

Variability and consequences of seagrass  
vegetation effect on macrobenthic  
invertebrate communities

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## **ABSTRACT**

Seagrass vegetation plays an important role in marine coastal ecosystem. It provides habitats, shelter and food to associated-animal communities, enhancing their abundance and biodiversity. For macrobenthic invertebrate communities, however the vegetation effects are not always positive. To examine the factors affecting the variability in the vegetation effects on macrobenthic communities, and to investigate the interacting effects of seagrass vegetation with other types of factors affecting their abundance and diversity, I carried out broad-scale analyses of benthic community using several different approaches.

In Chapter 2, I used a hierarchical nested design to examine effects of eelgrass vegetation on benthic community at large spatial scale by comparing data collected at several different stations (1-10 km apart) within each of several different sites (10-50 km apart). I found no significant variation among sites in the vegetation effects, which are represented by differences in macrobenthic density, diversity and dissimilarity. This suggests that the variation in vegetation effects mostly occur at small-spatial scale such as among seagrass beds in one locality or within a single seagrass bed.

In Chapter 3, I investigated the effect of spatial structure of seagrass landscape and its temporal dynamics on abundance and density of macrobenthic community by combination of field sampling and remote sensing analysis. I also examined relative importance of vegetation types, coverage and stability on observed variation in macrobenthic communities by a model selection method. Seagrass coverage was most correlated with diversity and abundance of benthic animals when I observed the seagrass coverage at the extent of 10-15 m. Model selection showed that not only

vegetation types but also coverage at surrounding area explained variability in macrobenthic abundance and diversity.

In Chapter 4, I examined the impacts of tsunami (catastrophic disturbance) on seagrass macrobenthic communities by comparing data collected before and after the tsunami, and those collected inside and outside the seagrass vegetation. Macrobenthic animals were collected from vegetated and nonvegetated areas of 2 sites that had received different levels of tsunami disturbances. The temporal changes in assemblage structure were not solely related to the magnitude of the tsunami disturbance. I also found that the presence or absence of seagrass vegetation can alter the patterns of temporal changes in macrobenthic assemblages and recovery processes after disturbance.

My results revealed that the variability and consequence of seagrass vegetation effects on macrobenthic animal community over different spatial and temporal scales. Finding on the importance of seagrass vegetation is further discussed in relation to conservation and management of coastal ecosystems.

## **CHAPTER 1**

### **General introduction**

#### **1.1. Importance of seagrass community**

Seagrasses are marine flowering plants that represent important communities in coastal areas throughout the world (Hemminga and Duarte, 2000; Green and Short, 2003). There are about 60 species of seagrass in 12 genera (Hemminga and Duarte, 2000; Kuo and Hartog, 2006). Typically, seagrass bed is found in areas dominated by soft bottom such as sand and mud, but some species can grow on hard substrate such as rock. Seagrasses need enough light for photosynthesis which limits their distribution in shallow areas (Lipkin, 1979). Seagrass species are more diverse in tropical regions where multispecific meadows are developed than in temperate regions that mostly have monospecific beds (Spalding et al., 2003).

Seagrass beds play an important key in the ecological roles of the marine coastal ecosystem. They are major primary producers, supporting high productivity and high diversity of associated marine animals including commercially important fish and large endangered vertebrates such as sea turtles, dugongs, and manatees (Mukai et al., 2000; Beck et al., 2001; Heck et al., 2003; Larkum et al., 2006; Valentine and Duffy, 2006). They also have a relatively complex physical structure, providing food source and nursery grounds for many species such as blue swimming crabs and black tiger prawn (Spalding et al., 2003; Waycott et al., 2004). Seagrasses are ecosystem engineers in coastal environment. They accumulate and stabilize sediment, and regulate water quality and nutrient cycle, contributing to organic carbon



production and trophic transfers to adjacent habitats (Spalding et al., 2003; Orth et al., 2006; McGlathery et al., 2007). Economic value of ecosystem services provided by seagrass beds is estimated to be very high (Costanza et al., 1997).

Despite importance of seagrass beds as described above, they are declining rapidly from the world (Duarte, 2002; Duarte, et al., 2006; Waycott et al., 2009). Decrease of seagrass bed has been also reported in Asian regions (Green and Short, 2003; Sanbanze Restoration Plan Committee, 2004; Nakamura, 2009). The causes of decline in seagrass vegetation are various types of disturbance, some of which due to natural, non-anthropogenic causes such as disease and strong storm, but most of which due to human-induced disturbances such as coastal development and the deterioration of water quality (Orth et al., 2006). However, quantitative reports on the patterns of decline and possible causes are still insufficient in Asian regions (Waycott et al., 2009). More studies on seagrass beds in these regions are required to quantitatively evaluate their role in coastal ecosystems, which information is necessary to plan effective conservation and adaptive management of coastal areas.

## **1.2. Macrobenthic invertebrate community in seagrass beds**

As explained in above section, seagrass beds host a wide variety of associated animal communities. Animal community in seagrass bed can be classified to 4 major functional groups based on life habitat (Boström et al., 2006; Duffy, 2006). Among benthic organisms that are associated with sea bottom, epifaunal animals live by attaching to the surface hard substratum such as seagrass leaves, whereas infaunal animals live partly or fully below the sediment. Many swimming animals such as fishes and shrimps are called nekton. Because benthic animals are often collected and

separated by sieve, we can classify benthic organisms based on size; macrofaunal animals (body size greater or equal to 0.5 mm); meiofaunal animals (smaller than 0.5 mm but greater than 0.1 mm) and microfaunal animals (less than 0.1 mm in size) (Levinton, 1995).

Studies have addressed the importance of seagrass beds by showing the various types of their positive effects on macrobenthic invertebrate community. Macrobenthic animals in seagrass beds, defined here as benthic animals larger than 0.5 mm in body length but smaller than 5 cm, consist of major marine invertebrate taxa such as polychaetes; small crustaceans; gastropods and bivalves. Most species of macrobenthic invertebrate community are either grazer or decomposer in the seagrass beds, and they are mostly consumed by higher level consumers such as large decapod crustaceans (shrimps and crabs) and variety of fish species (Watanabe et al., 1996; Nakamura et al., 2006). They thus provide a key link in food web of seagrass beds. They also play an important role in the nutrient cycling in the sediment (Williams and Heck, 2001; Hasegawa et al., 2008).

Seagrass provides both food and habitats to macrobenthic invertebrates. For food supply, it should be emphasized that major food for invertebrate grazers is not seagrass leaves itself, but epiphytic organisms (e.g., biozoa, algae and benthic phytoplankton) that attached to seagrasses (Jernakoff et al., 1996; Valentine and Heck, 1999; Kaiser et al., 2005). For decomposers like most deposit feeders, decayed seagrass may be a major source of their food (Williams and Heck, 2001). However, fewer studies have addressed their feeding ecology and roles in nutrient material flow in detail (Williams and Heck, 2001).

### **1.3. Variation in vegetation effects on macrobenthic invertebrate community**

Seagrasses generally enhance abundance and biodiversity of animals in most functional groups (Kikuchi and Pérès, 1977; Hemminga and Duarte, 2000). There are many studies showing that seagrass vegetation has positive effects on animal groups, particularly on fish and shrimp communities (Hovel and Lipcius, 2001; Duffy, 2006). For macrobenthic invertebrate community, however, vegetation effects are not always positive. For example, Allen and Williams (2003) showed that growth and reproduction of mussels were negatively affected by eelgrass.

Variable and elusive effects of seagrass vegetation on macrobenthic animal community, especially on infauna, are primary due to the fact that infauna do not necessarily require seagrass for its habitats, as opposed to epiphytic fauna for which the presence of seagrass leaves are prerequisite. It is highly likely that environmental conditions of seagrasses, for example, hydrodynamic conditions, physical disturbance regime, water and sediment conditions interfere with the effects of seagrass vegetation. Focusing on either hydrodynamic conditions or disturbance may be plausible, i.e., if the disturbance is too strong, the seagrass may act as shelter for infauna, whereas if the hydrodynamic condition is not strong enough, the presence of seagrass retard water flow and inhibit feeding activity of suspension feeders.

In conclusion, the effects of seagrass vegetation is highly variable on macrobenthic infauna compared with other types of seagrass-associated animals, and we need to investigate how the variability is caused in relation to environmental set-ups and nature of seagrass vegetation.

#### **1.4. Integrated approach to examine variable effects of seagrass vegetation on seagrass-associated benthic community**

To examine factors and processes of variable effects of seagrass vegetation on macrobenthic invertebrate, several different approaches are proposed in this study. They are (1) hierarchical analysis of seagrass vegetation effects at broad-spatial scales, (2) landscape approach using remote sensing and GIS, and (3) long-term monitoring of seagrass community at different seagrass beds under different environmental conditions.

Comparison of community structure by nested hierarchical design is one of the effective approaches to understand multiple processes on population and community operating at different spatial scales. Using this approach, we can examine variation in functioning and ecological pattern at both a large variety of spatial and temporal scales (de Boer, 1992; Hughes et al., 1999). Especially, it is useful to examine at which spatial scale the community structure mostly varies. For example, Nakaoka et al. (2006) examined rocky intertidal community along the Pacific coast of Japan, and found that significant variation in similarities were found among regions and among shores within each region, with the former showing greater variation. Benedetti-Cecchi et al. (2010) examined spatial relationships between rocky shore polychaete assemblages and environmental variables over broad scales and found that most environmental variables were significantly related to spatial variation at the board scale. The approach can be used to clarify the context dependency in seagrass vegetation effects on macrobenthic animals that vary among regions, sites and patches in a seagrass bed.

Recently, remote sensing and GIS techniques have been increasingly utilized for broad-scale study of coastal ecosystems including seagrass beds (Kendrik et al., 1999; Fortin and Dale, 2005; Kendrik et al., 2008; Urbanski et al., 2009, Yamakita et al., in press). This tool enables one to analyze examine the effect of seagrass landscape structure on biodiversity and community of benthic animals at various spatial scales (Pittman et al., 2004; Kendall, 2005; Mellin et al., 2007). By integrating remote sensing data to identify habitat variables and field collection, it is now possible to examine effects of seagrass structure on benthic animals simultaneously at different spatial scales.

Finally, long-term monitoring of seagrass community is an essential method to understand how seagrass community responds to variable changes in environmental factors. Effective monitoring of biodiversity over the long run can be used for various purposes, such as prediction and evaluation of ecosystem changes in relation to climate changes (Kendrik et al., 1999; McKenzie et al., 2001; Frederiksen et al., 2004; Bernard et al., 2007). The long-term monitoring data can also be useful to assess the impact of sudden catastrophic disturbance to coastal ecosystems, such as caused by typhoon and tsunami. Because these catastrophic events occur in unpredictable way, it is difficult to assess the impact by pre-planned assessments. However, if long-term monitoring data are available at impacted sites before the occurrence of the event, it is then possible to assess their impact based on before/after comparisons using the same monitoring methods.

## 1.5. Scope of study

The main objective of this thesis is to examine the variability in seagrass-associated benthic communities among different positions in seagrass beds that are affected by different combination of environmental parameters and geographical setups. Throughout the thesis, I defined “seagrass vegetation effects” as the difference in abundance and diversity of macrobenthic invertebrates between seagrass vegetation and nonvegetated position (gap) in a seagrass bed. I set up the two major research questions; (1) “How does the seagrass vegetation effect vary spatially and temporally?”, and (2) “How does the effect contribute to the dynamics of macrobenthic invertebrate community?”. I examine the former question by two different approaches, i.e., by hierarchical sampling design (Chapter 2) and by landscape approach (Chapter 3), and the latter question by focusing on a catastrophic disturbance by a tsunami (Chapter 4).

In Chapter 2, spatial scale dependency in the seagrass vegetation effect on macrobenthic invertebrates are tested by setting the sampling stations according to a hierarchical nested design, i.e., several seagrass beds (or several positions in a seagrass bed) nested within a single local site, and several local sites nested within a coastal region. I examine at which scale the seagrass vegetation most vary. I also examine factors affecting the variability of the vegetation effect by collecting broad-scale data on environmental and geographical variables.

In Chapter 3, I examine the effect of spatial structure of seagrass vegetation on macrobenthic invertebrate community by developing an integrated approach using field sampling and remote sensing analysis. By changing the scale of observation continuously, I examine at which spatial scale (extent) seagrass vegetation has the

highest positive effects on benthic community. Temporal variability in seagrass coverage at each sampling point is also analyzed using time-series data on seagrass spatial distribution. Finally, I examine relative importance of vegetation types, coverage and stability on observed variation in macrobenthic invertebrate community by a model selection method.

In Chapter 4, I focus on the contribution of the seagrass vegetation effects on the dynamics of benthic invertebrate community which faced catastrophic disturbance. I examine the effects of a tsunami on seagrass macrobenthic community by comparing data collected before and after the tsunami. Patterns of temporal changes in community structure are compared between 2 seagrass beds that received different degrees of disturbance and between vegetated and nonvegetated areas within seagrass bed to examine whether the changes are related to the magnitude of the tsunami disturbance and to the presence or absence of seagrass vegetation.

Finally in Chapter 5, I synthesize my findings on the causes for variability and consequences of seagrass vegetation effects. I discuss the importance of seagrass landscape structure and small local environmental and geographical conditions on the intensity of vegetation effect. I set up a conceptual model describing how the seagrass vegetation effects can be a cause and consequence of variability in associated-animal community base on comparisons with other related studies.

My findings on the importance of seagrass vegetation effect are further discussed in relation to conservation and management of coastal ecosystems, i.e., how the understanding of seagrass vegetation effect contribute to maintain the stability of biodiversity and ecosystem function of seagrass beds which harbor wide array of biodiversity in coastal areas.

## **CHAPTER 2**

### **Spatial and seasonal variation in the seagrass vegetation effect on benthic community in Tokyo Bay, Japan**

#### **2.1. Introduction**

Eelgrass (*Zostera marina*), a marine flowering plant that occur in shallow soft bottom, is the most dominant species in coastal and estuarine areas of temperate regions in the Northern Hemisphere (Den Hartog, 1970; Hemminga and Duarte, 2000; Short et al., 2007). Seagrass beds, including those consisting of eelgrass, play important roles in marine ecosystems. They enhance diversity and abundance of numerous animals by providing food, shelter and nursery ground (Hemminga and Duarte, 2000; Williams and Heck, 2001). In the recent years, however, eelgrass beds are significantly reduced worldwide due to human-induced disturbances and stresses such as coastal development and water pollution (McRoy, 1996; Duarte, 2002; Waycott et al., 2009). The elucidation of factors affecting variation and dynamics of seagrass community is necessary for planning effective conservation of seagrass ecosystem functions and biodiversity against the human-induced threats.

Providing three-dimensional structure on shallow sea bottom, seagrass beds provide habitats for diverse animal community. A variety of epifaunal invertebrates such as sessile animals (such as bryozoans and the spirobid polychaetes) (Hamamoto and Mukai, 1999; Kouchi et al., 2006) and motile animals (such as small crustaceans and gastropods) are present on leaf blade (Jernakoff et al., 1996; Kaiser et al., 2005). Numerous infaunal benthic organisms, such as polychaetes and bivalves inhabit the



sediment of seagrass beds (Cloern, 1982; Cole et al., 1992). These small invertebrates are consumed by larger animals such as decapods crustaceans and fish, providing a key link between primary producers and higher-level consumers including commercially important species (Watanabe et al., 1996; Nakamura et al., 2006).

Numerous studies have been conducted to examine the effects of seagrass bed on biodiversity and abundance of benthic community (Lewis, 1984; Hemminga and Duarte, 2000; Lee et al., 2001). One of the most effective methods to evaluate the effect of vegetation is to compare abundance and diversity of animal communities between seagrass vegetated areas and surrounding nonvegetated areas (Orth et al., 1984). Seagrass beds have positive effects on abundance of fish and epiphytic animals by providing areas for feeding and breeding, and refuge from predators (Virnstein, 1977; Heck and Thoman, 1981; Edgar 1983; Bell and Pollard, 1989; Edgar et al., 1994; Heck et al., 2003). For infaunal benthic community, however, the effects of seagrass vegetation are highly variable. Seagrass vegetation shows positive effect on some infauna by increasing food availability and shelters against predators (Virnstein, 1977; Hemminga and Duarte, 2000; Kneer et al., 2008). In the other end, a negative effect of seagrass vegetation was also detected in some studies in which seagrasses decrease habitat and food for benthic animals such as mussel and blue crab (Boström and Bonsdorff, 1997; Reusch and Williams, 1999; Allen and Williams, 2003).

The variable effects of seagrass vegetation on infauna are partly due to the fact that infaunal benthic animals do not necessarily require seagrasses as a habitat as for epifauna animals (Nakaoka, 2005). More importantly, seagrass beds can develop on soft bottoms under various environmental conditions, ranging from sheltered muddy bottom to semi-open sandy bottom with different hydrodynamic and biogeochemical setups (Nakaoka and Aioi, 2001). Most previous studies examined the community

structure of benthic organisms through comparisons at very small spatial scales (Boström and Bonsdorff, 1997; Lee et al., 2001). However, recent studies on community dynamics pointed out the importance of processes operated at different spatial scales (Irlandi, 1994; Underwood and Chapman, 1996; Noda et al., 2009). To understand the nature and variability of seagrass vegetation effects, one of the promising approaches is to compare the effect at broad spatial scales by setting each seagrass bed or each vegetation patch as a replicate unit. The use of hierarchical sampling design is especially useful to determine the appropriate scales at which key ecological processes vary (Noda, 2004; Nakaoka et al., 2006).

The aim of the study is to examine the variability in the vegetation effects of seagrass on macrobenthic organisms. The sampling stations were established according to a hierarchical nested design, i.e., (1) replicate samples collected within a sampling station of each seagrass bed (or a part of large seagrass bed) at the smallest spatial scale (within a distance of 10-100 m), (2) several stations set within a local area at an intermediate scale (within 5-10 km distance), and (3) several local area established located within a coastal region of Tokyo Bay, Japan at the broadest spatial scale (within a distance of 50-100 km). At each sampling station, macrobenthic organisms were collected within and outside the seagrass vegetation by the same procedure, and variation in abundance, species diversity and similarity in species composition were compared between vegetated and nonvegetated positions of each station. By utilizing broad-scale data on environmental and geographical variables, I also examined factors affecting the variability of the vegetation effects.

## **2.2. Materials and methods**

### 2.2.1 Study sites

Tokyo Bay locates along the Pacific coast of middle Honshu, Japan.

It is 80 km long trending north to south, and divided into inner and outer parts by a narrow strait (Uraga Strait) between Futtsu Cape and Kannon Cape (Fig. 2.1). At the inner part (Inner Bay), average depth is less than 20 m, with limited water exchange with outer part (Outer Bay) due to Uraga Strait (Furukawa and Okada, 2006). Outer Bay is deeper with deep trench (>500 m) located at the center. Water exchange rate from/to the Pacific Ocean is high.

Up to the early 20<sup>th</sup> Century, seagrass beds were present throughout Inner Bay (Yamakita et al., 2010 in press). Most seagrass beds, however, have disappeared during the 20<sup>th</sup> Century due to land reclamation and eutrophication, and only three seagrass beds remains in Inner Bay (Yamakita et al., 2005; Yamakita et al., 2010 in press). Coastlines of Outer Bay are mostly rocky, and numerous small seagrass beds are found in sedimentary bottoms in small coves and sheltered areas (Furukawa and Okada, 2006; Shoji and Hasegawa, 2008). Three seagrass species are found in Tokyo Bay; *Zostera marina*, *Z. caulescens* and *Z. japonica*. *Zostera marina* is dominant in all the seagrass beds, whereas *Z. japonica* and *Z. caulescens* were found only in the shallowest and deepest parts of several large seagrass beds, respectively.

In this study, I selected the study site according to the nested, hierarchical design. Firstly I selected three areas (sites); FT (Futtsu in Inner Bay), TK (Takeoka in northern Outer Bay) and TT (Tateyama in southern Outer Bay). Then I selected three to four stations within each area; P1, P2, F1, F2 in FT; T, S, U in TK; and H1, H2, O in TT (Fig. 2.1). *Z. marina* dominates in all the seagrass beds with *Z. japonica* and *Z. caulescens* observed partially in some bed (Table. 2.1).

### *2.2.2. Field census*

The fieldwork was carried out in summer 2006 (between June and August), and in autumn 2006 (between September and November). The benthic collection was conducted by SCUBA. Three replicate samples were collected from each of seagrass-vegetated positions and non-vegetated points within each station by a PVC core sampler of 15 cm diameter. The core was inserted to sediment 10 cm deep to take benthic samples quantitatively. Collected samples were sieved by 1 mm mesh opening, and fixed with 10% neutralized seawater formalin. In the laboratory, macrobenthic animals were sorted and identified to possible lowest taxonomic level, and the number of individuals was counted for each taxa. Due to the lack of relevant taxonomic information, some groups such as amphipods were identified only to genus level. Throughout this study, I used the term “taxa” rather than “species” (“taxa richness” rather than “species richness”). The biomass of aboveground and belowground parts of eelgrass was measured to a nearest 0.1mg by an electrical balance after drying them at 60°C to a constant weight.

