Growth of seagrass *Halophila ovalis* at dugong trails compared to existing within-patch variation in a Thailand intertidal flat

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ABSTRACT: We studied small-scale variation in morphology and growth rate of the seagrass *Halophila ovalis* in an intertidal flat of Thailand coast where the seagrass bed is subjected to grazing by dugongs. Our objectives were to examine whether morphology and growth rate differ between rhizomes in different positions within a patch (center, edge and dugong trails), and to test whether *H. ovalis* shows plastic growth response to disturbance by dugong feeding. Seagrass biomass and leaf density were 3 to 4 times greater at the patch center than the patch edge and the dugong trails. In contrast, branching rate and internode length of rhizomes were significantly greater at the patch edge and dugong trails than at the patch center. The results of marking experiments of *H. ovalis* revealed that net production, leaf production and rhizome elongation rates were 2 to 3 times greater at the patch edge than at the center. Growth and production rates at the edge of the dugong trails and artificial trails mimicking dugong trails were not significantly higher than at the patch center. Nevertheless, significant differences in some morphological parameters such as branching frequency and internode length between the dugong trails and the patch center suggest that morphological changes in *H. ovalis* can be induced over short time scales. Recovery of *H. ovalis* after disturbance by dugong herbivory was estimated to be quite rapid (< 20 d). High growth rates of *H. ovalis* were probably responsible for its persistence under grazing by dugongs.

KEY WORDS: *Halophila ovalis* · Seagrass · Within-patch variation · Growth · Production · Dugong herbivory · Morphological plasticity · Thailand · Small-scale heterogeneity

INTRODUCTION

Seagrasses are clonal plants that sometimes form dense beds or patches. In terrestrial clonal plants, it is known that growth rate and morphology are not always uniform among different positions within a patch or even a single genet (Keddy 1981, 1982, Adachi et al. 1996, Steuer et al. 1996, Hutchings & Wijesinghe 1997). In general, better growth of modules is expected at peripheral rather than at central positions of a patch, when modules are released from crowding effects or competition at the periphery (ecological factors), or when there are aging effects on growth or morphology at the center (autogenic factors).

This general prediction can also apply to clonal seagrasses, although only a few studies have examined small-scale variation in growth or morphology within a patch or a single genet (Zieman 1972, Brouns 1987a, Duarte & Sand-Jensen 1990, Marbà & Duarte 1995, Turner et al. 1996, Vermaat et al. 1997).

The seagrass species belonging to the genus *Halophila* occur on intertidal and subtidal soft bottoms of tropical and subtropical coasts. Among various tropical seagrass species, *Halophila ovalis* is known to be preferred by dugongs *Dugong dugon* (Preen 1995). Dugongs leave unvegetated feeding trails in seagrass patches (Heinsohn et al. 1977), but sometimes their intensive feeding activity changes dense unfragmented seagrass beds into bare sand flats (Preen 1995). However, *H. ovalis* is the fastest growing seagrass species in tropical seagrass beds (Vermaat et al.

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1995), and this may play an important role in maintaining population size in the face of extensive herbivory (Preen 1995). For example, Supanwanid (1996) observed in a Thailand intertidal flat that *H. ovalis* biomass in artificial trails mimicking dugong trails recovered to original levels within 2 mo. It is possible that such rapid recovery is dependent on a plastic response in growth because shoots and rhizomes in central positions of a patch can suddenly become peripheral when subjected to the disturbance caused by dugong herbivory.

The main objectives of the present study are (1) to examine whether morphology and growth rate of *Halophila ovalis* differ between different positions within patches, i.e. the patch center and patch edge, and (2) to test whether *H. ovalis* shows plastic growth response to disturbance by dugong herbivory. We conducted a quantitative sampling and a marking experiment at several different positions in *H. ovalis* patches, as well as at edges of dugong feeding trails and artificially made trails resembling dugong feeding trails.

