

亜熱帯性の海草のシュート密度, シュート構造, 摂餌痕の地域変異

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Local variations in shoot density, shoot morphology, and bite mark frequency of subtropical seagrasses in Japan

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Abstract This study demonstrated local variations in seagrass species composition, biomass, shoot density, shoot morphology and the frequency of bite marks in seagrass leaves at coastal sites in the Yaeyama Islands, subtropical Japan. Seven seagrass species (*Zostera japonica*, *Halodule pinifolia*, *H. uninervis*, *Cymodocea rotundata*, *C. serrulata*, *Thalassia hemprichii* and *Halophila ovalis*) were sampled, and *T. hemprichii* was the most dominant. Total biomass did not vary between the four sampling sites, but there were considerable local variations in shoot density and shoot morphology of the larger three species (*C. rotundata*, *C. serrulata* and *T. hemprichii*). At the sites with a low shoot density (19-29 shoots per 625cm²), the shoots of *T. hemprichii* had a lower number of leaves, wider and longer leaves, and a longer “sheath+erect shoot” length than the shoots at the sites with a high shoot density (44-93 shoots). The frequencies of bite marks on leaves of *C. rotundata* and *T. hemprichii* varied between sites, but they did not correspond to local variations in the leaf length structure. The relation between the seagrass shoot morphology and the balance of production and consumption requires further clarification.

Key words: Seagrass, density, size structure, herbivory, biomass

Seagrass beds provide habitats for many types of algae and animals. Density and diversity of organisms associated with seagrass beds are affected by the shoot density (Orth *et al.*, 1984; Edgar *et al.*, 1994), leaf length (Horinouchi *et al.*, 1999), leaf morphology (Trautman and Borowitzka, 1999), and heterogeneity of the seagrass bed structure (Horinouchi and Sano, 1999). On the other hand, recent studies indicate that large herbivores (i.e. fishes, sea urchins, and green turtles) consume considerable quantities of seagrass leaves (Thayer *et al.*, 1984; Valentine and Heck, 1999), which in turn affects the shoot density and leaf length structure of the seagrass bed. Therefore, variation in seagrass bed structures with an evaluation of leaf herbivory is important as basic information to understand the possible relationships

between local variations in seagrass bed structure and its associated organisms.

Tropical and subtropical seagrass beds in the western Pacific usually form mixed species vegetations (Brouns, 1987; Poiner *et al.*, 1989; Tomasko *et al.*, 1993; Vermaat *et al.*, 1995; Bach *et al.*, 1998; Terrados *et al.*, 1998). Spatial variations in species composition have been observed not only on a geographic scale (Mukai, 1993), but also on local scales (Kanamoto and Watanabe, 1981; de Iongh *et al.*, 1995). In subtropical Japan, including the Yaeyama Islands, several species of seagrass occur in shallow coastal lagoons and they usually form mixed seagrass beds (Nozawa, 1972; Tsuda and Kamura, 1990). In the Yaeyama Islands, a quantitative study on the seagrass community was carried out on a small scale (<10km) at the Nagura Bay

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(Kanamoto and Watanabe, 1981), but local variations over a larger scale (10-100km) were not investigated. Kanamoto and Watanabe (1981) suggested that the species composition of subtropical seagrass beds varies primarily with depth, with the maximum diversity around the Mean Low Water Spring (MLWS) tide level. Therefore, comparison between seagrass samples around the MLWS would be a good indicator of the local variations in seagrass vegetation.

The objectives of this work are three-fold. First, seagrass species compositions on the coast of the Yaeyama Islands, subtropical Japan, were determined to substantiate earlier reports of mixed-species vegetation. Second, the range of local variations in shoot density and shoot morphology (number of leaves per shoot, leaf width, leaf length, and "sheath+erect shoot" length) of seagrass are evaluated within the mixed vegetation at the MLWS level in lagoons. Third, local variations of the impact of herbivory were assessed by observing the frequency of bite marks on seagrass leaves.

