生物圏科学
Biosphere Sci.
54 : 29－44 (2015)

Production of *Zostera marina* with different shoot size and stand structures in the Seto Inland Sea, Japan – production in the luxuriant season in 2012 –

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Abstract In June 2012, production was measured and compared among *Zostera marina* stands with different shoot sizes and stand structures, at a total of seven stations in three *Z. marina* beds in the Seto Inland Sea, Japan. Production per shoot depended on the shoot size, and was larger (50.9 - 73.2 mg DW shoot $^{-1}$ d^{-1}) at the stands in the bed of Ikuno-shima Is. (Hiroshima Pref.; Aki-Nada Sea), where large shoots formed stands with lower densities, than at stands in the bed of Heigun-jima Is. (Yamaguchi Pref.; Suo-Nada Sea) (7.7 - 27.4 mg DW shoot $^{-1}$ d^{-1}) where small shoots exhibited higher densities. Though the areal production estimated was compensated by shoot density, it was still larger at the bed of Ikuno-shima Is. (2.89-5.38 g DW m^{-2} d^{-1}) than at Heigun-jima Is. (1.63 - 2.56 g DW m^{-2} d^{-1}). Sediment characteristics were quite different between the two *Z. marina* beds and considered to affect the stand structures and productivity, *i.e.*, the sediment at Ikuno-shima Is. was muddy and rich in organic matter and the sediment at Heigun-jima Is. was dominated by sand indicating severer physical conditions induced by waves.

In Aba-shima Is. (Hiroshima Pref.; Aki-Nada Sea), the third research site, the *Z. marina* bed was on the way of recovery after catastrophic damage due to heavy grazing of rabbitfish (*Siganus fuscescens*) which had occurred in autumn of 2011, and young shoots developed from seeds forming a patchy stand with a low shoot density and biomass. Though the production was lowest (0.60 g DW m^{-2} d^{-1}), the turnover of the biomass was higher (6.5 % d^{-1}) at the stand in Aba-shima Is. than values (1.7-3.3% d^{-1}) at the other two beds.

Keywords: biomass, production, shoot size, stand structure, *Zostera marina*

INTRODUCTION

Seagrass *Zostera marina* forms dense beds and contributes substantially to coastal primary production (Sand-Jensen, 1975; Jacobs, 1979), providing variable ecosystem services which benefits human welfare (Costanza *et al.*, 1997). Because of its ecological and industrial importance, production of this cosmopolitan species has been evaluated worldwide (Duarte and Chiscano, 1999).

Though it is a cosmopolitan species, recent studies have shown extensive genetic variations among *Z. marina* populations observed within its regional or, in some cases, local distributions (Rhode and Duffy, 2004; Ort *et al.*, 2012; Shimabukuro *et al.*, 2012). In addition, diversities in shoot morphology

Accepted on September 9, 2015 ＊ E-mail: gorogoro@affrc.go.jp

and structures of stands are often observed even within the same sea area. In previous papers (Yoshida *et al.*, 2013ab), we reported both shoot size and stand structures were highly variable among *Z. marina* populations in the western Seto Inland Sea and eastern area of Bungo-Channel. There, shoot size and density exhibit a reciprocal pattern among (or often within) local *Z. marina* populations, where *Z. marina* with smaller shoots tends to have a higher density, and *vice versa*. Though similar results have been obtained in other regions (Aioi, 1980), it has not been examined how the ecological potentials and functions of those *Z. marina* stands differ.

In this study, we conducted a preliminary survey in the Seto Inland Sea to compare the primary production among *Z. marina* with different shoot sizes and stand structures. Based on this research, we wish to answer: how differences arise under approximately identical climatic conditions due to their close proximity? Can smaller *Z. marina* shoots compensate for their productivity by higher densities or higher turnover rates? Production measured in this study is also compared with values obtained in other regions worldwide to understand the ecological characteristics of *Z. marina* in the Seto Inland Sea.

These results offer better understanding of the ecological diversity of *Z. marina* populations in the relevant sea area, and ideas for the preservation measures of this ecologically important species.

Materials and methods

This study was conducted in June 2012, when *Z. marina* in the Seto Inland Sea is most luxuriant (Fujiwara *et al.*, 2009) and is supposed to show the highest production in a year.

Study sites

Three subtidal *Zostera marina* beds with different characteristics were chosen. That is, 1): a bed occupied by relatively large shoots, 2): by smaller shoots but with a higher density, and 3) by young shoots which had just grown up from seedlings germinated during the last winter to spring. The topographic characteristics were also quite different among the three beds.

The bed 1) was located at Ikuno-shima Is. in the Aki-Nada Sea, one of the sub-sea areas of the Seto Inland Sea (Figs 1, 2). The *Z. marina* bed was formed within a vast, sheltered inlet with most of the area shallower than 1.0 m in depth (below Chart Datum Level; depths are stated based on the same criterion in the following description). The *Z. marina* bed occupied ca. 21 ha in the inlet area. Three stations for production measurements were set, two (St. 1 and St. 2, 0.2 and 0.4 m in depth, respectively) at the innermost area, and one (St. 3, depth; 0.6 m) near the mouth of the inlet (Fig. 2).

The bed 2) was located at Kona of Heigun-jima Is., in the Iyo-Nada Sea, and formed in a relatively open inlet and within a depth range of 0-6 m (Figs 1, 2). The area of the bed was estimated to be ca. 0.6 ha. Three measurement stations were set along the depth gradient of the bed, which was St. 5 (depth; 0.2 m), St. 6 (1.2 m) and St. 7 (3.1 m) (Fig. 2).