MATERIALS AND METHODS

Study site. We carried out the fieldwork during March 11 through March 24, 1998, in an intertidal flat at Koh Bae Na, located at Haad Chao Mai Marine National Park, on the southwestern coast of Thailand (Fig. 1). The tidal range during the research period
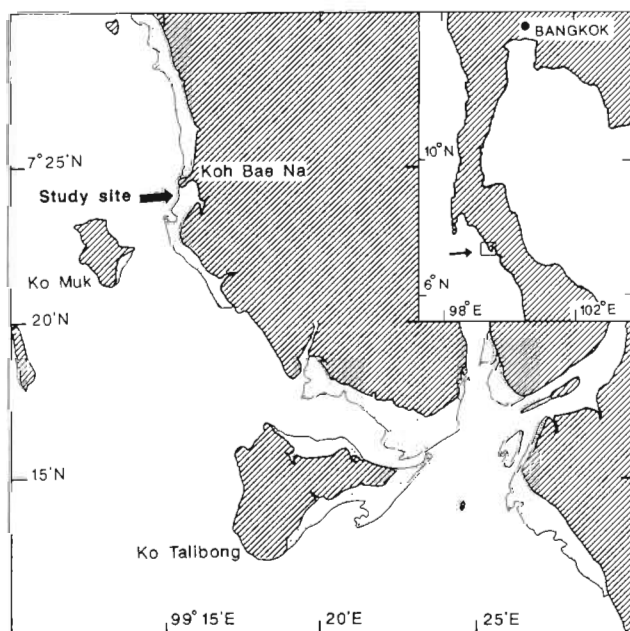

Fig. 1. Study site at Koh Bae Na, Haad Chao Mai National Park, in Thailand

varied between 0.7 m (neap tide) and 2.8 m (spring tide). At spring ebb, the intertidal flat extends about 400 m from the shoreline. A seagrass bed of ca 3 ha area covers the lower half of the intertidal flat. The most dominant seagrass species is *Halophila ovalis*, followed by *Cymodocea rotundata*, *C. serrulata* and *Enhalus acoroides*. Each seagrass species forms monospecific stands of patches of various sizes (<1 to 100 m²) and shapes. Coverage of each seagrass species measured at a 10 000 m² quadrat was 61% *H. ovalis*, 10% *C. rotundata*, 1% *C. serrulata*, and <1% *E. acoroides*, while 28% was unvegetated mudflat (H. Mukai unpubl. data).

Six individuals of dugongs were observed around the study site (intertidal and subtidal seagrass beds between Ko Muk and Koh Bae Na; Fig. 1) by an aerial survey conducted on April 9, 1997 (Adulyanukosol et al. 1997). During our research period, 1 dugong (probably the same individual) was observed in the tidal flat for 7 d at high tide in the daytime, leaving 6 to 29 (15 on average) new feeding trails per day in the 1 ha quadrat (H. Mukai unpubl. data). The average size of feeding trails is 200 cm in length, 15 cm in width and 3 cm in depth. Dugongs feed more efficiently on the aboveground part of *Halophila ovalis* than the belowground, leaving in the feeding trails only 6.1% (±1.3 SD) of initial biomass of the former, and 39% (±13.2 SD) of the latter (T. Suzuki unpubl. data).

Within-patch variation in abundance and morphology. We compared abundance, biomass and vegetative morphology of *Halophila ovalis* at 3 different positions within the patches; (1) in the center of the *H. ovalis* patches ('patch center'), (2) at the edge of the patches adjoining the unvegetated mud flat ('patch edge'), and (3) along the edge of the dugong feeding trails ('dugong trails'). The patch center is defined as the area >3 m inside the patch margin, and the patch edge within 20 cm from the margin. We collected *H. ovalis* at each position from within a 20 × 20 cm quadrat (4 samples from the patch center and the patch edge, and 3 from the dugong trails) by digging down to a depth of 10 cm using a hand shovel, and removing the sediment using sieves of 1 mm mesh opening. We counted the numbers of leaves and rhizome apices in each sample. We then measured the length and width of leaf blade, the distances between successive nodes of rhizomes (individual internode length), and the branching frequency (expressed by the ratio of the number of nodes with a branch axis to the total number of nodes) of 20 haphazardly selected ramets from each sample. Individual leaf area was approximated as an area of ellipse with leaf length as the longer axis and leaf width as the shorter axis. Finally, we separated aboveground parts (leaves and petioles) and belowground parts (rhizomes and roots)

