Small-scale Variation in a Benthic Community at an Intertidal Flat in Thailand: Effects of Spatial Heterogeneity of Seagrass Vegetation

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Abstract: I examined the diversity and abundance of benthic animal communities in an intertidal seagrass bed at Haad Chao Mai National Park, Thailand, in relation to small-scale spatial heterogeneity of the seagrass vegetation. In this seagrass bed, two dominant seagrasses, *Halophila ovalis* and *Thalassia hemprichii*, coexist in a mosaic of monospecific vegetation. I collected benthic animals at the center, edge and outside of the *H. ovalis* vegetation at one site that bordered an unvegetated sand flat and at another site surrounded by *T. hemprichii* vegetation. A total of 3146 benthic animals from 61 taxa were collected. The most numerous species was the lucinid bivalve *Pillucina* sp., composing more than 60% of the individuals. Although the species composition of benthic animals did not differ largely among the three positions at each site, taxa richness (the number of taxa) was higher in the center of the *H. ovalis* vegetation than the edge of and outside the vegetation. Among the four dominant taxa, *Pillucina* sp. and a sabellid polychaete were generally more abundant in the center of the vegetation than at the edge of and outside the vegetation, whereas significant variation among positions was not detected in the densities of capitellid and spionid polychaetes. Significant among-position variation was also detected in the relative abundance of some taxa. The patterns of among-position variation in taxa richness and abundance did not differ between the two sites. These findings suggest that small-scale spatial heterogeneity of seagrass vegetation has a great impact on the diversity and abundance of benthic communities in intertidal seagrass beds, and that the responses of benthic animals to habitat heterogeneity are species specific.

Key words: abundance, benthic animals, diversity, seagrass, spatial heterogeneity, Thailand

INTRODUCTION

Spatial structure in habitats plays a critical role in determining community dynamics (Bell et al. 1991; Tilman 1994; Tilman & Kareiva 1997). The effects of habitat structure on community dynamics is a central topic in conservation ecology, especially in relation to the effects of habitat fragmentation (Saunders et al.

1991; Robinson et al. 1995). In marine systems, experimental analyses on the effects of spatial structure within habitats have been carried out intensively in rocky intertidal communities (Paine & Levin 1981; Sousa 1984; Noda 1999), and more recently, in soft bottom communities (Irlandi 1994; Robbins & Bell 1994; Bell et al. 1995; Reusch & Williams 1999).

The presence of marine macrophytes, such as seagrasses and kelps, enhances the abundance and diversity of associated animal assemblages by providing food, habitat and shelter (see reviews in Orth & van Montfrans 1984; Mazzella et al. 1992; Orth 1992; Jernakoff et al. 1996). In general, the vegetation patterns of these macrophytes are not uniform. Rather,

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they show large spatial heterogeneity in their distribution, containing monospecific and/or multispecific patches and unvegetated gaps of various sizes often arranged in complex configurations (Marbà & Duarte 1995; Vidondo et al. 1997; Nakaoka & Aioi 1999). Recent studies on the effects of the spatial heterogeneity of macrophyte distribution on animal populations and communities found that spatial structure of macrophytes (e.g., size and shape of patches, and their spatial arrangements) influences the species richness and abundance of animal communities, and the population dynamics of the component species (Stoner & Lewis 1985; Bell & Hicks 1991; Bologna & Steneck 1993; Irlandi 1994, 1996, 1997; Eggleston et al. 1998; Reusch & Williams 1999). However, the directions and magnitudes of the responses of animals to habitat spatial structures vary from case to case, precluding the establishment of general patterns. In particular, very few data are available on the variation that occurs in animal communities at small spatial scales, e.g., within a single macrophyte patch (Reusch & Williams 1999). Examination of small-scale variation in benthic communities is important because the presence of such variation may influence the accuracy of benthic abundance and diversity estimates over large scales.