Silt-clay content of sediment at vegetated and nonvegetated positions of each station was obtained by collecting three sediment samples at each position for a ca. 300 g wet weight by shovel to a depth of 5 cm. The collected sediment was dried to a constant weight at 110°C and sieved through a 0.063mm mesh sieve, and the relative percentage of dry weight of the fraction < 0.063 mm among total dry weight was determined as the silt-clay content (%).

### *2.2.3. Broad-scale environmental conditions*

Water quality (water temperature, salinity, nitrogen and phosphate contents) at each sampling point was represented by the long-term observation at the near most station of each seagrass bed conducted by Chiba Prefecture Environmental Research Center. The observation has been carried out monthly or bimonthly since 1998. Average data between 1998 and 2005 was used for the analyses in this study.

The effect of river discharge on seagrass community was investigated by calculating the “river effect index (REI)” by the following formulae:

$$REI = A / d^2$$

Where  $A$  is a catchment area of a near most river of each seagrass bed, and  $d$  is the distance between the seagrass bed and the mouth of the river. I assumed that effect of river discharge such as the siltation and nutrient discharge was greater from rivers with greater catchment area and for seagrass beds closer to river mouth. The catchment area of rivers and the distance from the mouth river to the sampling points were calculated by GIS (Arc GIS 9.3, ESRI).

Area of each seagrass bed was obtained by BIODIC (2007) in which areas of major seagrass beds along eastern coast of Tokyo Bay was determined based on aerial photographs taken in 2005.

#### *2.2.4. Data analysis*

From species composition and density data of each core sample, I estimated the following variables: (1) the abundance represented by density of all macrobenthic invertebrates, (2) density of top three dominant taxa of macrobenthic in each season, and (3) taxa richness of all macrobenthic animals.

Spatial and temporal variations in abundance and taxa richness of all macrobenthic animals were tested by three-way nested ANOVA using the presence/absence of vegetation, season, site and station (within site) as dependent variables. Variation in the density of top three dominant taxa at each season was tested by two-way nested ANOVA using the presence/absence of vegetation, site and station (within site) as fixed factors. The data on density was log-transformed to account for normality and homoscedicity. In cases when significant interactions were found between vegetation types and other factors, post-hoc comparison was carried out using t-test for each station and seasons after adjusting an type I error rate of each comparison to be  $\alpha' = 0.005$ .

The variation in vegetative effect on macrobenthic organisms at each station was represented by the following two variables; (1) the difference in density (log-transformed) between vegetated and nonvegetated sites;  $\log(n_v) - \log(n_u)$ , and (2) dissimilarity in taxa compositions between vegetated and nonvegetated positions. For the latter, the average value of Bray-Curtis dissimilarity for all the combination of 3 replicate samples from two vegetation types (a total of 9 data) was obtained for each station using untransformed density data and the presence/absence data. The scale-dependency of these two variables was then tested using one-way ANOVA using site as a random variable and station as replicate unit (residual). The analysis was carried out separately for summer and autumn samples.

I finally examined factors affecting the observed variation in vegetation effects on macrobenthic animals using general linear model. Candidate environmental variables parameters for the test were: four variables on water quality (average annual temperature, average annual salinity, total nitrogen content and total phosphate content in water column), the river effect index, two variables on sediment condition

(silt-clay content in vegetated area, and the difference in silt-clay content between vegetated and nonvegetated area), four variables on seagrass-related parameters (seagrass bed size, seagrass shoot density, seagrass biomass) and season (summer and autumn). Except for season (binary data), some of these variables may covary. I first excluded several variables by collinearity analysis. Because all the four variables on water quality were highly correlated with each other (nitrogen content correlated positively with phosphate content, water temperature and negatively with salinity), I only used nitrogen content as independent variable. Similarly, I excluded the difference in silt-clay content between vegetated and non-vegetated area and seagrass shoot density from the model because the former was highly correlated with silt-clay content in the vegetation, and the latter with seagrass biomass.

## **2.3. Results**

### *2.3.1. Spatial variation in environmental parameters*

Annual average water temperature was minimum in Futtsu and maximum in Tateyama. It tended to be lower at Inner Bay (Table 2.2). Average annual salinity was lower at Inner Bay, Futtsu than at Outer Bay (Table 2.2). Total nitrogen and total phosphate contents were highest in Futtsu, and decreased gradually to the outer part of Tokyo Bay (Table 2.2). River effect index varied greatly among stations within sites and stations with the lowest in F2 and the highest in H1 (Table 2.2). Seagrass bed size was the largest in Futtsu tidal flat, which contains stations F1 and F2, followed by Hojo Beach in Tateyama (H1 and H2) and Futtsu Port (P1 and P2) (Table 2.2).

Seagrass biomass tends to be smaller in the autumn than in summer (Fig. 2.2). In summer, it was maximum in Shimatogura (S), and minimum in P2 of Futtsu. In autumn, biomass of seagrass was maximum at Okinoshima (O) and the minimum in H1. Silt-clay content varied greatly among sites and between vegetation types, but generally higher in seagrass vegetation than in non-vegetated positions (Fig. 2.3).

### 2.3.2. Abundance and diversity of macrobenthic community

A total of 14857 individuals  $\text{cm}^{-2}$  of macrobenthic animals were collected from 120 core samples, which were classified into 190 taxa (Table 2.3). Bivalves were the most dominant (33.4 %), followed by polychaetes (31.7 %), amphipods (22.3%), and other (8.3%). The dominant taxa varied between seasons. In summer, *Jassa* sp. (Amphipod) were the most dominant, followed by *Platynereis bicanaliculata* (Polychaete), and *Spiophanes bombyx* (Polychaete), whereas in autumn, *Musculista senhousia* (Bivalve) were the most abundant, followed by *P. bicanaliculata* and *Iwakawatrochus urbanus* (Gastropod).

Pattern of variation in the total density of macrobenthic animal, and those in top three dominant taxa varied among sites and stations, and between seasons and vegetation types. For the total density, three-way nested ANOVA showed significant higher order interactions among season, site and vegetation type, and among season, station and vegetation types, suggesting that the vegetation effects vary with seasons, stations and sites (Table 2.4). Post-hoc comparisons revealed that the density was significantly greater in the vegetation than non-vegetated positions for P1, F1 and H2 in summer, and for F2, T, S and O in autumn. In contrast, the density in nonvegetated positions was higher P1 in autumn (Fig. 2.4).



Patterns of variation in abundance of top three dominant taxa were totally different between seasons and among species (Table 2.5). Two-way nested ANOVA showed no significant interactions among vegetation, station and sites of all three dominant taxa; *Jassa* sp., *Platynereis bicanaliculata*, and *Spiophanes bombyx* in summer. For *Jassa* sp. and *P. bicanaliculata*, it was significantly higher in vegetation than in non-vegetated points, whereas the difference between vegetation types was not significant for *S. bombyx*. In autumn, significant higher order interactions between site and vegetation, and/or between station and vegetation were detected for the dominant three species (Table 2.5). Post-hoc comparisons revealed that the density was significantly greater in the vegetation than non-vegetated positions for F2, T and H2 of *Musculista senhousia*, for P1, P2, F2, S, H1, H2 and O of *Platynereis bicanaliculata*, and for F1 of *Iwakawatrochus urbanus*. In contrast, the density in nonvegetated positions was higher for P1 of *Musculista senhousia* and P2 of *Iwakawatrochus urbanus* in autumn (Fig. 2.5).

For taxa richness, ANOVA showed no significant interactions among season, vegetation, station and sites. Only additive effects of these factors were found (Table 2.6); i.e., it was higher in summer than in autumn, higher in seagrass vegetation than in non-vegetated position. Taxa richness tended to be greater at stations in Futtsu than those in Tateyama (Fig. 2.6).

Two-way ANOVA for the differences in total density and for Bray-Curtis dissimilarity between seagrass vegetation and non-vegetated positions showed no significant effect of site and seasons for both dependent variables (Table 2.7).

General linear model relating environmental factors to the vegetation effects on density and dissimilarity had low predictable power ( $R^2 \leq 0.367$ ; Table 2.8). The

model detected no significant independent variables accounted for the observed variation in the dependent variables (Table 2.8).

## **2.4. Discussion**

Present study provides the first comprehensive data on abundance and diversity of seagrass-associated macrobenthic assemblages in Tokyo Bay. The comparisons between seagrass vegetation and adjacent unvegetated areas revealed that the abundance is not always higher in seagrass vegetation, as repeatedly reported in previous studies (Edgar et al., 1994; Boström and Bonsdorff, 1997; Attrill et al., 2000; Lee et al., 2001). Most notably, significant high-order interactions among season, vegetation, and site/station were found for the total density of macrobenthic organisms, suggesting that the seagrass vegetation effects on their abundance vary spatially and seasonally. For taxa richness, however, only additive effects of season, vegetation, and site/station were detected, with greater taxa richness in the seagrass vegetation sites, which agrees with general notion that seagrass vegetation enhances animal diversity (Hemminga and Duarte, 2000). The contrasting results between dependent variables suggest that processes and mechanisms determining abundance and diversity of benthic community may totally different.

The results of ANOVA testing variation in seagrass vegetation effects revealed no significant effects of sites on the observed differences in macrobenthic density and dissimilarity. This demonstrates that the variation in vegetation effects mostly occur at smaller spatial scales, such as among seagrass beds in one locality (< 10 km distance) or even within a single seagrass beds. Previous studies pointed out the important of local (small scale) processes in determining the abundance and

diversity of benthic communities (Irlandi, 1994; Underwood and Chapman, 1996). For example, Edgar and Barrett (2002) reported that faunal density showed greater response to factors that vary within an estuary (<10 km) than to factors that vary between estuaries. Similarly, Hovel et al. (2002) showed that abundance of benthic fauna is mostly related to variation in energy regime and habitat structure within a local site (<1m).

I firstly expected that the vegetation effects were greater at seagrass beds with greater seagrass biomass or shoot density because they may provide better habitat for macrobenthic animals (Attrill et al., 2000; Hovel et al., 2002). I also expected that abundance of seagrass vegetation effects were greater in the seagrass beds with more disturbed habitats such as low water quality, high heat and salinity stress and greater river discharge effects, where presence of seagrass may be more important for increasing survivorship of associated animals. Multiple regressions analysis, however, failed to detect any environmental factors responsible for the variation in the vegetation effects; i.e., The effects of vegetation effects could not ascribed to the variation in water quality, river effect index, seagrass biomass, seagrass bed size and bottom profiles in my study. Concerning variables on water quality (temperature, salinity and nutrient concentration), it mostly varies among-site scale, which may not be responsible for causing variation in seagrass vegetation effects at smaller spatial scale. It remains unknown, however, why variables representing quantity of seagrass did not affect the vegetation effects.

Patterns of variation in abundance of dominant taxa between vegetation types varied greatly among species and between seasons. Two dominant taxa in summer, *Jassa* sp. and *Platynereis bicanaliculata* showed higher density in seagrass vegetation than in nonvegetated area regardless of sites and stations (indicated by no significant

interaction terms). The result is expected because they are mobile epifauna which requires seagrass blade as their main habitats (Nakaoka et al., 2001). For the third dominant species, *Spiophanes bombyx* is a suspension feeder inhabiting surface and/or in the sediment. To this species, seagrass vegetation showed no positive response. Seagrass vegetation effect varies with life styles and habitat requirement of macrobenthic animals, with more positive effects likely exhibited for epifauna than in infauna.

For the dominant species in autumn, the significant interaction was found between vegetation types and site/stations, suggesting that seagrass vegetation effects vary spatially. This is especially true for *Musculista senhousia* which are suspension feeder living in the surface of sediment (Crooks, 1998; Reusch and Williams, 1999). Seagrass beds may either enhance or decrease food availability for suspension feeders, depending on their effects on hydrodynamic conditions. They also decrease habitat for benthic animals such as mussel (Allen and Williams, 2003), but may enhance their survivorship by protecting them from predators (Hemminga and Duarte 2000). It is likely that relative importance of these multiple processes varies among sites and stations, leading to site/station-specific effects of seagrass vegetation.

However, it is unexpected that similar site/station-specific effects were also found for dominant epifauna in autumn, i.e., *Platynereis bicanaliculata* and *Iwakawatrochus urbanus*. For *P. bicanaliculata*, the results are also different between summer and autumn. This is one of the important findings of this study; the seagrass vegetation effects can vary with seasons even within a same station. One of the major factors for the seasonal variation may be changes in seagrass biomass and shoot size which generally decreases from summer to autumn in temperate areas of Japan (Mukai et al., 1979; Aioi et al., 1981). In the present study sites in Tokyo Bay,

however, the seagrass biomass did not decrease drastically from summer to autumn to account for the observed change in the effect.

Species composition also changes greatly with seasons in some stations. For example, *Musculista senhousia*, the most dominant taxa in my study sites increases greatly in some seagrass beds from summer to autumn, but not in other sites. This mussel species is known as an ecosystem engineer of soft bottoms, affecting community structures of benthic animals (Crooks, 1998; Crooks and Khim, 1999). Other important, but uninvestigated factors include seasonal changes in major predatory species in eelgrass beds such as fish and crustacean decapods which abundance and diet generally changes with seasons (Yamada et al., 2010). More detailed studies on biological interactions such as predation and competition may answer the processes affecting the seagrass vegetation effects on macrobenthic invertebrate community, which vary at small spatial and temporal scales.

Table 2.1  
Seagrass species composition at each station along the east coast of Tokyo Bay.

Seagrass beds (Region)	Study sites (Station)	No. of seagrass species	Seagrass species		
			<i>Zostera marina</i>	<i>Zostera japonica</i>	<i>Zostera caulescens</i>
Inner Bay					
Futtsu (FT)	Futtsu port (P1, P2)	1	○	-	-
	Futtsu tidal flat (F1, F2)	3	○	○	○
Northern Outer Bay					
Takeoka (TK)	Tsuhama (T)	2	○	-	○
	Ushiyama (U)	1	○	-	-
	Shimatogura (S)	1	○	-	-
Southern Outer Bay					
Tateyama (TT)	Hojo Beach (H1, H2)	1	○	-	-
	Okinoshima (O)	2	○	○	-

Table 2.2  
 Environmental factors at 10 stations in 3 sites (FT, TK, TT) along east coast of Tokyo Bay. Data on water temperature, salinity, total nitrogen content and total phosphate content were obtained from Chiba Prefecture Environmental Research Center. Among those, the data of nearest measuring point were used for analysis. For river effect index, see the text. Seagrass bed sizes were cited from BIODIC (2007).

Seagrass beds (Region)	Study sites	Water temperature (°C)	Salinity (PSU)	Nitrogen content (mg/L)	Phosphat content (mg/L)	River effect index	Seagrass bed size (m <sup>2</sup> )
Inner Bay Futtsu (FT)	Futtsu port (P1)					24.95	67752
	Futtsu port (P2)	17.6	31.5	0.72	0.061	22.30	
	Futtsu tidal flat (F1)					6.06	721425
	Futtsu tidal flat (F2)					5.84	
Northern Outer Bay Takeoka (TK)	Tsuhama (T)	18.7	33.3	0.40	0.031	34.11	4018
	Ushiyama (U)	19.2	33.9	0.30	0.021	11.79	1646
	Shimatogura (S)	19.2	33.9	0.30	0.021	11.77	500
Southern Outer Bay Tateyama (TT)	Hojo Beach (H1)	19.6	33.9	0.22	0.021	452.57	303848
	Hojo Beach (H2)	19.6	33.7	0.24	0.021	241.09	
	Okinoshima (O)	19.6	33.9	0.21	0.021	12.68	4277

Table 2.3. List of macrobenthic invertebrate species collected at Tokyo Bay in 2006.

Polychaeta		Gastropoda
Ampharetidae sp.	<i>Owenia fusiformis</i>	<i>Reticuasssa festiva</i>
<i>Arenicola brasiliensis</i>	<i>Aricidea eximia</i>	Pyrgiscilla
<i>Capitella</i> sp.	<i>Aricidea pacifica</i>	<i>Thais (Reishia) clavigera</i>
Capitellidae gen. sp.	<i>Paraonides nipponica</i>	<i>Iwakawatrochus urbanus</i>
Capitellidae gen. sp. 2	<i>Lagis bocki</i>	<i>Pupsyrnola inturbida</i>
<i>Heteromastus</i> spp.	<i>Anaitides maculata</i>	<i>Umbonium multiferum</i>
<i>Notomastus</i> sp.	<i>Eteone longa</i>	<i>Orinella pulchella</i>
<i>Chrysopetalum</i> sp. ( <i>occidentale</i> )	<i>Eulalia viridis</i>	<i>Angustassiminea castanea</i>
<i>Chaetozone</i> sp.	<i>Eumida sanguinea</i>	<i>Epitium (Papyriscala) clementinum</i>
<i>Ciriformia</i> cf. <i>comosa</i>	<i>Genetyllis castanea</i>	<i>Phasianella solida</i>
<i>Cirratulus cirratus</i>	<i>Phyllodoce</i> sp.	<i>Alaba picta</i>
<i>Cirriformia tentaculata</i>	<i>Sigambra</i> spp.	<i>Turbonilla multigrata</i>
Dorvilleidae spp.	<i>Harmothoe imbricata</i>	<i>Lacuna turrita</i>
<i>Eunice indica</i>	Polynoidae sp.	<i>Antalis weinkauffi</i>
<i>Lysidice collaris</i>	Polynoidae sp. 2	<i>Glossaulax didyma</i>
<i>Marphysa sanguinea</i>	Sabellariidae sp.	<i>Zafra mitriformis</i>
<i>Glycera alba</i>	<i>Laonome albicingillum</i>	<i>Eulima bifascialis</i>
<i>Glycera americana</i>	<i>Paradialychone edomae</i>	<i>Lirularia pygmaea</i>
<i>Glycera</i> sp.	Sabellidae sp.	<i>Reticunassa multigranosa</i>
<i>Ophioglycera distorta</i>	Serpulidae spp.	<i>Tricolia variabilis</i>
<i>Gyptis capensis</i> (?)	<i>Sigalion</i> sp.	<i>Batillaria cumingii</i>
<i>Hesione reticulata</i>	Sigalionidae sp.	<i>Olivella japonica</i>
<i>Hesiospina</i> sp.	<i>Aonides oxycephala</i>	<i>Agatha virgo</i>
<i>Lumbrineris heteropoda</i>	<i>Polydora flava orientalis</i>	<i>paracingulina triarata</i>
<i>Lumbrineris longifolia</i>	<i>Prionospio (Aquilaspio) krusadensis</i>	<i>Mitrella bicincta</i>
<i>Megelona japonica</i>	<i>Prionospio (Minuspio) multibranchiata</i>	<i>Olivella fulgurata</i>
<i>Asychis disparidentata</i>	<i>Prionospio (Prionospio) caspersi</i>	<i>Niotha livescens</i>
<i>Microclumene caudata</i>	<i>Prionospio (Prionospio) paradisea</i>	<i>Mytilus galloprovincialis</i>
<i>Praxillella pacifica</i>	<i>Prionospio (Prionospio) sp.</i>	<i>Cingulina cingulata</i>
<i>Nephtys</i> sp.	<i>Pseudopolydora antennata</i>	<i>Telasco sufflatus</i>
<i>Ceratonereis erythraeensis</i>	<i>Pseudopolydora kempii japonica</i>	<i>Odstomia hirotamurana</i>
<i>Ceratonereis moorei</i>	<i>Pseudopolydora paucibranchiata</i>	Haminoeidae sp.
<i>Neanthes caudata</i>	<i>Rhynchospio glutaea</i>	Muricidae sp.
<i>Neanthes succinea</i>	<i>Scolelepis (Parascolelepis) texana</i>	Acteonidae sp.
<i>Nectoneanthes oxypoda</i>	<i>Scolelepis (Scolelepis) branchia</i>	<i>Crepidula onyx</i> sp.1
<i>Nereis neoneanthes</i>	<i>Spio filicornis</i>	<i>Crepidula onyx</i> sp.2
<i>Nereis pelagia</i> (?)	<i>Spiophanes bombyx</i>	Naticidae sp.
<i>Nereis zonata</i>	<i>Spiophanes kroeyeri</i>	Columbellidae sp.
<i>Nicon japonicus</i>	<i>Exogone verugera</i>	Rissoidae sp.1
<i>Nicon misakiensis</i>	Syllidae sp.	Rissoidae sp.2
<i>Platynereis bicanaliculata</i>	<i>Typosyllis prolifera</i>	Aplysiidae sp.
<i>Diopatra sugokai</i>	Terebellidae gen. sp. 1	Opisthobranchia
<i>Armandia lanceolata</i>	Terebellidae gen. sp. 2	
<i>Haploscoloplos elonatus</i>	Terebellidae gen. sp. 3	
<i>Haploscoloplos</i> sp.		