The bed 3) was located at Aba-shima Is., which is adjacent to Ikuno-shima Is. (Fig. 1). The *Z. marina* bed was formed in front of an open beach on the western coast of the island, exhibiting a belt-like form with an estimated area of ca. 1.5 ha (Fig. 2). Originally, *Z. marina* distributed from 0 to, at least, 3 m in depth, but the stand had been damaged and disappeared due to grazing by rabbitfish, *Siganus fuscescens*, in the autumn of 2011. When we conducted this study (June 2012), the *Z. marina* stand was composed of numbers of young shoot patches. From the morphology of their rhizomes with nodes per shoot in relatively small numbers, we made sure that these shoot patches were originated from one or a few seedlings and their subsequent laterally-branching. Production measurements were

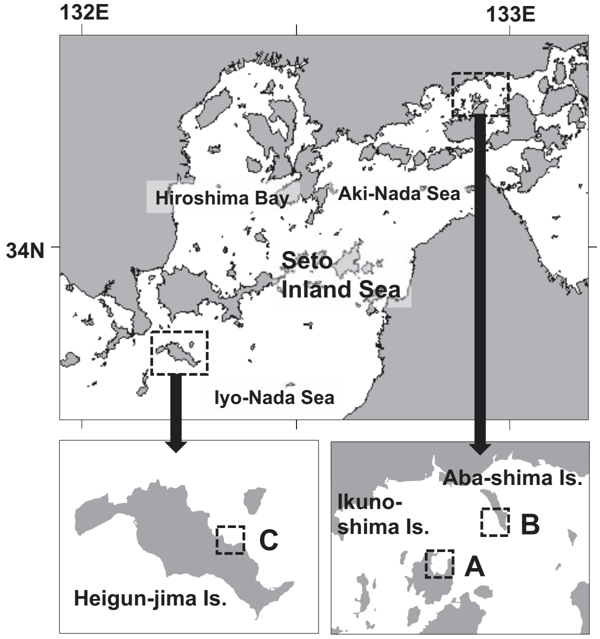

Fig. 1.Three study sites (islands) where the *Zostera marina* beds examined in this study are located. The grids A, B and C indicate the locations of the *Z. marina* beds, which coincide with those shown in Fig. 2.

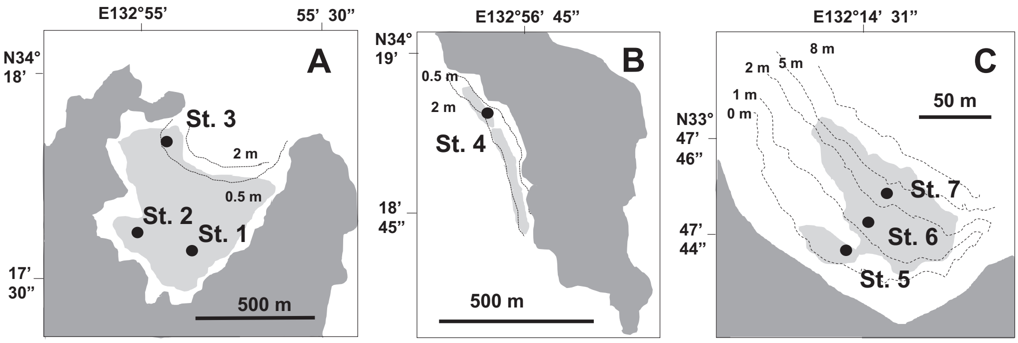

Fig. 2.Topography of the three *Z. marina* beds (area shaded light gray) and locations of the seven stations where production of the *Z. marina* stands was measured. A: the *Zostera* bed in Ikuno-shima Is., B: in Aba-shima Is., C: in Heigun-jima Is.

conducted on these shoots at the point of 0.6 m in depth (Fig. 2, St. 4).

Shoot size, density and biomass of *Zostera marina*

Shoot size, density and biomass were surveyed at the 7 stations in early June 2012. At each station, three 50 × 50 cm quadrats were set in the *Z. marina* stand. All shoots within the quadrat were sampled with their rhizomes and roots using a shovel, and put in a mesh bag. Dead rhizomes which were black in color and fragmented were discarded. After being brought back to a laboratory, vegetative and flowering shoots in each bag were counted respectively. Then each shoot was separated into the above- and under-ground parts using a knife, at the root primordium close to the meristematic region assumed to be the boundary of the both parts (Yoshida *et al.*, 2013a). The above-ground part (sheath and leaves) of each vegetative shoot was measured in total length (as ‘shoot length’) and the maximum width of the leaf just above the sheath. The below-ground parts of vegetative and flowering shoots were separated into rhizomes and roots. The length and major axis in the section of the second rhizome node of each vegetative shoot were measured. The weight of each part was determined after being dried under 85 ℃ for a few days.

***Zostera marina* production measurement**

In this study, production of *Zostera marina* was measured by a leaf-marking technique, a common method for seagrass production measurements (Short and Duarte, 2001). For the estimation of the above-ground part (*i.e.*, leaves) production, we used the ‘conventional’ leaf-marking method (Fig. 3) so-called by Gaeckle and Short (2002), and for the below-ground part (rhizomes and roots) production, we took a more improved and recommended (Short and Duarte, 2001) method (the plastochrone method) based on the plastochrone interval (the time interval between the new initiation of two successive leaves on one shoot) determined by the leaf-marking (Fig. 3).

