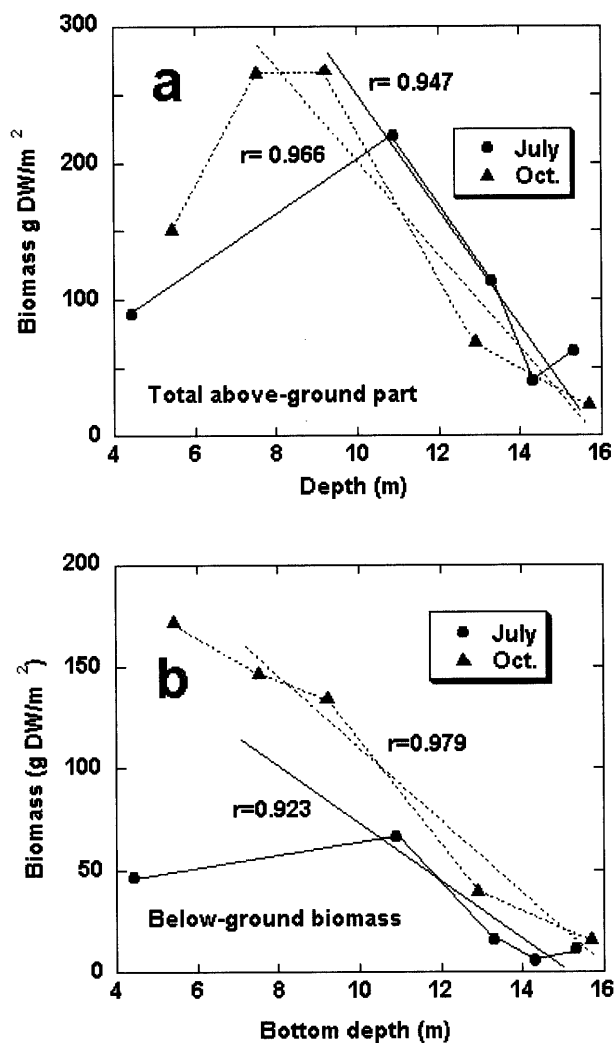


Fig. 3. Total above-ground biomass (a) and below-ground biomass (b) per m² at five different bottom depths in July (closed circles) and in October (closed triangles). Regression lines showing the relationship between biomass and bottom depths, except for the shallowest depths in July and in October are represented with solid and dotted lines, respectively.

the flowering shoot density was the greatest (40 shoots/m²) at the depth of 10.9 m and the lowest (12 shoots/m²) at the depth of 14.3 m. In autumn, the vegetative shoot density ranged from 68–428 shoots/m² and flowering shoots ranged from 16–80 shoots/m² (Fig. 2). Vegetative shoot density was the highest (428 shoots/m²) at the bottom depth of 7.5 m and the lowest (68 shoots/m²) at the bottom depth of 12.9 m. Vegetative shoot densities along the bottom depth in autumn were greater than those in summer.

Biomass

In both seasons, the above- and below-ground biomass of *Z. caulescens* had a tendency to be negatively correlated to the bottom depth except at the shallowest sampling depths (Fig. 3). In summer, the above- and below-ground biomass ranged between 40.2 (a bottom depth of 14.3 m) and 220.6 g DW/m² (a bottom depth of 10.9 m) and between 6.1 (a bottom depth of 14.3 m) and 66.7 g DW/m² (a bottom depth of 10.9 m), respectively (Fig. 3). In autumn, the above- and below-ground biomass were the greatest (268.8 g DW/m²) at a bottom depth of 9.2 m and (172.7 g DW/m²) at a bottom

