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Benthic macrofaunal assemblages in multispecific seagrass meadows of the southern Philippines: Variation among vegetation dominated by different seagrass species

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ABSTRACT

Although the influence of seagrasses on the diversity and abundance of associated fauna is generally well understood, the effects of seagrass specific identity are not. To determine whether benthic epifaunal and infaunal assemblage patterns vary by the identity of dominant seagrass species in shallow water meadows, we compared quantitative measures of faunal species richness, abundance, and assemblage structure among beds dominated by *Cymodocea rotundata*, *Enhalus acoroides*, and *Thalassia hemprichii*; the study site was at Lopez Jaena, Misamis Occidental Province in the southern Philippines. The *Cymodocea*-dominated vegetation had higher seagrass shoot density and lower seagrass biomass than those dominated by *Enhalus* and *Thalassia*. Across vegetation types, we encountered 30 and 15 species of epifauna and infauna at average densities of 1.73 and 0.82 animals/core (0.0314 m²), respectively. Neither densities and species richnesses of epifauna and infauna nor species composition varied significantly by vegetation type. Multivariate analyses of macrofaunal assemblage structure and abiotic/biotic environmental factors demonstrated that seagrass aboveground biomass explained a significant proportion of the multivariate variation in epifaunal species composition (39%); none of the potential explanatory variables was related to variation in ecological parameters of the infauna. Thus, seagrass specific identity is not a good predictor of either macrofaunal abundance or diversity patterns. Although the ecological parameters of the benthic macrofauna may be influenced by seagrass biomass and structure, responses differ between epifauna and infauna.

Keywords: Biodiversity, Epifauna, Infauna, Macrobenthos, Plant-animal interaction, Tropical seagrasses

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1. Introduction

Seagrasses are marine flowering plants that grow on sedimentary substrata in the shallow waters of tropical, temperate, and boreal regions (den Hartog and Kuo, 2006). Compared to the striking numbers of other marine taxa (e.g., fishes, corals), seagrass diversity is relatively low, with only about 60 species worldwide. Nevertheless, the extent of individual seagrass meadows can be very large; some occupy kilometers of coastline, although others occur in small fragmented patches (Orth et al., 2006). Seagrass beds provide physical structure for complex assemblages of associated species, and along with phytoplankton, periphyton, and macroalgae, they provide many essential ecosystem services. Seagrass meadows are among the most productive ecosystems on the planet (Costanza et al., 1998; Short et al., 2007). While the meadows function as major natural sinks of blue carbon in the ocean (Fourqurean et al., 2012), they are also important in carbon production and export (Ziegler and Benner, 1999; Eyre and Fergusson, 2002), nutrient cycling (Hemminga et al., 1991; Flindt et al., 1999), sediment stabilization (Fonseca, 1989), and trophic transfers (Heck et al., 2008). Finally, seagrass beds enhance biodiversity. For example, more faunal elements are attracted to seagrass vegetated areas than to bare sand or non-vegetated estuarine seabed plots (Ferrer and Bell, 1991; Lee et al., 2001; Hosack et al., 2006). Despite the many ecosystem services that seagrass beds provide, a growing realization indicates that seagrasses are declining worldwide due to increases in natural and human-induced disturbances (Short and Wyllie-Echeverria, 1996; Duarte, 2002; Orth et al., 2006; Waycott et al., 2009). The link between biodiversity and ecosystem functions in seagrass ecosystems (Duffy, 2006) implies that accelerating the decline of seagrass beds will threaten the sustainability of their ecosystem services (Duarte, 2000). Efforts to maintain, protect, and conserve coastal biodiversity should be especially focused on the conservation and management of seagrasses.

The effect of seagrasses on associated fauna is generally well understood; seagrass beds enhance faunal diversity by providing structural habitat, food, nursery grounds, protection from predators, and a much larger range of available niches than areas devoid of vegetation. Much of the previous works on plant–animal interactions in seagrass beds has focused on epifauna, including fish and epibenthic invertebrates (e.g., Pollard et al., 1984; Jenkins et al., 1997; Gillanders, 2006); however, it is becoming increasingly clear that infaunal assemblages of seagrass beds have important roles in the ecological processes operating in the meadows (e.g., Peterson and Heck, 2001; Johnson et al., 2002; van der Heide et al., 2012; Blackburn and Orth, 2013). Because the emergent structures of seagrass beds are readily observable, the aboveground benthic epifauna has been subjected to more intense investigation (e.g., Bell and Westoby, 1986; Edgar, 1990; Nakaoka et al., 2001) than infaunal assemblages associated with seagrass belowground structures (root–rhizome complex; e.g., Harrison,

1987; Berkenbusch et al., 2007; see also the review by Orth et al., 1984 and references therein). Are infaunal elements as dependent on seagrass structures as epifaunal taxa; do positive and negative interactions belowground depend on diverse interacting factors, including environmental conditions and biological traits of component species (see review by Nakaoka, 2005)? The current knowledge base is insufficient to provide comprehensive answers to these questions. One approach to resolving the issues is a comparative analysis of epifaunal and infaunal diversity structures in seagrass beds. In particular, it is essential to determine the ecological responses of epifauna and infauna in mixed meadows dominated by different seagrass species. Different seagrass species in mixed meadows have diverse above- and belowground structures (Duarte, 1991; Kuo and den Hartog, 2006; Hori et al., 2009). If the responses of associated faunas differ among seagrass species, then seagrass identity within a meadow may directly or indirectly determine the structure of the benthic faunal communities, and may be a good predictor of faunal abundance and biodiversity patterns (see Gillanders, 2006).

We examined effects of the identities of different seagrass species on associated benthic macrofauna through quantitative comparative studies of meadow epifaunas and infaunas. Our premise was that the benthic epifaunal assemblage depends more strongly on seagrass structure than the infaunal assemblage (see Orth et al., 1984 and Nakaoka, 2005 for extensive reviews). Thus, we postulated that interspecific differences in the aboveground structures of seagrass beds will affect the assemblage structure of the benthic epifauna, but not the assemblage structure of the benthic infauna. To test this postulate, we made quantitative comparisons among benthic epifaunas and infaunas in tropical seagrass vegetation types dominated by three different seagrass species: *Cymodocea rotundata* Ehrenb. & Hempr. ex Aschers., *Enhalus acoroides* (L.f.) Royle, and *Thalassia hemprichii* (Ehrenb) Aschers. The study was conducted in the southern Philippines.