Table 2.3. (continued)

<b>Bivalvia</b>	<b>Gammaridea</b>	
<i>Ruditapes philippinarum</i>	Pontogeneiidae sp.	Tanaidacea
<i>Nitidotellina minuta</i>	<i>Gammaropsis</i> sp.	Cumacea
<i>Phacosoma japonicum</i>	<i>Paradexamine</i> sp.	Myodocopida
<i>Petrasma pusilla</i>	<i>Jassa</i> sp.	Caridea
<i>Solidicorbula erythron</i>	<i>Erichthonius</i> sp.	Anomala
<i>Nitidotellina hokkaidoensis</i>	<i>Cerapus</i> sp.	Thalassinidea
<i>Lynsia ventricosa</i>	Oedicerotidae sp.	Brachyura
<i>Scapharca kagoshimensis</i>	Ampeliscidae sp.	Mysidacea
<i>Theora fragilis</i>	Stenothoidae sp.	Cirripedia
<i>Fulvia mutica</i>	Amphilochidae sp.	Asellota
<i>Placamen tiara</i>	Urothoidae sp.	Anthuridae
<i>Mactra chinensis</i>	<i>Pleustes</i> sp.	Flabellifera
<i>Modiolus nipponicus</i>	<i>Parapleistes</i> sp.1	Valvifera
<i>Macoma incongrua</i>	<i>Parapleistes</i> sp.2	Actiniaria
<i>Cryptomya busensis</i>	Liljeborgiidae sp.	Brachiopoda
<i>Musculista senhousia</i>	Corophiidae sp.1	Enteropneusta
<i>Solen strictus</i>	Corophiidae sp.2	Porifera
<i>Perna viridis</i>	Podoceridae sp.	Nemertea
<i>Mytilus galloprovincialis</i>	<i>Ampithoe</i> sp.	Sipuncula
Hiatellidae sp.	Phoxocephalidae sp.	Platyhelminthes
Lucinidae sp.	Atylidae sp.	Chordata
Tellinidae sp.	Lysianassidae sp.	Echiura
Thyasiridae sp.	Melitoidae sp.	Asteroidea
Arcidae sp.	Hyalidae sp.	Pycnogonida
Tellinidae sp.	Aoridae sp.	
Bivalvia sp.1	Maxillipiidae sp.	
Bivalvia sp.2	Caprella	
Bivalvia sp.3		
Bivalvia sp.4		
Bivalvia sp.5		

Table 2.4  
 Results of three-way nested ANOVA testing spatial and temporal variation in density (log-transformed) of macrobenthic animals collected at seagrass-vegetation and nonvegetated positions at 10 stations in 3 sites.

Factor	df	MS	F	P
Season	1	0.004	0.051	0.822
Vegetation	1	1.691	21.934	<0.001
Site	2	3.945	51.163	<0.001
Station (Site)	7	0.535	6.933	<0.001
Season * Vegetation	1	0.012	0.156	0.694
Season * Site	2	0.040	0.520	0.597
Season * Station (Site)	7	0.039	0.508	0.826
Site * Vegetation	2	0.109	1.417	0.248
Station (Site) * Vegetation	7	0.210	2.718	0.014
Season * Site * Vegetation	2	0.839	10.875	<0.001
Season * Station (Site) * Vegetation	7	0.576	7.466	<0.001
Error	80	0.077		

Table 2.5

Results of two-way nested ANOVA testing variation in density (log-transformed) of top three dominant taxa collected at seagrass-vegetation and nonvegetated positions at 10 stations in 3 sites.

Factor	df	MS	F	P
<b>Summer</b>				
1. <i>Jassa</i> sp.				
Vegetation	1	5.306	4.969	0.031
Site	2	20.423	19.127	<0.001
Station (Site)	7	1.578	1.478	0.203
Site * Vegetation	2	1.268	1.188	0.315
Station (Site) * Vegetation	7	1.186	1.111	0.375
Error	40	1.068		
2. <i>Platynereis bicanaliculata</i>				
Vegetation	1	45.412	48.542	<0.001
Site	2	0.058	0.062	0.940
Station (Site)	7	1.991	2.128	0.063
Site * Vegetation	2	0.336	0.359	0.701
Station (Site) * Vegetation	7	1.734	1.854	0.103
Error	40	0.936		
3. <i>Spiophanes bombyx</i>				
Vegetation	1	0.125	0.258	0.614
Site	2	18.646	38.136	<0.001
Station (Site)	7	8.760	18.093	<0.001
Site * Vegetation	2	0.485	1.003	0.376
Station (Site) * Vegetation	7	0.502	1.036	0.422
Error	40	0.484		
<b>Autumn</b>				
1. <i>Musculista senhousia</i>				
Vegetation	1	16.259	41.928	<0.001
Site	2	34.329	88.526	<0.001
Station (Site)	7	6.432	16.586	<0.001
Site * Vegetation	2	3.415	8.807	0.001
Station (Site) * Vegetation	7	3.355	8.651	<0.001
Error	40	0.388		
2. <i>Platynereis bicanaliculata</i>				
Vegetation	1	40.764	207.298	<0.001
Site	2	5.345	27.180	<0.001
Station (Site)	7	3.538	17.990	<0.001
Site * Vegetation	2	2.407	12.242	<0.001
Station (Site) * Vegetation	7	0.538	2.737	0.020
Error	40	0.197		
3. <i>Iwakawatrochus urbanus</i>				
Vegetation	1	0.097	0.251	0.619
Site	2	7.674	24.303	<0.001
Station (Site)	7	7.472	23.663	<0.001
Site * Vegetation	2	0.634	2.007	0.148
Station (Site) * Vegetation	7	1.918	6.074	<0.001
Error	40	0.316		

Table 2.6  
 Results of three-way nested ANOVA testing spatial and temporal variation in taxa richness of macrobenthic animals collected at seagrass-vegetation and nonvegetated positions at 10 stations in 3 sites.

Factor	df	MS	F	P
Season	1	189.178	5.769	0.019
Vegetation	1	746.972	22.779	<0.001
Site	2	665.841	20.305	<0.001
Station (Site)	7	111.088	3.388	0.003
Season * Vegetation	1	2.813	0.086	0.770
Season * Site	2	83.041	2.532	0.086
Season * Station (Site)	7	61.850	1.886	0.083
Site * Vegetation	2	2.313	0.071	0.932
Station (Site) * Vegetation	7	24.406	0.744	0.635
Season * Site * Vegetation	2	34.847	1.063	0.350
Season * Station (Site) * Vegetation	7	34.977	1.067	0.393
Error	80	32.792		

Table 2.7  
 Results of two-way nested ANOVA testing difference in density (log-transformed) and dissimilarity of macrobenthic animals between seagrass-vegetation and nonvegetated positions at 10 stations.

Dependent variables	df	MS	F	P
<b>Dissimilarity (4th root transformed)</b>				
Season	1	35.793	0.687	0.421
Site	2	73.697	1.414	0.276
Season * Site	2	19.053	0.366	0.700
Error	14	52.116		
<b>Density (log transformed inds.m<sup>-2</sup>)</b>				
Season	1	0.009	0.007	0.934
Site	2	0.516	0.406	0.674
Season * Site	2	2.058	1.621	0.233
Error	14	1.270		

Table 2.8  
 Results of general linear model testing variation in vegetation effects on macrobenthic animals. Dependent variables were difference of density (log-transformed) and dissimilarity index at seagrass vegetation and nonvegetated areas.

Dependent variables	Independent variables												R <sup>2</sup>	F	P
	Total nitrogen content			River effect index			Silt-clay content (at seagrass vegetation)			Seagrass bed size					
	t	P		t	P		t	P		t	P	t	P	t	P
Dissimilarity (4th root transformed)	-0.755	0.463	0.906	0.380	0.448	-0.781	1.309	0.212	0.842	0.414	0.367	1.626	0.217		
Density (log transformed inds.m <sup>-2</sup> )	-1.085	0.296	-0.429	0.675	0.725	-0.359	0.778	0.450	-0.822	0.425	0.103	0.320	0.893		

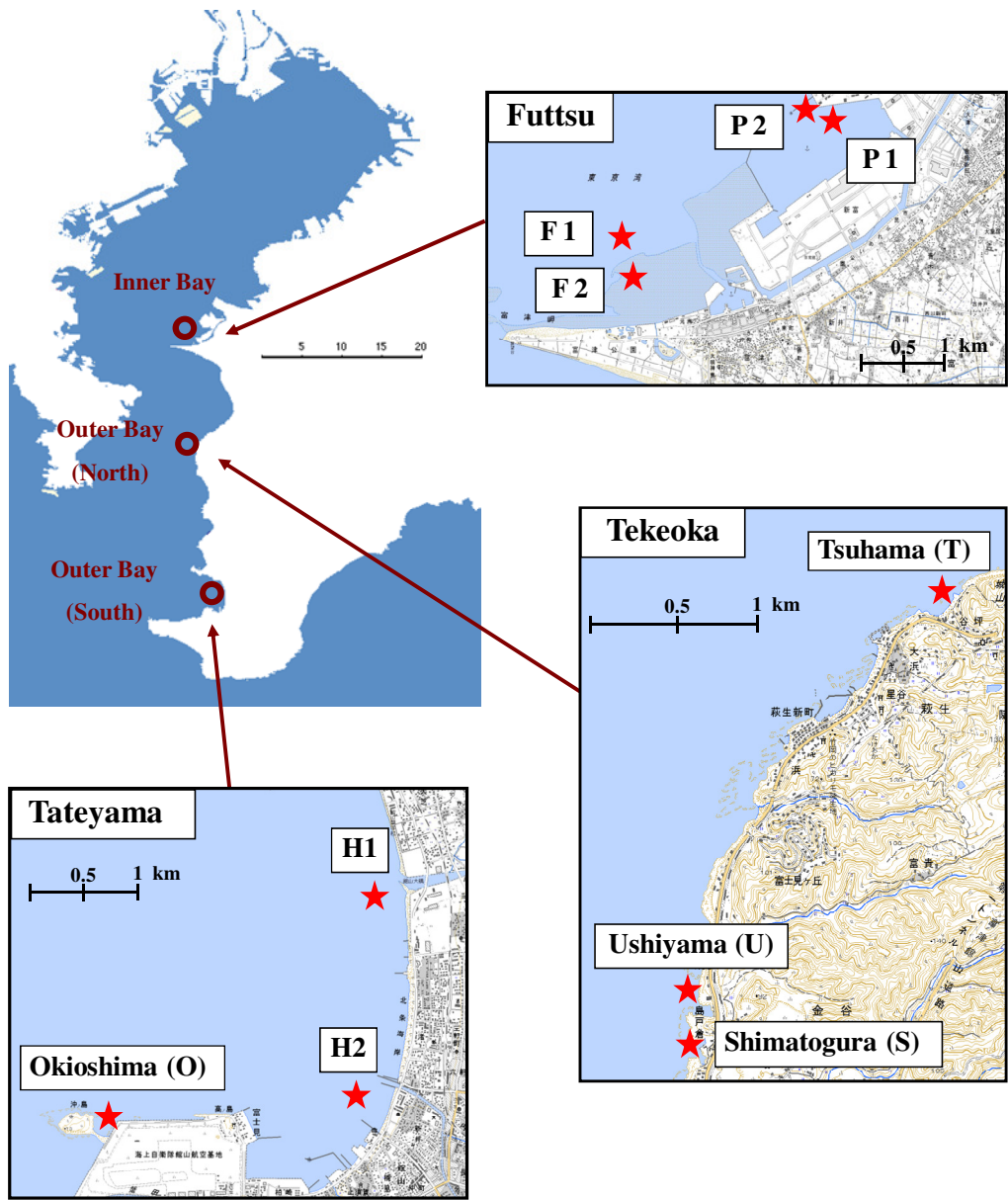


Fig. 2.1. Maps showing study sites. ★ indicates 10 stations in 3 areas along the east coast of Tokyo Bay.

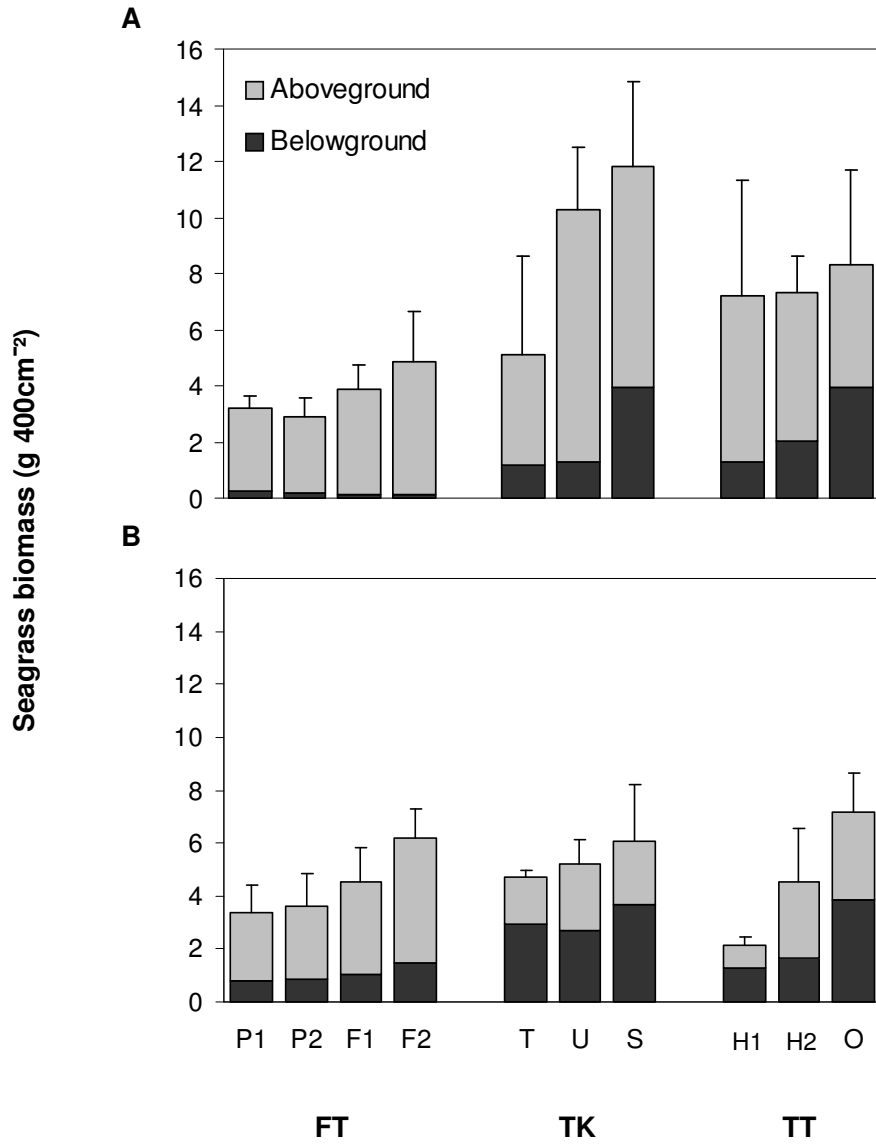


Fig. 2.2. Aboveground and belowground biomass of eelgrass (g 400cm<sup>-2</sup>) in summer; June – August 2006 (A) and autumn; September – November 2006 (B) in Tokyo Bay. Bars denote standard deviation of the total biomass.



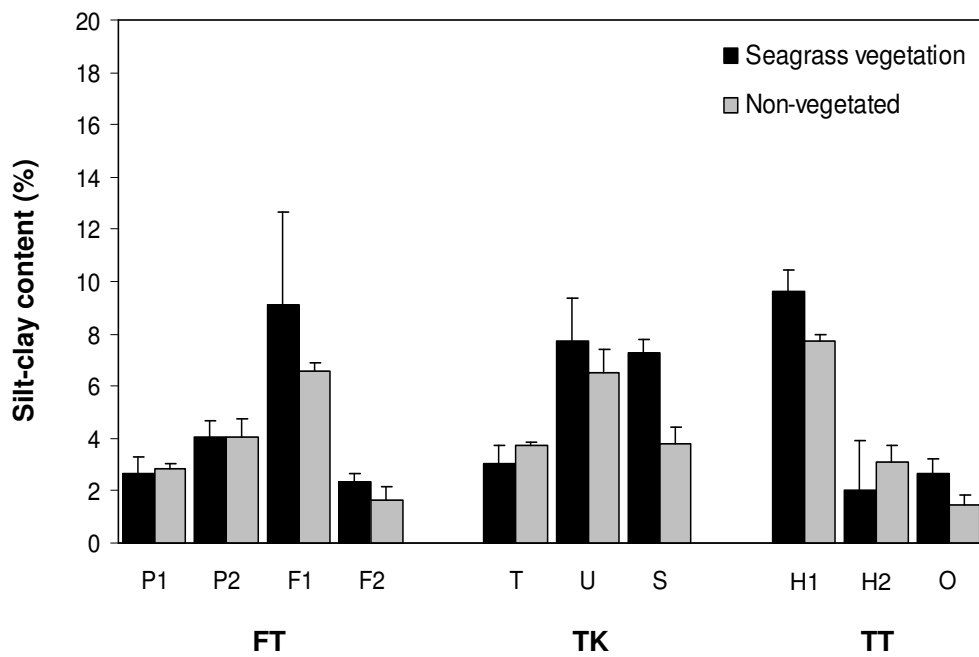


Fig. 2.3. Silt-clay content of sediment in seagrass vegetation and nonvegetated areas at each station in Tokyo Bay. Bars denote standard deviation of the mean.

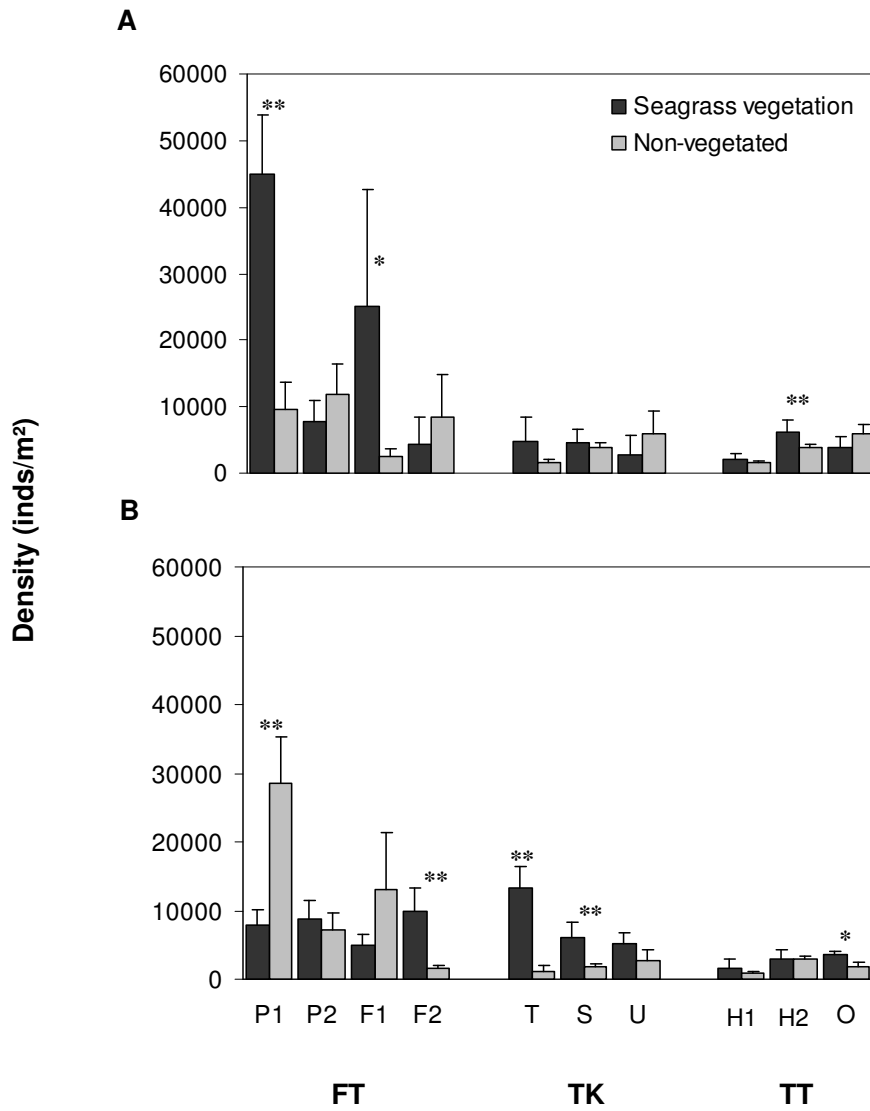


Fig. 2.4. Density of macrobenthic animals collected at seagrass-vegetation and nonvegetated areas of 10 stations (P1, P2, F1, F2, T, S, U, H1, H2 and O) at 3 sites (FT, TK, TT) in summer; June - August 2006 (A) and autumn; September - November 2006 (B). Bars denote standard deviation of the mean. Asterisks indicate the pairs of vegetation types with significant differences by post-hoc comparisons ( $p < 0.005$ , t-test).