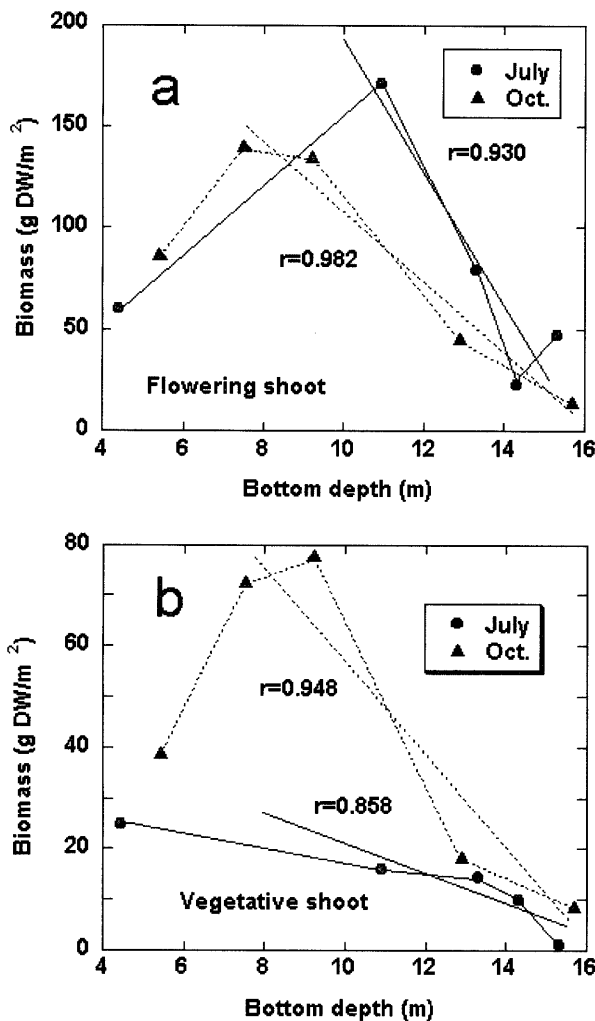


Fig. 4. Above-ground biomass of flowering (a) and vegetative (b) shoots per m² at five different bottom depths in July (closed circles) and in October (closed triangles). Regression lines showing the relationship between biomass and bottom depths except for the shallowest depths in July and in October are represented with solid and dotted straight lines, respectively.

depth of 5.4 m, and the lowest (24.0 g DW/m²) and (16.5 g DW/m²) at a bottom depth of 15.7 m, respectively (Fig. 3).

The biomass of vegetative and flowering shoots were negatively correlated to the bottom depth except the shallowest sampling depths in both seasons (Fig. 4). The biomass of flowering shoots along the bottom in summer were greater than those in autumn while the biomass of vegetative shoots at different bottom depths in summer were smaller than those in autumn. In summer, the biomass of vegetative shoots ranged between 1.3 (a depth of 15.3 m) and 25.2 g DW/m² (a depth of 4.4 m) and decreased with increasing bottom depth. Flowering shoot biomass was the greatest (171.2 g DW/m²) at a bottom depth of 10.9 m and the lowest (23.5 g DW/m²) at a bottom depth of 14.3 m, and decreased with increasing bottom depth below depths of 10.9 m. In autumn, the flowering shoot biomass was the greatest (140.8 g DW/m²) at a bottom depth of 7.5 m and the lowest (14.2 g DW/m²) at a bottom depth of 15.7 m. The biomass of vegetative shoots and flowering shoots tended to decrease with increasing bottom depth, except at 5.3 m. Vegetative shoot biomass was the greatest (77.9 g DW/m²)