To provide a first step to elucidate the effects of spatial heterogeneity of seagrass distribution on benthic communities, I conducted a quantitative study at a seagrass bed in Haad Chao Mai National Park, one of the largest seagrass beds along the southwestern coast of Thailand (Lewmanomont et al. 1996; Lewmanomont & Supanwanid 2000). The intertidal part of the seagrass bed consists of eight seagrass species (Lewmanomont & Supanwanid 2000). *Halophila ovalis* and *Thalassia hemprichii* are dominant and form a mosaic of monospecific patches that overlap only at patch margins (Nakaoka & Iizumi 2000; Nakaoka & Supanwanid 2000). Such spatial heterogeneity in seagrass distribution can have a great influence on seagrass growth and productivity, and on epifaunal communities (Nakaoka & Aioi 1999; Nakaoka & Iizumi 2000; Nakaoka & Toyohara 2000). It is expected that the effects further extend to benthic animals, including infaunal animals, in the seagrass bed.

The aim of the present paper is to determine whether the diversity and abundance of benthic animals vary with small-scale spatial heterogeneity of the vegetation of *H. ovalis*. I collected and compared benthic communities among two different positions within the *H. ovalis* vegetation and one position outside the vegetation. These comparisons were made at one site where

the *H. ovalis* vegetation bordered an unvegetated sand flat and at another site surrounded by *T. hemprichii* vegetation to investigate the possible effects of adjacent vegetation on small-scale variation in benthic communities.

MATERIALS AND METHODS

Study site

I carried out the fieldwork in December 1998 at an intertidal seagrass bed in Laem Yong Lam, Haad Chao Mai National Park (Fig. 1A). The area of the intertidal flat is ca 3 km² (Nakaoka & Supanwanid 2000). The tidal range in the area varies between 0.7 m (neap tide) and 2.8 m (spring tide). At the upper parts of the intertidal flats (shallower than -1 m deep at Lowest Low Water), *H. ovalis* and *T. hemprichii* are the dominant species, followed by *Enhalus acoroides*, *Cymodocea rotundata* and *Halodule uninervis* (Nakaoka & Supanwanid 2000).

The two dominant seagrass species coexist in a mosaic of monospecific patches (hereafter called "vegetation") that border either vegetation of another species or an unvegetated sand flat. I established two study sites (each ca 20 × 20 m in area) containing *H. ovalis* vegetation. At one site (called "HS site"), the *H. ovalis* vegetation bordered an unvegetated sand flat, and at the other site ("HT site"), the vegetation was surrounded by adjoining *T. hemprichii* vegetation (Fig. 1B). The two sites were located 100 m apart.

Halophila ovalis vegetation at both sites was located at the same tidal level (-1.5 m at LLW). *Thalassia hemprichii* vegetation at the HT site was depressed 5–7 cm below the *H. ovalis* vegetation, forming tide pools at low tide. The tidal elevation was the same both outside and inside of the *H. ovalis* vegetation at the HS site.

To examine the sediment characteristics, sediment samples were randomly collected to a depth of 5 cm with a cylindrical tube of 5 cm diameter inside and outside of the *H. ovalis* vegetation at both sites. Four replicate samples were collected from each position. The collected sediment samples were dried in an oven at 60 °C to constant weight and weighed on an electronic balance. They were then sieved through a series of sieves consisting of 1, 0.5, 0.25, 0.125 and 0.063 mm mesh openings. Each fraction was dried and weighed again. The median diameter, silt-clay content and inclusive graphic standard deviation (sorting coefficient) were then calculated according to the method of Buchanan

(1984).

Collection and measurement of benthic animals

Quantitative sampling of benthic animals was carried out when the intertidal flat was exposed to air during the daytime low tide. I collected sediments using a 10 cm × 10 cm square core to a depth of 10 cm. At each site, I randomly collected eight replicate samples from each of three positions: (1) at the center of the *H. ovalis* vegetation (center), (2) at the outer edge of the vegetation (edge), and (3) outside the vegetation (outside; i.e., from the unvegetated sand flat at the HS site, and from the *T. hemprichii* vegetation at the HT site). The border of the vegetation was determined visually, although a small amount of *H. ovalis* (less than 0.06 g dry weight per 0.01 m² area; Nakaoka, unpublished data) was sometimes found outside the vegetation. The center was defined as positions more than 1 m inside the border of the *H. ovalis* vegetation, and the edge was defined as locations less than 30 cm from the borders. Outside locations were located more than 1 m from the borders.