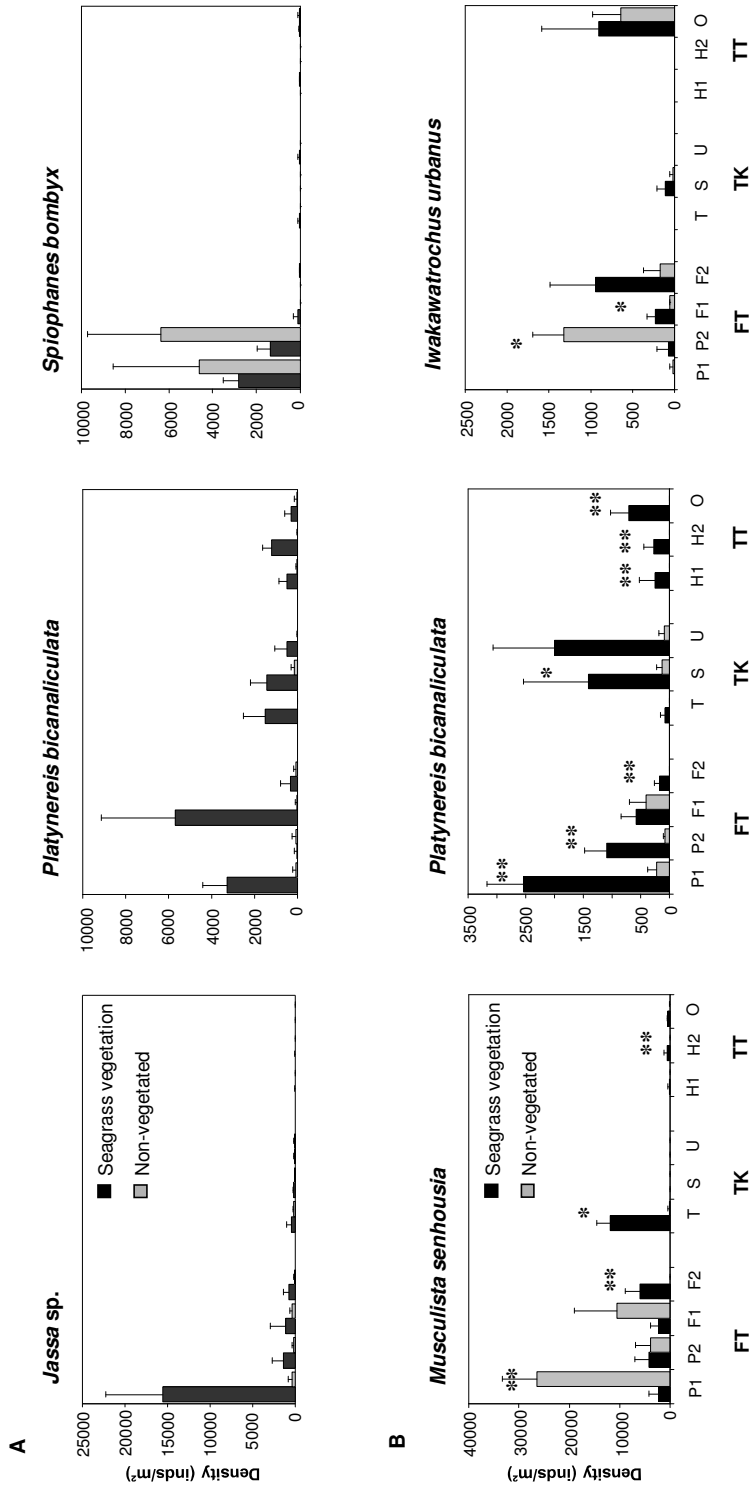


Fig. 2.5. Density of three dominant taxa of macrobenthic animals collected at seagrass-vegetation and nonvegetated areas of 10 stations (P1, P2, F1, F2, T, S, U, H1, H2 and O) at 3 sites (FT, TK, TT) in summer; June – August 2006 (A) and autumn; September – November 2006 (B). Bars denote standard deviation of the mean. Asterisks indicate the pairs of vegetation types with significant differences by post-hoc comparisons conducted for Autumn data ( $p < 0.005$ , t-test).

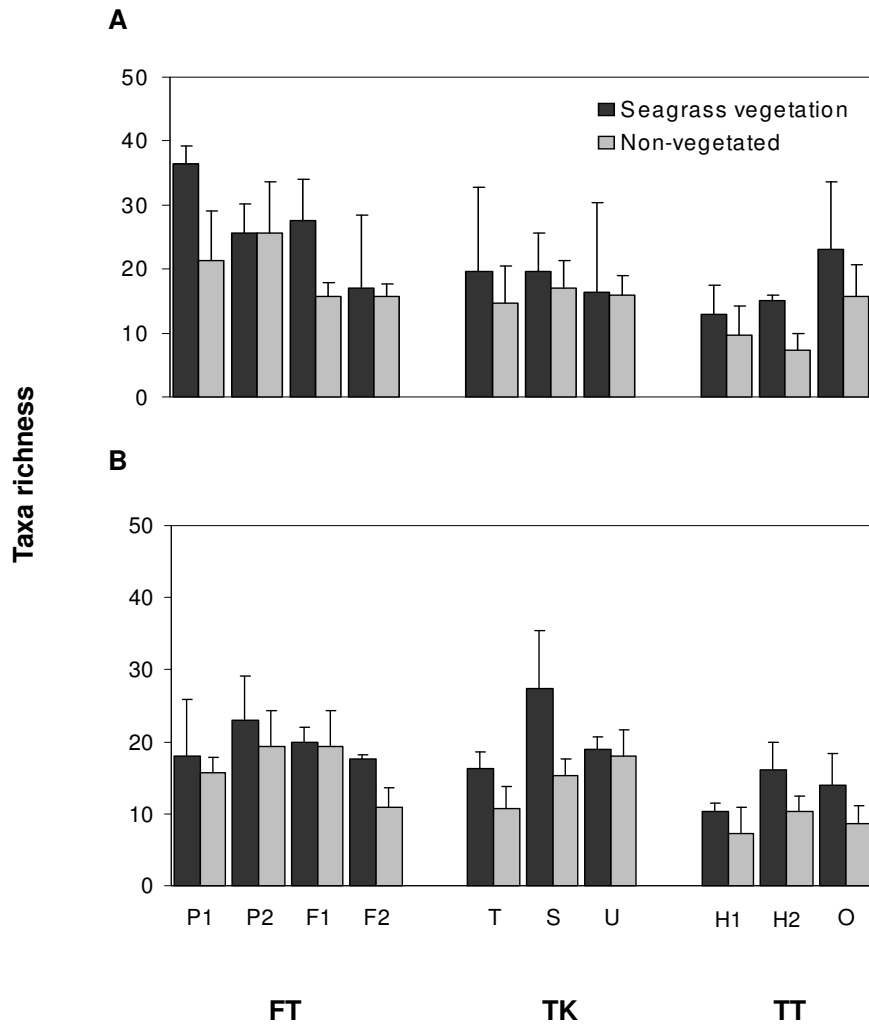


Fig. 2.6. Taxa richness of macrobenthic animals collected at seagrass-vegetation and nonvegetated areas of 10 stations (P1, P2, F1, F2, T, S, U, H, N and O) at 3 sites (FT, TK, TT) in summer; June – August 2006 (A) and autumn; September – November 2006 (B). Bars denote standard deviation of the mean.

## **CHAPTER 3**

### **Effect of Spatial Structure of Seagrass Vegetation on Macrobenthic invertebrate Community: An integrated approach using field sampling and remote sensing analysis**

#### **3.1. Introduction**

Seagrass beds are one of the most important components in coastal ecosystems (Costanza et al., 1997; Hemminga and Duarte, 2000; Green and Short, 2003). Seagrass provides complex habitat structure, shelter, nursery ground and food for macrobenthic animals (Kikuchi and Pérès, 1977; Beck et al., 2001; Heck et al., 2003; Valentine and Duffy, 2006). For epifauna, the presence of seagrass leads to higher density and diversity compared to nonvegetated area (Orth et al., 1984; Lee et al., 2001). For infauna animals, however, the effect of vegetation can vary among habitats and target organisms. For example, the density and diversity of infaunal animals were greater in a seagrass bed than in other vegetation types such as coral areas or sand areas (Sheridan, 1997; Nakamura and Sano, 2005; Alfaro, 2006 ). In addition, the survivorship of macrobenthic invertebrates such as clams, scallops and blue crabs increased with an increase in seagrass habitat complexity (Irlandi, 1994; Irlandi et al, 1995; Hovel and Lipcius, 2001). However, negative effects of seagrass vegetation were also reported for some benthic organisms, as shown by lower growth and survivorship of mussels in seagrass vegetation compared to nonvegetated area (Reusch and Williams, 1999; Allen and Williams, 2003).

Seagrass bed is not uniform, but consists of patches and gaps of various sizes and shapes (Robbins and Bell, 1994). It also exhibits great temporal fluctuations (Frederikson et al., 2004; Burkholder et al., 2007; Micheli et al., 2008; Yamakita et al., in press). Spatial/temporal variability of seagrass beds affects macrobenthic abundance and diversity (Bell and Westoby, 1986; Tanner, 2005; Nakaoka, 2005; Berkenbusch and Rowden, 2007). However, most previous studies examined effects of vegetation and its spatial/temporal variability by arbitrarily setting a scale of observation at different scales. For example, some studies examined the effects of seagrass vegetation by comparing seagrass beds and other types of habitats locating >1 km apart (Jenkins et al., 1998; Jenkins and Hamer, 2001), whereas others compared benthic abundance at very fine scales, such as between a seagrass patch and a gap within a few meters (Nakaoka et al., 2002). In what spatial extent does the seagrass vegetation affect abundance and diversity of benthic animals? To address this question, it is worthwhile to examine the effects of seagrass vegetation by changing scale of observation continuously in a single study. Recent development of remote sensing and GIS enables one to analyze the effect of seagrass landscape structure on biodiversity and community of benthic animals at various spatial scales (Pittman et al., 2004; Kendall, 2005; Kendrik et al., 2008; Urbanski et al., 2009). By integrating remote sensing data and field collection, it is now possible to examine effects of seagrass structure on benthic animals at different spatial scales simultaneously.

A seagrass bed in Futtsu is the largest in Tokyo Bay. Here, aerial photographs are available annually since 1980's at a fine resolution of 0.5 m (Yamakita and Nakaoka, 2009; Yamakita et al, in press). Using the spatial data on seagrass landscape change, we were

able to collect benthic animals at points of seagrass beds with different coverage at different spatial scales. Also, time-series remote sensing data on vegetation allowed us to compare benthic diversity and abundance among sites with different past history of vegetation status, e.g., between sites where seagrass vegetation was stable over past 5 years and those where vegetation fluctuated greatly.

The objective of this study is to examine the influences of spatial structure and dynamics of seagrass landscape on macrobenthic invertebrate community by an integrated analysis of field census data and using remote-sensing/GIS data. The vegetation coverage around the sampling points was estimated at different spatial extent by a buffering method (Gerrard et al., 2001; Ciarniello et al., 2007; Miyashita et al., 2007). In addition, temporal variability in seagrass coverage at each sampling point was analyzed using time-series data on seagrass spatial distribution. I address two specific hypotheses as follows; (1) the abundance and diversity of benthic communities are higher at sites with more seagrass vegetation at large spatial extent; and (2) the abundance and diversity of benthic communities are higher at sites with more stable seagrass vegetation (less temporal fluctuation). I also examined relative importance of vegetation types, coverage and stability on observed variation in macrobenthic invertebrate communities by a model selection method.

## **3.2. Materials and methods**

### *3.2.1 Study sites*

Futtsu seagrass bed in Tokyo Bay consists of three seagrass species, *Zostera marina* L., *Z. japonica* Aschers and Graebn and *Z. caulescens* Miki. The dominant species is *Z. marina*, whereas *Z. caulescens* and *Z. japonica* occurs in deepest and shallowest edge of the bed, respectively. Patterns of temporal change in seagrass vegetation varied among positions in the bed (Yamakita et al., in press).

In this study, a research plot of 0.375 km<sup>2</sup> (the distance of 500 m × 750 m) was established at a southern part of the seagrass bed (Fig. 3.1). The plot covered intertidal and shallow subtidal zones (water depth less than 5 m) (Furukawa and Okada, 2006), in which heterogeneous vegetation of *Z. marina* and *Z. japonica* was observed. The bottom consisted of medium sand.

### 3.2.2. Sampling of macrobenthic invertebrates

Macrobenthic invertebrate assemblages were collected from patches of *Zostera marina* vegetation, *Z. japonica* vegetation and non-vegetated gaps in June 2006. The sampling was carried out during daytime low tide. We used a core sampler of 177 cm<sup>2</sup> (diameter of 15 cm) which was inserted into the sediment to a depth of 10 cm. For each vegetation type, 10 replicate samples were collected within the research plot. The exact location of each sampling point was recorded by GPS at the accuracy of 5 m.

Collected macrobenthic samples were sieved on 0.5 mm mesh with seawater. All macrobenthic invertebrates retained on the sieve were transferred to polyethylene bags and fixed with a 10% seawater–formalin solution. In the laboratory, macrobenthic animals were sorted and transferred to 70 % ethanol for identification and counting. All



organisms were classified into lower taxonomic levels using available taxonomic keys, and the number of individuals in each taxon was counted.

### *3.2.3. GIS analysis on spatial structure and temporal dynamics of seagrass vegetation*

Spatial configuration and temporal variability of seagrass vegetation at the research plot was examined from aerial photographs that were taken annually between 1997 and 2007. The images were ortho-rectified by GIS and seagrass distribution was extracted using the supervised classification method (Yamakita and Nakaoka, 2009; Yamakita et al., in press).

I plotted the macrobenthic sampling points on the GIS maps showing spatial structure of seagrass vegetation for the 5 years. To examine at which spatial scale seagrass vegetation gave positive effect on abundance and diversity of macrobenthic animals, the percent coverage of seagrass around each sampling point was calculated at different spatial extents by generating buffers of different sizes (1, 5, 10, 15, 20, 30, 40, 50 m diameter around each point). Temporal variation in seagrass coverage during 2003-2007 was then determined at each buffer, and the stability of vegetation was represented by coefficient of variation (CV 5 yrs). Year since no seagrass vegetation (< 5% cover) was also calculated for each sampling point.

#### 3.2.4. Data analysis

Diversity of macrobenthic invertebrate from each core sample was represented by Simpson diversity index ( $D' = 1 - \sum p_i^2$ , while  $p_i$  is the relative abundance of taxon  $i$ ). Preliminary analyses revealed that other indices of diversity, such as taxa richness and Shannon's index, showed the similar patterns of variation with Simpson.

Density and diversity were compared among three vegetation types using one-way ANOVA with vegetation type as fixed factor. In cases of significant variation, post-hoc comparison was carried out using Tukey HSD method.

The relationship between benthic abundance/diversity and seagrass coverage in 2006 for each buffer size was analyzed by a linear regression analysis. Using the buffer size with the highest correlation, I then examined the relationship between benthic abundance/diversity and temporal variability of seagrass coverage by a linear regression analysis. The temporal variability of the eelgrass vegetation at each point was represented by (1) coefficient of variation between 2003 and 2007 (CV 5 yrs), and by (2) years since no seagrass vegetation (< 5% cover).

To examine relative importance of vegetation types, coverage and stability of seagrass vegetation on macrobenthic invertebrate community, a general linear model was made using the vegetation type, coverage in 2006 and CV 5 yrs as explanatory variables and benthic abundance/diversity as independent variables. I did not use years since no seagrass vegetation (< 5% cover) as explanatory variables because it highly correlated with CV 5 yrs. The best model was selected based on AIC.

### 3.3. Results

#### 3.3.1. Seagrass landscape structure and temporal variation

Seagrass vegetation at the research plot, extracted from aerial photographs, was spatially and temporally variable (Fig. 3.2). Main vegetation occurred at the center of the research plot, whereas vegetation at the edge of the plots was mostly patchy.

Magnitude of temporal variation in coverage, estimated for each sampling point of macrobenthic animals was stable in the center of the vegetation, whereas it tended to be unstable near the edge of the vegetation (Fig. 3.2f).

#### 3.3.2. Abundance and diversity of macrobenthic invertebrate at different vegetation types

A total of 132 taxa were found from 30 replicate samples collected at 3 vegetation types. Polychaete worms were the most dominant taxa, followed by amphipods and mollusks (Table 3.1). Abundance and taxa diversity of macrobenthic varied significantly among different vegetation types (Fig. 3.3) (ANOVA,  $F = 5.165$ ,  $df = 2, 27$ ,  $p < 0.001$  for density,  $F = 10.170$ ,  $df = 2, 27$ ,  $p < 0.001$  for Simpson diversity). Post-hoc comparisons revealed that the difference was significant for both variables between *Z. marina* vegetation and non-vegetated area, but not between *Z. marina* and *Z. japonica*, nor between *Z. japonica* and non-vegetated area.

### *3.3.3. Effect of seagrass landscape structure and dynamics on macrobenthic invertebrate community*

Density of macrobenthic was positively correlated with seagrass coverage at all buffer size between 1 and 50 m diameter of each sampling point (Table 3.2). The correlation coefficient increased gradually with the buffer size between 1 and 15 m, highest in 15 m, and then gradually decreased with larger buffer size. Simpson diversity index was also positively correlated with seagrass coverage at all buffer sizes, with a peak at 10 m buffer size (Table 3.2).

Both the density and Simpson index of macrobenthic invertebrates correlated negatively with CV of seagrass coverage (estimated at 15 m buffer for the density data and at 10 m for the diversity data), showing higher abundance and diversity in more stable vegetation (Fig. 3.4 A-B). They showed positive correlation with years since no seagrass vegetation (< 5 %cover) (Fig. 3.4 C-D).

General linear model revealed that the variation in benthic abundance and diversity was best explained when vegetation types and coverage were selected as dependent variables (Table 3.3). Including seagrass coverage as dependent variable greatly improve the model fit, whereas inclusion of CV did not contribute to better fit of the model for both abundance and diversity.

### 3.4. Discussion

The positive effects of seagrass vegetation on abundance and diversity of associated-fauna have been repeatedly reported for a variety of taxa in different regions (Hemminga and Duarte, 2000). By an integrated use of field samplings and RS/GIS data, the present study shed lights on two new aspects on this general rule. First, the degree of positive effects varies with spatial scale of observation on seagrass abundance, with a highest correlation between seagrass coverage and benthic abundance/diversity observed at an intermediate scale of observation (10-15 m diameter of sampling point). Secondly, degree of temporal variation in seagrass bed has some influence on benthic community, with higher abundance and diversity with more stable seagrass vegetation.

Abundance and diversity of macrobenthic animals varied among vegetation types, which are highest at *Z. marina* vegetation, followed by *Z. japonica* vegetation, and the lowest at nonvegetated area. This agrees with most previous research showing higher abundance and diversity of macrobenthic in vegetated areas (Orth, 1992; Hemminga and Duarte, 2000; Lee et al., 2001; Nakaoka, 2005). Seagrass vegetation play important roles in food supply (Lee et al., 2001; Kasim and Mukai, 2006; Vonk et al, 2008), predator avoidance (Virnstein, 1977; Boström and Mattila, 1999; Horinouchi, 2007), and modification of physical environment for macrobenthic animals (Koch and Gust, 1999; Madsen et al., 2001; Komatsu et al., 2004). In my study, the positive effect was more pronounced for *Z. marina* vegetation than *Z. japonica* vegetation. This is likely due to the difference in seagrass size. *Z. marina* is larger in size for both aboveground and

belowground than *Z. japonica*, and thus the effect of vegetation are expected to be greater in the former species.

In the present study, seagrass coverage was most correlated with diversity and abundance of macrobenthic animals when I observed the seagrass coverage at the extent of 10-15 m. Our result agrees with that of Darcy and Eggleston (2005) which showed that macrobenthic groups respond positively to seagrass corridors at the scale of 10 m. The biological causes for the high correlation at the intermediate spatial scales can be ascribed to characteristics and the natural history of animal species such as behavior, biological interactions, mobility and dispersal range (Thrush, 1991; Doak et al., 1992; Underwood and Chapman, 1996). The major macrobenthic invertebrates collected in my study are spionid polychaetes, gastropod and gammarids which have limited dispersal ability compared to other types of macrobenthic such as decapod crustaceans with higher mobility. It is likely that the ability to detect and respond to seagrass vegetation is determined at this spatial scale. At the larger buffer, the coverage data may be affected by the presence or absence of vegetation at too far area from the sampling points where the macrobenthic organisms can not detect and response, resulting in decreased correlation. The lower correlation at the smaller extent ( $\leq 5$  m diameter) can be ascribed for biases in positioning by a portable GPS (5 m accuracy), which may not truly represent vegetation status at very fine spatial scale. Due to these reasons, the correlation becomes highest at the intermediate spatial scales.

Macrobenthic invertebrate assemblages showed higher abundance and diversity at sites where seagrass vegetation was more stable, i.e., lower CV and longer years since vegetation was developed, which supports our hypothesis. Lower abundance and

diversity in unstable sites and younger vegetation would probably reflect time-lag in colonization and recruitment of macrobenthic after the vegetation is developed (Levingston, 1984; de Paz et al., 2008). Boström et al. (2002) reported that total abundance and biomass of macrobenthic animal increased with increasing of seagrass density in long-term changes. As it takes time for macrobenthic to settle and colonize seagrass vegetation, unstable seagrass vegetation which developed just recently can not have enough time to have large number of animals and diversity.

Results of the model selection demonstrated that not only vegetation types, but also seagrass coverage at 10-15m extent have considerable contribution to explain variability in macrobenthic invertebrate abundance and diversity. The temporal stability, however, was not a major factor that accounts for the variation. The present outcome has highlighted the importance of choosing appropriate of scale of observation for evaluating the effects of seagrass on associated macrobenthic communities, which has large implication for applied purposes, such as designing area and positions of marine protected area for conservation and sustainable use of biodiversity and resources.