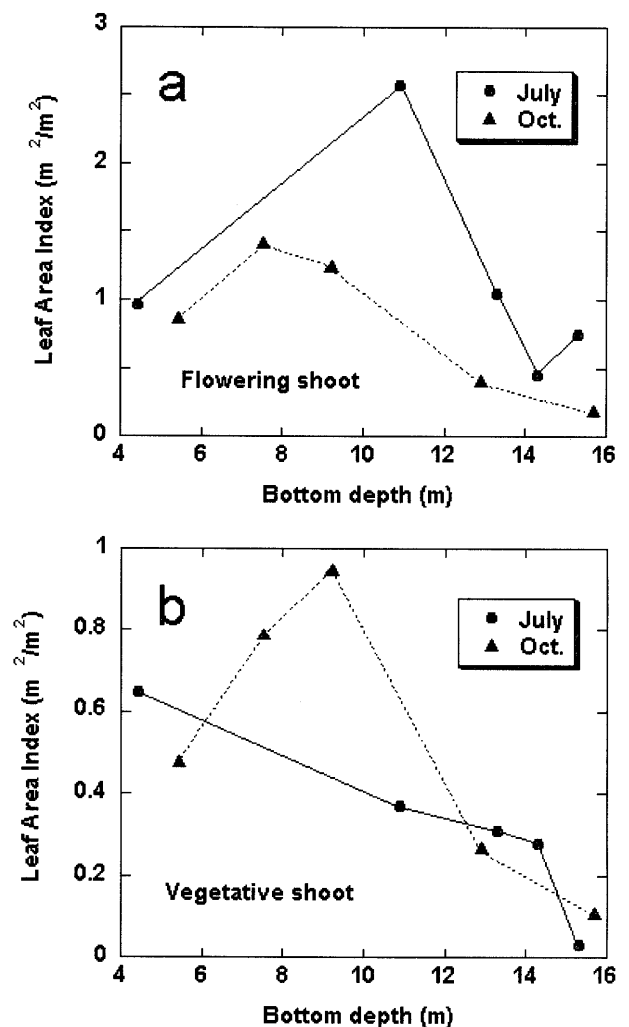


Fig. 5. Leaf Area Index of flowering (a) and vegetative (b) shoots per m² at five different bottom depths in July (closed circles) and in October (closed triangles).

at a bottom depth of 9.2 m and the lowest (8.8 g DW/m²) at a bottom depth of 15.7 m (Fig. 4).

Leaf area index (LAI)

The LAIs of vegetative and flowering shoots in both seasons appeared to be related to the bottom depth and the season. The maximum LAI of flowering shoots along the bottom in summer was higher than that in autumn, while that of vegetative shoots in autumn was higher than in summer. In summer, the LAI of flowering shoots of *Z. caulescens* was the greatest (2.57 m²/m²) at the bottom depth of 10.9 m and the lowest (0.45 m²/m²) at the bottom depth of 14.3 m. The LAI of vegetative shoots was the greatest (0.65 m²/m²) at the shallowest depth (4.4 m) and the lowest (0.03 m²/m²) at the deepest depth (15.3 m) (Fig. 5). In autumn, the LAI of flowering *Z. caulescens* was the greatest (1.42 m²/m²) at a depth of 7.5 m and the lowest (0.19 m²/m²) at a bottom depth of 15.7 m. The LAI of vegetative shoots ranged between 0.11 (a depth of 15.7 m) and 0.95 m²/m² (a depth of 9.2 m).

The relationships of LAI to biomass of flowering in July and October (Fig. 6) were examined with the null hypothesis that the slopes of two regression lines are equal. These hypothesis were rejected by ANCOVA ($P < 0.002$). The null