Materials and Methods

Quantitative seagrass sampling was carried out at four coral lagoons around the Yaeyama Islands (124°N, 24°E, Fig. 1) in July, 1997: two sites (Ibaruma and Urasoko) on the northern side of Ishigaki Island and two sites (Nagahama and Takahama) on the southern side of Iriomote Island. Nagahama and Takahama are more exposed to oceanic swells than Ibaruma and Urasoko because the distances between the reef edge and the shore are less at Nagahama and Takahama (0.2-0.4km) than at Ibaruma and Urasoko (1.7-2.4km).

To minimize any possible effects of microtopographic variations between samples, at each site a sampling area (20m diameter) was selected at the center of the seagrass bed, where the sandy bottom was flat (heterogeneity of height <5cm, mainly by mounds of infauna) at a depth of 0-30cm below the MLWS. Four replicate samples of seagrasses were taken using a quadrat (25×25cm, 15cm depth) randomly set within each sampling area.

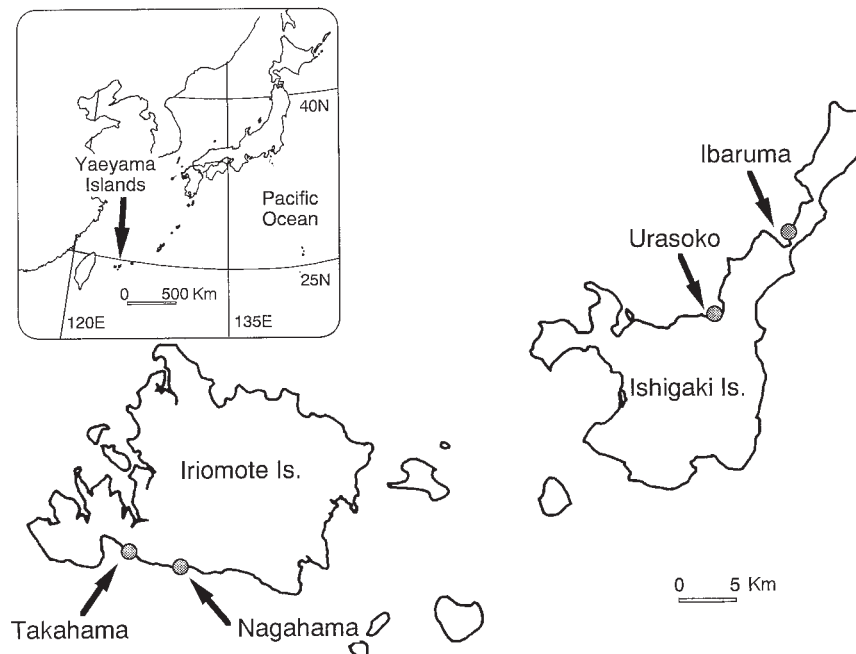


Fig. 1. Locations of the four study sites (Ibaruma, Urasoko, Nagahama and Takahama) in the Yaeyama Islands, Japan.

Seagrass samples were sorted to species. Live and dead tissues were separated and only live tissues were used in the following analyses. Live tissues were separated into three parts (leaf, sheath + erect shoot, and horizontal rhizome) and their dry weights (60 °C, 24 hours) were measured.

For the larger three species (*Cymodocea rotundata* Ehrenberg and Hemprich ex Ascherson, *C. serrulata* (R. Brown) Ascherson and Magnus, and *Thalassia hemprichii* (Ehrenberg) Ascherson), the number of shoots per quadrat and the number of leaves per shoot were counted. Budding shoots without any leaves were excluded from the analysis. The length of “sheath+erect shoot” was measured for each shoot. The length and the width of the leaves were measured in the order of the leaf in each shoot (Fig. 2). Mostly, the width of the leaves was the same over whole positions on a leaf and leaves within a shoot. Otherwise, the maximum width of the leaves within a shoot was measured. Leaf areas of each species per quadrat were estimated by summing up the products of leaf length and width. Four types of leaves were recognized according to bite marks (Fig. 2) : (1) no bite marks, (2) intact leaf length with round bite marks, (3) leaf shortened by round bite marks, (4) leaf shortened by straight or irregular shaped bite marks. For *C. rotundata*, the leaf types 3 and 4 were not distinguishable because of its narrower leaf width. These bite marks may be made by various