Table 3.1. List of macrobenthic invertebrate taxa collected at Futtsu, Tokyo Bay in June 2006.

List of macrobenthic invertebrates in the study area		
Polychaeta	<i>Scolecipis (Scolecipis) planata</i>	<i>Jassa</i> sp.
<i>Arenicola brasiliensis</i>	<i>Spio filicornis</i>	Lysianassidae gen. sp.1
<i>Capitella</i> sp.1	<i>Spiophanes bombyx</i>	Lysianassidae gen. sp.2
<i>Capitella</i> sp.2	<i>Exogone verugera</i>	Lysianassidae gen. sp.3
<i>Capitellethus</i> sp.	<i>Sphaerosyllis erinaceus</i>	<i>Melita</i> sp.
Capitellidae gen. sp.	<i>Trypanosyllis (Trypanosyllis) sp.</i>	<i>Nebaria</i> sp.
<i>Heteromastus</i> spp.	<i>Typosyllis ehlersioides</i>	Oedicerotiidae gen. sp.
<i>Chrysopetalum</i> sp. ( <i>occidentale</i> )	<i>Typosyllis prolifera</i>	<i>Paradexamine</i> sp.
<i>Chaetozone</i> sp.	Terebellidae gen. sp.	<i>Pleustes</i> sp.
<i>Cirratulus cirratus</i>	Bivalvia	<i>Pontogeneia</i> sp.
<i>Cirriformia</i> sp.	<i>Macoma incongrua</i>	Tanaidacea
<i>Cirriformia tentaculata</i>	<i>Macra chinensis</i>	<i>Sinelobus stanfordi</i>
<i>Marphysa sanguinea</i>	<i>Macra veneriformis</i>	Copepoda
<i>Marphysa tamurai</i>	<i>Musculista senhousia</i>	Copepoda gen spp. 1
<i>Glycera alba</i>	<i>Mytilus galloprovincialis</i>	Copepoda gen sp. 2
<i>Ophioglycera distorta</i>	<i>Nitidotellina hokkaidoensis</i>	Ostracoda
<i>Hesione reticulata</i>	<i>Nitidotellina minuta</i>	<i>Vargula hilgendorffii</i>
<i>Lumbrineris heteropoda</i>	<i>Phacosoma japonicum</i>	<i>Xenoleberis yamadai</i>
<i>Lumbrineris longifolia</i>	<i>Ruditapes philippinarum</i>	Cumacea
<i>Chlymenura (Cephalata) longicaudata</i>	<i>Trapezium bicarinatum</i>	Cumacea sp.1
<i>Microclymene caudata</i>	Thyasiridae gen sp.	Cumacea sp.2
<i>Nephtys</i> sp.1	Bivalvia gen sp. 1	Cumacea sp.3
<i>Nephtys</i> sp.2	Bivalvia gen sp. 2	Cumacea sp.4
<i>Ceratonereis erythraeensis</i>	Bivalvia gen sp. 3	Cumacea sp.5
<i>Ceratonereis moorei</i>	Gastropoda	Isopoda
<i>Neanthes caudata</i>	<i>Alaba picta</i>	<i>Synidotea hikigawaensis</i>
<i>Platynereis bicanaliculata</i>	<i>Cantharidus callithroa</i>	Decapoda
<i>Diopatra sugokai</i>	<i>Haloa japonica</i>	<i>Pinnixa tumida</i>
<i>Armandia lanceolata</i>	<i>Iwakawatrochus urbanus</i>	Small crustacean
<i>Polyophthalmus pictus</i>	<i>Reticunassa multigranosa</i>	<i>Cyathura muromiensis</i>
<i>Phylo</i> sp.	<i>Reticunassa festiva</i>	<i>Nihonotrypaea japonica</i>
<i>Owenia fusiformis</i>	<i>Retusa (Decolifer) insignis</i>	<i>Upogebia major</i>
<i>Anaitides maculata</i>	<i>Umbonium costatum</i>	<i>Pagurus minutus</i>
<i>Eteone longa</i>	<i>Umbonium moniliferum</i>	Penaeidae sp.
<i>Eumida sanguinea</i>	Acteonidae gen sp.	Platyhelminthes
<i>Genetyllis castanea</i>	Amphipoda	<i>Notoplana japonica</i>
<i>Phyllodoce</i> sp.	<i>Ampithoe</i> sp.	<i>Planocera pellucida</i>
<i>Sigambra</i> sp.	<i>Aoroides</i> sp.	Platyhelminthes gen sp.
<i>Harmothoe imbricata</i>	<i>Byblis</i> sp.	Actiniaria
<i>Iphione muricata</i>	<i>Caprella penantis</i>	<i>Haliclystus</i> sp.
Sabellidae gen. sp.	<i>Caprella tsugarensis</i>	Actiniaria gen spp.
<i>Aonides oxycephala</i>	Caprellidae gen. sp.	Nemertinea
<i>Polydora flava orientalis</i>	<i>Corophium</i> sp.1	<i>Cephalothrix</i> sp.
<i>Prionospio (Aquilaspio) krusadensis</i>	<i>Corophium</i> sp.2	<i>Paradrepanophorus</i> sp.
<i>Prionospio (Minuspio) multibranchiata</i>	<i>Erichthonius</i> sp.	Nemertinea gen sp. 1
<i>Prionospio (Minuspio) pulchra</i>	<i>Gammaropsis</i> sp.	Nemertinea gen sp. 2
<i>Pseudopolydora paucibranchiata</i>	Haustoriidae sp.1	Echinodermata
<i>Rhynchospio glutaea</i>	Haustoriidae sp.2	<i>Ophiactis</i> sp.
<i>Scolecipis (Parascolecipis) texana</i>	<i>Hyale</i> sp.	<i>Ophiothrix (Ophiothrix) sp.</i>



Table 3.2

The result of regression analyses relating benthic abundance and diversity to seagrass vegetation at different extent of seagrass vegetation.

Dependent variable	Coverage at different extent (m)	df	<i>F</i>	<i>p</i>	<i>r</i>
Density of macrobenthic invertebrate					
	1	1, 28	6.57	0.016	0.436
	5	1, 28	8.14	0.008	0.475
	10	1, 28	12.28	0.002	0.552
	15	1, 28	17.84	< 0.001	0.624
	20	1, 28	15.60	< 0.001	0.598
	30	1, 28	13.36	0.001	0.568
	40	1, 28	8.45	0.007	0.481
	50	1, 28	8.50	0.007	0.483
Simpson diversity index of macrobenthic invertebrate					
	1	1, 28	12.74	0.001	0.559
	5	1, 28	19.12	< 0.001	0.637
	10	1, 28	22.40	< 0.001	0.667
	15	1, 28	18.02	< 0.001	0.626
	20	1, 28	13.60	0.001	0.572
	30	1, 28	12.91	0.001	0.562
	40	1, 28	9.93	0.004	0.512
	50	1, 28	7.93	0.009	0.470

Table 3.3  
General linear models examining factors contributing to the observed variables in the density and diversity of macrobenthic invertebrates.

Dependent variable	Model description	R <sup>2</sup>	df	F	P	AIC
Density of macrobenthic invertebrate						
Dn = Veg +Cover.in.15m.2006 +CV.5yr.at.15m + Cover.in.15m.2006*CV.5yr.at.15m		0.333*	5, 24	3.89	0.010	626.524
Dn = Veg +CV.5yr.at.15m		0.222	3, 26	3.76	0.023	629.520
Dn = Veg +Cover.in.15m.2006		0.370	3, 26	6.68	0.002	<u>623.204</u>
Dn = Veg		0.223	2, 27	5.17	0.013	628.620
Simpson diversity index of macrobenthic invertebrate						
Simp = Veg +Cover.in.10m.2006 +CV.5yr.at.10m + Cover.in.10m.2006*CV.5yr.at.10m		0.478	5, 24	6.30	0.001	-54.042
Simp = Veg +CV.5yr.at.10m		0.441	3, 26	8.62	< 0.001	-53.603
Simp = Veg +Cover.in.10m.2006		0.517	3, 26	11.36	< 0.001	<u>-58.020</u>
Simp = Veg		0.387	2, 27	10.17	0.001	-51.734

Dn: Density of macrobenthic invertebrate; Simp: Simpson diversity index of macrobenthic invertebrate; Veg: Vegetation types;  
Cover.in.15m.2006: Seagrass coverage at buffer size 15 m diameter in 2006; Cover.in.10m.2006: Seagrass coverage at buffer size 10 m diameter in 2006;  
CV.5yr.at.15m: The stability of seagrass vegetation expressed by coefficient of variation for 5 years at buffer size 15 m diameter ;  
CV.5yr.at.10m: The stability of seagrass vegetation expressed by coefficient of variation for 5 years at buffer size 10 m diameter.

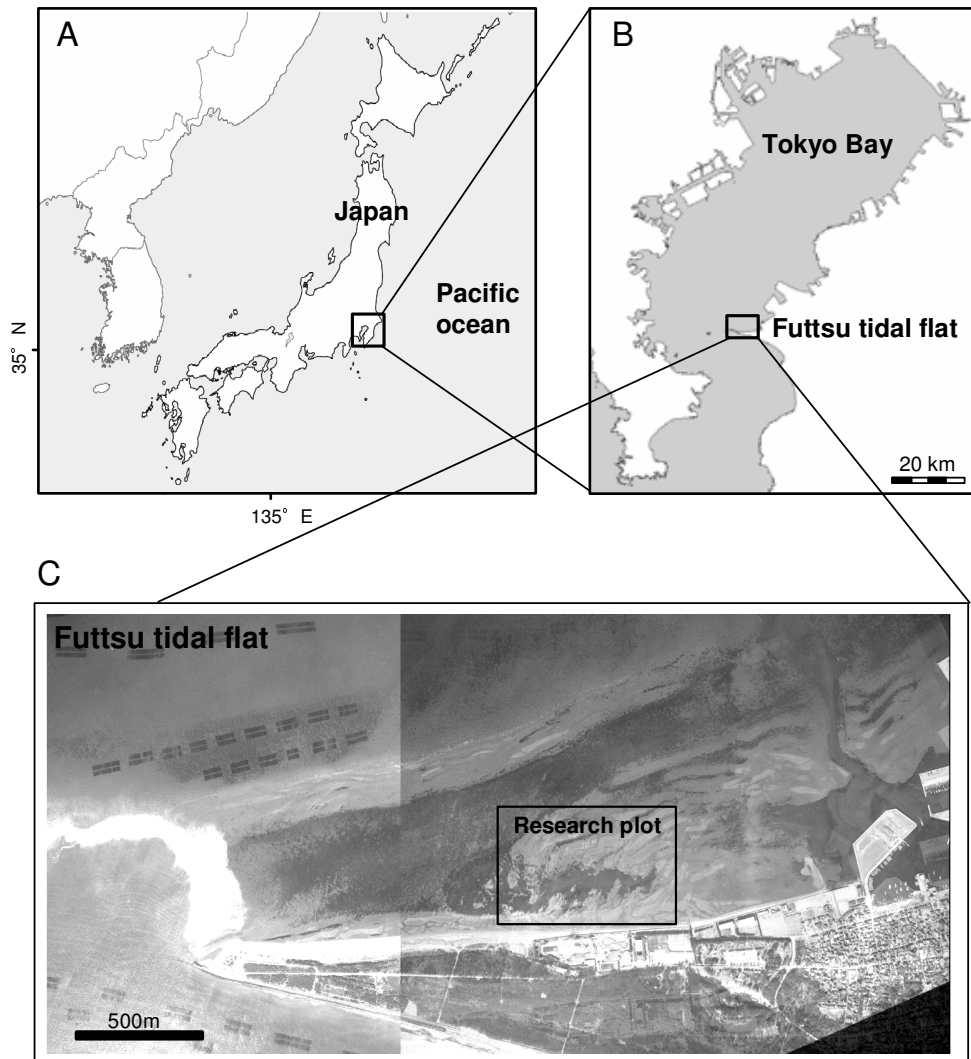


Fig. 3.1. Study site at Futtsu tidal flat in Tokyo Bay, Japan, showing the research plot of 0.375 km<sup>2</sup> area (500 m × 750 m).

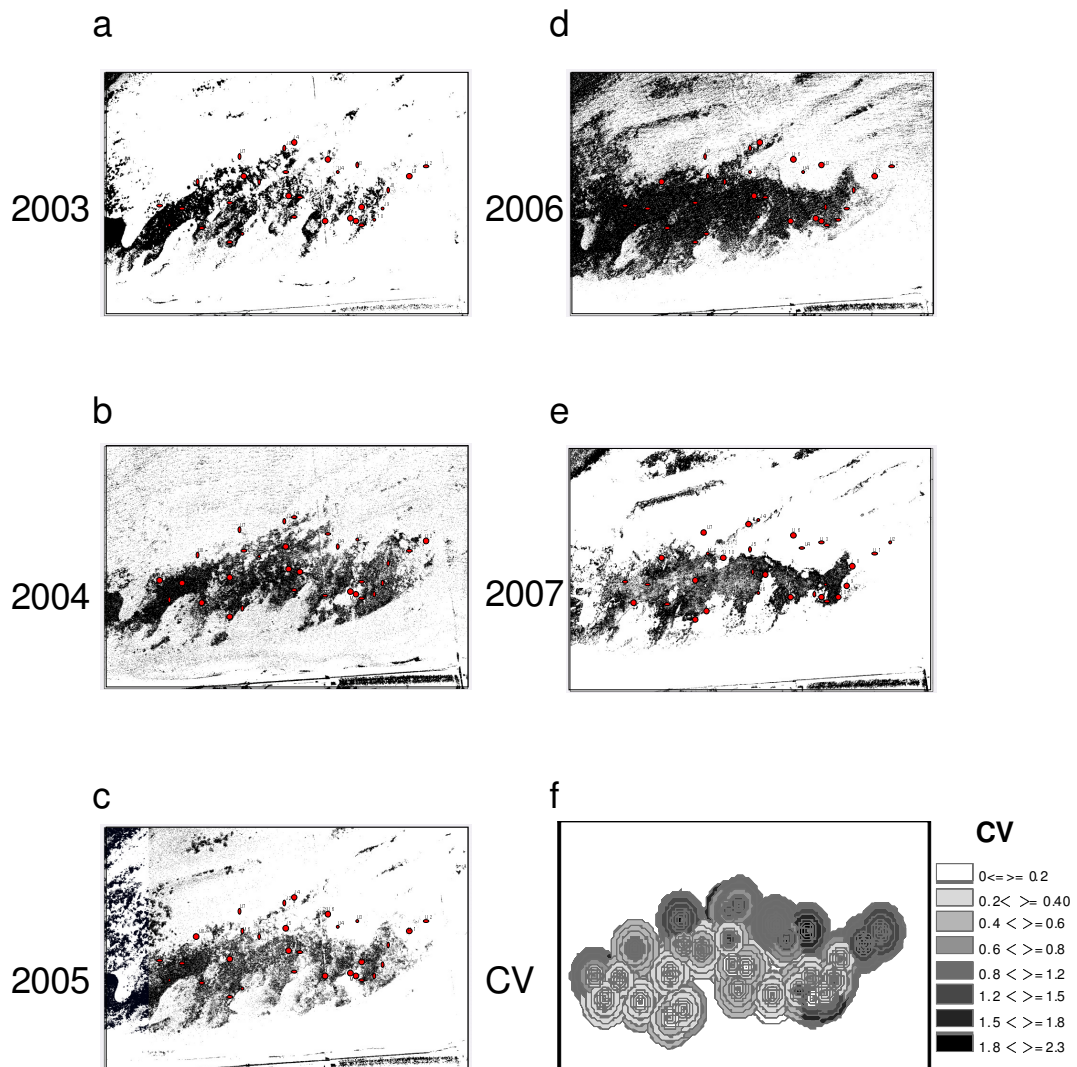


Fig. 3.2. Temporal changes in seagrass coverage at the research plot from 2003 to 2007 (a-e) analyzed by remote sensing and GIS. Dark areas indicate vegetation by either *Zostera marina* or *Z. japonica*. Bottom right plot (f) shows the degree of temporal variation (expressed by coefficient of variation) around each of 30 sampling points at different spatial extents (1, 5, 10, 15, 20, 30, 40, 50 m diameter).

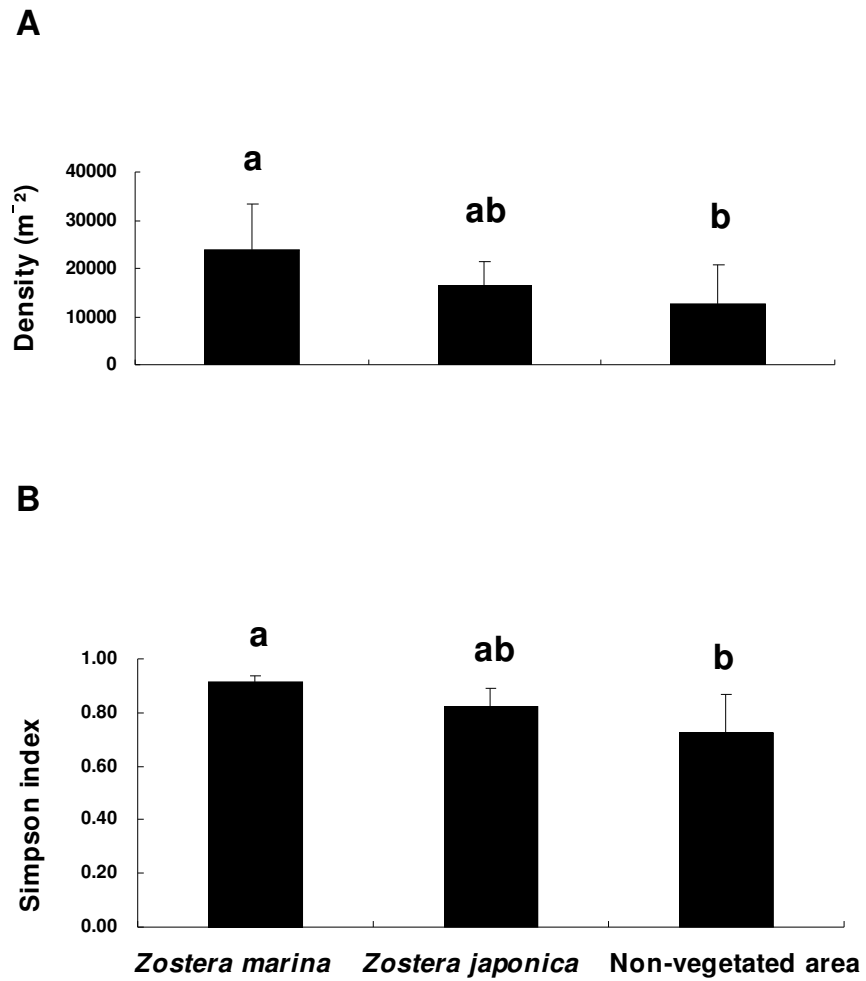


Fig. 3.3. Temporal variation in (A) density and (B) Simpson diversity index of macrobenthic invertebrates collected at *Zostera marina* vegetation, *Z. japonica* vegetation and nonvegetated areas. Bars denote standard deviation of the mean. Unlike letters denote pairs of vegetation types with significant differences by post-hoc comparisons.