2. Material and methods

2.1. Study area

We sampled in the months of September and December 2010 in Lopez Jaena municipality, Misamis Occidental Province (southern Philippines; Fig. 1). This municipality was previously reported to have 526.2 ha of aggregated seagrass meadows (de Guzman et al., 2009). We sampled three sites in these meadows (Mansabay Bajo, Danlujan, and Capayas; Fig. 1). The sites differed by topography. Mansabay was located in a beach area

where the fine sandy sediments were mostly dominated by pioneer seagrasses such as *Halodule* sp. and *C. rotundata*. In contrast, Danlunan had a muddy seagrass area dominated by *E. acoroides* and *T. hemprichii*; this site was located in the vicinity of mangrove stands and an old wharf left standing in an abandoned fishing port. Capayas, a marine protected area near Capayas Island, was located approximately 0.32 km offshore; the water depth ranged from about 20 cm at low tide to about 200 cm at high tide. The substratum comprised coarse sediments and supported at least five seagrass species dominated (in no particular order) by *T. hemprichii*, *C. rotundata*, and *E. acoroides*. Although all of the locations had heterogeneous seagrass beds, we limited our sampling to the three chosen sites due to logistical constraints, including the lack of a nearby laboratory facility, and limited budget and time for sampling.

2.2. Target seagrass species

C. rotundata, *E. acoroides*, and *T. hemprichii* were targeted for this study because they are the most common species in seagrass meadows of Southeast Asia (Menez et al., 1983; Fortes, 1986; Vermaat et al., 1995), and because they were the most abundant in the study area (Rollon et al., 1999; de Guzman et al., 2009). *C. rotundata* has a monopodial rhizome; it is herbaceous and has leaf blades that shed before the leaf-sheaths (den Hartog and Kuo, 2006). The species occurs widely along the coasts of the tropical Indo–West Pacific region, and is considered to be a pioneer seagrass with rapid rhizome elongation rates, low reproductive output, and limited seed dispersal (Olesen et al., 2004). Although *C. rotundata* is relatively small compared to the other two targeted seagrasses, it frequently has the highest shoot density, albeit with reduced biomass. *E. acoroides*, a very coarse plant with a thick rhizome and strap-shaped leaves, is the largest tropical seagrass species; *T. hemprichii*, a medium-sized species, is moderately coarse. *E. acoroides* and *T. hemprichii* are slow-growing, but produce large, widely dispersed seeds that dominate seagrass sexual colonization; they are capable of forming climax communities (Olesen et al., 2004). *E. acoroides* and *T. hemprichii* are widely distributed in the coastal waters of the Indian Ocean and the western Pacific (den Hartog and Kuo, 2006).

2.3. Field sampling

We established duplicate sites for each of three seagrass vegetation types: *C. rotundata*-, *T. hemprichii*-, and *E. acoroides*-dominated types (hereafter referred to as Cr, Th, and Ea vegetation, respectively). We collected

samples from Th and Ea vegetation in the Danlugan and Capayas sites; Cr vegetation was sampled in Capayas and Mansabay. Each of the duplicate sites comprised a multispecific seagrass meadow with an estimated area of $\geq 100 \text{ m}^2$. The parameters of the vegetation types were based on shoot density because core samples sometimes contained more than one seagrass species. In each replicate core, the target seagrass species had a shoot density $>50\%$ greater than those of other seagrass species found in the same core. We used a stainless steel cylindrical sediment sampler (20 cm diameter) to simultaneously collect the benthic epifauna, infauna, and seagrasses down to a depth of 10 cm (0.0314 m^2 surface area for each core sample). Five core samples were obtained from within each seagrass vegetation type in each of the duplicate sites. We sampled without regard to edge effects or the presence of patches; instead, we collected the cores haphazardly in the selected seagrass areas. Core samples were initially sieved in the field using a wooden mesh box (1.0-mm mesh size) and then taken to the laboratory for processing. We also haphazardly collected five additional sediment samples per vegetation unit in each site using a smaller PVC core (0.0026 m^2 surface area) to 10 cm depth and took them to the laboratory to determine the silt–clay content of the surrounding sediment. We sampled twice in the months of September and December 2010.

2.4. Laboratory analyses

All benthic macrofaunal samples were preserved in 75% ethanol. They were sorted to lowest taxonomic level using appropriate literature (Hinton, 1975; Okutani, 2000; Schoppe, 2000) and the World Register of Marine Species online database (WoRMS, <http://www.marinespecies.org>). The density of each taxon was recorded. Epifaunal and infaunal animals were distinguished in the samples based on knowledge of their biology or their predominant mode of life (Lee et al., 2001).

The seagrass samples were cleaned with seawater. They were identified to species, after which shoot density was recorded. The shoots and sheaths were then separated from the roots and rhizomes and dried for ≥ 2 days to constant weight.

Samples for sediment analyses were first air-dried. We collected 100.0 g of dried sediment (free of organic debris) from each replicate core for dry-sieving (Buchanan, 1934) through six sets of sieves (2 mm, 850 μm , 710 μm , 180 μm , 150 μm , 45 μm). Following the Udden–Wentworth scale (Wentworth, 1922), we set the size cutoff for the silt–clay fraction at 45 μm .

2.5. Statistical analysis

All of the statistical analyses were performed with R v.3.0 software (R Core Team, 2013). The variation among seagrass vegetation types was our primary interest; we replicated sampling in different sites in each of 2 months to account for random variation in space and time. Thus, our data set contained one fixed effect (seagrass vegetation types) and two random effects (site, month). In addition, we had a partially crossed sampling design because while the design had three sites levels, collections from all three vegetation types were conducted only at the Capayas site; collections from two vegetation types (Th and Ea) were made at Danlunan, and collections from one vegetation type (Cr) were made at Mansabay. Therefore, the design was asymmetrical.