On the same day as the quadrat sampling, we pierced pin-holes using a needle in the leaf bundle just above the sheath of each vegetative shoot (Fig. 3). This marking method was carried out on 30 vegetative shoots at each station and marked shoots were distinguished by being tied with pink-colored tape at their base. After 2 weeks, marked shoots were recovered with their rhizomes and roots and brought back to the laboratory. Tissues needed for the production measurement were sampled (see below), dried and weighed in the same way as the biomass measurement.

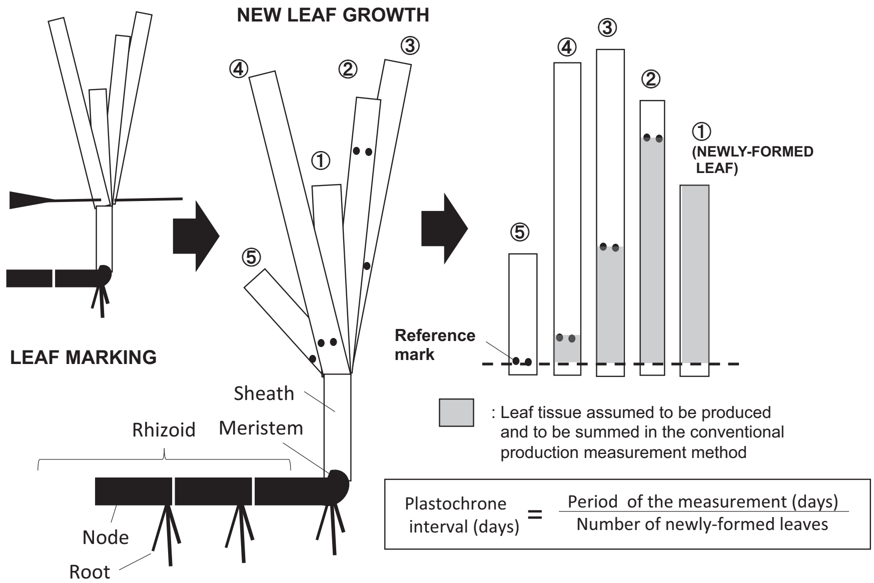

Fig. 3.Leaf-marking method in *Z. marina* production measurement (modified figure of Short and Duarte, 2001). The ‘conventional method’ (Gaeckle and Short, 2002) of the production measurement and determination procedure of plastochrone interval are shown.

For each marked shoot, leaf production was determined from the weight of leaf tissue between the reference pin-hole, being marked on the outermost (and the oldest) leaf assumed to have terminated growth, and the holes on the younger leaves that has moved up as they grow (Fig. 3). Leaves newly-formed during the period and distinguished by being without pinholes were counted for each shoot and the plastochrone interval was determined (Fig. 3). The weight of new leaves was also added to the leaf production. This 'conventional' method has been reported to possibly miss the maturation of leaf tissues above the holes and growth of newly-formed leaves enclosed in a sheath (therefore, invisible) and cause an underestimation of the production (Gaeckle and Short, 2002). However, this underestimation had been reported to be negligible when the measurement period is sufficiently longer than the plastochrone interval, allowing the new leaf tissue to mature during the period. The period we took for the production measurement (2 weeks) was longer than the plastochrone interval of the marked shoots (see the Results), so underestimation was supposed to be small.

For the below-ground part production measurement, we took the plastochrone method (Gaeckle and Short, 2002). In this method, leaf or under-ground production is simply estimated by weight of a mature leaf (usually, the 3 rd leaf) or rhizoid node with its root bundles (g) divided by a plastchrone interval of leaves (days), as the plastochrone intervals of leaves and nodes of *Z. marina* are the same (Short and Duarte, 2001). In our study, we used the mean biomass of the 3 rd to 5 th nodes with their root bundles as a mature node weight.

The estimated daily production of one shoot (above- + below-ground parts) is multiplied by vegetative shoot density within the sampled quadrat and assumed to be the daily areal (m^{-2}) production of the *Z. marina* stand at each station. We ignored the production of the flowering shoots, which constitute some parts of the *Z. marina* stand in its luxuriant season. When we conducted our measurements, most of the flowering shoots were observed to be beginning to wither. Therefore, we assumed that the production of the flowering shoots was negligible during the period, though the seeds in a spathe could be getting matured.

Production of newly-formed lateral shoots

During the period of the production measurement, active formation and branching of new lateral shoots was observed. In this study, the whole biomass of new lateral shoots, which had branched out from the marked shoots after the pin-hole marking, was assumed to be new production during the period of the measurement. This could be a somewhat overestimation because some parts of the new lateral shoots could have already been produced and existed but were not visible within the sheath of the marked shoots when the marking was performed.

Frequency of new lateral shoot formation in the marked shoots and the mean biomass of the new lateral shoot were recorded. The frequency was applied to the vegetative shoot density of quadrat sampling, and production of newly-formed lateral shoots was estimated on an areal basis.

When the marked shoots were recovered, some marked shoots were observed to have new lateral shoots before branching in their sheaths. When the leaves of these new shoots were visible above the reference pin-hole of the 'parent' marked shoots, the weight of visible part of the leaves was measured and included in the leaf production of the parent shoot, but not counted as 'newly-formed' leaves.

Environmental characteristics at each station

Water temperature was recorded every 60 minutes at Sts 1, 3, 4, 5 and 7 by data-loggers (HOBO

Pendant temp/light loggers, Onset Computer Corporation) during the period of the production measurement. Decrease of underwater irradiance along the depth was recorded by an underwater radiation sensor and a data-logger (LI-193SA spherical quantum sensor and LI-1400 data-logger, LI-COR) at an offshore site of each *Zostera* bed and extinction coefficient was calculated. Sediment of surface layer up to 10 cm was sampled by sediment cores (4 cm in diameter) at each station. Ignition loss and grain-size composition of the sediments was evaluated by ordinary methods (Oceanographic Society of Japan, 1986).