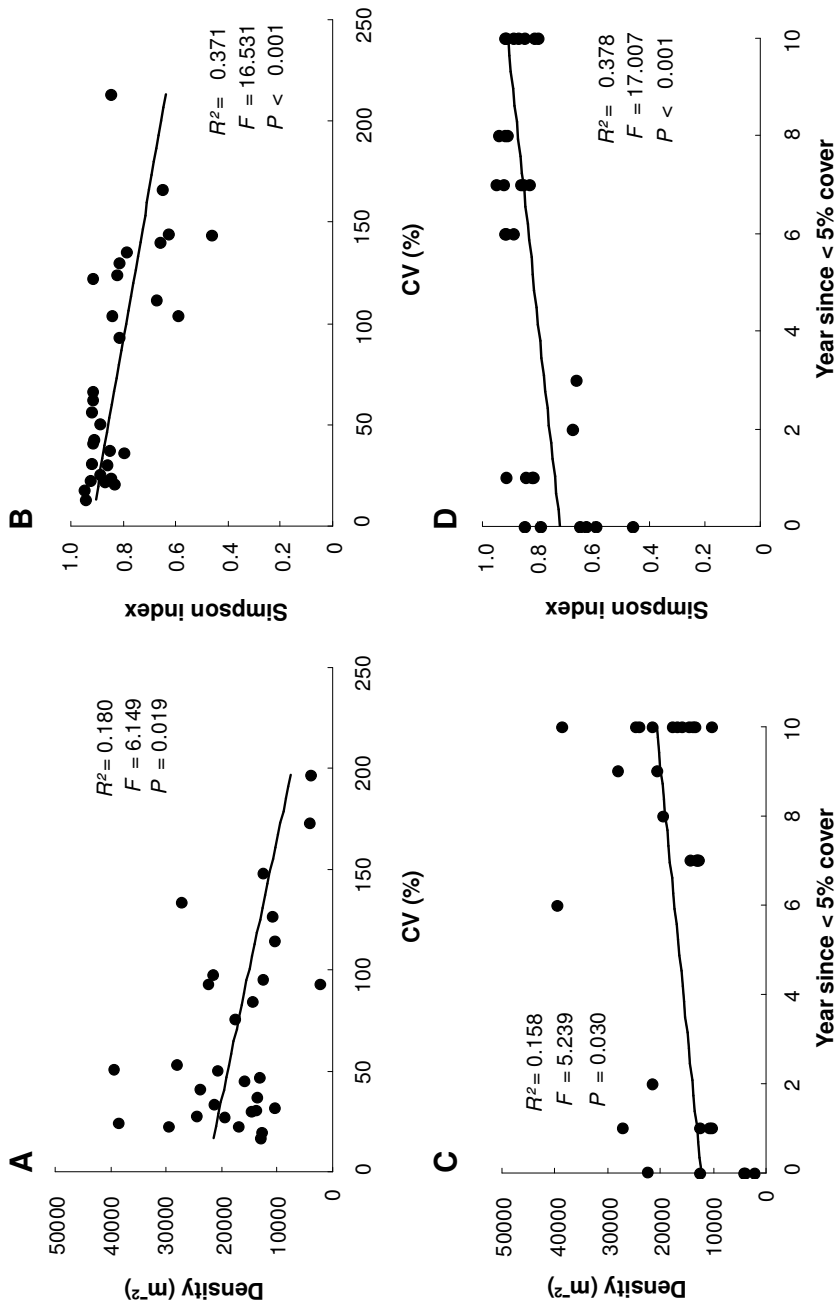


Fig. 3.4. Relationship between stability of seagrass vegetation represented by coefficient of variation for 5 years of data and (A) the density and (B) Simpson diversity index, and between years since no vegetation (<5 % cover) and (C) the density and (D) Simpson diversity index. The coverage was calculated at 15 m diameter of sampling point for the density and at 10 m diameter for the Simpson diversity index.

## **CHAPTER 4**

### **Temporal changes in benthic communities of seagrass beds impacted by a tsunami in the Andaman Sea, Thailand**

#### **4.1. Introduction**

Seagrasses are marine flowering plants that occur in nearshore areas around the world (Hemminga and Duarte, 2000; Green and Short, 2003). Seagrasses play key ecological roles in the marine environment, including organic carbon production and trophic transfers to adjacent habitats (Costanza et al., 1997). They are major primary producers, supporting the high productivity of associated animals including commercially important fish and large invertebrates as well as endangered marine animals such as sea turtles, dugongs, and manatees (Mukai et al., 2000; Beck et al., 2001; Heck et al., 2003; Valentine and Duffy, 2006). Seagrasses also support a variety of meiobenthic/macrobenthic organisms such as polychaetes, mollusks, and small crustaceans that play important roles in food web, nutrient cycling, and decomposition processes of the beds (Kikuchi and Pérès, 1977; Duarte and Cebrián, 1996; Williams and Heck, 2001; Tanner, 2005). Seagrass beds are susceptible to various natural and human-induced disturbances such as extreme climatic events (e.g., cyclones, monsoons, and tsunamis), fishing activities, eutrophication, bioturbation, dredging, and coastal development (Short and Wyllie-Echeverria, 1996; Duarte, 2002; Orth et al., 2006). These disturbances are expected to affect not only the seagrasses but also the abundance and diversity of the associated macrofauna.

The effects of physical disturbances on benthic animals have been studied extensively in various types of soft-bottom communities (see Lenihan and Micheli, 2001, for a review). For macrobenthic animals in seagrass beds, the presence or absence of seagrass vegetation may modify the degree of impact caused by the physical disturbance. This is because the vegetation acts as a buffer, reducing water current velocity and sediment erosion (Fonseca and Fisher, 1986; Koch and Gust, 1999; Madsen et al., 2001). Recovery processes in macrobenthic communities after a disturbance may also vary greatly among different community types, habitats, and locations. Recovery rate can be affected by a variety of abiotic and biotic factors including magnitude and spatial scale of the disturbance, changes in physical and chemical characteristics of the sediment, immigration and colonization rates of organisms from undisturbed habitats, and species interactions after colonization (Meadow and Tait, 1989; Wallace, 1990; Karakassis et al., 1999; Ferns et al., 2000). These abiotic and biotic factors may operate interactively. For example, the physical and chemical properties of a habitat must recover before the colonization and succession of benthic communities can occur (Dernie et al., 2003b).

Coastal ecosystems of Southeast Asia, especially those along the Andaman Sea of Thailand and Indonesia, were greatly affected by the tsunami of December 26, 2004. A broad-scale coastal census after the tsunami revealed that the effects on seagrass beds were spatially variable; some seagrass beds disappeared completely, whereas others were only negligibly impacted (Department of Marine and Coastal Resources of Thailand, 2005). In 2001, we monitored the taxa composition and abundance of seagrass-associated animals at several seagrass beds in these regions. By repeating the monitoring in 2005 and 2006, we had the rare opportunity to evaluate the impact of the tsunami on benthic communities.



The objective of this paper is to examine the effects of a tsunami on seagrass macrofaunal communities by comparing data collected before and after the tsunami. Patterns of temporal changes in abundance, diversity, and similarity of macrofaunal community structure were compared between 2 seagrass beds that received different degrees of disturbance and between vegetated and nonvegetated areas within seagrass bed to examine whether the changes are related to the magnitude of the tsunami disturbance and to the presence or absence of seagrass vegetation.

## **4.2. Materials and methods**

### *4.2.1. Study sites*

Study sites were located in seagrass beds at the mouth of the river Khlong Khura, Phang-nga Province, along the Andaman Sea coast of Thailand (Fig. 4.1). In this region, mangroves cover the upper intertidal zone, and several seagrass beds occur from the lower intertidal to the shallow subtidal zone. Seven seagrass species occur in these beds: *Halophila ovalis*, *Enhalus acoroides*, *Syringodium isoetifolium*, *Halodule uninervis*, *H. pinifolia*, *Cymodocea rotundata*, and *C. serrulata*.

Benthic samples were collected at the 2 sites, K2 (Mai Hang; 9°13'25"N; 98°19'40"E) and K3 (Thung Nang Dam; 9°15'02"N; 98°20'30"E) (Fig. 4.1). The K2 seagrass bed developed at the intertidal to shallow subtidal zone (less than 0.5 m deep at MLW). The bed was located close to the river mouth and, thus, would be highly affected by river discharge. The bottom consisted of medium-coarse sand. Here, mixed vegetation of *H. ovalis*, *C. serrulata*, *C. rotundata*, and *H. uninervis* developed,

among which *C. rotundata* was the most dominant. The K2 seagrass bed received moderate disturbance from the tsunami, and fresh nonvegetated gaps within the seagrass were observed in 2006 (T. Suzuki, personal observation). Coverage and biomass of seagrass were stable between 2001 and 2006 (Fig. 4.2) (Nakaoka et al. 2007).

The K3 seagrass bed occurred in a shallow subtidal area (0.5-1.0 m deep at MLW). This site faced the outer ocean and, thus, the effect of a monsoon was expected to be severe. Here, seagrass coverage expanded rapidly in the late 1990s due to sand dune development surrounding the seagrass bed. (S. Nimsantijaroen, personal communication). K3 was covered with *C. serrulata* vegetation in 2001 but was severely disturbed by the tsunami, and almost all of the seagrass disappeared due to sand accumulation (Nakaoka et al., 2007). Seagrass coverage and biomass dropped to zero in 2005 and did not recover in 2006 (Fig. 4.2).

#### 4.2.2. Sampling procedure

Macrobenthic organisms were sampled in January 2001 (approximately 4 years before the tsunami), February 2005 (2 months after the tsunami), and December 2006 (approximately 2 years after the tsunami). The sampling was carried out during low tide. The sites were approached either on foot (under emerged conditions) or by snorkeling (under submerged conditions). A research plot approximately 50 m by 50 m in size containing areas with both seagrass vegetation and nonvegetated gaps was established at each site. At K3, samples were collected only from nonvegetated areas in 2005 and 2006 because no vegetated areas remained.

At each site, 5 replicate cores were collected randomly from a seagrass-vegetated area and a nonvegetated area using a 15-cm-diameter (PVC) corer. Cores were inserted into the sediment to a depth of 20 cm, resulting in a sampling area of 177 cm<sup>2</sup> (2540 cm<sup>3</sup> in volume). Five replicates were taken in each vegetation type in 2001, 2005, and 2006. Macrobenthic samples were sieved through a 0.5-mm mesh sieve. All animals retained on the sieve were transferred to polyethylene bags and fixed with a 10% seawater–formalin solution. In the laboratory, macrobenthic animals were sorted and transferred to 80 % ethanol for identification and counting. All organisms were classified into lower taxonomic levels using available taxonomic keys, (Table 4.1) and the number of individuals in each taxon was counted.

To determine the grain size composition of the sediment, 5 replicate sediment samples were collected from each site and vegetation type using a 5-cm-diameter PVC corer to a depth of 5 cm. Approximately 30 g of sediments were sieved through 2-, 1-, 0.5-, 0.25-, 0.125-, and 0.063-mm mesh sizes and were dried for 24 h at 105 °C. Each fraction was weighed to the nearest 0.1 g. The median grain size and inclusive graphic standard deviation (sorting coefficient) were determined graphically using a cumulative percentage curve (Holme and McIntyre, 1984).

#### *4.2.3. Data analysis*

Changes in diversity of benthic animals were assessed for 2001, 2005, and 2006 using the 2 diversity indices taxa richness (the number of taxa per core) and Simpson diversity index ( $D' = 1 - \sum p_i^2$ , where  $p_i$  is the relative abundance of taxon  $i$ ). Temporal variations in the average densities of whole macrofauna and of some dominant taxa (in which density is higher than 7 individuals/5 cores = 395

individuals/m<sup>2</sup>), taxa richness, and Simpson diversity index were compared for the seagrass-vegetated area and nonvegetated areas of K2 and only the nonvegetated areas of K3 because seagrass vegetation was not found in 2005 and 2006 (see above). At K2, variations in density, taxa richness, and diversity index were tested by a 2-way analysis of variance (ANOVA) using year and vegetation type as fixed factors. At the nonvegetated areas of K3, a 1-way ANOVA was used to test variation among the 3 years. In cases where significant variation was detected by the ANOVA, post-hoc comparisons were carried out using Tukey's method. At K3, the difference in the univariate indices between 2 groups of samples from the different vegetation types in 2001 was tested using a Student's *t*-test. Data were log-transformed in case of heterogeneous variation.

Temporal changes in community structure were further examined by multivariate analyses. Similarity of assemblage was calculated using the Bray-Curtis dissimilarity index for all pairs of the 10 groups by combining data from 5 replicate samples for each group. Two types of similarity matrices were developed using nontransformed abundance data and presence/absence data to examine whether relative abundance of component taxa and taxa composition vary similarly among years for each site and vegetation type. Variation in similarity was graphed using a nonmetric multidimensional scaling (nMDS) ordination method based on 20 iterations of data (Clarke and Warwick, 2001).

Tests for differences in similarity among years for each site and vegetation type were performed using a 1-way analysis of similarities (ANOSIM). The samples from nonvegetated areas in K2 were not used because they contained too few taxa and individuals (fewer than 3 taxa and 5 individuals in most cores). The degrees of dissimilarity among samples from different years were represented by a test statistic *R*.

$R$  is 1 when samples are entirely different and 0 when samples are identical. ANOSIM was carried out based on the following null hypotheses ( $H_0$ ): there are no differences among years within each site and vegetation type in (1) relative abundance (using the nontransformed data) and (2) taxa composition (using the presence/absence data). All of the multivariate analyses were carried out using the software PRIMER-E (ver. 5; Plymouth Marine Laboratory, UK).

### 4.3. Results

#### 4.3.1. Change in sediment composition

Sediment composition varied greatly among sites, between vegetation types, and among the 3 years (Fig. 4.3).

In K2, the 2-way ANOVA showed significant year-by-vegetation type interaction in median grain size ( $F = 3.63$ ;  $df = 2, 24$ ;  $P = 0.042$ ). Median grain size decreased in nonvegetated areas from 2001 to 2005 but recovered by 2006 to a value similar to that in 2001 (Fig. 4.3A). In seagrass vegetation, however, median grain size showed no significant difference among years. At nonvegetated areas of K3, median grain size varied significantly among the 3 years (ANOVA:  $F = 14.07$ ;  $df = 2, 12$ ;  $P < 0.001$ ). Post-hoc comparison revealed that median grain size was greater in 2005 than in 2001 and 2006 (Fig. 4.3A). In 2001, median grain size was significantly higher in the seagrass-vegetated areas of K3 than in the nonvegetated areas ( $t$ -test:  $t = 3.435$ ,  $df = 8$ ,  $P = 0.009$ ).

Sorting coefficients also showed significant year-by-vegetation type interaction in K2 ( $F = 4.59$ ;  $df = 2, 24$ ;  $P = 0.021$ ). In the nonvegetated areas, sorting coefficients was higher in 2001 than in 2005 and 2006, and in the seagrass-vegetated areas, sorting coefficients was higher in 2005 than in 2006 (Fig. 4.3B). Among-year variation was significant at the nonvegetated areas of K3 (ANOVA:  $F = 98.08$ ;  $df = 2, 12$ ;  $P < 0.001$ ), where it was significantly higher in 2001 than in 2005 and 2006 (Fig. 2.3B). In 2001, the sorting coefficient was significantly lower in the vegetated areas of K3 than in the nonvegetated areas ( $t$ -test:  $t = -5.295$ ,  $df = 8$ ,  $P = 0.001$ ).

#### 4.3.2. Abundance and diversity of macrofauna

A total of 137 macrofaunal taxa were recorded from the study area (Table 4.1). Total macrofaunal abundance at the 2 sites was 3119, 3153, and 4102 individuals  $m^{-2}$  in 2001, 2005, and 2006, respectively. Polychaetes were the most abundant, occupying more than 50% of the total abundance.

Macrofaunal density, taxa richness, and diversity varied greatly among sites, between vegetation types, and among the 3 years (Fig. 4.4). In K2, patterns of temporal changes in the density of total macrofauna differed between vegetation types, as shown by significant year-by-vegetation type interaction in a 2-way ANOVA ( $F = 11.95$ ;  $df = 2, 24$ ;  $P < 0.001$ ). In nonvegetated areas, the densities decreased greatly from 2001 to 2005 but were not statistically different between 2001 and 2006 or between 2005 and 2006 (Fig. 4.4A). In seagrass vegetation, density increased from 2001 to 2005 and was not significantly different between 2005 and 2006.

In nonvegetated areas of K3, the densities decreased from 2001 to 2005 but increased greatly from 2005 to 2006. One-way ANOVA results showed significant

variation among the 3 years ( $F = 12.44$ ;  $df = 2, 12$ ;  $P < 0.001$ ), and a post-hoc comparison revealed that the difference was significant between 2001 and 2005, and between 2005 and 2006, but not between 2001 and 2006 (Fig. 4.4A). Density was not statistically different between the 2 vegetation types of K3 in 2001 ( $t$ -test:  $t = 0.453$ ,  $df = 8$ ,  $P = 0.663$ ).

The results of temporal changes in abundance of dominant taxa showed significant difference among vegetation types and among years (Table 4.2). In the vegetated areas of K2, *Ophelina* sp. A was more abundant in 2001 than in 2005 and 2006, whereas *Armandia intermedia* and *Sipunculidea* sp. A were significantly more abundant in 2005 than in 2001 with 2006 showing intermediate values. *Goniada* spp. and *Prionospio* (*Prionospio*) *membranacea* did not show significant variation among years. In the nonvegetated areas of K2, *Goniada* spp. was the most abundant in 2001, and *Aricidea* sp. 2 was the most abundant in 2006. In the nonvegetated areas of K3, the density of *Aricidea* sp. 2 was significantly higher in 2001 than in 2005, and the density of *Umbonium* sp. A and *Tanaidacea* sp. B was higher in 2006 than in 2001 (Table 4.2).

Temporal changes in taxa richness of macrofauna showed the same patterns of variation among vegetation types as those shown in total density (Fig. 4.4B). At K2, a significant interaction between year and vegetation type was detected by a 2-way ANOVA ( $F = 10.83$ ;  $df = 2, 24$ ;  $P < 0.001$ ). In nonvegetated areas, taxa richness was significantly lower in 2005 than in 2001, but in seagrass-vegetated areas, taxa richness was significantly lower in 2001 than in 2005 and 2006. At the nonvegetated areas of K3, taxa richness varied significantly among the 3 years (ANOVA:  $F = 31.39$ ;  $df = 2, 12$ ;  $P < 0.001$ ), and was lower in 2005 than in 2001 and 2006. Taxa richness did not

differ significantly between the nonvegetated and seagrass-vegetated areas in 2001 (*t*-test:  $t = 0.641$ ,  $df = 8$ ,  $P = 0.539$ ).

Patterns of temporal changes in the Simpson diversity index of macrofauna also showed a significant year-by-vegetation type interaction in K2 by a 2-way ANOVA ( $F = 7.74$ ;  $df = 2, 24$ ;  $P = 0.003$ ). In the nonvegetated areas, diversity was higher in 2001 than in 2005 but was not statistically different between 2001 and 2006 (Fig. 4.4C). In seagrass vegetation, however, diversity showed no significant difference among years. At the nonvegetated areas of K3, diversity varied significantly among the 3 years (ANOVA:  $F = 1.93$ ;  $df = 2, 12$ ;  $P = 0.188$ ). Post-hoc comparison revealed that diversity was higher in 2001 than in 2005 but was not statistically different between 2001 and 2006 or between 2005 and 2006 (Fig. 4.4C). In 2001, the Simpson diversity index in the seagrass-vegetated areas of K3 was not statistically different from the nonvegetated areas (*t*-test:  $t = 0.342$ ,  $df = 8$ ,  $P = 0.741$ ).

The nMDS plots based on abundance data and presence/absence data showed a different pattern of temporal variation among different sites (Fig. 4.5). For both data types, macrofauna assemblage in the seagrass-vegetated areas at K2 was similar among the 3 years, whereas it was less similar in the nonvegetated areas at K2 and K3. The results of ANOSIM showed significant variation in similarity among years for both data types in all sites and vegetation types (Table 4.3). Post-hoc comparisons showed that the variation was only significant between 2001 and 2006 at nonvegetated areas at K3, whereas it was significant for all pairs of years at vegetated areas at K2 (Table 4.3).



#### 4.4. Discussion

Using the pre-existing quantitative data collected before the tsunami, we evaluated its impact on benthic communities by quantifying animal diversity and abundance. Our findings were based on data collected at only 2 seagrass beds in one locality, and thus their general applicability remains unknown. Nevertheless, our study offers some insight into the variability of benthic organisms in general, i.e., the pattern of temporal changes in benthic animals varies between sites with different disturbance levels and between positions with and without seagrass vegetation.

Comparative analysis on seagrass biomass and coverage before and after the tsunami revealed that the seagrass bed in K3 was more severely affected by the tsunami than the seagrass bed in K2 (Nakaoka et al., 2007). Changes in sediment composition were also different between K2 and K3 and between nonvegetated and seagrass-vegetated areas of K2. The difference between sites may be due to the different types of disturbance caused by the tsunami. At K3, the bed was buried more than 50 cm, whereas at K2, the bed was only partly eroded (Nakaoka et al., 2007). More importantly, the presence of seagrasses may buffer changes in sediment composition at K2 because no significant temporal variation was found in the median diameter of the seagrass-vegetated site.

One notable finding is that the patterns of temporal changes in benthic abundance and diversity differed between vegetated and nonvegetated areas at K2. A large decline in abundance and diversity after the tsunami was observed in the nonvegetated areas at K2, whereas an increase was detected in the seagrass-vegetated areas. The positions of vegetated and nonvegetated areas in K2 did not change to a great extent either before or after the tsunami, as shown by the consistent coverage at

this site (Fig. 4.2A). Thus, the contrasting pattern of temporal changes in benthic animals was most likely related to the presence or absence of seagrass vegetation because seagrass can buffer the impacts of the physical disturbance. Complex networks of belowground rhizomes and roots prevent sediment erosion, (Fonseca and Fisher, 1986; Fonseca, 1989) and the presence of a seagrass canopy efficiently attenuates waves and reduces current velocity (Koch and Gust, 1999; Verduin and Backhaus, 2000; Madsen et al., 2001; Komatsu et al., 2004). The buffering effects of seagrass may be irrelevant at K3, where the strong physical disturbance created by the tsunami resulted in the loss of all vegetation, but they may play a significant role at K2, where the impact of the tsunami was less intense and the seagrass cover and biomass did not change before or after the tsunami. It remains unknown, however, why abundance and diversity increased in the vegetated areas. Processes that may explain these increases include the aggregation of benthic organisms after the tsunami due to the reduction of vegetation elsewhere (such as at K3) and the rapid dispersal and recruitment from neighboring, less-disturbed areas.