In the field, the collected sediment was sieved through a sieve with a 0.5 mm mesh opening, and fixed and preserved in 10% neutralized seawater formalin. In the laboratory, all animals retained on a 1 mm mesh sieve were sorted out, counted and classified to species or higher taxa depending on the taxonomic information available. Most animals were classified to species-level taxon based on observations under a microscope. For some groups, such as diastomid gastropods and capitellid polychaetes, however, it was not possible to identify all individuals to species level due to a lack of taxonomic information and to logistical constraints. For example, the capitellid polychaetes comprised several different genera, such as *Heteromastus* sp., *Mediomastus* sp. and *Notomastus* sp. (K. Yabe, personal communication). These groups were categorized into one taxon.

To examine spatial variation in seagrass abundance and composition, I collected four additional samples using a 20 cm × 20 cm square quadrat to a depth of 10 cm at both the center and edge of the HS and HT sites, and outside of the *H. ovalis* vegetation at the HT site (i.e., in the *T. hemprichii* vegetation). Above-ground and belowground parts of the two seagrasses were sorted, dried in an oven at 60°C to a constant weight, and weighed on an electronic balance.

Fig. 1. (A) Location of the study site (Laem Yong Lam) at Haad Chao Mai National Park in Thailand, and (B) schematic presentation of spatial structure of the seagrass vegetation and positions of benthic collection (C: center of the *Halophila ovalis* vegetation, E: edge of the vegetation, O: outside the vegetation) at the two study sites (HS and HT sites).

Data analyses

Differences in sediment composition (median diameter, silt-clay content and inclusive graphic standard deviation) between the inside and outside of the *H. ovalis* vegetation at each site were tested using a *t*-test.

Benthic community structure was analyzed by comparing the taxa richness (the number of taxa occurring in each sample) and the densities and the relative abundances of the dominant animals at each site. Only four dominant taxa (*Pillucina* sp., Capitellidae spp., Sabellidae sp.1 and Spionidae sp.1) were analyzed because abundances of the other species were too low (average of < 0.5 individuals per quadrat) for powerful statistical testing.

The effects of position in and near the *H. ovalis* vegetation on taxa richness were tested for each site using one-way ANOVA. To test among-position variation in the densities of dominant taxa, multivariate ANOVA (MANOVA) was carried out using the logarithm of the densities of the four dominant species as dependent variables. In cases when significant variation was detected by MANOVA, ANOVA was carried out separately for each dominant taxon. Prior to the ANOVA, homoscedasticity of the data was tested using Cochran's *C* test (Underwood 1997), and in cases where a significant difference in variance was detected, data were log-transformed to secure the homogeneity of variances. When significant variation among the three positions was detected by ANOVA, post-hoc comparisons were carried out using the Student-Newman-Keuls (SNK) test by setting the error rate at $P = 0.05$.

Within-site variation in relative abundance of the dominant taxa (i.e., the proportion that each taxon formed of the total number of benthic animals collected at each position of the two sites) was tested using a χ^2 test against the null hypothesis that the proportion of each taxon was the same at the three positions. Data from eight replicate samples were pooled for each position in this analysis.

RESULTS

Sediments at the two sites consisted of fine sand (median diameter of 2 to 3 in phi unit), with the silt-clay content varying between 4 and 7%, and the inclusive graphic standard deviation between 0.58 and 0.78 (Table 1). These parameters differed significantly between the inside and outside of the HT site, where the sediment was finer and less sorted inside the *H. ovalis* vegetation than outside (i.e., in the *T. hemprichii* vegetation). At the HS site, on the other hand, the sediment composition did not differ significantly inside and outside the *H. ovalis* vegetation (Table 1).

The seagrass vegetation was composed of only *H. ovalis* at the HS site, where the aboveground and belowground biomass was about twice as high at the center than the edge (Fig. 2). Seagrass at the HT site consisted of only *H. ovalis* at the center, of only *T. hemprichii* outside, and of both species at the edge, with *T. hemprichii* occupying more than 80% of the total biomass. The aboveground and belowground biomass of *H. ovalis* was 3–5 times higher in the center than the edge of the HT site, although seagrass biomass was greater at the edge when *T. hemprichii* was

included. The aboveground and belowground biomass of *T. hemprichii* was slightly higher outside than at the edge at the HT site.