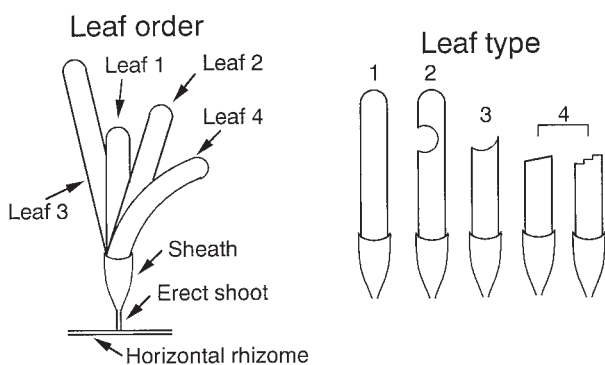


Fig. 2. Schematic representations of seagrass leaf order and leaf types with bite marks.

herbivores including amphipods and fishes (McClanahan *et al.*, 1994). In the Yaeyama Islands, preliminary observations showed that green turtles (*Chelonia mydas* (Linnaeus)) make straight bites and sea urchins (*Tripneustes gratilla* (Linnaeus)) make irregular shaped bite marks.

Results

Species composition and biomass

Overall, seven species of seagrass were sampled during this study: *Zostera japonica* Ascherson and Graebner, *Halodule pinifolia* (Miki) den Hartog, *H. uninervis* (Forsskål) Ascherson, *Cymodocea rotundata*, *C. serrulata*, *Thalassia hemprichii* and *Halophila ovalis* (R. Brown) Hooker f. Species compositions were the same at Nagahama and Takahama (4 species, Table 1), but different at Ibaruma (3 species) or Urasoko (5 species). *C. rotundata* and *T. hemprichii* occurred at all the four sites. *T. hemprichii* was the most dominant species in dry weights of the whole tissue and the three separated parts (leaf, “sheath+erect shoot”, and horizontal rhizome) at all sites except Ibaruma where the leaf dry weight of *C. serrulata* was dominant. Dry weights of whole tissue and the three separated parts of *T. hemprichii* were significantly different between four sites (Kruskal-Wallis tests, $p < 0.05$) Total dry weight of *T. hemprichii* at Takahama (16.96g per quadrat) was 2.5 times larger than at Ibaruma (6.79g). However for all the species combined, the total dry weights were not significantly different between the four sites (Kruskal-Wallis tests, $p > 0.05$).

Shoot density and shoot morphology

Shoot and leaf density of the larger three species (*C. rotundata*, *C. serrulata* and *T. hemprichii*) varied between the four sites (Table 2). *C. serrulata* occurred only abundantly at Ibaruma. Differences in the leaf area, numbers of shoots and leaves of *T. hemprichii* and *C. rotundata* were statistically significant between the four sites (Kruskal-Wallis tests, $p < 0.05$). For *T. hemprichii*, number of shoots and leaves at Takahama were 4.9 and 6.4 times higher than at Ibaruma,

Table 1. Mean (+SD) seagrass dry weight (g, 60°C 24h) at four sites (per 25cm×25cm quadrat, n=4). Zj: *Zostera japonica*, Hp: *Halodule pinifolia*, Hu: *Halodule uninervis*, Cr: *Cymodocea rotundata*, Cs: *Cymodocea serrulata*, Th: *Thalassia hemprichii*, and Ho: *Halophila ovalis*.