Statistical analysis

Difference in means of all data of *Z. marina* and its stand structures was tested by non-parametric Welch test, because most of the data sets did not show homogeneity of variance. When significant differences were detected, Games-Howell test was performed as a post-hoc test. All these analyses were conducted by SPSS 20.0 Statistic (IBM). Afterwards, the results of these analyses are mentioned only when it is necessary.

RESULTS

Shoot size, density and biomass

Mean length of vegetative shoots (above-ground part) was significantly different among the seven stations ($p<0.001$ in Welch test). Shoots in Ikuno-jima Is. were longer than those in the other islands (Fig. 4, Table 1 ①). Within the stations of Ikuno-shima Is., shoots in the inner area of the bed (Sts 1 and 2) were longer than shoots growing near the edge of the bed (St. 3; $p< 0.05$ in Games-Howell test). In Heigun-jima Is. (Sts 5-7), the length of shoots significantly increased in the deeper stations ($p< 0.05$ in Games-Howell test). In general, longer shoots had wider leaves and larger rhizomes (Table 1 ② - ④).

Total shoot density (vegetative + flowering shoots) was also significantly different ($p<0.001$ in

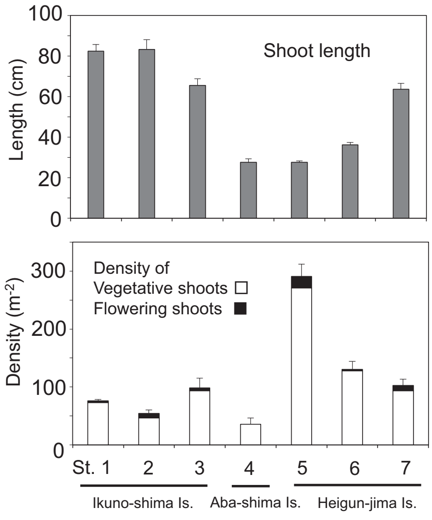

Fig. 4. Mean length of the vegetative shoots (above-ground part) and shoot density of the seven *Z. marina* stands in the three beds in June 2012. Standard errors are shown only in the positive direction and for the total (vegetative + flowering shoots) density in case of the density.

Welch test) and exhibited a reciprocal pattern with the shoot size among the stations except for St. 4 (Fig. 4, Table 1 ⑤). The largest shoots at Sts 1 and 2 exhibited a relatively low density (76 and 55 shoots m^{-2}). The highest density (291 shoots m^{-2}) was observed at St. 5, the shallowest station in Heigun-jima Is, and the densities decreased as the constituent shoots became larger in the deeper stations. An exceptional case was shown in Aba-shima Is. (St. 4), where short young shoots exhibited a relatively low density (36 shoots m^{-2}). This was because the *Z. marina* bed at St. 4 was composed of small patches with a scattered distribution pattern, and the quadrat sampling could only cover a patch per a quadrat.

Proportion of flowering shoots in total shoots was quite different among stations, and even among quadrats at a station. Mean proportion of all stations ranged from 0 to 14.6 %. Young shoots at St. 4 did not contain any flowering shoots (Table 1 ⑥).

Table 1. Shoot size, stand structures and production of *Z. marina* measured in this study. All data are shown in means with SE