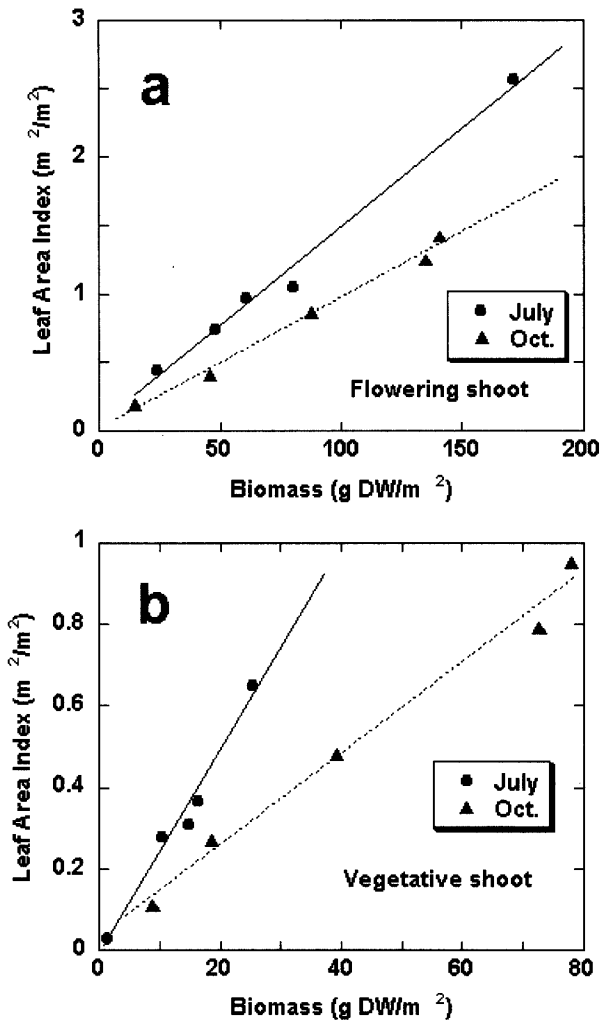


Fig. 6. Leaf Area Index to biomass of flowering (a) and vegetative (b) shoots per m² in July (closed circles) and in October (closed triangles). Regression lines showing the relationship between LAI and biomass except for the shallowest depths in July and in October are represented with solid and dotted straight lines, respectively.

hypothesis that the slopes of the two regression lines of vegetative shoots in July and in October are equal was also rejected by ANCOVA ($P < 0.003$, respectively). Therefore, LAI in relation to biomass of both shoots in July were significantly greater those in October.

The LAI of the flowering and vegetative shoots in July and October were compared. The mean values of LAI per flowering shoot at five bottom depths in July were greater than in October and this was also true for vegetative shoots (Fig. 7).

DISCUSSION

The erect flowering shoots of *Z. caulescens* typically lay down or detach from the subterranean stem after ripening. In Sagami Bay, Omori (1994) observed no flowering shoots but only vegetative shoots in September. In Funakoshi Bay, flowering shoots of *Z. caulescens* were found erect at bottom depths of 5.4–15.7 m in late October. Omori and Aioi (2000) also studied their flowering shoots at depths of 5.5 m and 7.5 m in Funakoshi Bay in mid-October and in mid-November by sampling 11 to 12 shoots. They observed that

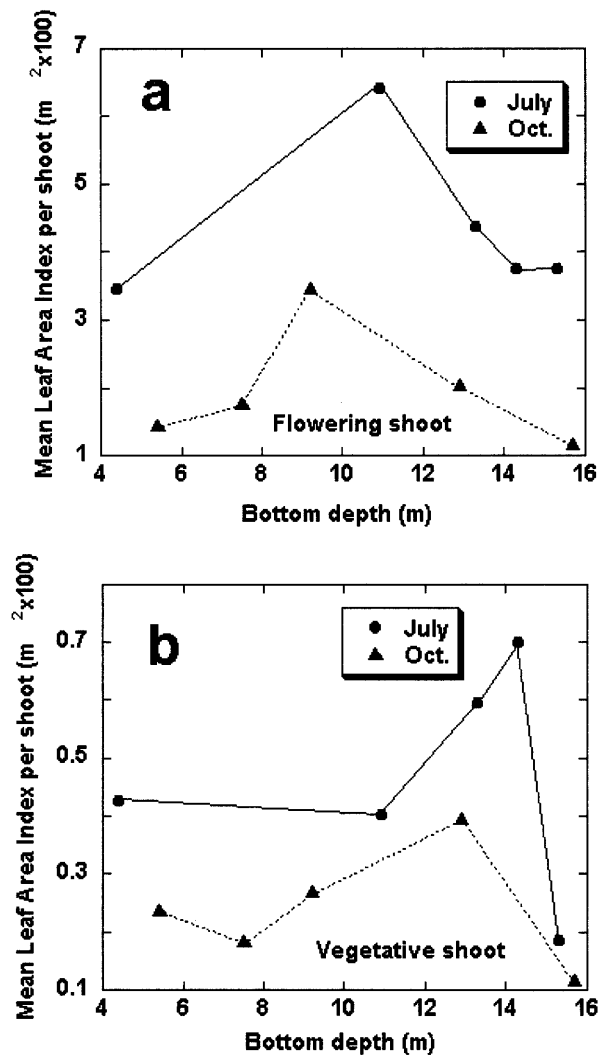


Fig. 7. Mean Leaf Area Index per shoot per m² in July (closed circles) and in October (closed triangles) of flowering (a) and vegetative shoots (b).

flowering shoots lay on the bottom in November but not in mid October. Our results corresponded to Omori and Aioi’s (2000) observations of the erect flowering shoots even in different observation years and could extend their observation to flowering shoots at a depth of 15.7 m in October.