In general, benthic community recovery from the disturbance occurred more rapidly in sites receiving less impact (Dernie et al., 2003a as observed experimentally). After the tsunami, we expected that the decline in abundance and diversity of the macrobenthic community would be greater and that the recovery rate would be slower in the seagrass bed at K3 than K2, with K3 receiving greater impacts (Nakaoka et al., 2007). However, the magnitude of decline and subsequent recovery of macrobenthic animals in nonvegetated areas were similar between the 2 sites. This suggests that the temporal changes in macrofauna observed here were not solely related to the magnitude of the tsunami disturbance. Temporal changes in macrofaunal abundance and community structure can be affected simultaneously by a variety of factors such

as physical disturbance caused by monsoon storms, sedimentation due to river discharge during rainy seasons, sporadic recruitment and colonization, and changes in food availability and predation pressures (e.g., Virnstein, 1977; Breitburg, 1996; Frost et al., 1999; Nakaoka et al., 2004). These factors can interactively affect macrofaunal community composition in addition to the physical disturbance caused by the tsunami.

The analysis of temporal changes in population size of the dominant taxa revealed that each taxon showed a different temporal pattern before and after the tsunami. However, it is difficult to explain how the increase and decrease are related to biological features of these taxa. Most of the dominant taxa are deposit-feeding animals living in the subsurface of the sediment, except *Goniada* spp., which are carnivorous, and *Umbonium costatum*, which is a suspension feeder (Table 4.4). We could not establish whether the increase or decrease is related to their feeding modes or living position. Furthermore, some species (*Goniada* spp. and *Aricidea* sp. 2) showed different temporal patterns at different vegetation types or at different sites. More life history information such as dispersal ability and recruitment dynamics is needed for each species to explain how and why different patterns were observed among dominant species.

Multivariate analysis revealed that similarity of the benthic animals differed greatly among the 3 years at the nonvegetated areas, whereas it varied less at the seagrass-vegetated areas. This is consistent with the fact that dominant taxa were almost totally replaced before and after the tsunami at nonvegetated areas of K2 and K3, whereas the abundance of some dominant taxa did not change significantly at vegetated areas of K2. Thus, the tsunami effect varied between seagrass-vegetated and nonvegetated areas not only in abundance and diversity but also in changes of taxa composition. The observed pattern was similar between the 2 data types (abundance

data and presence/absence data), indicating that temporal change in similarity occurred both in relative abundance of dominant animals and in the composition of rare taxa. The finding suggests that the community structure in nonvegetated areas had changed and had not recovered to the same composition that existed before the tsunami even though total abundance and taxa richness had recovered by 2006. Ongoing, long-term monitoring of seagrasses and associated animals will clarify whether or not the taxa composition in 2005 and 2006 was in a transitional stage of recovery.

#### **4.5. Conclusion**

The present study revealed that the patterns of temporal changes in abundance and diversity of macrofaunal assemblages before and after the tsunami were highly variable among sites, and that the degree of temporal changes in assemblage structure was not solely related to the magnitude of the tsunami disturbance. More importantly, our results suggest that the presence or absence of seagrass vegetation can alter the patterns of temporal changes in macrofaunal assemblages and recovery processes after a tsunami disturbance. This may highlight the importance of seagrass vegetation for coastal management, such as in retarding increasing levels of physical disturbance in the face of global climate changes and in maintaining the stability of biodiversity and ecosystem function.

Table 4.1. List of macrofauna taxa collected at the two study sites in 2001, 2005 and 2006

List of macrofauna in the study area		
Annelida	<i>Scoloplos (Scoloplos) sp. A</i>	Anthuridea sp.B
<i>Isolda pulchela</i>	<i>Scoloplos (Scoloplos) sp. B</i>	Sphaeromatidae sp.
<i>Lynopherus sp. A</i>	<i>Aricidea sp. 1</i>	Tanaidacea sp.B
<i>Lynopherus sp. B</i>	<i>Aricidea sp. 2</i>	Tanaidacea sp.C
<i>Lynopherus sp. C</i>	<i>Levinsenia sp.</i>	Cumacea sp.
<i>Arabella sp.</i>	<i>Pilargis sp.</i>	<i>Nikoides sp.</i>
<i>Capitella sp.</i>	Polynoidae Indet. genus 1	<i>Processa sp.</i>
Capitellidae Genus indet. 1	Polynoidae Indet. genus 2	<i>Alpheus sp.</i>
<i>Heteromastus sp.</i>	<i>Chone sp. A</i>	<i>Diogenes sp.</i>
<i>Notomastus sp.</i>	<i>Fimbriosthenelais sp.</i>	<i>Paratymolus sp.</i>
<i>Parheteromastus tenuis</i>	<i>Leanira sp.</i>	<i>Thalamita spp.</i>
<i>Caulleriella sp.</i>	<i>Sigalion sp.</i>	<i>Parapilumnus sp.</i>
<i>Chaetozone sp.</i>	<i>Aonides sp.</i>	Penaeidae sp.
<i>Monticellina sp. A</i>	<i>Malacoceros cf. indicus</i>	<i>Sicyonella sp.</i>
<i>Monticellina sp. B</i>	<i>Prionospio (Minuspio) sp.</i>	<i>Crangon sp.</i>
<i>Euniphysa sp. A</i>	<i>Prionospio (Prionospio) cf. andamanensis</i>	Mollusca
<i>Pherusa sp.</i>	<i>Prionospio (Prionospio) cf. caspersi</i>	<i>Umbonium sp.</i>
<i>Glycera sp. A</i>	<i>Prionospio (Prionospio) cf. cornuta</i>	<i>Cerithium sp. aff. dialeucum</i>
<i>Glycera sp. B</i>	<i>Prionospio (Prionospio) cf. runei</i>	<i>Rhinoclaris sordidula</i>
<i>Glycinde sp.</i>	<i>Prionospio (Prionospio) membranacea</i>	<i>Niotha sp. aff. albescens</i>
<i>Goniada spp.</i>	<i>Scololepis sp. 1</i>	<i>Zeuxis sp. aff. margaritifera</i>
<i>Hesione sp.</i>	<i>Spio sp.A</i>	<i>Gibberula sp.</i>
<i>Leocrates indicus</i>	<i>Spio sp.B</i>	<i>Neritina paralella</i>
<i>Kuwaita sp.</i>	Spionidae sp. indet.	<i>Nuculana sp.</i>
<i>Lumbrineris sp. A</i>	<i>Sternapsis sp.</i>	<i>Anadara sp.</i>
<i>Lumbrineris sp. B</i>	<i>Pionosyllis sp.</i>	<i>Thyasira sp.</i>
<i>Tainokia sp.</i>	<i>Syllis spp.</i>	<i>Jactellina sp.</i>
<i>Magelona sp.</i>	<i>Pista sp.</i>	<i>Nitidotellina sp.</i>
<i>Axiothella sp.</i>	Terebellidae Indet. genus 1	Veneridae sp.A
<i>Clymenella koellikeri</i>	Unidentified genus 1	Veneridae sp.B
Maldanidae Indet. genus 1	Arthropoda	<i>Musculus sp.</i>
Maldanidae Indet. genus 2	Ostracoda sp.	<i>Musculista senhousia</i>
<i>Paraxiella sp.</i>	<i>Balanus sp.</i>	Cnidaria
<i>Inermonephthys sp.</i>	<i>Balanus reticulatus</i>	Edwardsiidae sp.
<i>Micronephthys spp.</i>	<i>Ampelisca sp.</i>	Nemertinea
<i>Namalycastis sp.</i>	<i>Byblis sp.</i>	Anopla sp.
Nereididae sp. indet.	<i>Amphithoe sp.</i>	Anopla sp.B
<i>Nereis sp.</i>	<i>Grandidierella sp.A</i>	Sipuncula
<i>Perinereis sp.</i>	<i>Erichthonius sp.B</i>	Sipunculidea sp.A
<i>Platynereis dumerilii</i>	<i>Erichthonius sp.E</i>	Echinodermata
<i>Platynereis sp. A</i>	Podoceridae sp.	Ophiuroidea sp.
<i>Diopatra claparedii</i>	<i>Pontogeneia ? sp.</i>	Fibulariidae sp.
<i>Diopatra sp.A</i>	Melitidae sp.	Synaptidae sp.
<i>Armandia intermedia</i>	Melitidae sp.B	Echinoidea sp.
<i>Ophelina sp. A</i>	<i>Monocluades sp.</i>	Chordata
Orbiniidae sp. indet.	<i>Tipimegus sp.</i>	Branchiostomidae sp.
<i>Scoloplos (Leodamas) brevithorax</i>	Phoxocephalidae sp.	Vertebrata
<i>Scoloplos (Leodamas) dubia</i>	Gammaridae sp. A	Osteichthyes sp.A
<i>Scoloplos (Leodamas) gracillis</i>	Anthuridea sp.	

Table 4.2  
Results of temporal changes in abundance of dominant species (inds. /m<sup>2</sup>) in two seagrass beds .

Taxa	2001		2005		2006		ANOVA		Post-hoc comparisons*			
	mean	sd	mean	sd	mean	sd	F	P				
<b>K2-Vegetated area</b>												
<i>Ophelina</i> sp. A	180.8	197.3	11.3	25.3	0.0	0.0	7.09	0.009	**	2001	2005	2006
<i>Armandia intermedia</i>	11.3	25.3	655.4	470.3	56.5	69.2	21.04	0.000	**	2005	2006	2001
<i>Sipunculidea</i> sp.A	11.3	25.3	542.4	275.6	350.3	269.2	7.28	0.009		2005	2006	2001
<i>Goniada</i> spp.	90.4	85.7	214.7	92.8	158.2	101.1	2.22	0.151		-	-	-
<i>Prionospio (Prionospio) membranacea</i>	90.4	30.9	158.2	134.9	101.7	73.7	0.81	0.470		-	-	-
<b>K2-Non-vegetated area</b>												
<i>Goniada</i> spp.	259.9	162.8	11.3	25.3	22.6	30.9	14.51	0.001	**	2001	2006	2005
<i>Aricidea</i> sp. 2	0.0	0.0	0.0	0.0	135.6	147.3	5.33	0.022	**	2006	2005	2001
<b>K3-Non-vegetated area</b>												
<i>Aricidea</i> sp. 2	79.1	75.8	0.0	0.0	11.3	25.3	4.03	0.046	**	2001	2006	2005
<i>Umbonium</i> sp.	0.0	0.0	0.0	0.0	870.1	811.5	5.98	0.016	**	2006	2005	2001
<i>Tanaidacea</i> sp.B	0.0	0.0	0.0	0.0	203.4	30.9	773.52	0.000	**	2006	2005	2001

\* Underline denote pairs of years without significant differences

\*\* Data were log-transformed for ANOVA to reduce heterogeneity of variance (Mark all which were transformed)

Table 4.3

Results of ANOSIM testing variation in similarity among years. Bray-Curtis similarity was calculated between pairs of core samples using non-transformed abundance data and presence/absence data.

Sites	Among years		Post-hoc comparisons <sup>a</sup>			
	Global <i>R</i>	<i>P</i>	among years			
Non-transformed abundance						
K3-Non-vegetated area	0.822	< 0.001	<u>2001</u>	<u>2005</u>	<u>2006</u>	2006
K2-Non-vegetated area <sup>b</sup>	0.731	0.029	-	-	-	-
K2-Seagrass area	0.658	< 0.001	2001	2005	2006	2006
Presence / absence						
K3-Non-vegetated area	0.727	< 0.001	<u>2001</u>	<u>2005</u>	<u>2006</u>	2006
K2-Non-vegetated area <sup>b</sup>	0.454	0.029	-	-	-	-
K2-Seagrass area	0.600	< 0.001	2001	2005	2006	2006

<sup>a</sup> The pairs of years without significant differences are underline.

<sup>b</sup> Post-hoc comparisons were not undertaken because data on 2005 was not used for the analysis.

Table 4.4  
Biological features of dominant macrofaunal taxa in the study area

<b>Taxa name</b>	<b>Family, Taxa group</b>	<b>Feeding modes</b>	<b>Living position</b>	<b>Reference</b>
<i>Ophelina</i> sp. A	Opheliidae, Polychaeta	Subsurface deposit feeder	A slender torpedo-shaped active burrower in sandy sediments	Fauchald and Jumars (1979)
<i>Goniada</i> spp.	Goniadidae, Polychaeta	Carnivorous	Burrower or free-living(?) in sandy sediment	Gaston (1987)
<i>Prionospio</i> ( <i>Prionospio</i> ) <i>membranacea</i>	Spionidae, Polychaeta	Surface deposit feeder	Live in mud tubes, tubicolous worms in shallow water on all substrata	Fauchald and Jumars (1979)
<i>Armandia intermedia</i>	Opheliidae, Polychaeta	Surface deposit feeder	Burrower in the upper layer of sediment	Pagliosa (2005)
Sipunculidea sp.A	Sipunculidae, Sipuncula	Deposit feeder	Inhabit semi-permanent burrows in coarse or silty sand	Edmonds (2000)
<i>Aricidea</i> sp. 2	Paraonidae, Polychaeta	Surface deposit feeder	Shallow burrowers	Gaston (1987)
<i>Umbonium</i> sp.	Trochidae, Gastropoda	Suspension feeder	Surface sand bottom in intertidal to shallow subtidal zone	Noda (1991)
Tanaidacea sp.B	Tanaidacea, Malacostaca	Raptorial feeder	Live in shallow waters, in sandy or muddy bottoms	Brusca and Brusca (2003)



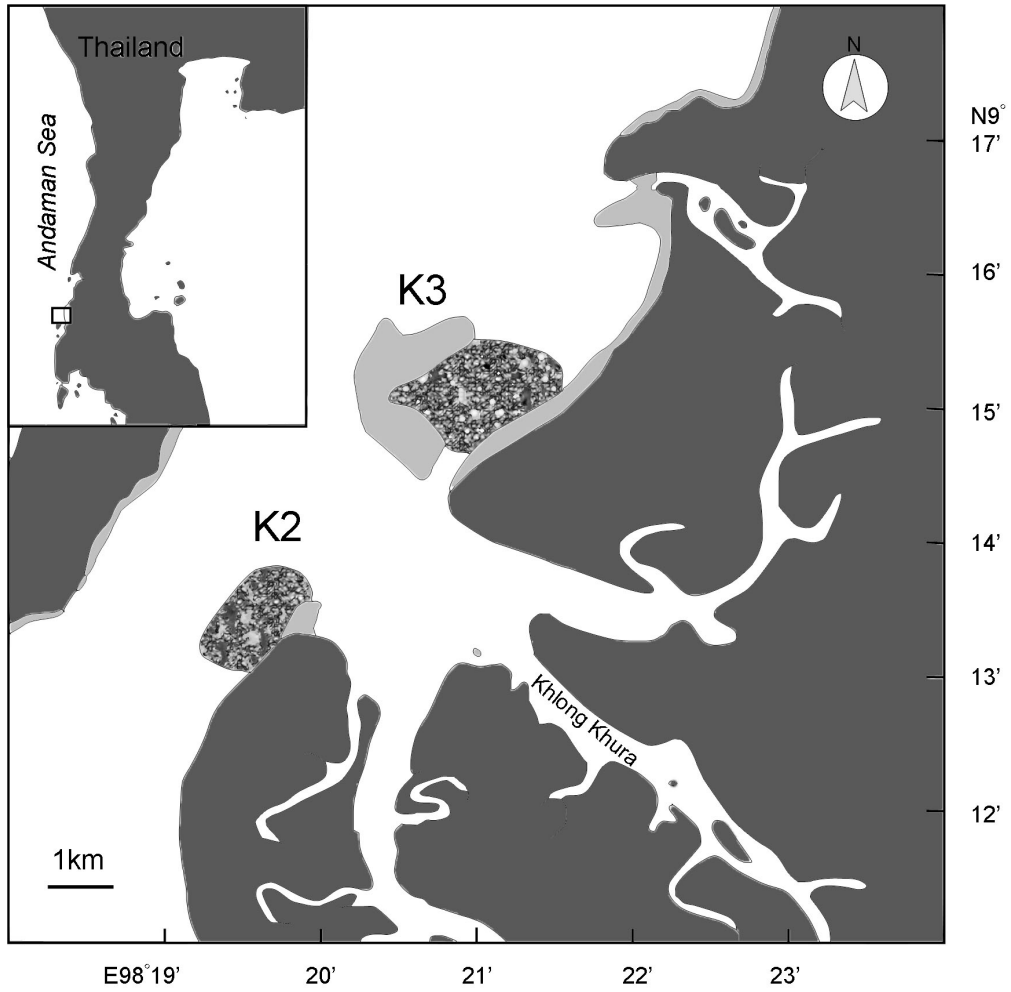


Fig. 4.1. Study sites at Kuraburi along the Andaman Sea coast of Thailand. Fine dot areas indicate positions of major seagrass beds in 2001. Dark and light grey areas denote the land and sand dunes, respectively.

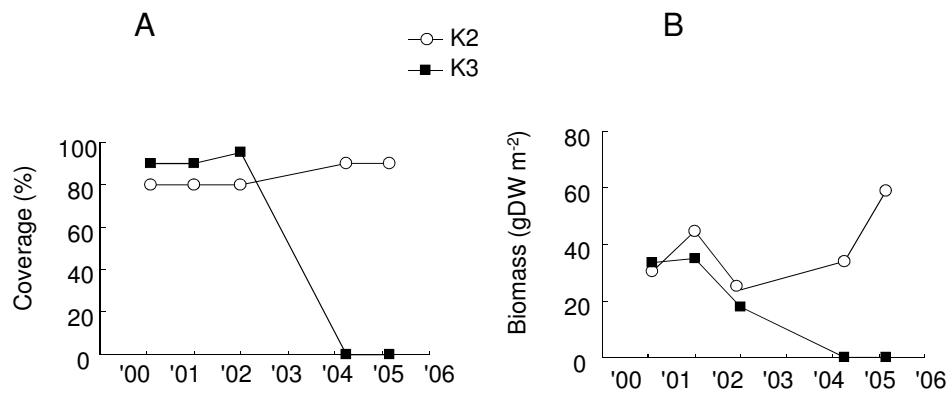


Fig. 4.2. Temporal changes in seagrass coverage (A) and biomass (B) at the two research sites in Kuraburi from 2001 to 2006 (cited from Nakaoka et al., 2007).

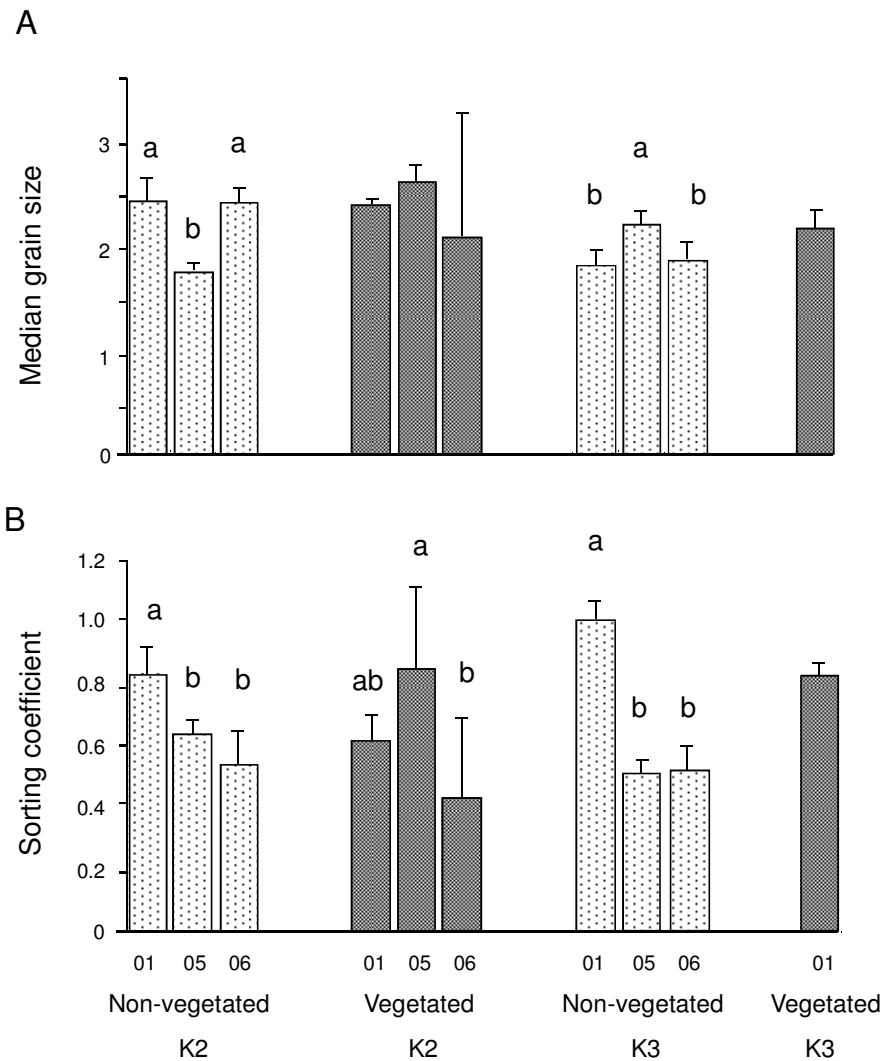


Fig. 4.3. Average value of the median grain size (A) and sorting coefficient (B) measured in seagrass-vegetated and non-vegetated areas in 2001 (01), 2005 (05) and 2006 (06) at two sites (K2 and K3) in Kuraburi. Bars denote standard deviation of the mean. Unlike letters denote pairs of years with significant differences by post-hoc comparisons.