2.5.1. Univariate analyses

We first tested among-vegetation type variation in seagrass shoot density, aboveground biomass, belowground biomass, and surrounding sediment silt-clay content to clearly determine the structure of the seagrass vegetation sampled. We used generalized linear mixed models (GLMMs) to analyze the seagrass vegetation structure by species. Untransformed core data from the vegetation structures were analyzed [assuming Poisson distribution and penalized quasi-likelihood (PQL) approximation] using the *glmmPQL* function of the *MASS* library (Venables et al., 2002). We used the PQL estimation since it allows overdispersion, and the mean numbers of all measured structures per seagrass vegetation type within site and month groups usually exceeded 5 (Bolker et al., 2008). Model selection is not easily implemented in *glmmPQL* (e.g., AIC and log-likelihood are apparently meaningless in the PQL approximation), but a likelihood-based test can be used for model selection. We performed the likelihood ratio test (LRT) using the *anova* function in the *lmer* (linear mixed-effects model) routine of the *lme4* library (Bates et al., 2013) to find the difference between the null model and the reduced model (full-model) after excluding an 'effect' term. The null-intercept model did not contain the fixed effect (seagrass), but varied among two crossed random effects (random group intercepts), i.e., site and month; the full model included seagrass and intercepts varying among sites and months. When the full model was not significant in the LRT, the null model was chosen as the best selection, although by default, LRT does not compute χ^2 degrees of freedom, or χ^2 or p values for the null model. We did not test the significance of the random effects to avoid the pitfall of pseudoreplication (Hurlbert, 1984). We subsequently

used the Tukey contrasts in the *multcomp* library (Hothorn et al., 2008) for multiple comparisons between the levels of seagrass species (fixed effect) whenever the effect itself was found significant at $\alpha = 0.05$.

After determining the structures of the sampled seagrass vegetation types, we also used the GLMM to examine variation in overall abundance and species richness of both epifaunal and infaunal assemblages using zero-inflation models. We analyzed all core data ($n = 60$) using the *glmmADMB* library (Skaug et al., 2012); this has been built with the open-source *AD Model Builder* (Fournier et al., 2012), which is able to handle zero-inflated data (many of our core data had zero values) and has a negative binomial distribution to allow for overdispersion (Martin et al., 2005). We fitted five candidate models (that were mostly non-nested and suitable for a crossed-factor design) based on multilevel model specifications of the *lme4* library (Bates et al., 2006; Bates, 2010, 2011). In addition, to account for differences in seagrass vegetation structures, log shoot density and aboveground biomass were used as offsets in the linear predictor for epifauna; the log of belowground biomass was used as the offset for infauna. An offset is used to specify as *a priori* known component that is to be included in the linear predictor during fitting (Bolker et al., 2012). That is, for any given vegetation type, the expected abundances or species richnesses of the epifauna or infauna were assumed to be proportional to the structure of seagrass species in that vegetation type. Silt-clay content data were excluded as offsets as they did not show a clear pattern across vegetation types (based on our prior analysis of the seagrass vegetation structures). Other models other than the null model had offset terms. The candidate models were generally built as follows: (i) null model, only the levels were defined, contained only site and month (random group intercepts); (ii) full model 1, with seagrass plus the offset term and intercept varying among sites and months; (iii) full model 2, with seagrass plus the offset and random slope of seagrass within sites and within months with the correlated intercept; (iv) full model 3, with seagrass plus the offset and random slope of seagrass within site and within month, no variation in intercept; and (v) full model 4, with seagrass plus the offset and uncorrelated random intercept and random slope within seagrass and within month. We used the Akaike information criterion (AIC; Akaike, 1973) for model selection; the preferred model had the lowest AIC value, the smallest difference between its AIC value and the maximum AIC (dAIC), and the maximum weight. We used the *AICtab* function in the *bbmle* library (Bolker and R Core Team, 2013) to obtain the dAIC, degrees of freedom (df), and weights.

2.5.2. Multivariate analyses

For graphic visualisation of variation in benthic species composition of epifauna and infauna, we performed nonmetric multidimensional scaling (NMDS) on a matrix of Bray-Curtis distances (Bray and Curtis, 1957) using the *metaMDS* function in *vegan* library (Oksanen et al., 2013). Because zero or empty rows are undefined (meaningless) in method "Bray" and since our core data had many zero-occurrences, we pooled the data for the five replicate cores for each vegetation type, site, and month. The pooled replicate measure was coded by species-site-month, e.g., CrCS: *Cymodocea rotundata*-dominated vegetation at Capayas in September. We analyzed data from 12 sampled locations for epifauna, and 10 sampled locations for infauna (2 missing data points to exclude those replicate cores without any infaunal occurrence). We then performed non-parametric multivariate analysis of variance (PERMANOVA; Anderson, 2001) on same data set and distance measure using the *adonis* function in *vegan*. The PERMANOVA calculated using *adonis* is able to handle an unbalanced sampling design. We consistently used 9999 permutations for NMDS ordination and PERMANOVA.

Finally, to determine the relationships between species compositions of epifauna and infauna and the environmental variables (seagrass vegetation structures), we conducted a direct gradient analysis using canonical correspondence analysis (CCA; Ter Braak, 1986, 1987; Ter Braak and Verdonschot, 1995) using the *cca* function of *vegan* (Oksanen et al., 2013). We separately analyzed data from 12 and 10 sampled locations for epifauna and infauna, respectively. The data for each sampled location were mean values of both the response and explanatory environmental variables. The response variables were mean density ($n = 5$) of each macrofaunal species log-transformed to reduce the skewness in the data set (Ter Braak, 1986). Some of the species had a mean of less than one individual per observation; we added a constant value of 1 to circumvent the impossibility of finding the log of zero [$\log(x + 1)$] (Ter Braak and Verdonschot, 1995; Underwood, 1997). Mean data ($n = 5$) for structures of seagrass vegetation were used as environmental variables and all were log-transformed, except for the percentage data of silt-clay proportions, which were arcsine-transformed (Snedecor and Cochran, 1967). We decided to match every environmental variable to macrofaunal type and we limited the number of macrofaunal species in the plots to obtain a clear interpretation of the results. Thus, we used shoot density, aboveground biomass, and silt-clay content of sediment as environmental variables for epifauna; for infauna, we used belowground biomass instead of aboveground biomass. We also plotted the scores for the top ranking four and three species of epifauna and infauna, respectively. The CCA ordination diagram displayed the species, sampling locations, and classes of environmental variables in coordinate space. The weighted mean (WA)

species and site scores were used for plots of species and sites since WA is unaffected by noisy environmental variables (Ter Braak, 1986). For easy interpretation, we limited our ordinations to two-dimensional plots for convenience in visualization (Ter Braak, 1986). The eigenvalues of the CCA were tested through 9999 permutations to statistically determine whether any set or single dominating environmental variable had significant effects on the faunal assemblage, or alternatively, had none. We focused on testing the significance of eigenvalues in the framework of canonical axes and environmental constraints (variables) to corroborate patterns emerging from the CCA diagram. The variances explained (%) by any constrained axis and the environmental variables were also computed as the proportion of the (the constrained axis) eigenvalue in total eigenvalues multiplied by 100.