A total of 3146 benthic animals were collected from 48 sediment samples and classified into 61 taxa (Table 2). Annelid polychaetes were the most numerous in taxon (25 taxa), followed by molluscs (21 taxa) and arthropods (10 taxa). The most abundant species was a lucinid bivalve *Pillucina* sp. This species occurred in all core samples, and composed 62% of the total number of benthic animals. Other abundant species included several polychaetes. Capitellidae spp. was the second most abundant taxon (2.7% of the total number), followed by Sabellidae sp. (1.4%) and Spionidae sp.1 (1.3%). Other species contributed to less than 0.8% of the total number of benthic animals.

Most taxa were collected from various positions at the two sites (Table 2). Seven of the ten dominant taxa (i.e., with a total of ≥ 20 individuals) were collected from all positions. The three exceptions were *Anadara* sp., Syllidae spp. and Sabellidae sp., which were collected only within the *H. ovalis* vegetation at the HS site (Table 2). Taxa composition was thus largely similar among the three positions within each site.

The taxa richness of benthic animals tended to be higher at the center of *H. ovalis* vegetation than at the edge and outside the vegetation at the HS site (Fig. 3), although the variation among positions was marginally significant (ANOVA; $F = 2.877$; d.f. = 2, 21; $P = 0.079$). At the HT site, the variation was statistically significant among positions (ANOVA; $F = 4.237$; d.f. = 2, 21; $P = 0.028$), and post-hoc comparison revealed that the taxa richness was highest in the center of the *H. ovalis* vegetation (Fig. 3).

For the four dominant benthic taxa, MANOVA revealed significant variation in densities among positions at both the HS site (Pillai's trace = 0.823; $F = 3.319$; d.f. = 8, 38; $P = 0.006$) and the HT site (Pillai's trace = 0.924; $F = 4.076$; d.f. = 8, 38; $P = 0.001$). Taxa-by-taxa comparisons showed that the density of *Pillucina* sp. was significantly higher at the center than at the edge and outside at both sites, whereas no significant variation was found between the latter two positions (Table 3). The density of Sabellidae sp. showed a similar pattern of variation among positions. The variation was marginally significant at the HS site, but not significant at the HT site (Table 3). For the densities of Capitellidae spp. and Spionidae sp.1, significant variation was not detected among positions at either site (Table 3).

The relative abundances of *Pillucina* sp. and

Table 1. Sediment composition at the two study sites (HS and HT) compared between inside and outside of *Halophila ovalis* vegetation.

	Inside		Outside		T-test		
	mean	se	mean	se	t	df	P
HS site							
Median diameter (phi unit)	2.51	0.02	2.57	0.02	2.151	6	0.075
Silt-clay content (%) ^a	4.23	0.33	4.89	0.77	0.682	6	0.521
Inclusive graphic standard deviation	0.59	0.01	0.58	0.03	0.092	4 ^b	0.930
HT site							
Median diameter (phi unit)	2.65	0.02	2.44	0.02	9.655	6	< 0.001
Silt-clay content (%) ^a	7.31	0.83	3.58	0.29	4.643	6	0.004
Inclusive graphic standard deviation	0.78	0.03	0.69	0.01	2.805	5 ^b	0.042

^a Data were arcsine transformed for the *t*-test^b Welch's correction was applied to account for heterogeneous variances**Table 2.** Numbers of benthic animals collected in the present study. Data on eight replicate samples (each covering 0.01m² area) were combined for each position of the two sites.