	St.1	St.2	St.3	St.4	St.5	St.6	St.7
Size of vegetative shoots							
① Vegetative shoot length (cm)	79.8 ± 3.3	85.2 ± 4.8	63.5 ± 3.3	28.8 ± 1.8	26.5 ± 0.7	36.4 ± 1.1	61.5 ± 2.8
② Max. leaf width (mm)	10.6 ± 0.3	10.1 ± 0.3	8.0 ± 0.2	4.9 ± 0.2	4.2 ± 0.1	5.1 ± 0.1	5.9 ± 0.2
③ Length of 2nd internode (mm)	16.7 ± 0.7	18.7 ± 1.1	18.0 ± 0.8	14.0 ± 1.2	10.3 ± 0.4	11.4 ± 0.5	14.0 ± 0.7
④ Diameter of 2nd internode (mm)	5.7 ± 0.2	5.3 ± 0.2	4.4 ± 0.1	2.7 ± 0.1	2.4 ± 0.1	3.1 ± 0.1	3.3 ± 0.1
Density (n=3)							
⑤ Total density of shoots (m^{-2})	76.0 ± 2.3	54.7 ± 5.8	98.7 ± 16.7	36.0 ± 10.6	290.7 ± 21.3	130.7 ± 13.3	102.7 ± 10.9
⑥ % of flowering shoots	3.7	14.6	4.0	0	6.5	1.9	9.3
Biomass (n=3)							
⑦ Total biomass ; TB (g DW m^{-2})	259.8 ± 43.6	174.8 ± 38.2	167.0 ± 53.2	9.3 ± 2.0	83.4 ± 3.4	55.1 ± 9.4	78.4 ± 9.3
⑧ Above-ground ; AGB (g DW m^{-2})	211.4 ± 33.5	148.6 ± 34.2	136.8 ± 43.6	6.1 ± 1.4	53.1 ± 2.8	39.7 ± 7.1	65.4 ± 7.9
⑨ % of flowering shoots in AGB	9.5	33.2	10.0	0	13.4	3.4	16.8
⑩ Below-ground ; BGB (g DW m^{-2})	48.3 ± 10.2	26.2 ± 4.8	30.3 ± 10.2	3.2 ± 0.6	30.4 ± 1.9	15.4 ± 2.3	13.0 ± 2.1
⑪ Proportion of BGB in TB (%)	18.3	15.3	17.6	34.4	36.4	28.1	16.6
Data of marked shoots (Initial n= 30)							
⑫ Number of recovered shoots	29	29	28	28	22	24	27
⑬ Plastochrone interval (days)	9.9	8.7	9.3	11.2	12.6	13.8	10.8
⑭ Leaf number of recovered shoots	7.4 ± 0.1	7.3 ± 0.2	7.4 ± 0.2	6.2 ± 0.1	5.1 ± 0.1	5.8 ± 0.1	6.2 ± 0.2
⑮ Daily turn-over of leaves (% d^{-1})	1.3	1.6	1.5	1.4	1.6	1.3	1.5
Production of marked shoots							
⑯ Total (mg DW $shoot^{-1}$ d^{-1})	73.2 ± 2.9	62.0 ± 3.4	50.9 ± 2.0	16.7 ± 0.7	7.7 ± 0.4	12.7 ± 0.6	27.4 ± 1.3
⑰ Above-ground (mg DW $shoot^{-1}$ d^{-1})	53.9 ± 2.7	44.5 ± 3.0	35.1 ± 1.6	12.7 ± 0.6	5.1 ± 0.3	10.2 ± 0.5	19.3 ± 1.3
⑱ Below-ground (mg DW $shoot^{-1}$ d^{-1})	19.3 ± 1.1	17.4 ± 1.0	15.8 ± 0.8	3.9 ± 0.3	2.6 ± 0.2	2.4 ± 0.2	7.6 ± 0.5
Areal production (n=3)							
⑲ Total production; TP (g DW m^{-2} d^{-1})	5.37 ± 0.35	2.89 ± 0.41	5.38 ± 0.66	0.60 ± 0.18	2.08 ± 0.10	1.63 ± 0.15	2.56 ± 0.31
⑳ Above-ground (g DW m^{-2} d^{-1})	3.95 ± 0.26	2.08 ± 0.30	3.91 ± 0.48	0.46 ± 0.14	1.38 ± 0.07	1.31 ± 0.12	1.80 ± 0.22
㉑ Below-ground; BGP (g DW m^{-2} d^{-1})	1.42 ± 0.09	0.81 ± 0.12	1.48 ± 0.18	0.14 ± 0.04	0.70 ± 0.04	0.31 ± 0.03	0.71 ± 0.09
㉒ Proportion of BGP in TP (%)	26.4	28.0	27.5	23.3	33.7	19.0	27.7
㉓ Daily turn-over of total biomass (% d^{-1})	2.1	1.7	3.2	6.5	2.5	3.0	3.3
New lateral shoot formation							
㉔ New lateral shoot emergence (New lateral shoot $shoot^{-1}$ d^{-1})	0.021	0.048	0.030	0.046	0.009	0.007	0.025
㉕ Production of new lateral shoot ; PNLS (g DW m^{-2} d^{-1}) (n=3)	0.43 ± 0.03	0.73 ± 0.10	0.46 ± 0.06	0.15 ± 0.04	0.05 ± 0.00	0.04 ± 0.00	0.22 ± 0.03
㉖ % of PNLS to areal total production	8.1	25.2	8.6	25.1	2.6	2.3	8.8

The largest biomass among the three islands was observed in Ikuno-shima Is, in which mean total biomass ranged 167.0 - 259.8 g DW m^{-2} among Sts 1- 3 (Fig. 5, Table 1 ⑦). However, the total biomass was not significantly different among Sts 1- 3 ($p > 0.05$ in Games-Howell test). Total biomass among Sts 5 - 7 was not also significantly different in Heigun-jima Is. ($p > 0.05$ in Games-Howell test), despite of the significant difference in shoot size and density among them. The biomass was smallest in Aba-shima Is. (St. 4) among all seven stations (Fig. 5, Table 1 ⑦).

Proportion of below-ground biomass to total biomass was also significantly different among stations. The proportions at Sts 4 and 5 were high (34.4 and 36.4 %, respectively) than at other stations. In Heigun-jima, the proportion became lower in the deeper stations, up to 16.6 % at St. 7 (Table 1 ⑪).

Production of the marked shoots

Among thirty shoots marked at each station, 22 - 29 shoots were recovered after 2 weeks (Table 1 ⑫). Heavy grazing on leaves during the measurement period, as in autumn 2011, was not observed at all stations.

Estimated plastochrone intervals ranged between 8.7 - 13.8 days among the seven stations (Table 1 ⑬). Generally, the intervals were slightly shorter (< 10 days) at stations in Ikuno-shima Is. than at the other stations. In Table 1, the number of leaves per shoot which were marked is also shown (Table 1 ⑭). Generally, shoots at stations in Ikuno-shima Is. had more leaves on them than shoots at other stations. Daily turnover rate of leaves was calculated, as:

Daily turnover rate of leaves = 1 / plastochrone interval / number of leaves $\times 100$

and they ranged 1.3 -1.6 % d^{-1} which were not largely different among stations (Table 1 ⑮).

Daily production per shoot is apparently dependent on the shoot size. Generally, larger shoots exhibit a larger daily production per shoot (Fig. 6, Table 1 ⑯). The largest production per shoot (73.2

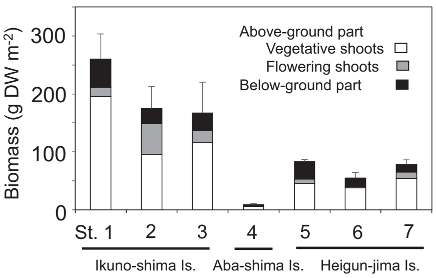

Fig. 5. Mean biomass of the seven *Z. marina* stands in the three beds in June 2012. Standard errors are shown only in the positive direction and for the total (above- + below- ground parts) biomass.