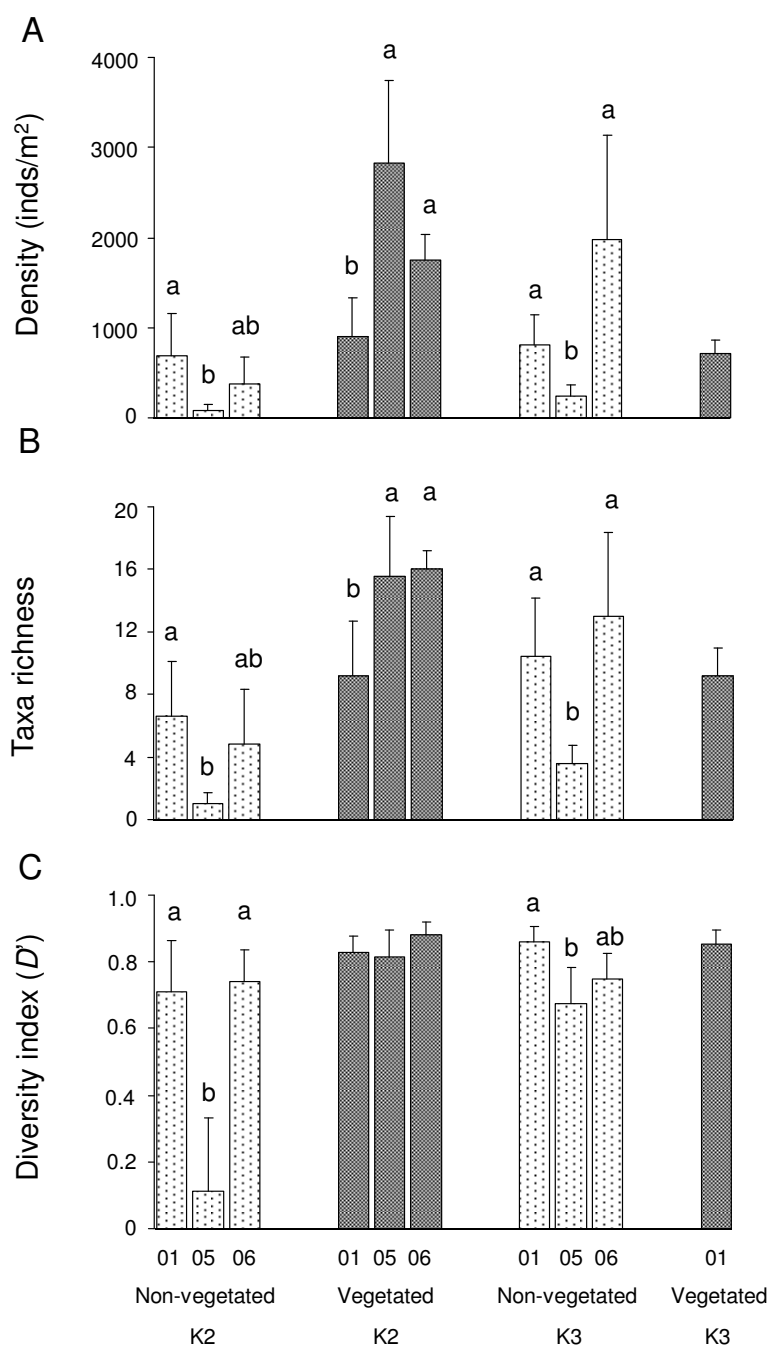
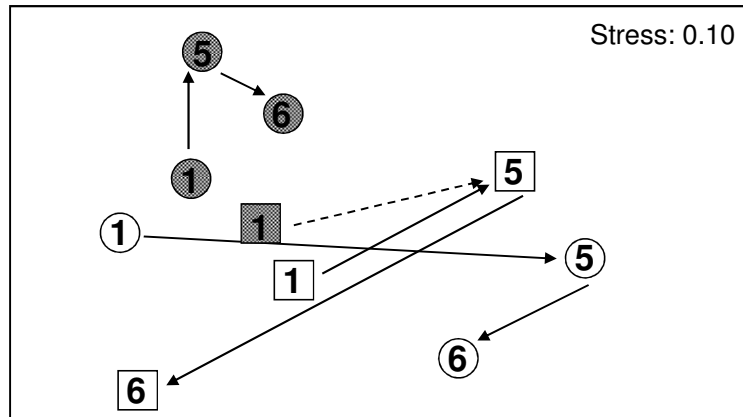


Fig. 4.4. Temporal variation in (A) density, (B) taxa richness, and (C) Simpson diversity index ( $D'$ ) of macrobenthic animals collected at seagrass-vegetated and nonvegetated areas of 2 sites (K2 and K3) in 2001 (01), 2005 (05), and 2006 (06). Bars denote standard deviation of the mean. Unlike letters denote pairs of years with significant differences by post-hoc comparisons. Untransformed data were presented for graphical purposes.

A



B

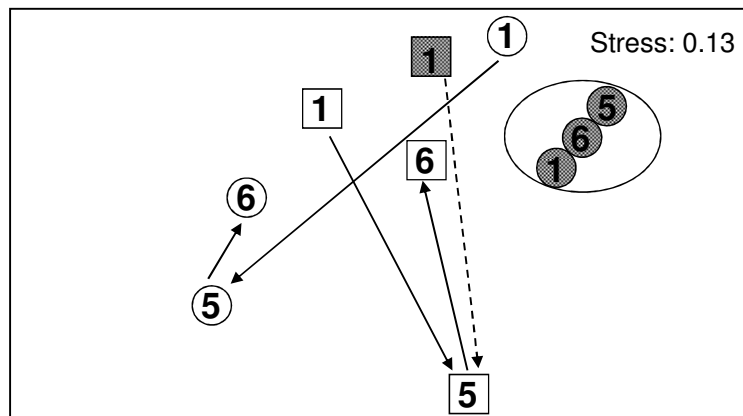


Fig. 4.5. Non-dimensional MDS ordination of macrobenthic assemblages in seagrass-vegetated (shaded symbols) and non-vegetated (clear symbols) areas at two sites (circles for K2 samples and squares for K3) in 2001 (1), 2005 (5) and 2006 (6). The nMDS plots were made based on (A) non-transformed abundance data, and (B) presence/absence data. Solid arrows indicate temporal changes in assemblages for each site and vegetation types, and dotted arrows those from vegetated to non-vegetated states at K3 due to the tsunami disturbance.

## **CHAPTER 5**

### **General discussion**

#### **5.1. Variability in seagrass vegetation effects**

Seagrass vegetation plays important roles in habitat complexity, food availability, shelter, and nursery ground for associated animals (Kikuchi and Pérès, 1977; Hemminga and Duarte, 2000; Beck et al., 2001; Heck et al., 2003; Valentine and Duffy, 2006). The presence of seagrass vegetation, therefore, generally enhances their abundance and diversity. The positive effects of seagrass vegetation are most obvious for nekton and epiphytic animals which require seagrass aboveground as habitat and shelter. However, the effects are variable for infaunal benthic animals which do not necessarily require seagrass as habitat (see Chapter 1).

Comparisons of abundance and diversity of animals between vegetated and non-vegetated position in seagrass beds is one of the most effective methods to examine the seagrass vegetation effects. In my study, comparisons are made according to this design for seagrass beds in Tokyo Bay (Chapters 2 and 3), and in Thailand (Chapter 4). Non-significant effects or even negative effects were found in some seagrass beds such as Futtsu Port in autumn and Takeoka in summer (Chapter 2), but the positive effects of vegetation were found in most seagrass beds such as Futtsu Tidal Flat in Tokyo Bay (Chapter 3), and Kuraburi in Thailand (Chapter 4). The results confirm my notion that the vegetation effect was highly variable among seagrass beds for macrobenthic animals. In this thesis, I attempted to investigate

factors causing the variability (Chapter 2), and appropriate scales to consider the vegetation effects (Chapter 3).

## **5.2. Broad-scale analyses of variability in seagrass vegetation effects on macrobenthic invertebrate community**

There are several different approaches to elucidate factors and processes of variable effects of seagrass vegetation on macrobenthic invertebrate (Fig. 5.1). In this study, I used a nested hierarchical approach to understand spatial heterogeneity of the seagrass vegetation effect on benthic animals over many seagrass beds occurring discretely along a region (eastern part of Tokyo Bay) (Chapter 2). This approach enables us to examine variation in ecological patterns across a large variety of spatial scales from local patch scale (<1 m) to a cross-continental scale (de Boer, 1992; Hughes et al., 1999; Noda, 2004; Nakaoka et al., 2006, Benedetti-Cecchi et al., 2010). In Chapter 3, I used remote sensing and GIS techniques to examine the effect of seagrass vegetation structure on animals at different spatial scales in a continuous landscape. Finally, the result of a long-term monitoring of seagrass community at different seagrass beds with different environmental conditions was examined in Chapter 4. It provides a baseline data to understand how seagrass community responds to variable changes in environmental factors. It can be useful to assess the impact of sudden catastrophic disturbance to coastal ecosystems and to predict and evaluate for the changes in marine community with climate changes and other human-induced threats (Kendrik et al., 1999; McKenzie et al., 2001; Bernard et al., 2007).

Importance of scaling has recently been recognized in studies of marine community (Heck et al., 2003; Mumby et al., 2004). In Chapter 3, I investigated the

influences of spatial (scale) structure and dynamics of seagrass landscape on macrobenthic invertebrate community. Here, I examined the relative importance of vegetation types, coverage and stability on observed variation in macrobenthic communities. One of the most notable findings is that abundance and diversity of macrobenthic invertebrate were most correlated with seagrass coverage at the extent of 10-15 m (small scale), possibly related to mobility and dispersal range of component species, and their biological interactions (Doak et al., 1992; Underwood and Chapman, 1996). I also found that temporal stability of the vegetation is also important to explain variability in abundance and diversity of macrobenthic invertebrate community.

In contrast to Chapter 3, which considers the spatial effects of seagrass at continuous landscapes, I investigated broader-scale processes for causing variability of the vegetation effects in a discrete, nested design (Chapter 2). Whereas additive effects of sites, station and vegetation was found for the variation in taxa richness, variability in abundance was greater at smaller spatial scale (within a site; < 5 km distance) rather than at broad spatial scale (between sites; > 10 km). I failed to detect any significant environmental parameters relating to the observed variability in the vegetation effects on abundance and similarity. Based on the results of these two chapters, I can conclude that the small-scale processes can be more important for explaining the variability in the effects of seagrass vegetation on macrobenthic invertebrate community. There are many studies showing that macrobenthic abundance and diversity vary most greatly at small scale (Underwood and Chapman, 1996; Hovel et al., 2002; Tanaka and Leite, 2003), suggesting the importance of local processes such as species interactions and microenvironmental variation for determining the community structure.



### **5.3. Roles of seagrass vegetation on maintenance of macrobenthic invertebrate biodiversity against the catastrophic disturbance**

Coastal ecosystems, including seagrass beds, are susceptible to various environmental disturbances such as extreme climatic events (e.g., cyclones, monsoons, and tsunamis), eutrophication, and coastal development (Short and Wyllie-Echeverria, 1996; Duarte, 2002; Orth et al., 2006). These disturbances are expected to affect not only seagrass, but also the abundance and diversity of the associated macrobenthic invertebrate. In relation to this point, I examined the effect of tsunami on seagrass macrobenthic communities by comparing data collected before and after the tsunami, and between vegetated and nonvegetated positions of seagrass beds (Chapter 4). Although one seagrass bed disappeared due to tsunami, I found that changes in macrobenthic assemblage structure were not solely related to the magnitude of the tsunami disturbance. I found that the presence or absence of seagrass vegetation can alter the patterns of temporal changes in macrobenthic assemblages and recovery processes after disturbance. Notably, the abundance and diversity are enhanced in the vegetation after the tsunami whereas they are greatly reduced outside the vegetation. This suggests that the presence of seagrass vegetation can buffer the impact of physical disturbance against benthic community.

It has been pointed out that the presence of coastal vegetation such as mangrove, seagrass and saltmarsh is important not only for enhanced productivity, but also as barriers for physical disturbances. My finding add another important values of seagrass vegetation; i.e., maintaining biodiversity of associated-organisms in the face of catastrophic disturbance likes tsunami, which otherwise causes great negative

impacts. The same lines of argument can be applicable to the buffering effects of seagrass vegetation to other types of disturbances, such as typhoon, monsoon, and stresses such as increased temperature and desiccation due to global climate change, which should be tested in future studies.

#### **5.4. Conclusions**

Various types of responses of macrobenthic invertebrate community to seagrass vegetation were found in this study, which was carried out over relatively broad spatial scales. The approach, which examined local processes (such as seagrass vegetation effects) over the context of broader temporal and spatial scales has been successfully elucidating processes and mechanisms of benthic community organization, that are highly context-dependent to be solved by single studies conducted at small scales (Hovel et al., 2002; Tanner, 2005; Mill and Berkenbusch, 2009). The approach is promising to elucidate the general aspects of “vegetation effects” which cannot be explained by focusing only one factor in limited local setups.

In summary, my results highlight the variability and importance (consequence) of seagrass vegetation effects on macrobenthic invertebrate community over broad spatial and temporal scales (Fig. 5.2). Particularly for the spatial aspect, the seagrass vegetation effects vary greatly among region, sites, and seasons. I specially found that the variability is partly explained by selecting the appropriate spatial scale for the observation in a continuous seagrass landscape. The approached developed here can be applied to other regions, other types of coastal vegetation, and so on.

My findings lead to more general aspects concerning the importance of aquatic vegetation on coastal biodiversity, and its functioning, which information is

essential for planning effective and efficient management plans for conservation and sustainable management of coastal ecosystems threatened by various nature and human-induced stresses. For example, my outcome on the importance of choosing appropriate scale of observation for evaluating the effects of vegetation on associated animal communities may be useful for designing area and positions of marine protected area for conservation and sustainable use of biodiversity and resources. Furthermore, we can conserve seagrass vegetation not only for the purpose of enhancing productivity of commercially important species, but also for ameliorating stresses and disturbances in the face of global climate changes to maintain the stability of biodiversity and ecosystem functions.

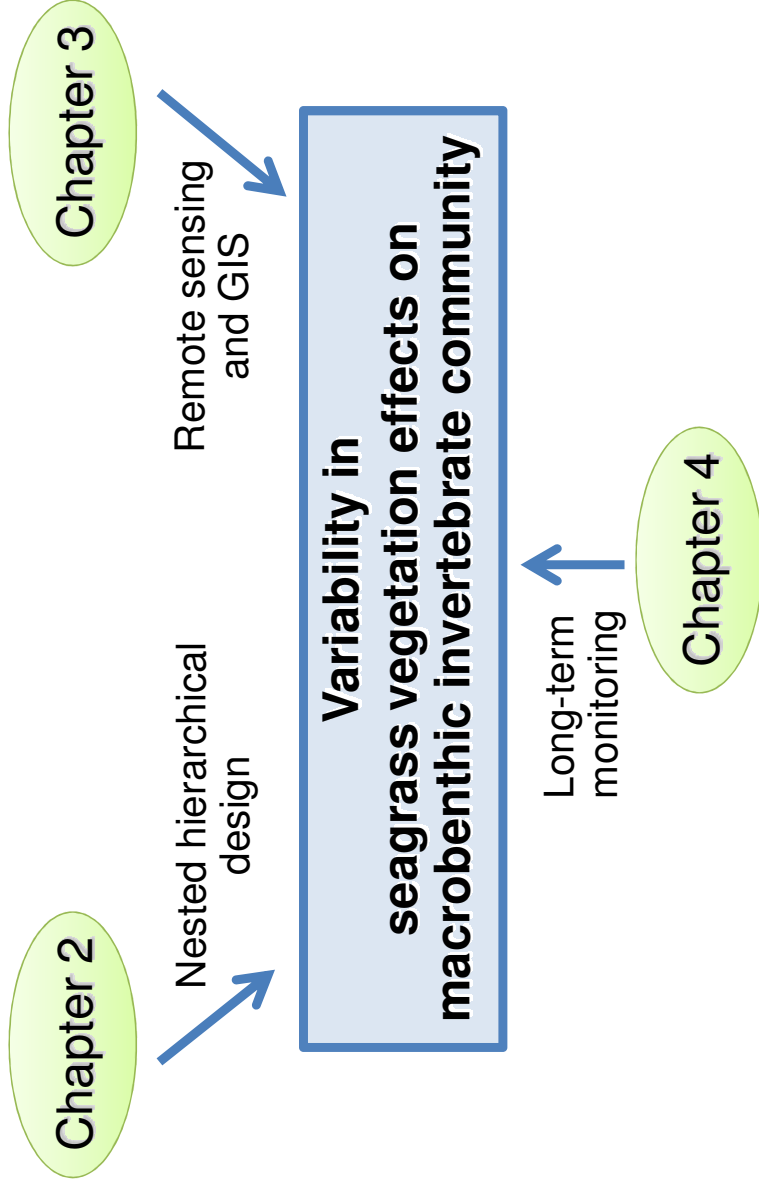


Fig. 5.1. A schematic diagram showing different approaches to elucidate factors and processes of variable effects of seagrass vegetation on macrobenthic invertebrate community.

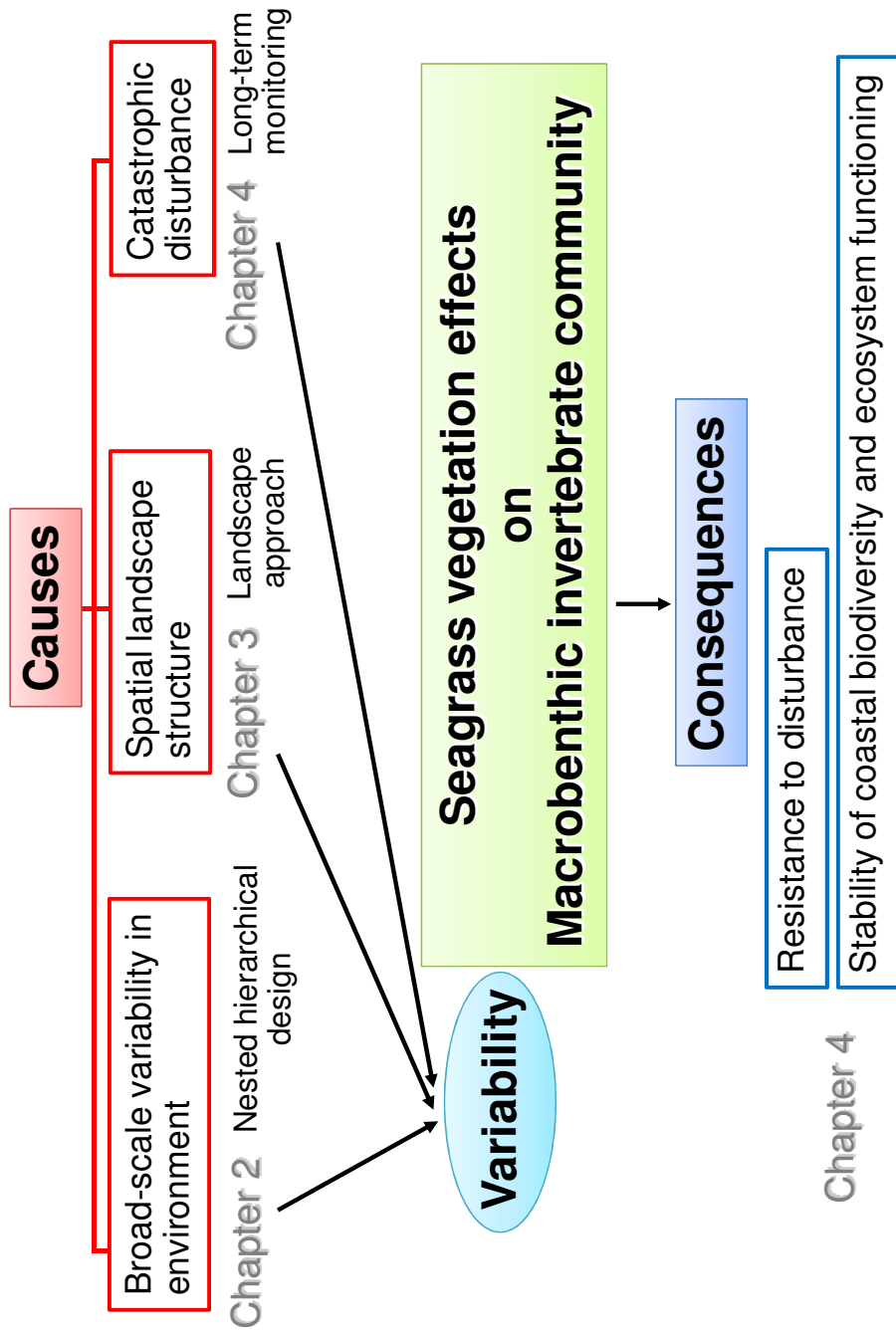


Fig. 5.2. Schematic diagram of causes for variability and consequences of seagrass vegetation effects on macrobenthic invertebrate community.

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