of all the collected seagrasses, dried them in an oven at 60°C for 48 h, and measured them on an electronic balance (to the nearest 0.1 mg) to obtain the dry weight of each part. The root:shoot ratio was expressed as the weight of belowground parts divided by that of aboveground.

Within-patch variation in growth rate. We measured the growth rate of *Halophila ovalis* at 4 different positions in patches; (1) at patch centers, (2) at patch edges, (3) at the edge of the dugong trail, and (4) at the edge of artificial trails. Two artificial trails to resemble dugong feeding trails (each 2 m long and 15 cm wide) were made in the center of a patch by digging up the sediment in the seagrass bed to a depth of 10 cm with a hand shovel and then by replacing the sediment once the *H. ovalis* had been removed manually.

We marked rhizomes of *Halophila ovalis* by tagging plastic-coated steel wire (3 mm in width and 0.5 mm in thickness) around the second node from the growing apex. Marking was carried out at low tide on March 12 to 15, 1998, when the *H. ovalis* bed was exposed or shallower than 10 cm deep. Some disturbance to the seagrass may have been caused when we dug the sediment by hand at a depth of about 1 to 3 cm to look for growing apices. However, the impact appeared to be minor because the marked rhizomes were observed to retain their position underground after the arrival of the first high tide. Ten seagrass rhizomes were marked at each of the 3 sites of patch centers, 3 at patch edges, 2 at dugong trails and 2 at artificial trails. The marked rhizomes were recovered on March 22, 1998 (7 to 10 d later) at the lowest tide. During the experimental period, 40 to 80% of plants with tags were washed away at each site. Nevertheless, we retrieved 6 to 12 marked rhizomes per position which is sufficient to perform statistical analyses (see below). The number of new leaves, length and the branching frequency of extended rhizomes, and dry weight of newly produced aboveground and belowground parts were measured as described above.

Statistical analyses. Some of the parameters representing seagrass abundance, morphology and growth were expressed on a sample basis (per unit area), and other parameters on a ramet basis (per ramet within each sample). We tested within-patch (among-position; center, edge and trail-edge) variation in the former parameters using 1-way ANOVA, and among- and within-position variation in the latter using 1-way nested ANOVA. The data were log transformed before the analyses when significant differences in variance were detected among data (tested with Cochran's test). When significant variation among positions was detected by ANOVA, post-hoc comparisons were carried out with the Tukey-Kramer method (at a significance level of α = 0.05). For the branching fre-

quency of newly produced rhizomes in the marking experiment, among-position variation was tested with non-parametric Kruskal-Wallis test instead of ANOVA because the data did not fulfill the assumption of normality. Post-hoc comparisons were made with Mann-Whitney *U*-test after adjusting the probability of overall Type I error (α = 0.05) by the Dunn-Sidák method.