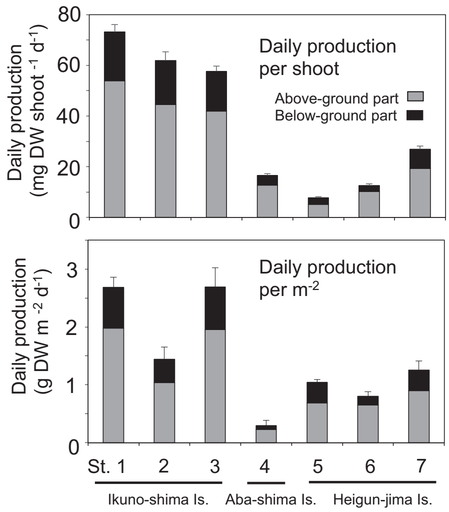

Fig. 6. Mean daily production per shoot and areal production (per m^2) of the seven *Z. marina* stands in the three beds in June 2012. Standard errors are shown only in the positive direction and for the total (above- + below- ground parts) production.

mg DW shoot $^{-1}$ d^{-1}) was observed at St. 1, which was approximately ten times larger than the smallest value (7.7 mg DW shoot $^{-1}$ d^{-1}) at St. 5.

Areal production (Fig. 6, Table 1 ⑲) was dependent on the vegetative shoot density, and the difference among the stations in the same island was relatively small. In Heigun-jima Is., for example, areal production was not significantly different among Sts 5 - 7 ($p>0.05$ in Games-Howell test), though production per shoot was different by approximately 4 times between Sts 5 and 7. At St. 4, daily areal production was smallest (0.60 g DW m $^{-2}$ d^{-1}) among all stations due to the lowest shoot density. However, daily turnover of biomass (% d^{-1}), which was calculated as:

Daily turnover of biomass (% d^{-1}) = daily areal production / biomass × 100,

was far larger (6.5 % d^{-1}) at St. 4 than the values (1.7 - 3.3 % d^{-1}) at the other stations (Table 1 ㉓).

Production of newly-formed lateral shoots

New lateral shoot formation on the marked shoots was observed at all stations, but the frequency was different among the stations (Table 1 ㉔). Most active formation was observed at Sts 2 and 4. On the contrary, frequency at Sts 5 and 6 in Heigun-jima Is. was small. At Sts 2 and 4, the daily production of new lateral shoots amounted to 25 % of the daily areal production of vegetative shoots (Table 1 ㉖).

Environmental characteristics at each station

The means (and range) of water temperature during the measurement period at Sts 1, 3, 4, 5 and 7 were 18.3 (17.1-20.6) ℃ , 18.0 (16.9-19.7) ℃ , 18.0 (16.9-19.9) ℃ , 17.4 (16.2-19.9) ℃ and 17.2 (16.2-18.8) ℃ , respectively. The mean of the extinction coefficient measured offshore of the three *Z. marina* beds on the days of marking and recovery of the shoots were 0.27 for Ikuno-shima Is., 0.27 for Aba-shima Is. and 0.19 for Heigun-jima Is.

Sediment characteristics were quite different among the three *Z. marina* beds. Sediment at stations of Ikuno-shima Is. was mainly composed of mud (< 63 μ m) and the ignition loss was 8-10 % (Fig. 7). Sediment at Aba-shima Is. and Heigun-jima Is. was coarser and main components were medium and fine sand (125 - 500 μ m). Also, less organic matter was contained (Fig. 7).

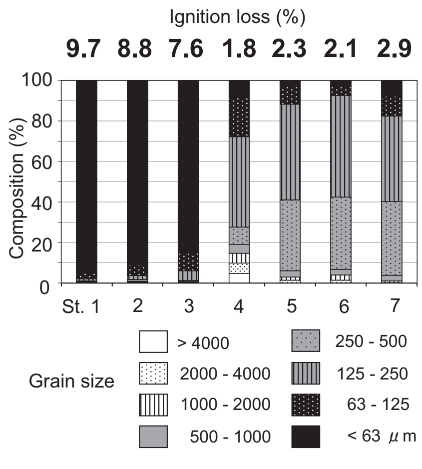

Fig. 7. Grain size composition and ignition loss of the sediments at the seven *Z. marina* stands in the three beds.

DISCUSSION

Biomass and production characteristics of *Z. marina* in the Seto Inland Sea

Biomass and production of seagrass has been measured worldwide, and data distribution pattern and its species-specific or geographic (latitudinal) characteristics were reassessed by Duarte and Chiscano (1999). According to their reassessment, mean maximum biomass and production of *Z. marina* measured worldwide were 298.4 (above-ground) and 149.7 (below-ground) g DW m^{-2} for biomass, and 5.2 (above-ground) and 1.7 (below-ground) g DW m^{-2} d^{-1} for production. As the data distribution was skewed, the medians of those data were smaller than the mean values (Duarte and Chiscano, 1999). However, both *Z. marina* biomass and production measured in this study are below the medians in the worldwide data distribution.