	Leaf	Sheath+Erect shoot	Horizontal rhizome	Whole tissue
Ibaruma				
Cr	0.15+0.17	0.26+0.19	0.29+0.25	0.70+0.56
Cs	1.45+0.63	1.24+0.15	1.75+0.38	4.43+0.72
Th	0.51+0.27	4.23+2.33	2.05+0.85	6.79+3.25
Total	2.10+0.82	5.73+2.34	4.07+0.70	11.92+3.21
Urasoko				
Zj	0.41+0.13	0.57+0.22	0.39+0.17	1.36+0.45
Cr	0.09+0.07	0.38+0.42	0.11+0.06	0.57+0.59
Cs	0.03+0.06	0.02+0.04	0.15+0.21	0.16+0.32
Hu	0.06+0.03	0.12+0.05	0.19+0.10	0.36+0.15
Th	1.33+0.56	6.62+3.23	3.61+1.16	11.56+4.30
Total	1.91+0.64	7.70+3.44	4.44+1.17	14.04+4.49
Nagahama				
Hp	0.17+0.06	0.26+0.11	0.60+0.29	1.03+0.44
Cr	0.31+0.10	1.40+0.63	1.28+0.47	2.98+1.09
Th	0.85+0.27	5.76+1.30	2.59+0.29	9.20+1.29
Ho	0.05+0.01	0.03+0.01	0.06+0.04	0.14+0.06
Total	1.37+0.31	7.45+1.35	4.52+0.49	13.34+1.75
Takahama				
Hp	0.00+0.01	0.01+0.02	0.01+0.01	0.02+0.03
Cr	0.08+0.04	0.21+0.03	0.28+0.01	0.57+0.07
Th	1.20+0.06	9.96+2.08	5.81+1.60	16.96+2.81
Ho	0.01+0.01	0.01+0.01	0.01+0.01	0.01+0.03
Total	1.28+0.07	10.18+2.10	6.10+1.59	17.56+2.82
Results of Kruskal-Wallis test				
Cr	ns	*	***	*
Th	*	*	***	**
Total	ns	ns	ns	ns

ns:no significance, *:p<0.05, **:p<0.01 and ***:p<0.005

respectively. The difference in leaf area between Takahama and Ibaruma was 2.2 times, which is similar to the leaf dry weight (2.4 times). On the other hand, combined for the three species, total leaf area did not differ significantly between the four sites (Kruskal-Wallis tests, p>0.05).

Variations in the shoot morphology between the sites were also recognized (Table 3). Differences in the number of leaves per shoot, leaf width and the length of “sheath + erect shoot” of *T. hemprichii* and *C. rotundata* were statistically significant between the sites (Kruskal-Wallis tests, p<0.005). For *T. hemprichii*, shoots at Ibaruma and Urasoko could be characterized

by their lower number of leaves, wider leaf width, and longer “sheath + erect shoot” length than at Nagahama and Takahama (Table 3). The maximum leaf length was also longer at Ibaruma and Urasoko than at Nagahama and Takahama. Similar variations in shoot morphology between the sites were observed in *C. rotundata*, except for the number of leaves per shoot (Table 3).

Leaf length structure and bite marks

Leaf length structure of *T. hemprichii* varied between the four sites (Fig. 3), which corresponded to the between-site variation in the

Table 2. Mean (+SD) number of shoots, number of leaves and leaf area at four sites (per 25cm×25cm quadrat, n=4). Cr: *Cymodocea rotundata*, Cs: *Cymodocea serrulata* and Th: *Thalassia hemprichii*.

	No. shoots	No. leaves	Leaf area (cm ²)
Ibaruma			
Cr	7.8+ 6.9	21.5+19.6	57.5+ 53.4
Cs	19.0+ 4.7	57.8+12.6	448.4+147.8
Th	18.8+ 6.8	43.0+16.6	167.4+ 84.8
Urasoko			
Cr	3.8+ 3.3	9.3+ 8.1	29.6+ 29.0
Cs	0.5+ 1.0	1.3+ 2.5	10.0+ 20.0
Th	29.3+ 5.9	75.3+15.1	453.9+184.2
Nagahama			
Cr	53.8+22.3	139.0+53.8	138.1+ 41.4
Th	43.5+ 8.1	156.5+35.4	287.5+ 83.9
Takahama			
Cr	12.0+ 5.0	30.8+12.3	26.4+ 9.6
Th	93.0+15.0	273.3+35.8	361.7+ 26.8
Results of Kruskal-Wallis test			
Cr	***	***	*
Th	***	***	***

*:p<0.05 and ***:p<0.005

Table 3. Mean (+SD) number of leaves, leaf width and sheath length (per shoot, n = number of shoots) at four sites. Maximum leaf length at each station is also listed. Cr: *Cymodocea rotundata*, Cs: *Cymodocea serrulata* and Th: *Thalassia hemprichii*.