RESULTS

Within-patch variation in abundance and morphology

Total biomass, aboveground and belowground biomass, densities of leaves and rhizome apices were about 3 to 4 times greater at patch centers than at patch edges or dugong trails (Fig. 2). One-way ANOVA revealed significant among-position variation in these parameters (p = 0.010 for total biomass; p =
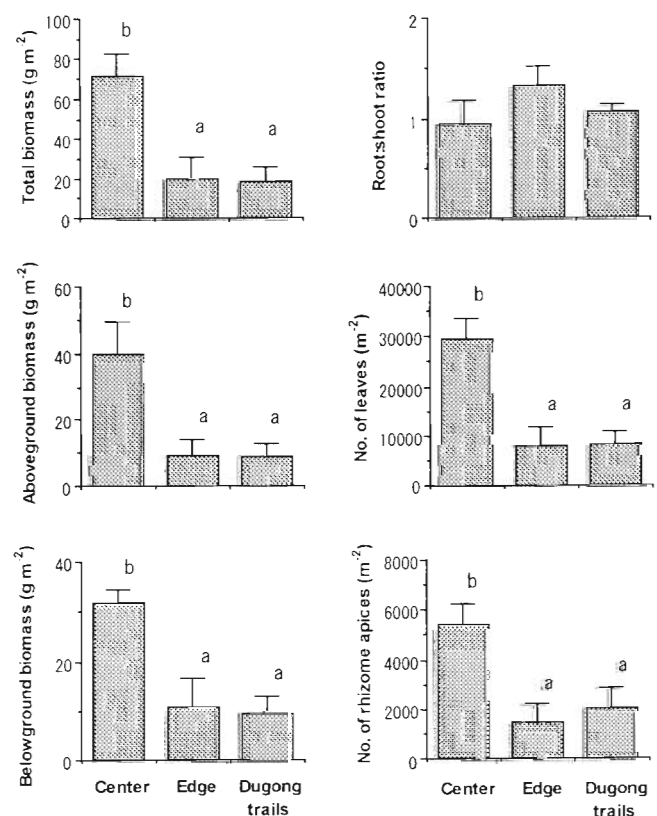

Fig. 2. *Halophila ovalis*. Variation in parameters representing abundance among 3 position types within patches. Bars are the means of 4 (center and edge) and 3 (dugong trails) replicates and error bars are standard errors of the mean. Different letters denote pairs of positions where significant among-position variation was detected by the post-hoc comparisons
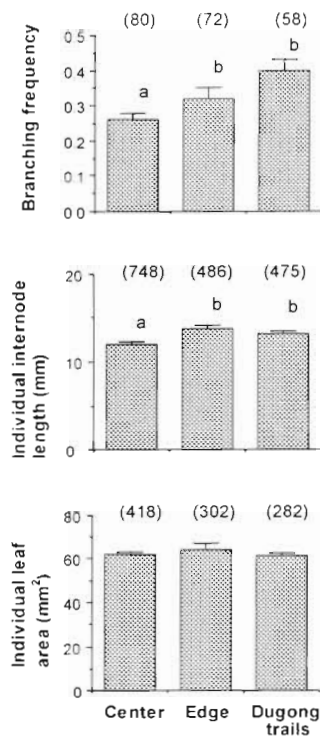
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Fig. 3. *Halophila ovalis*. Variation in morphology among positions within patches. Bars indicate the means, and error bars are standard errors of the mean. The numbers in parentheses indicate sample sizes. Different letters denote pairs of positions where significant among-position variation was detected by the post-hoc comparisons

0.024 for aboveground biomass; p = 0.011 for belowground biomass; p = 0.005 for density of leaves; and p = 0.016 for density of rhizome apices). Post-hoc comparison showed that parameters at patch centers were significantly higher than at patch edges and at dugong trails, whereas the differences between the latter two were not significant (Fig. 2). In contrast, branching frequency and individual internode length of rhizomes were significantly greater at patch edge and dugong trails than at patch center although significant within-position variation was also detected for these parameters (Fig. 3; 1-way nested ANOVA; p = 0.002 for among-position and p = 0.001 for within-position variation of branching frequency; and p < 0.001 for both among-position and within-position variation of individual internode length). Among-position variation was not obvious for root:shoot ratio and individual leaf area (Figs. 2 & 3). No significant among-position variation was found for either parameters, although individual leaf area varied significantly among samples within each position (1-way ANOVA: p = 0.397 for root:shoot ratio; 1-way nested ANOVA: p = 0.884 for among-position and p < 0.001 for within-position variation of individual leaf area).