In Japan, biomass and, in a less frequency, production of *Z. marina* has also been measured along the geographical distribution of *Z. marina*, from Hokkaido to Kyushu regions. For these values, no clear relationship has been found between the maximum biomass and latitude or geographical location of *Z. marina* populations (Nakaoka and Aioi, 2001). Above-ground biomass of 300-600 g DW m^{-2} was reported in many sites, such as Notsuke Bay (Mizushima, 1985) and Akkeshi-ko estuary (Hasegawa *et al.*, 2007) in Hokkaido, Ise Bay on the Pacific coast (Abe *et al.*, 2004) and Maizuru Bay (Douke *et al.*, 2000) on the Japan Sea coast. Above-ground biomass measured in this study was lower than the biomass of those sites, and close to the biomass reported in Nabeta Bay (Mukai *et al.*, 1979) and Odawa Bay (Aioi, 1980) on the Pacific coast and Iida Bay (Taniguchi and Yamada, 1979) on the Japan Sea coast.

Even within the Seto Inland Sea area, biomass measured at our study sites, which are located in the western area of the Seto Inland Sea, were lower than the biomass reported in the eastern Seto Inland Sea. *Z. marina* stand at Shodo-shima Is. in Kagawa Prefecture was reported to have a seasonal maximum biomass of 355.2 g DW m^{-2} for the above-ground part and 173.6 g DW m^{-2} for the below-ground part (Fujiwara et al., 2009). Also, at Ushimado in Okayama Prefecture, above-ground biomass of 300-500 g DW m^{-2} was reported (Azuma and Harada, 1969). Contrary to these sites, biomass reported from the western Seto Inland Sea and eastern area of Bungo Channel, such as Hiroshima Bay (Terawaki *et al.*, 2002; Yoshida *et al.*, 2013a), Yanai Bay (Kawabata *et al.*, 1993; Yoshida *et al.*, 2013a) and the coast of Ehime Prefecture (Yoshida *et al.*, 2013b), rarely reached > 200 g DW m^{-2} in total biomass.

Comparing the stand structures between the populations exhibiting high biomass (300-500 g DW m^{-2} in above-ground biomass) and the populations in the western Seto Inland Sea, the former populations are composed of larger shoots with higher densities than the latter populations. For example, the modes in the shoot length frequency during the luxuriant season are generally 120 cm < and the shoot densities are 200 m^{-2} <, for the *Z. marina* populations with a large biomass (*e.g.*, Mizushima, 1985; Douke *et al.*, 2000; Abe *et al.*, 2004; Fujiwara *et al.*, 2009). Contrary to this, *Z. marina* populations in the western Seto Inland Sea are commonly characterized by relatively lower density and smaller shoots. At present, we are not sure whether these characteristics are due to environmental aspects or biological traits of *Z. marina*, which are endemic to this region. To clarify if these characteristics are regionally specific or not, long-term observations are also needed as *Z. marina* beds generally exhibit large year-to-year fluctuations (Terawaki *et al.*, 2002; Fujiwara *et al*., 2006).

Comparisons within the stands in this study

The size and stand structures of *Z. marina* were diverse among the stations in this study, and larger shoots exhibited higher production per shoot than smaller shoots. Leaf turnover rates of shoots were similar among the 7 stands, indicating no relation between leaf turnover and shoot size. Further, plastochrone intervals were rather shorter in large shoots of the bed in Ikuno-shima Is. than small shoots of the other two beds, indicating that leaf productivity is higher in larger shoots.

Though the productivity of the stands of small shoots was not compensated by leaf turnover, it could be compensated by shoot density. For the *Z. marina* bed in Ikuno-shima Is. and Heigun-jima Is., though production per shoot is different, no significant difference in areal production was observed among the stations of each bed. This is prominent in Heigun-jima Is., where the shoot size and density exhibited a clear reciprocal pattern among the stations along the depth gradient. Within this depth range, no light limitation for *Z. marina* production occurred under the extinction coefficient of seawater (0.19) indicating favorable water quality for the growth of *Z. marina* (Abe *et al.*, 2003).

Though significant difference in the areal production was not observed among the stations in each bed, a difference in productivity was still observed between the bed in Ikuno-shima Is. and in Heigun-jima Is. The difference in local environmental conditions between the two beds was prominently shown in sediment characteristics. It was reported that seagrass production in temperate regions is often nitrogen-limited and shoot size and growth of *Z. marina* are promoted in muddy sediments which contain more interstitial nutrients than sandy sediments (Short, 1987). Experimental addition of fertilizer to sediment resulted in an increase in shoot size and biomass of *Zostera* species (Orth, 1977; Udy and Dennison, 1997). It is possible that a difference in nutrient availability, due to the difference in sediment characteristics, could affect the productivity of the two *Z. marina* beds.

However, all of the differences in the stand characteristics could not be explained by the nutrient availability, especially in case of the difference in shoot density. In previous reports (Orth, 1977; Udy and Dennison, 1997), fertilization to the sediment caused shoot density to increase. In general patterns of *Z. marina* beds in the western Seto Inland Sea, stands developed on shallow and sandy beds (as at St. 5 in this study) have larger shoot densities than the stands developed on muddy beds (Yoshida *et al.*, 2013ab). Such stands also exhibit larger relative allocation of biomass to the lower-ground part (Yoshida *et al.*, 2013ab). Also in our study, more production in a relative abundance was allocated to the below-ground part at the stand of St. 5 compared to the other stands (Table 1 ㉒).