3. Results

3.1. *Seagrass habitat structure*

Seagrass density ranged from 4.8 ± 2.8 to 62.0 ± 8.9 shoots/0.0314 m² (Table 1), and was significantly higher in Cr and Th vegetation than in Ea vegetation (GLMM, $\chi^2 = 15.42$, $P < 0.001$; Table 2). Aboveground and belowground biomasses were within the following ranges: 2.4 ± 0.6 – 12.8 ± 3.6 g dw/0.0314 m² and 7.5 ± 4.9 – 64.4 ± 38.1 g dw/0.0314 m², respectively (Table 1). Seagrass biomasses (both above ground and below ground) were higher in Ea vegetation than in Th and Cr vegetation (GLMM, $P < 0.0001$; Table 2). The silt–clay proportion in the surrounding sediment was within the range of 6.4 ± 0.6 – $33.4 \pm 1.3\%$ (Table 1). The GLMM demonstrated that the full model (with seagrass as a fixed effect) was not significant (Table 2).

3.2. *Macrofaunal assemblage structure*

Sixty core samples collected in 2 months yielded 153 individuals, most of which were molluscs and polychaete annelids. The 45 species collected belonged to five invertebrate phyla and 41 families (Table 3). Epifaunal species belonged to 3 phyla and 26 families; infaunal collections fell into 3 phyla but only 15 families. The epifauna (30 species) was more speciose than the infauna (15 species). The average densities of benthic epifauna and infauna were 1.73 ind./0.0314 m² and 0.82 ind./0.0314 m², respectively.

Overall benthic macrofaunal density and species richness did not vary significantly among the three vegetation types (Fig. 2A, B; GLMM in Table 4) even after taking into account the seagrass vegetation structures as offset terms. The species composition structures of epifaunal and infaunal assemblages did not vary consistently across the three seagrass vegetation types (NMDS, Fig. 3A, B). PERMANOVA detected no significant overall effects of vegetation type on either epifauna or infauna, although the effect on epifauna was significant among sites (Table 5).

3.3. Relationships among macrofaunal assemblage structure and environmental variables

3.3.1. Epifauna

The CCA for the epifaunal assemblage explained 41% of the total variation (Table 6). The first canonical axis (horizontal CCA1) was significant ($F = 2.409$, $P = 0.015$) and explained 43% of the captured total constrained variation (Fig. 4A). This axis represented silt–clay content, and decreasing gradients of seagrass shoot densities and aboveground biomass. The second axis in the two-dimensional plot was not significant, but all environmental variables tracked decreasing gradients along its length, with the steepest decreases in silt–clay content. Among the three environmental variables tested, aboveground biomass of seagrass significantly explained 39% of the multivariate variation on epifaunal species composition ($F = 2.200$, $P = 0.010$; Table 6).

Epifaunal assemblage structure was not clearly differentiated among different vegetation types; instead, assemblage structure varied among different sites (Fig. 4A). For example, the locations Capayas and Mansabay Bajo (for Cr vegetation) were widely separated in the coordinate space of the CCA diagram, and so were the coordinate locations of Capayas and Danluga (for Th vegetation).

The relationship between seagrass vegetation type and epifaunal assemblage structure was also ambiguous when focusing only on dominant taxa (Fig. 4A). For example, *Bulla ampulla* was a dominant component of the epifauna in Th vegetation at Danluga, but this was not the case at Capayas, where the dominant component was *Brissus latecarinatus*. Similarly, *Canarium urceus* characterized the assemblages in Cr vegetation at Capayas, but not at Mansabay Bajo. The variation in epifaunal assemblage structure in Ea vegetation was difficult to interpret because all of the components were located near the centroid of the CCA plot.

3.3.2. Infauna

The CCA plot for the infaunal assemblage explained 35% of the constrained variation, and 71% of this proportion was explained by CCA1 (Table 6). The first axis was significant and correlated positively with seagrass belowground biomass and shoot density (Fig. 4B). CCA2 represented an increasing proportion of silt–clay and a decreasing gradient of seagrass belowground biomass and shoot density, but the axis itself was not significant (Table 6). None of the environmental variables significantly influenced infaunal community variation ($P > 0.05$; Table 6). Although infaunal assemblage structure tended to vary along the silt–clay gradient, it was not clearly related to either vegetation type or site. The contributions of the dominant infaunal elements to the observed assemblage pattern were neither consistent nor clear (Fig. 4B). For example, *Golfingia* sp. was located in the coordinate space of the CCA diagram closest to in assemblage in Th vegetation at Capayas, but not at Danlugan.

4. Discussion

Numerous investigations of seagrass–faunal interactions have shown that the presence of seagrass is a strong determinant of faunal diversity. However, effects of differences among seagrass species with different morphological characters on faunal abundance and diversity are much less well understood (Ansari et al., 1991; Nakaoka et al., 2001; Paula et al., 2001; Somerfield et al., 2002). Importantly, we found no significant variation in epifaunal and infaunal assemblage abundance or taxon diversity across different seagrass vegetation types. Nevertheless, our multivariate analyses of relationships between assemblage structures and environmental variables (using CCA) demonstrated that a significant epifaunal variation was best explained by seagrass aboveground biomass, but we were unable to detect an equivalent determinant for infauna. The different responses of epifauna and infauna are in partial agreement with our premise that epifauna would be more dependent on seagrass structure than infaunal elements, which do not necessarily depend on the presence of seagrass belowground biomass as a key habitat component.

The overall species diversity of benthic macrofauna we recorded at Lopez Jaena (45 species; Table 2) was less than half of that reported previously for other areas (e.g., Lewis and Stoner, 1983; Nacorda and Yap, 1997; Webster et al., 1998; Nakaoka et al., 2001; Klumpp and Kwak, 2005). These earlier reports also describe higher macrofaunal densities than at Lopez Jaena, where we found approximately 1–2 individuals per core (0.0314 m²).