	HS site			HT site			Total		HS site			HT site			Total
	Center	Edge	Outside	Center	Edge	Outside			Center	Edge	Outside	Center	Edge	Outside	
CHIDARIA								ANNELIDA (continued)							
Ceriantharia sp.	0	1	0	0	2	0	3	Orbiniidae sp.	1	1	2	1	0	0	5
								Glyceridae sp.	4	5	10	4	2	2	27
MOLLUSCA								Lumbrineridae sp. 1	0	1	0	1	1	1	4
Mytillidae sp. 1	3	1	0	10	0	1	15	Lumbrineridae sp. 2	5	2	0	7	0	1	15
Mytillidae sp. 2	0	0	0	3	0	0	3	Maldanidae sp.	5	10	10	2	2	1	30
Pillucina sp.	697	321	351	639	244	243	2495	Sigambra sp.	2	3	4	2	3	0	14
Anadara sp.	12	1	0	4	2	1	20	Syllidae spp.	10	4	0	4	2	2	22
Myasidae sp.	1	2	0	0	2	1	6	Chaetopteridae sp.	0	0	0	4	9	3	16
Veremolpa sp.	3	0	2	3	2	2	12	Oweniidae sp.	1	0	0	0	0	0	1
Mactridae sp.	0	0	0	0	0	1	1	Opheliidae sp.	3	2	0	1	3	4	13
Tellinidae sp.	2	0	0	1	0	2	5	Sabellidae sp.	19	8	0	18	5	5	55
Anomalocardia squamos	0	0	0	0	1	6	7	Terebellidae sp.	1	0	0	0	0	1	2
Paphia gallus	2	0	0	0	1	0	3	Eunicidae sp.	0	1	0	0	0	0	1
Unidentified bivalve sp.	0	0	0	0	1	0	1	Unidentified polychaete spp.	0	0	0	2	0	1	3
Nassariidae sp.	1	2	1	1	0	0	5	ECHIUURA							
Pyramidellidae sp.	1	1	0	2	0	0	4	Echiura sp.	1	1	4	0	2	0	8
Zafra spp.	3	1	0	2	0	0	6	SIPUNCULA							
Turridae sp.	1	0	7	1	0	1	10	Sipunculidae sp.	0	0	0	0	1	1	2
Diastomidae spp.	2	2	0	0	0	0	4	ARTHROPODA							
Clypeomorus trailli	4	1	0	1	1	0	7	Macrophthalmus quadratus	1	1	0	0	0	0	2
Clithon chlorostoma	1	0	0	4	0	2	7	Unidentified crab sp.	4	0	0	0	0	0	4
Rissoridae sp.	9	6	1	1	1	7	25	Anomura sp.	9	2	0	0	2	0	13
Decorifer sp.	0	1	0	0	0	0	1	Alpheidae sp.	4	2	1	0	4	3	14
Unidentified gastropod sp.	4	0	0	0	0	0	4	Latreutes sp.	1	1	0	0	1	0	3
ANNELIDA								Corophiidae sp.	2	2	0	0	1	0	5
Polydora sp. 1	4	1	0	10	0	0	15	Anthuridea sp.	0	0	0	1	0	0	1
Polydora sp. 2	0	0	2	2	0	0	4	Tanaidacea sp.	1	1	0	2	1	0	5
Spionidae sp. 1	17	15	4	7	3	8	54	Ostracoda spp.	1	1	0	0	0	1	3
Spionidae sp. 2	2	1	0	0	0	0	3	Pycnogonida sp.	0	0	0	1	0	0	1
Spionidae sp. 3	3	0	0	0	0	0	3	ECHINODERMATA							
Spionidae sp. 4	0	1	0	4	0	2	7	Archaster typicus	0	0	0	1	0	0	1
Nereis sp.	7	2	7	4	3	2	25	Ophiuroidea sp.	1	0	0	1	0	0	2
Polynoidae sp.	2	0	1	0	0	0	3	Total	871	419	437	783	325	311	3146
Capitellidae spp.	13	10	27	32	22	6	110								
Phyllodoce longipes	1	0	3	0	0	0	4								
Nephtyidae sp.	0	1	0	0	1	0	2

Fig. 2. Aboveground and belowground biomass (in dry weight) of the two seagrasses (*Halophila ovalis* and *Thalassia hemprichii*) at various positions of the two study sites (HS and HT sites). Error bars indicate standard errors of the mean. The number of replicates is four for each position.

Fig. 3. Taxa richness of benthic animals at three positions within and near the *Halophila ovalis* vegetation. Error bars indicate standard errors of the mean. Eight replicate samples were collected at each position. Unlike letters denote pairs of positions where significant differences were detected by post-hoc comparison (SNK test; $P = 0.05$).