The flowering shoots of this species appear to reach great lengths because they continue to grow even after flowering and production of fruits. Omori (1991) made comparative observations of the young and mature flowering shoots of *Z. Caulescens* in Sagami Bay based on longitudinal and serial cross sections. His observations showed that the apex of the flowering shoots have indeterminate growth that continues to elongate the shoot after the ripening of the fruit. Shoot growth was stopped in August in Sagami Bay due to high water temperature above 25°C from August to September (Omori, 1991). On the other hand, our observations showed that the flowering shoots grew on bottom depths of 4–5 m to 15–16 m from July to mid October in Funakoshi Bay. The difference in shoot growth between Funakoshi Bay and Sagami Bay is probably due to the difference in water temperature. The maximum water temperature in Otsuchi Bay neighbouring to Funakoshi Bay in a year was still under 25°C (21.2°C) lower than in Sagami Bay

from summer to autumn (Omori and Aioi 2000). Because this maximum water temperature is also applicable to Funakoshi Bay, flowering shoots continue to grow even in mid October.

It is very interesting to consider why the maximum total length of flowering shoots of *Z. caulescens* can reach 6–7 m (Aioi et al. 1998, Sultana and Komatsu 2000), but the shoots were much shorter in shallower depths. Only *Z. caulescens* have blades at the apex of the flowering shoots, which is different from other *Zostera* species (Omori 1991), and this can be explained as an adaptation of *Z. caulescens* to acquire light in a low light environment. At the shallowest depths in both seasons the maximum shoot lengths were less than the bottom depth even though *Z. caulescens* can grow to 6–7 m in shoot length. This fact suggests that it is difficult for the flowering shoots to grow parallel to the sea surface due to the drag forces of the wind and waves in the surface layer, which can cause the blades to break off. As a consequence, the lengths of flowering shoots at the shallowest depths are limited by the water depth and are smaller than those at deeper bottom depths where the seagrass can grow nearly to the sea surface. However, the flowering shoots may be limited by the light availability per shoot at these deeper bottom depths.

Nakaoka and Aioi (2001) concluded that *Z. marina* had no consistent tendency between shoot density and bottom depth. However, shoot densities of *Z. caulescens* along the bottom in Funakoshi Bay were proportional to the bottom depth except at the shallowest depths, which are protected from waves and currents by the breakwaters. The biomass of above-ground parts, flowering shoots and vegetative shoots of *Z. caulescens* were all negatively proportional to the bottom depth, as were the flowering and vegetative shoot densities. Nakaoka and Aioi's conclusion was based on the data of *Z. marina* growing on the bottom at depths shallower than 5 m in various areas with different light attenuation coefficients in seawater. In our case, the densities of flowering and vegetative shoots were obtained from a wide range of bottom depths in the same area where the light attenuation coefficients may be nearly the same except at the shallowest depths. Thus, in Funakoshi Bay, the shoot densities depended on the depth, which is negatively proportional to light availability.

The production of vegetative shoots appears to be related to the side-branching of rhizomes and the season. The vegetative shoots of the rhizomes differentiate into flowering shoots after supplying one or two branches (Omori 2002). Some branches of the rhizome don't become flowering shoots and differentiate into flowering shoots in the next year. Since *Z. caulescens* stop producing flowering shoots by autumn, the vegetative shoot densities continue to increase from summer to autumn. Nakaoka et al. (2000) studied the shoot age structure of *Z. caulescens* at a depth of 4–6 m in Funakoshi Bay from February to November and stated that the recruitment of vegetative shoots was low between June and October. However, our results suggest that the side-branching of rhizomes occurred from July to October and a greater number of vegetative shoots had accumulated by mid October (Fig. 1).

Compared to of *Z. marina* in some shallow areas, *Z. caulescens* may have a lower biomass. The maximum and

minimum biomass of *Z. marina* growing at depths of about 5 m in Otsuchi Bay was 370 g DW/m² in June and 30 g DW/m² in January (Iizumi 1996). At depths between 4 m and 5 m in Iida Bay the maximum and minimum biomass of *Z. marina* was 170 g DW/m² in July and 20–30 g DW/m² in November (Taniguchi and Yamada 1979). The above-ground biomass of *Z. caulescens* at a depth of 4.4 m in July and at 5.4 m in October during the season of long flowering shoots in Funakoshi Bay (90 g DW/m² in July and 152 g DW/m² in October) were less than those of *Z. marina* at similar depths in the season.