When we previously used the same sampling methodology at Bolinao Pangasinan in the northern Philippines, we recorded higher average densities of epifaunal ($12/0.0314 \text{ m}^2$) and infaunal ($22/0.0314 \text{ m}^2$) individuals than at Lopez Jaena (V.E. Leopardas, unpublished data). Currently, we do not have an explanation for the strikingly low abundance in our samples collected at Lopez Jaena. A comprehensive analysis of benthic population dynamics across broader spatial and temporal scales would be a first step to better understanding this issue.

The rather depauperate epifaunal assemblage at Lopez Jaena was nevertheless more speciose and more abundant than the infaunal assemblage. We attribute this difference to the association between epifauna and seagrass shoots, which we believe is closer than the interaction between infauna and belowground roots and rhizomes. Previous studies have also reported that epifaunal assemblages are more speciose than those in the sediments (e.g., Peterson et al., 1984; Bell and Westoby, 1986; Lee et al., 2001; Parker et al. 2001; cf. Stoner, 1980 and Vonk et al., 2010).

Although we found that shoot density and above- and belowground biomass varied greatly among the three dominant seagrass species, we detected no significant effects of these parameters on the abundance and diversity of either epifauna or infauna. This outcome is congruent with our predictions for seagrass–infaunal interactions but not for seagrass–epifaunal associations. A lack of significant seagrass species-specific effects on macrofauna has been previously documented (e.g., Nienhuis et al., 1989; Edgar, 1990; Nakaoka et al., 2001; Brito et al., 2005), although not universally (e.g., Virnstein and Howard, 1987; Hamilton et al., 2012; Somerfield et al., 2012; Gartner et al., 2013). Thus, Nakaoka et al. (2001) detected inconsistent patterns in epifaunal assemblages among *Zostera marina*, *Zostera caulescens*, and *Zostera caespitosa*, and Hamilton et al. (2012) suggested that individual seagrass species cannot act as surrogates for one another in the provision of habitat for epifaunal taxa. Edgar (1990) reported that epifaunal assemblages on different seagrass species subjected to the same environmental conditions are more often similar than epifaunal assemblages associated with the same seagrass species in different sites. Somerfield et al. (2012) demonstrated that the presence of several seagrass species promotes structural complexity of a seagrass meadow, which influences the range of habitats provided for associated benthic epifauna and infauna. Finally, the influence of seagrass species on associated fauna may be nonsignificant because of the very much larger swamping effects of other parameters, such as sediment chemistry (e.g., lack of oxygen; Brito et al., 2005), biological traits of the fauna (e.g., larvae of benthic decapods are unable to discriminate between beds with different structural complexities; Bell and Westoby, 1986), or combinations of several interacting factors (Edgar, 1990; Nakaoka et al., 2001), which were not assessed in this study.

Although variation in seagrass species identity did not have a significant influence on macrofaunal assemblages in this study, we did find that seagrass aboveground biomass explained a proportion of epifaunal variation among the sampled sites. This effect is not unexpected and is congruent with earlier works (e.g., Stoner, 1980; Lewis and Stoner, 1983; Ansari et al., 1991; Attrill et al., 2000; Klumpp and Kwak, 2005). The high degree of association between epifauna and seagrass standing biomass may be attributable to increased food availability, physical protection (Schneider and Mann, 1991; Edgar and Robertson, 1992), or the habitat complexity provided by elevated seagrass biomass; the long life spans of seagrass modular units promote higher population stability among epifaunal elements (Ansari et al., 1991). Attrill et al. (2000) emphasized that increased seagrass biomass does not reflect increased structural complexity, but does provide a larger surface area for occupancy by macroinvertebrates. Nevertheless, contradictory views have been published (e.g., Virnstein and Howard, 1987; Nienhuis et al., 1989). Lee et al. (2001) suggests that detritus accumulation enhances faunal species richness and abundance in seagrass habitats, and that the benefits of aboveground seagrass biomass are expressed indirectly through increased detrital accumulation, which is beneficial for both epifauna and infauna.

Finally, we did not detect a significant effect of belowground seagrass biomass on the associated infauna, a finding that was consistent with our expectations. This outcome is congruent with some previous investigations, but not all. Webster et al. (1998) found that root–rhizome measures are unimportant for infaunal assemblages, but Lee et al. (2001) and Paula et al. (2001) reported that the dense root–rhizome mat of seagrass beds provides protection from predators. Dense seagrass roots may also inhibit burrowing and tube-building activities, thereby exposing infauna to digging predators (e.g., Skilleter, 1994). However, the extent of the effects of seagrass belowground complexity on infauna depends on the behaviors of individual species. For example, juvenile infaunal elements are more susceptible to predators than adults, which are able to burrow deeper to escape digging carnivores (see review by Orth et al., 1984). Stoner (1980) demonstrated that increased belowground seagrass biomass decreases the abundance of deposit-feeding and omnivorous polychaetes, but enhances the abundances of suspension-feeding and carnivorous polychaetes. Increased total seagrass plant biomass reportedly increases the abundance of polychaetes and bivalves (Ogden and Ogden, 1982), although this work did not specifically report effects of the belowground vegetation.

5. Conclusion

We demonstrated that taxonomic identity of seagrass species is not a major determinant of variation in the abundance and taxon diversity of benthic macrofaunal assemblages at our study site in the southern Philippines. Nevertheless, we found that aboveground seagrass biomass did significantly influence variation in epifaunal assemblage structures. Thus, within multispecific meadows, seagrass species redundancy may exist according to the perceptions of macrobenthic invertebrates, even though morphological structures differ strikingly among seagrass taxa. Moreover, Hughes et al. (2009) demonstrated interdependence and facilitation among seagrass species. The effect of the global decline in seagrass biodiversity on the associated fauna has recently received detailed attention (e.g., Duarte, 2000; Duffy, 2006; Waycott et al., 2009), which has emphasized the importance of conserving seagrass ecosystems wherever possible (see also Hughes et al., 2009). Our study has significant implications for planning the conservation and management of biodiversity in seagrass meadows, which are rapidly declining in extent worldwide (Short and Wyllie-Echeverria, 1996; Duarte, 2002; Orth et al., 2006; Waycott et al., 2009).