Within-patch variation in growth rate

A total of 35 tagged rhizomes of *Halophila ovalis* was collected at 4 patch positions. Net production, leaf production and rhizome elongation rates differed significantly among patch positions: they were 2 to 3 times greater at patch edges than at patch centers, and those at the edge of dugong trails and artificial trails were not significantly different from the rates observed at the centers (Fig. 4, Table 1). These parameters varied significantly not only among positions, but also among different ramets of each position (Table 1).

Tagged rhizomes produced 1 to 5 branches at the patch edges and the 2 types of trails, but no branches were produced at the patch centers. The branching frequency of newly produced rhizomes varied significantly among positions (Kruskal-Wallis test; p < 0.001), and it was higher at patch edges and the dugong trails than at patch centers (Fig. 4). Individual internode
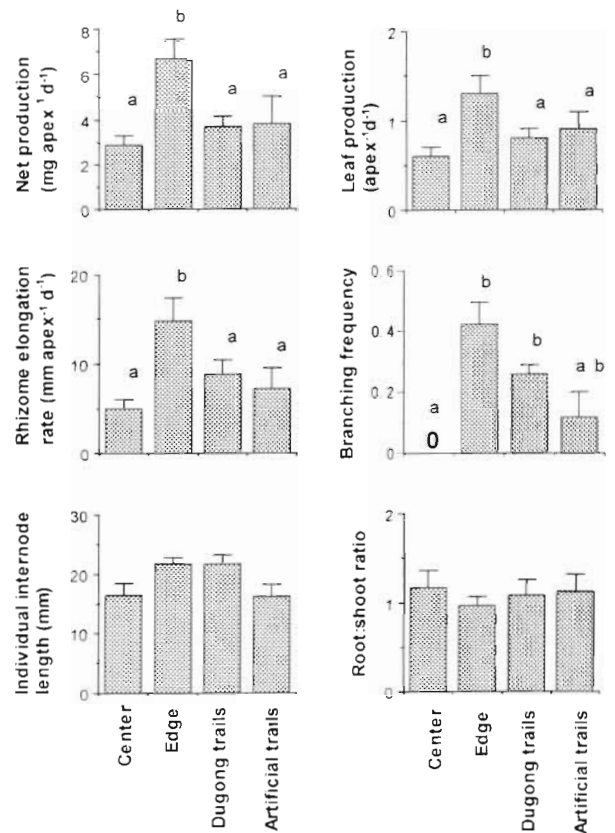

Fig. 4. *Halophila ovalis*. Variation in growth, production and morphology among positions within patches of newly produced modules in the marking experiment. Bars are the means of 12 (center), 10 (edge), 7 (dugong trails) and 6 (artificial trails) replicates and error bars are standard errors of the mean. Different letters denote pairs of positions where significant among-position variation was detected by the post-hoc comparisons. Branching frequency was 0 because no branches were produced at the patch centers

Table 1 *Halophila. ovalis*. Result of 1-way nested ANOVA testing within-patch variation in the growth rates and morphology of marked rhizomes

Factor	df	SS	F	p
Net production				
Position	3	52.92	8.101	0.001
Sample (position)	6	93.88	7.186	<0.001
Residual	25	54.43		
Leaf production				
Position	3	2.307	8.849	<0.001
Sample (position)	6	2.124	4.074	0.006
Residual	25	2.173		
Rhizome elongation rate				
Position	3	364.5	6.775	0.002
Sample (position)	6	513.1	4.769	0.002
Residual	25	448.3		
Individual internode length				
Position	3	173.7	2.796	0.061
Sample (position)	6	292.6	2.356	0.061
Residual	25	517.6		
Root:shoot ratio				
Position	3	0.456	0.778	0.517
Sample (position)	6	3.678	3.138	0.020
Residual	25	4.884		

length and root:shoot ratio did not vary among any of the habitat positions, although significant within-position (among-ramet) variation was detected for the root:shoot ratio (Table 1).