Seagrass roots develop not only to absorb nutrients but also to prevent the shoots from being broken off the substrate by the drag forces caused by waves and currents. Guidetti et al. (2002) stated that the below-ground components have an important structural role, such as mechanically anchoring the plants to the substrate, which accounts for the stability and persistence of seagrasses. Because the water movements by waves and currents are stronger at shallower bottom depths, it is likely that *Z. caulescens* growing at shallower bottoms need to develop larger below-ground components (root systems) than those on deeper bottoms, to anchor against the water movement. In fact, the below-ground components *Z. caulescens* that developed at shallower bottom depths in Funakoshi Bay were greater than the below-ground biomass at deeper bottom depths. However, another factor is that when the flowering shoots become taller with a similar leaf area, the drag force by waves and currents becomes stronger because the leaves approach the sea surface. Plants have to develop larger below-ground components to mechanically anchor them against stronger drag force in shallower layer, and because of the taller total lengths of *Z. caulescens* in October there is a greater need for the below-ground component than in July. Therefore the below ground-part, which is important for holding the plant on the bottom, appears to be proportional to the bottom depth due to the increased wave action, but also to the length of the shoots.

The LAI of different species of *Z. marina* at shallower depths appears to be higher than for *Z. caulescens* at slightly deeper depths. From various studies in Japan, the maximum LAI of *Z. marina* observed in Mangoku-Ura was 15–19 m²/m² (Mukai 1982), in Odawa Bay, 5.1–5.5 m²/m² (Aioi 1980) and in Otsuchi Bay, 3.2–4.8 m²/m² at bottom depths of 1–3 m (Aioi and Komatsu 1996). Our results provide new information on the total LAI of *Z. caulescens* including both flowering and vegetative shoots. These values ranged from 0.7 m²/m² to 2.9 m²/m² in July and from 0.3 m²/m² to 2.2 m²/m² in October at the depths of 4–5 m to 15–16 m, and were smaller than the LAIs of *Z. marina* at a shallower depth. It is possible that the differences in LAI between *Z. marina* and *Z. caulescens* is attributed to the light environment at different bottom depths and the morphological differences in their leaves that include the numbers of leaves and the shoot lengths.

The size of the leaves as measured by the LAI is very important for seagrass to survive at deeper depths because photosynthesis is limited by the light availability at the greater depths. In summer, the transparency of seawater measured with a secchi disk at the mouth of Otsuchi Bay neighboring Funakoshi Bay in August (6.5 m) and in

October (20 m) was the worse and the best in a year, respectively (Iizumi, unpublished). The LAI of flowering and vegetative shoots along the bottom in July was greater than that in October, so water transparency is one possible explanation for the seasonal change in LAI observed in this study. The ratio of LAI to biomass and mean LAI per shoot suggest that the seasonal change in LAI of flowering shoots can be explained by compensation for the lower transparency in summer than in autumn or that they are attempting to accumulate energy in summer for fruiting by increasing its LAI. The increase in mean LAI of vegetative shoots may also be a response to compensate for the lower light environment in summer.

CONCLUSION

In summer and autumn the shoot density and biomass of vegetative and flowering shoots of *Z. caulescens* were negatively proportional to bottom depth. This study also showed that *Z. caulescens* adapts to physical environmental factors such as light and water movement by varying shoot density, shoot lengths and above- and below-ground biomass. The biomass and densities of vegetative shoots at different bottom depths in autumn were higher than those in summer. However, the LAI of flowering and vegetative shoots at different depths in summer were higher than those in autumn. These results suggest that *Z. caulescens* has an increased LAI in summer, when there is the lowest transparency of seawater and then after its fruits ripen from summer to autumn, it also makes vegetative shoots for preparing for growth in the next spring. This ability of *Z. caulescens* to adapt to environmental conditions enables this species to grow in a wide range of bottom depths from depths of 4–5 m to 15–16 m.

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