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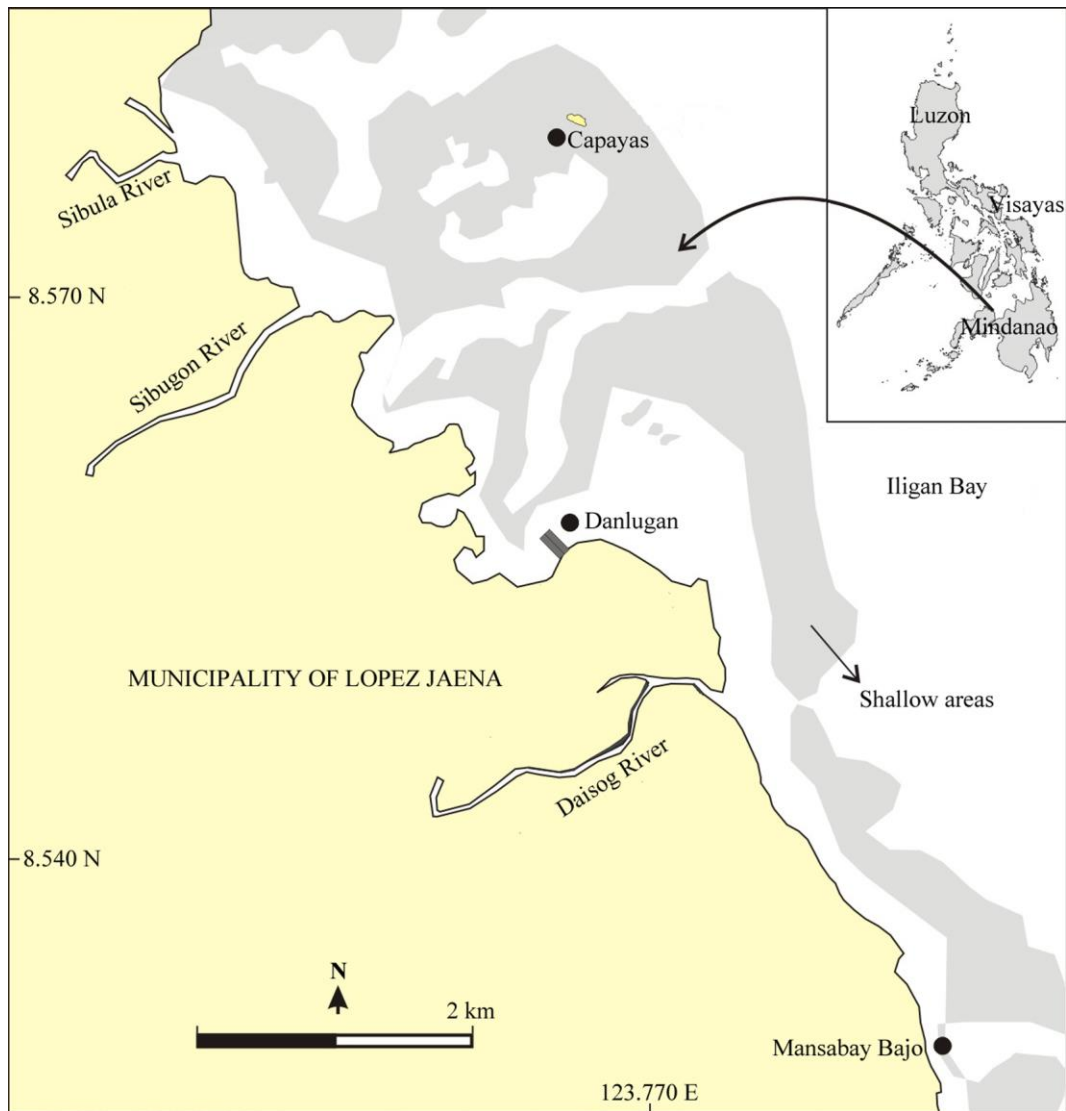


Fig. 1. Map of the study sites at Lopez Jaena, Misamis Occidental Province, southern Philippines. de Guzman et al. (2009) provided the base map.

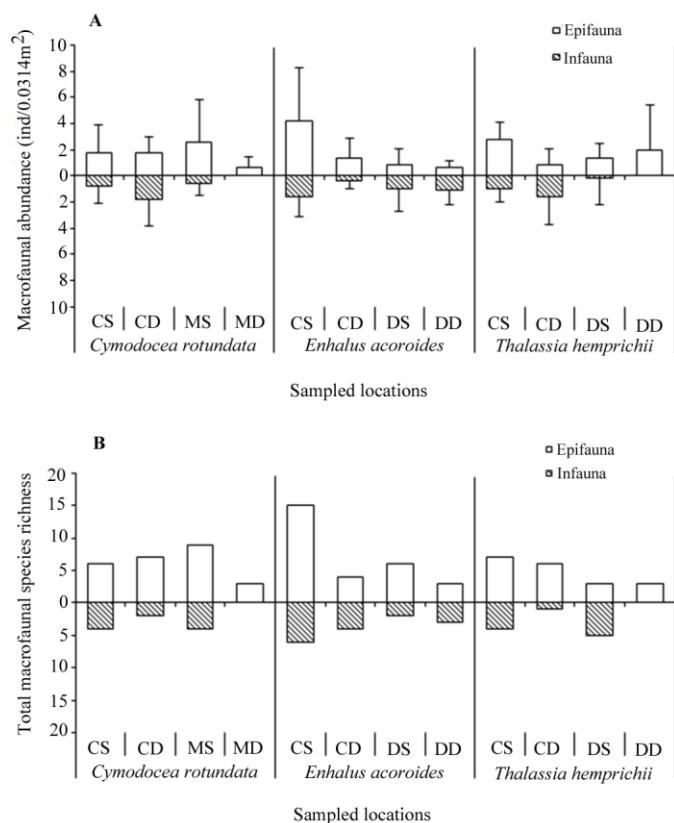


Fig. 2. (A) Mean benthic macrofaunal density (\pm SD, $n = 5$) and (B) total species richness of benthic macrofauna ($n = 5$) recorded in three seagrass vegetation types (dominated by *Cymodocea rotundata*, *Enhalus acoroides*, and *Thalassia hemprichii*) located in Capayas (C), Danlujan (D), and Mansabay (M) within the Lopez Jaena municipality, Misamis Occidental Province, southern Philippines; collections were made in September (S) and December (D) 2010. Abbreviations are configured as follows: CD, Capayas collection in December.