Table 3. Comparisons of abundance of four dominant benthic taxa among positions in and near the *Halophila ovalis* vegetation at the two sites.

Parameters	Density (0.01m ⁻² ±SE; top column) and relative abundance (%; lower column)			ANOVA (for density)					χ^2 test (for relative abundance)	
	Center	Edge	Outside	Sources	SS	df	F	P	SNK test (P=0.05)	χ^2_{cal} P
HS site										
Density of <i>Pillucina</i> sp. ^a	87.1±17.1 (80.0)	40.1±7.2 (76.6)	43.9±5.7 (80.3)	Habitat	0.485	2	6.068	0.008	C > E = O	0.497 > 0.90
				Error	0.840	21				
Density of Capitellidae spp.	1.6±0.7 (1.5)	1.3±0.6 (2.4)	3.4±1.0 (6.2)	Habitat	20.6	2	2.135	0.143		22.527 < 0.001
				Error	101.3	21				
Density of Sabellidae sp. 1 ^a	2.4±1.1 (2.2)	1.0±0.7 (1.9)	0.0±0.0 (0)	Habitat	0.577	2	3.429	0.051		9.083 < 0.05
				Error	1.766	21				
Density of Spionidae sp. 1	2.1±0.7 (2.0)	1.9±0.7 (3.6)	0.5±0.3 (0.9)	Habitat	12.3	2	2.083	0.150		7.382 > 0.05
				Error	61.8	21				
HT site										
Density of <i>Pillucina</i> sp. ^a	79.9±17.5 (81.6)	30.5±5.9 (75.1)	30.4±3.8 (78.1)	Habitat	0.758	2	7.420	0.004	C > E = O	1.309 > 0.70
				Error	1.073	21				
Density of Capitellidae spp. ^a	4.0±1.7 (4.1)	2.8±1.1 (6.8)	0.8±0.4 (1.9)	Habitat	0.479	2	1.645	0.217		8.950 < 0.05
				Error	3.061	21				
Density of Sabellidae sp. 1 ^a	2.3±1.0 (2.3)	0.6±0.5 (1.5)	0.6±0.3 (1.6)	Habitat	0.277	2	1.628	0.220		0.935 > 0.80
				Error	1.785	21				
Density of Spionidae sp. 1	0.9±0.5 (0.9)	0.4±0.2 (0.9)	1.0±0.4 (2.6)	Habitat	1.75	2	0.808	0.459		5.221 > 0.10
				Error	22.75	21				

^a Data were log-transformed for ANOVA to secure homogeneity variances.

Spionidae sp.1 did not differ significantly among positions, whereas those of Capitellidae spp. at both sites and Sabellidae sp. at the HS site did (Table 3). For Capitellidae spp., the relative abundance was highest outside of the *H. ovalis* vegetation at the HS site and lowest at the same position at the HT site (Table 3). For Sabellidae sp., relative abundance varied significantly at the HS site due to its absence outside the vegetation, whereas it did not differ significantly among the three positions at the HT site (Table 3).

DISCUSSION

The present study shows that the abundance and diversity of benthic animals in the seagrass bed at Laem Yong Lam varied greatly among positions in and near the *H. ovalis* vegetation. The density of *Pillucina* sp. was greater at the center than at the edge of the vegetation, but did not differ between the edge and outside of the *H. ovalis* vegetation (Table 3). Taxa richness showed a similar pattern of within-site variation, although most of the dominant taxa were found at various positions at each site (Table 3). The three positions at each site were close to each other (ca 3–5 m apart), but differed greatly both in seagrass species composition and in aboveground and belowground biomass, reflecting complex spatial configuration of the seagrass habitat (Fig. 1B). The present study demonstrated that such small-scale variation in habitat heterogeneity is important in determining abundance and diversity of benthic communities in the seagrass bed. In contrast to *Pillucina* sp. and Sabellidae sp., which showed significant among-position variation in density, no significant variation was detected for Spionidae sp.1 and Capitellidae spp. (Table 3). In addition, patterns of among-position variation in relative abundance also varied from taxa to taxa (Table 3). These results suggest that the responses of benthic animals to seagrass spatial heterogeneity are species specific.