	n	No. leaves per shoot	Leaf width (mm)	Sheath+Erect shoot length (cm)	Max. leaf length (cm)
Ibaruma					
Cr	31	2.77+0.62	3.58+0.90	4.68+1.94	16.9
Cs	76	3.04+1.38	8.50+1.92	4.39+2.04	17.8
Th	75	2.29+0.93	5.64+1.56	9.12+3.17	16.5
Urasoko					
Cr	15	2.47+0.64	4.00+0.57	5.97+3.19	19.0
Cs	2	2.50	6.50	4.20	13.1
Th	117	2.57+0.77	6.75+1.93	9.47+4.23	19.1
Nagahama					
Cr	215	2.59+0.84	2.76+0.77	2.78+1.54	8.8
Th	174	3.60+1.10	5.23+1.39	6.05+2.83	9.1
Takahama					
Cr	48	2.56+0.68	2.92+0.65	2.24+1.07	8.6
Th	372	2.94+0.74	4.51+1.67	3.98+1.37	7.7
Results of Kruskal-Wallis test					
Cr	***	***	***	***	
Th	***	***	***	***	

***:p<0.005

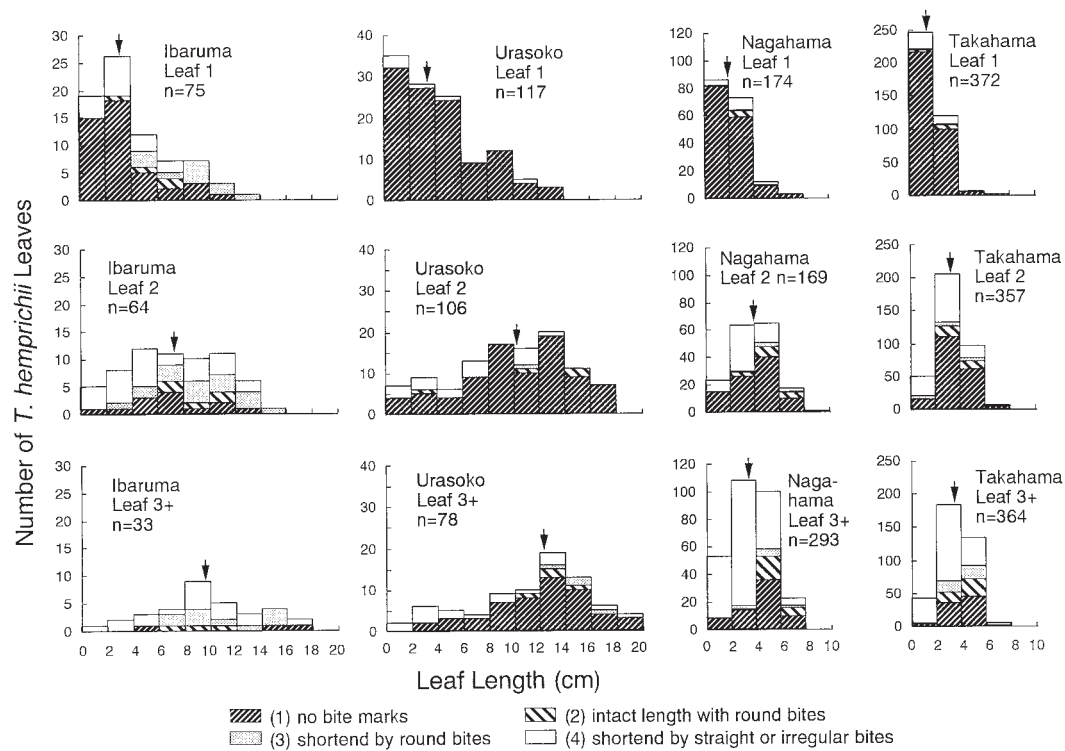


Fig. 3. Leaf length frequency histograms of *Thalassia hemprichii* at four sites. Leaves are classified by the order in the shoot and the type of their bite marks (see Fig. 2). The arrows indicate the median leaf length in each histogram. n = number of leaves.