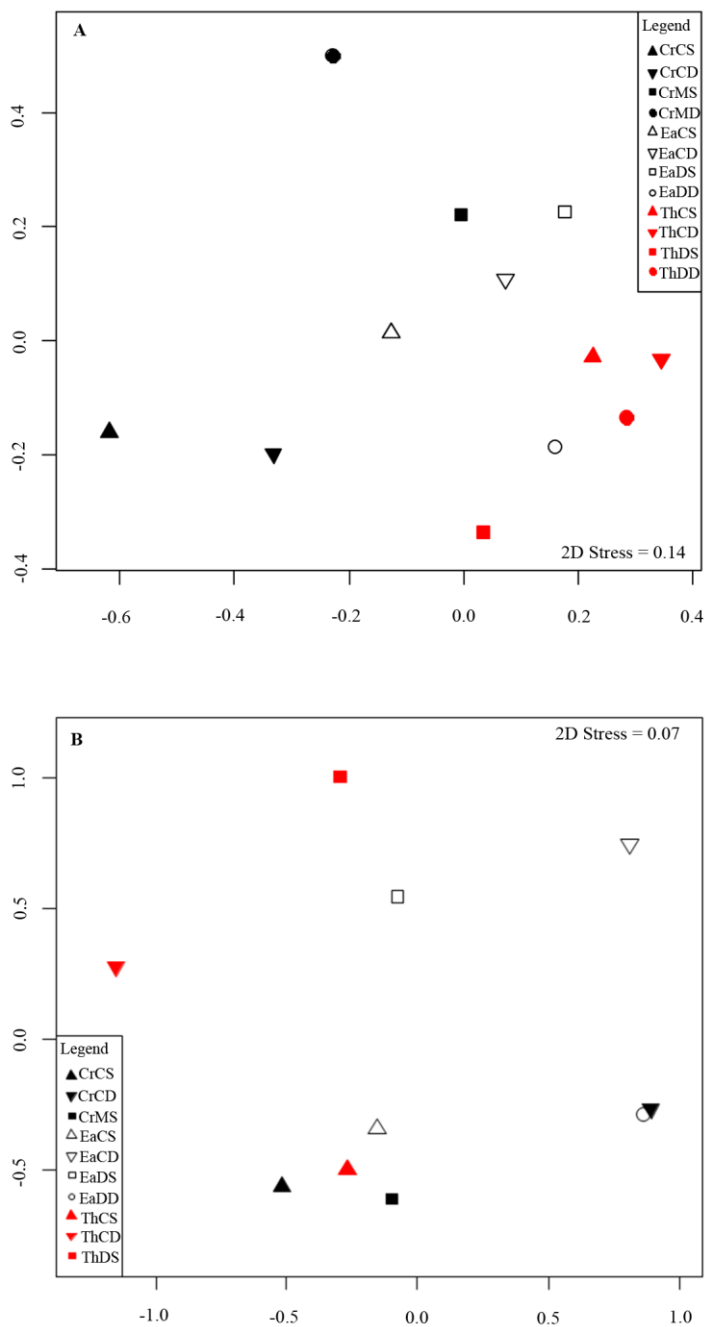


Fig. 3. Nonparametric multidimensional scaling (NMDS) plot based on a matrix of Bray–Curtis distance measures for (A) epifauna and (B) infauna based on total density ($n = 5$) in three vegetation types (Cr: *Cymodocea rotundata*, Ea: *Enhalus acoroides*, Th: *Thalassia hemprichii*) sampled at Capayas (C), Danlujan (D), and Mansabay (M) in Lopez Jaena, Misamis Occidental, southern Philippines, during September (S) and December (D) 2010. Sample code abbreviations are configured as follows: CrCS, *Cymodocea rotundata*-dominated vegetation at Capayas in September.

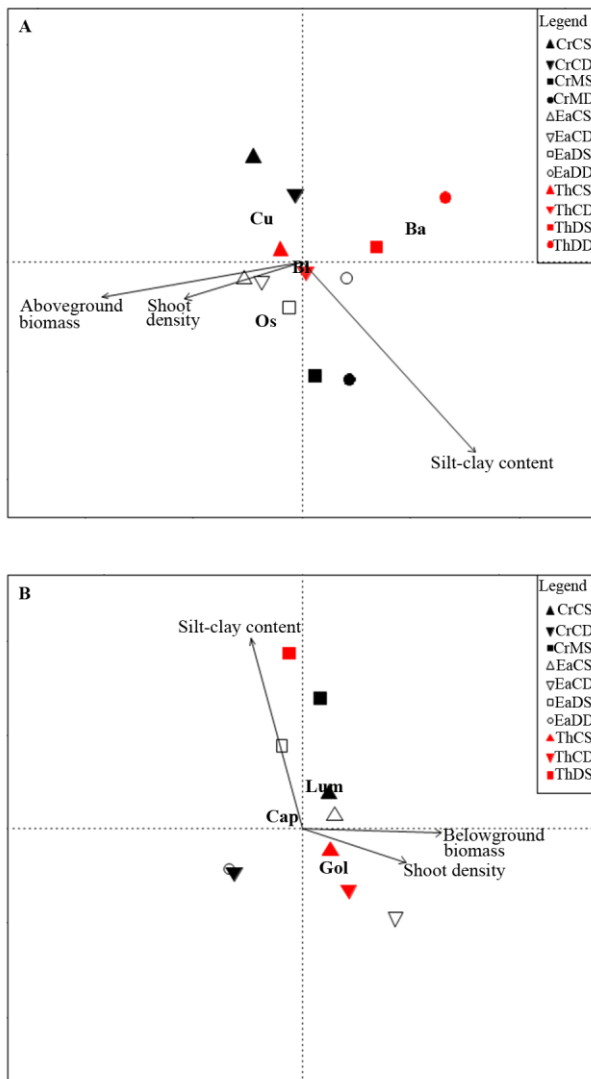


Fig. 4. Canonical correspondence analysis (CCA) ordination plots based on mean densities of each (A) epifaunal and (B) infaunal species in three vegetation types (Cr: *Cymodocea rotundata*, Ea: *Enhalus acoroides*, Th: *Thalassia hemprichii*) sampled in Capayas (C), Danlunan (D), and Mansabay (M) within Lopez Jaena municipality, Misamis Occidental Province, southern Philippines, during September (S) and December (D) 2010. CCA1, horizontal axis; CCA2, vertical axis. Environmental variables for epifauna were seagrass shoot density, aboveground seagrass biomass, and proportion of silt–clay; for infauna, they were seagrass shoot density, belowground seagrass biomass, and proportion of silt–clay. Plotted species are the four and three most abundant elements in the epifauna (Cu: *Canarium urceus*, Ba: *Bulla ampulla*, Bl: *Brissus latecarinatus*, Os: *Ophiactis savignyi*), and infauna (Lum: *Lumbrineris* sp., Cap: *Capitella* sp., Gol: *Golfingia* sp.), respectively. Other species are not included for graphical clarity. Sample code abbreviations are configured as follows: CrCS: *Cymodocea rotundata*-dominated vegetation at Capayas in September.