I expected the patterns of variation in the benthic community in *H. ovalis* vegetation to differ between the HS and HT sites because benthic animals at the vegetation edge are likely to be affected by the different types of surrounding environments. The surrounding environments at the two sites differed not only in the presence or absence of seagrass vegetation (*T. hemprichii*), but also in tidal level and sediment composition (Table 2). Compared to the unvegetated sand flat near the HS site, the *T. hemprichii* vegetation had coarser sediment and a shorter exposure time during

low tide. These factors may affect abundance of some benthic taxa. However, there were no differences in the patterns of among-position variation at the HS and HT sites (Fig. 3 and Table 3). Lower taxa richness and densities of some dominant animals in the *T. hemprichii* vegetation than at the center of *H. ovalis* vegetation indicate that *H. ovalis* provides better habitats for most benthic animals than *T. hemprichii*. Compared to *T. hemprichii*, *H. ovalis* covers a larger portion of the sediment surface by producing small but numerous leaves and petioles in the aboveground parts, and more complex networks of rhizomes at shallow parts of the sediment than *T. hemprichii* (Vermaat et al. 1995; Duarte et al. 1998). Such morphological characters of *H. ovalis* may favor the small-sized benthic animals collected here by providing habitats and refuges, although the mechanisms causing the variation in the benthic animals among different seagrass vegetation remain to be investigated.

Various factors can be considered to be responsible for producing the observed patterns of variation in the benthic community within vegetation, including predation intensity, food availability, physical disturbance, stress, larval supply and subsequent recruitment rate. Concerning predation intensity, major predators of the benthic animals collected at the study site (suspension feeders and deposit feeders mostly smaller than 1 cm in size) are large and mobile decapod crustaceans and carnivorous fish (Nojima, Junekitkarn & Duangdee, unpublished data), which were not efficiently collected by the core samples of 0.01 m² area. At the HS site, the predation rate on infaunal prey species by these large mobile predators may be higher at the edge of the vegetation than at the center because the biomass of *H. ovalis* is lower and predators have easier access to the edge. This may lead to lower densities of some benthic animals at the edge than the center of the vegetation. However, this cannot explain the similar patterns of variation at the HT site where seagrass biomass was highest outside the *H. ovalis* vegetation. *Pillucina* sp. and Sabellidae sp. are suspension feeders, while the other dominant polychaetes (spionid and capitellid species) are mostly deposit-feeders (Fauchald & Jumars 1979). It is possible that the presence of *H. ovalis* vegetation alters food conditions in favor of suspension-feeders. Previous studies, however, have shown that the presence of seagrass vegetation can both positively and negatively affect the food availability for suspension feeders (Irlandi & Peterson 1991; Reusch 1998; Reusch & Williams 1999). Examination of these possible factors, such as microhabitat variation in

predation intensity and food conditions, are necessary to elucidate how spatial heterogeneity of seagrass vegetation causes variation in benthic communities.

The growth rate of *H. ovalis* at the edge of the vegetation is rapid (rhizome growth rate: 15 mm/d) when the vegetation borders an unvegetated sand flat (Nakaoka & Aioi 1999; Nakaoka & Iizumi 2000). Therefore, the edge of the vegetation at the HS site was probably covered with *H. ovalis* quite recently (within 20 days, assuming a constant growth rate of the rhizomes). A similar level of abundance of benthic animals between the edge and outside of the vegetation is expected when the colonization rate to the newly-extended seagrass vegetation is lower than the expansion rate of the seagrass.

In conclusion, I showed that the benthic community in the seagrass bed at Laem Yong Lam is affected by small-scale spatial heterogeneity of *H. ovalis* vegetation, and that the pattern of variation among positions within the vegetation varied among benthic animals. These findings address the importance of the spatial structure of habitat heterogeneity in quantitative estimation of benthic communities. For example, choosing the center of habitats as sampling stations may lead to an overestimation of the density of some benthic animals when one extrapolates the data of benthic abundance to larger-scales, such as when estimating the biomass in an entire seagrass bed. Appropriate sampling designs taking the effects of small-scale habitat heterogeneity into consideration are thus necessary for precise estimation of abundance and diversity of benthic communities over large scales.

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