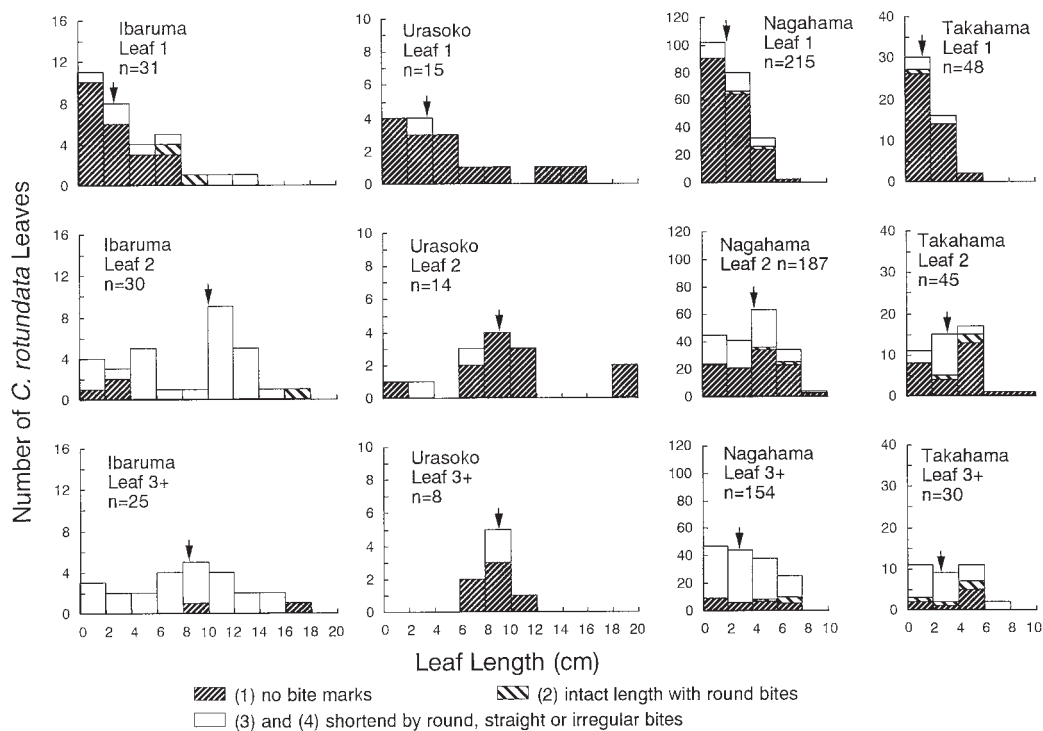


Fig. 4. Leaf length frequency histograms of *Cymodocea rotundata* at four sites. Leaves are classified by the order in the shoot and the type of their bite marks (see Fig. 2). The arrows indicate the median leaf length in each histogram. n = number of leaves.

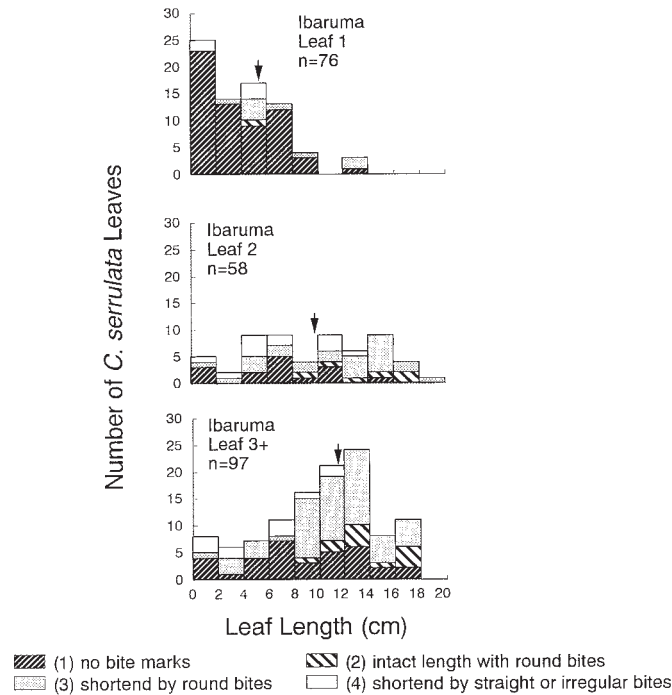


Fig. 5. Leaf length frequency histograms of *Cymodocea serrulata* at Ibaruma. Leaves are classified by the order in the shoot and the type of their bite marks (see Fig. 2). The arrows indicate the median leaf length in each histogram. n = number of leaves.