DISCUSSION

We found in the present study that the morphology and growth rate of *Halophila ovalis* differ significantly among positions within a seagrass patch. The observed pattern in within-patch variation in growth and production (better growth and greater production at the patch edges than at the centers) agrees with the review by Vermaat et al. (1997), which confirms that growth rates are faster at patch edges than inside patches in 4 out of 5 seagrass species (*Cymodocea nodosa, C. serrulata, H. ovalis* and *Syringodium isoetifolium*, but not in *Zostera noltii*).

The better growth and greater production at the patch edges can be caused by at least 2 (not fully exclusively) alternative factors; (1) release at patch edges from negative density effects or crowding effects (Antonovics & Levin 1980), and (2) aging effects of old ramets near patch centers (Masuzawa & Suzuki 1991). In the present *Halophila ovalis* population, the first factor is likely to be responsible because biomass and leaf density were more than 3-fold greater at the patch center. Mean LAI (leaf area index; the ratio of total leaf area to bottom area) was 1.82 at the patch centers, while it was 0.50 both at patch edges and dugong trails (calculated from data on individual leaf area in Fig. 3 and leaf density in Fig. 2). It is therefore likely that seagrasses may undergo competition for light at patch centers but not at patch edges. Furthermore, biomass at the patch center estimated in this study is among one of the highest estimates for *H. ovalis* when compared with other available data (Table 2). This might also suggest that crowding effects could play a role in within-patch variation. The second factor, on the other hand, seems unlikely because we found a large number of newly growing apices even at patch centers (Fig. 2).

Comparison of growth and morphology between the patch center and the dugong trails revealed the plastic change in some morphological parameters, such as rhizome branching frequency and individual internode

Table 2. *Halophila ovalis*. Comparisons of biomass, growth and production at different localities

Locality	Biomass (g dry wt m^{-2})	Rhizome elongation rate (mm apex^{-1} d^{-1})	Production (g dry wt m^{-2} d^{-1})	Source
Monospecific bed				
Arabian Sea coast of Oman	0.5–11.4	–	–	Jupp et al. (1996)
NE coast of Saudi Arabia	12–39	–	–	Kenworthy et al. (1993)
Ashtamudi estuary, SW India	≤48	–	–	Nair et al. (1983)
Swan/Canning Estuary, SW Australia	≤120	–	≤40	Hillman et al. (1995)
Moreton Bay, Australia	75	–	–	Preen (1995)
SW coast of Thailand	30	–	–	Supanwanid (1996)
SW coast of Thailand	72	5.0–14.8	7.5–15.6	Present study
Mixed bed				
Sinai, Northern Red Sea	16–20	–	–	Lipkin (1979)
Bolinao reef flat, Phillipines	0.2	3.9	0.04	Vermaat et al. (1995)
Bootless Inlet, Papua New Guinea	1.0	5.5	<0.02	Brouns (1987a,b)
Palau, Micronesia	2	–	–	Ogden & Odgen (1982)

length (Figs. 3 & 4). Such morphological changes are considered to be adaptive when open spaces appear due to sudden disturbance, because seagrass clones can invade and occupy open spaces quickly if they can extend more branches or increase the intervals of each node. A similar type of plastic change in seagrass morphology has been reported for other seagrass species in response to physical disturbance such as sedimentation and dune migration (Marbà & Duarte 1995, Duarte et al. 1997). The present study suggested that such morphological changes in seagrasses can also occur in response to biological disturbance by herbivorous animals, and that they can be induced in quite short time scale (within a week or 10 d).