Sediment grain size composition generally reflects the hydrodynamic conditions at the habitats. Sediment composed mainly of coarser grains indicates more exposure of the site to currents or wave actions (Oceanographic Society of Japan, 1986), and sandy sediments of *Z. marina* beds in Heigun-jima Is. and Aba-shima Is. indicated severer physical conditions than that of the bed in Ikuno-shima Is. Physical turbulence could also be a limiting factor affecting sustainability and distribution of *Z. marina* beds (Dan *et al.*, 1998; Moriguchi and Takagi, 2005). Shorter shoot size and relatively large below-ground parts could be adaptive under physically turbulent conditions, to relieve the dragging effect and increase an anchoring capacity. It was reported that *Z. marina* growing in the sediment with a high organic content developed long leaves and disproportionately short roots, which easily causes the shoot loss by uprooting (Wicks *et al.*, 2009). Effects of environmental conditions on shoot morphology and stand structures needs further studies to clarify any relationships between them.

Z. marina bed of Aba-shima Is., which is on the way of recovery after the heavy grazing of rabbit fish, exhibited the lowest biomass and production due to its small shoots and low densities. However, its daily turnover of biomass was larger than other stands. This indicates that more resources for growth, such as light and nutrients, are available for each shoot at St. 4 than at other stations, probably due to the low shoot density. Higher new lateral shoot emergence at St. 4 also supports this idea.

Future perspective

In the Seto Inland Sea, a considerable area of *Z. marina* beds has been lost due to the rapid coastal development and serious water pollution during the period of high economic growth in the 1960's to the early 1970's (Yoshida *et al.*, 2013a). Though recent improvements in water quality have been favorable to its gradual recovery, effective restoration of *Z. marina* beds and their ecological functions is still an urgent issue in the Seto Inland Sea (Terawaki *et al.*, 2005).

Among significant ecological functions of seagrass beds, recent social attention has been focusing on their potential as a long-term carbon sink. That is, seagrass beds, as well as salt marshes and mangroves, accumulate substantial amounts of organic matter of both endogenous and exogenous origins within them and sequester them through burial. It was reported that these vegetated coastal habitats contribute about 50 % of the total burial of organic carbon in global ocean sediments, though they cover only 0.2 % in seafloor (UNEP, 2009).

Our results indicate that the function as a carbon sink could be different among *Z. marina* beds with their ecological characteristics in two ways, *i.e.*, one is the difference in productivity among *Z. marina* beds, and the other is the accumulation efficiency of organic matter in the sediment. These functions are possibly affected by the topographic characteristics of the *Z. marina* beds, *e.g.*, the *Z. marina* bed in Ikuno-shima Is. formed under sheltered conditions with a vast muddy and high organic sediment area is potentially more effective as a carbon sink than the *Z. marina* beds in Heigun-jima Is. and Aba-shima Is.

However, high contribution of the latter two *Z. marina* beds could be possibly found in another important ecological function of *Z. marina* beds, *i.e.*, contribution to fisheries production. As the *Z. marina* beds in Heigun-jima Is. and Aba-shima Is. were formed under an open condition, fish assemblages can easily access and utilize the beds for various ecological usages. In addition, more benthic small animals as preys for fish are available in sandy sediments than in muddy sediments, which could heighten the value of the beds in the fisheries production.

The ecological characteristics of *Z. marina*, such as shoot size, stand structures and production are variable among its beds or stands even within the same proximate sea area. These variations arise from differences in physical conditions accompanied with topographic characteristics of each bed, and diversity in ecological functions of *Z. marina* beds could also be found with the varieties of their ecological and topographic characteristics. Though further studies are needed to prove this idea, it could be an important point to be reflected in the measures of conservation and restoration of *Z. marina* beds.

ACKNOWLEDGEMENT

We express our thanks to Mr. Kiyoshi Suzuki of Heigun Fishermen's Cooperative Association, Mr. Atsushi Kajita, Mr. Shun-ichi Miura and Mr. Koji Manabe of Aquatic Research Inc., for their technical support of our study. This study was partially funded by the project of Ministry of Agriculture, Forestry and Fisheries 'Technology development for circulatory food production systems responsive to climate change'.

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瀬戸内海における株サイズと群落構造の異なるアマモの生産量 ー2012年繁茂期の生産量ー

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要　旨　2012年６月に瀬戸内海の３つのアマモ場の，それぞれ異なる株サイズと群落構造を示す計7地点のアマモ群落において生産量を測定，比較した。株あたりの生産量は株サイズに依存し，大きい株が相対的に低い密度で生育する生野島（広島県；安芸灘）のアマモ場で50.0-73.2 mg DW shoot $^{-1}$ d^{-1}であり，小さい株が密生する平郡島（山口県；伊予灘）の株あたり生産量（7.7-27.4 mg DW shoot $^{-1}$ d^{-1}）より大きかった。面積あたり生産量において，株あたり生産量の差は株密度により相殺される傾向もみられたが，生野島のアマモ場の生産量（2.89-5.38 g DW m^{-2} d^{-1}）の方が平郡島のアマモ場の生産量 (1.63-2.56 g DW m^{-2} d^{-1}) よりも大きかった。これら２つのアマモ場では底質に大きな相違がみられ，アマモの群落構造や生産量に影響を与えていると考えられた。すなわち，生野島の底質はほとんど泥により構成され有機物含量も高い一方で，平郡島の底質は中砂・細砂を中心に構成されより厳しい波浪環境を反映していた。

2011年秋季のアイゴの食害による消失から回復途上にある阿波島（広島県；安芸灘）のアマモ場では新たに発芽した実生由来の株がパッチ状の群落を作り，株密度も現存量も低かった。調査した群落の中で生産量は最も低かったが (0.60 g DW m^{-2} d^{-1})，その現存量回転率（6.5% d^{-1}）は，他群落（1.7-3.3% d^{-1}）のそれよりも大きかった。

キーワード：アマモ，現存量，群落構造，株密度，生産量