maximum leaf length (Table 3). Generally, the youngest leaves (Leaf 1) were shorter than the older leaves (Leaf 2 and Leaf 3+). Leaves at Nagahama and Takahama were shorter than those at Ibaruma and Urasoko. Statistically significant differences in the median leaf length were detected between the leaf orders and the sites (Kruskal-Wallis tests, $p < 0.0001$). *C. rotundata* showed similar variations both in the leaf order and the sites (Fig. 4) and also in the leaf order of *C. serrulata* at Ibaruma (Fig. 5), where this species was abundant.

A large proportion of *T. hemprichii* leaves had bite marks (Fig. 3). The proportion of leaves with bite marks (number of leaf types 2, 3 and 4 against all the leaves) varied between the sites: the minimum of 17.6% at Urasoko (n=301), 45.6% at Takahama (n=1093), 50.9% at Nagahama (n=636), and the maximum of 65.1% at Ibaruma (n=172). Within the three types of bitten leaves, the proportion of type 4 (shortened leaf by straight or irregular bites) was the largest at all the sites. The proportion of type 3 (shortened leaf by round bites) was larger at Ibaruma than the other sites. In addition, the

proportion of leaves with bite marks increased with the leaf age: for example at Ibaruma, 41.3% for Leaf 1, 79.7% for Leaf 2 and 90.9% for Leaf 3+. Similar frequency patterns of bitten leaves were observed in *C. rotundata* (Fig. 4) and *C. serrulata* (Fig. 5): the proportion of leaves with bite marks increased with leaf age and was largest at Ibaruma. Comparison between the three species at Ibaruma showed that the frequency of bitten leaves was largest for *C. rotundata* (68.6%, n=86) followed by *T. hemprichii* (65.1%, n=172) and *C. serrulata* (58.9%, n=231), although the difference in the frequency of bites was not statistically significant (Goodness-of-fit test, $p > 0.05$).

Discussion

Previous surveys of seagrasses reported nine species around the Yaeyama Islands (Tsuda and Kamura, 1990) instead of seven species in this study. The two remaining species are *Enhalus acoroides* (Linnaeus f.) Royle, which has a patchy distribution and is found only in several bays (Nozawa, 1972), and *Syringodium isoetifolium*

(Ascherson) Dandy, which occurs in more wave-exposed areas (Kanamoto and Watanabe, 1981) than the areas of this study. Habitats of *Zostera japonica* are sometimes influenced by brackish water (Lee, 1997). Also in this study, *Z. japonica* occurred only at Urasoko Bay, where fresh water flowed from small brackish creeks and paddy fields behind the shoreline after heavy rain (Takada, personal observations).

Results of this study demonstrated that local variations in seagrass species composition, shoot density, shoot morphology and proportion of leaves with bite marks were considerable in the Yaeyama Islands within the same water depth in lagoons. According to the shoot density and the shoot morphology of *Thalassia hemprichii*, the four sites can be divided into two groups: (1) Ibaruma and Urasoko, and (2) Nagahama and Takahama. At Ibaruma and Urasoko, the shoot density was lower, and each shoot had a lower number of leaves, wider and longer leaves, and a longer "sheath+erect shoot" length than at Nagahama and Takahama. This grouping corresponds to the topographic characteristics of the shores. Ibaruma and Urasoko are north-facing and wave-protected shores, while Nagahama and Takahama are south-facing and wave-exposed shores. Interestingly, the pattern of site variation in the shoot morphology was almost identical between *T. hemprichii* and *Cymodocea rotundata*. Interspecific variations in shoot morphologies within a site appeared smaller than intraspecific variations between the sites. This suggests that some site-specific factors lead to phenotypic convergence in shoot morphology between these seagrasses.