Unlike the morphological parameters described above, we could not detect significant differences between the patch centers and the trail edges for parameters representing growth and production (Fig. 4, Table 1). We had expected that growth and production at the trails become similar to those at patch edges if the local release from clouding effects or competition were most responsible for producing within-patch variation in these parameters. Failure to detect significant differences may imply that the seagrass cannot attain higher growth rate or greater production on the short time scale. It is likely that the seagrass apices at the edges of dugong trails are damaged due to dugong foraging (e.g. either by herbivory or by disturbance of sediment during the feeding), which may be responsible for a delay in growth response.

Based on the data collected in the present study, it is possible to make rough estimates of the recovery rates of *Halophila ovalis* after disturbance by dugong feeding. Assuming that rhizomes at the margin of dugong trails can grow across dugong trails (width of 10 to 33 cm; H. Mukai unpubl. data) at the elongation rate of 8.8 mm apex^{-1} d^{-1} (Fig. 4), it takes only 6 to 19 d for rhizome apices to reach the center of the trails from both sides. Furthermore, based on daily net production per unit area at the dugong trails (7.5 g dry weight m^{-2} d^{-1}; see below for the method of calculation), it is estimated to take less than 10 d to reach the biomass at the center (72 g dry weight m^{-2}; Fig. 2) starting from an unvegetated state. In the present study site, Supanwanid (1996) demonstrated in a manipulative experiment that biomass of *H. ovalis* recovered in 2 mo to the initial level after its removal in an artificial trail resembling dugong feeding trails. Our estimates on the recovery rate of *H. ovalis* are much higher than the estimates of Supanwanid. In the present study, we have assumed constant growth rates and no mortality. Seagrass growth rates may decrease and shoot/leaf mortality rates may increase at the dugong trails as seagrass density and biomass increase during the course of recovery. In addition, we do not know whether all the

rhizome apices in our sampling quadrates (20 × 20 cm) produced new rhizomes and leaves towards the unvegetated feeding trails. Finally, *H. ovalis* may exhibit large seasonal and annual variation in growth and productivity, as revealed in other localities (Hillman et al. 1995). Such factors may have contributed to a discrepancy between our estimates and those of Supanwanid (1996). Longer-term studies on shoot demography and patch dynamics are necessary to gain more precise estimates on the recovery rates of *H. ovalis* in response to dugong feeding.

Daily production per unit area is estimated to be 7.5 g dry weight m^{-2} d^{-1} at the dugong trails, 9.9 g dry weight m^{-2} d^{-1} at the patch edge, and 15.6 g dry weight m^{-2} d^{-1} at the patch center (calculated from the data on the density of rhizome apices in Fig. 2 and the daily production rates per apex in Fig. 4). The growth and production rates estimated in the present study are mainly higher than those obtained for *Halophila ovalis* at other localities (Table 2). At our study site, daily consumption rate on *H. ovalis* by a dugong (visited by 1 individual during the research period) is estimated to be ca 0.06 g dry weight m^{-2} d^{-1} (H. Mukai unpubl. data). Therefore, the loss of seagrass by dugong feeding can be fully compensated by the high productivity of *H. ovalis*. Preen (1995) demonstrated that high productivity and rapid recovery rate of *H. ovalis* following intense grazing by dugongs are responsible for the persistence of this pioneer species among late successional species such as *Zostera capricorni* in Australia. A similar mechanism may explain the consistent persistence of *H. ovalis* in the present study site.

In conclusion, the present study demonstrated that growth and morphology of seagrasses can vary greatly even within a single patch, although it failed to detect plastic changes in growth and production in response to dugong herbivory. The fact that seagrass growth and production can vary greatly at small scales has large implications on studies of seagrass ecosystems at larger scale, because estimates of large-scale processes neglecting small-scale variation may lead to large biases in comparisons made over wider geographical scales (Thrush et al. 1997). The integrated approach to studying seagrass dynamics concurrently at several different scales (e.g. rhizome demography, patch dynamics and landscape patterns) is promising to understand effects of different scales on the dynamics of seagrass ecosystems (Turner et al. 1996).

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