On the other hand, the total dry weight (all species combined) and the total leaf area of the larger three species (*C. rotundata*, *C. serrulata* and *T. hemprichii* combined) did not show any variations between the sites. One of the reasons for these insignificant between-site variations in total dry weight and leaf area is that the within-site variations are larger than the between-site variations. For example, leaf areas at Urasoko ranged from 43.6% to 114.0%

against the area sampled (625cm²), while the mean values of the four sites ranged from 62.1% to 107.7%. Another reason is that the longer leaf length at Ibaruma and Urasoko may compensate for the lower shoot density and the fewer number of leaves per shoot. These compensated variations in shoot morphology decreased the between-site variations.

In comparison with mixed species seagrass beds in the Philippines (Tomasko *et al.*, 1993; Vermaart *et al.*, 1995; Bach *et al.*, 1998; Terrados *et al.*, 1998), the shoot density of *T. hemprichii* at Nagahama and Takahama were higher than in the Philippines. The leaf width of *T. hemprichii* and *C. rotundata* were narrower, and the leaf length of *C. rotundata* was shorter in the Yaeyama Islands than in the Philippines. But the leaf length of *C. serrulata* and *T. hemprichii* in the Philippines were similar at Nagahama and Takahama, which were shorter than at Ibaruma and Urasoko. According to these data, the shoot density and structure in Yaeyama Islands were more variable than in the Philippines. However, detailed comparison is difficult because of the wider range of scale in the above studies (1km-1000km) than in this study (10km-100km).

The results showed that the proportion of bite-marks on the seagrass leaves varied locally. At Ibaruma, 41.3-90.9% of leaves of *T. hemprichii* had bite marks, while 17.6% (pooled) at Urasoko. Although we did not estimate the ratio of consumption by herbivores against leaf production, the proportion of leaves with bite marks indicated that herbivory on the seagrass leaves was not negligible (for example, Valentine and Heck, 1999) and that the intensity of herbivory were also variable within a local scale. Zieman *et al.* (1984) noted that a reduction in the width of leaves indicated stress by heavy herbivory. The width of leaves at Urasoko being broadest may correspond to the least herbivory between the four sites.

A full discussions encompassing all the possible factors for these local variations are out of the scope of this paper. But, preliminary observations on the stomach contents of green

turtles (*Chelonia mydas*) suggest that the green turtles significantly consume seagrasses and contribute to the local variation in herbivory on seagrasses. Green turtles are known to forage repeatedly on seagrasses within a small (<6km²) area (Mendonça, 1983; Brill *et al.*, 1995). Presence (or absence) of green turtles may produce the observed local variation in the intensity of herbivory between the seagrass beds in this study area.

The proportion of leaves with bite marks did not correspond to the local variation of the leaf length structure. Although seagrasses at Ibaruma and Urasoko showed similar leaf length structures, the proportion of leaves with bite marks were the highest at Ibaruma and the lowest at Urasoko between the four sites. There is a possibility that the growth of these seagrass leaves is enhanced by herbivory (Thayer *et al.*, 1984) and the modification of leaf length structure is compensated for this. Experimental evidence is required to evaluate whether exact or over/under compensation would occur (Cebrián *et al.*, 1998). Thus, the present results show that the effects of herbivory on the leaf length structure are unclear in this study area.

In conclusion, this study demonstrated considerable variations of density, shoot morphology and levels of herbivory between seagrass beds within a local scale (10km-100km). The pattern of the local variations were almost identical between *Thalassia hemprichii* and *Cymodocea rotundata*, but the total biomass did not vary between sites. Effects of herbivory on the leaf length structure were unclear. Relation between the seagrass shoot morphology and the balance of production and consumption require further clarification.

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亜熱帯性の海草のシュート密度，シュート構造，
摂餌痕の地域変異(報文)

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八重山諸島沿岸の海草の種組成，現存量，シュート密度，シュート構造，および摂餌痕の地域変異を調べた。4地点で7種類の海草を採集した。現存量に地域差はなかったが，大型3種のシュート密度とシュート構造に違いがあった。シュート密度の低い地点では，リュウキュウスガモの葉数は少なく，葉長などは長かった。摂餌痕の頻度に地域差があったが，葉長組成の違いとは対応しなかった。今後は成長や被食量を調べる必要がある。

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