Table 1

Means and standard deviations (n=5) for seagrass vegetation structures measured in Lopez Jaena, Misamis Occidental, southern Philippines during September (S) and December (D) 2010 sample collection. nd = no data.

| | | <i>Cymodocea rotundata</i> | | <i>Enhalus acoroides</i> | | <i>Thalassia hemprichii</i> | |
|---|----------|----------------------------|-----------|--------------------------|-----------|-----------------------------|-----------|
| | | S | D | S | D | S | D |
| Shoot density (shoots/0.0314m ²) | Capayas | 62.0±8.9 | 31.6±10.8 | 19.4±7.8 | 31.2±11.9 | 36.6±14.3 | 46.2±20.7 |
| | Danlunan | nd | nd | 10.0±2.9 | 4.8±2.8 | 17.6±4.8 | 10.6±3.4 |
| | Mansabay | 53.2±9.1 | 59.4±18.1 | nd | nd | nd | nd |
| Aboveground biomass (g dw/0.0314m ²) | Capayas | 6.1±2.6 | 3.7±1.6 | 12.8±3.6 | 10.7±2.0 | 6.7±2.1 | 6.2±2.5 |
| | Danlunan | nd | nd | 11.3±6.3 | 6.3±3.5 | 6.8±2.1 | 3.3±1.5 |
| | Mansabay | 4.4±2.6 | 2.4±0.6 | nd | nd | nd | nd |
| Belowground biomass (g dw/0.0314m ²) | Capayas | 18.8±12.0 | 11.9±9.8 | 40.1±10.7 | 64.6±38.1 | 28.7±6.5 | 28.0±15.6 |
| | Danlunan | nd | nd | 30.4±14.9 | 23.0±27.4 | 15.5±8.0 | 8.9±3.7 |
| | Mansabay | 17.0±8.4 | 7.5±4.9 | nd | nd | nd | nd |
| Sediment silt-clay content (%/0.0314m ²) | Capayas | 6.4±0.6 | 7.6±1.2 | 6.8±0.6 | 7.2±0.9 | 7.0±0.9 | 7.2±0.8 |
| | Danlunan | nd | nd | 18.9±1.1 | 17.1±2.4 | 18.8±1.0 | 18.6±1.0 |
| | Mansabay | 32.9±1.3 | 33.4±1.3 | nd | nd | nd | nd |

Table 2

Summary results of Generalized Linear Mixed Models (GLMMs) via Penalized Quasi-Likelihood (PQL) estimation for testing variation in seagrass vegetation structures among three vegetation types (Cr: *Cymodocea rotundata*, Th: *Thalassia hemprichii*, Ea: *Enhalus acoroides*), wherein seagrass is set as fixed effect, and site and month as crossed random effects under Poisson distribution. The AIC, Chi-square df, χ^2 , and P values were obtained from testing the deviance using likelihood-ratio test to select the better model between null (reduced) and full model.

| Response variable | AIC | χ^2 df | χ^2 | P(> χ^2) | Post-hoc ^a |
|----------------------------|--------|-------------|----------|----------------|------------------------|
| Shoot density | 498.37 | 2.0 | 15.42 | < 0.001 | <u>Cr</u> <u>Th</u> Ea |
| Aboveground biomass | 313.14 | 2.0 | 34.09 | < 0.001 | Ea <u>Th</u> <u>Cr</u> |
| Belowground biomass | 523.07 | 2.0 | 22.85 | < 0.001 | Ea <u>Th</u> <u>Cr</u> |
| Sediment silt-clay content | 224.87 | 2.0 | 0.44 | 0.801 | |

^a Vegetation types are arranged from highest to lowest. Non-significant pair is connected by an underline.

Table 3

Taxonomic list of benthic macrofauna found and identified in Lopez Jaena, Misamis Occidental, southern Philippines during the September and December 2010 sampling.

| EPIFAUNA | | INFAUNA | |
|----------------------|--------------------------------|------------------|-------------------------------|
| Phylum/Family | Binomial name or species code | Phylum/Family | Binomial name or species code |
| Arthropoda | | Annelida | |
| Alpheidae | <i>Alpheus</i> sp. | Capitellidae | <i>Capitella</i> sp. |
| Calappidae | Unknown box crab | Eunicidae | <i>Eunice</i> sp. |
| Callianassidae | Unknown ghost shrimp | Glyceridae | <i>Glycera alba</i> |
| Corystidae | <i>Corystes</i> sp. | Hesionidae | Unknown hesionid |
| Epialtidae | <i>Menaethius</i> sp. 1 | Lumbrineridae | <i>Lumbrineris</i> sp. |
| | <i>Menaethius</i> sp. 2 | Nereididae | <i>Nereis</i> sp. |
| Paguridae | Unknown hermit crab | Orbiniidae | Unknown orbiniid |
| Penaedae | Unknown shrimp | Sphaerodoridae | Unknown sphaerodorid |
| Pilumnidae | <i>Pilumnus</i> sp. | Terebellidae | <i>Terebella</i> sp. |
| Portunidae | Unknown crab | Mollusca | |
| Echinodermata | | Arcidae | <i>Anadara antiquata</i> |
| Archasteridae | <i>Archaster typicus</i> | Lucinidae | <i>Codakia tigrina</i> |
| Brissidae | <i>Brissus latecarinatus</i> | Pinnidae | <i>Pinna</i> sp. |
| Holothuriidae | <i>Holothuria</i> sp. | Veneridae | <i>Gafrarium dispar</i> |
| | <i>Holothuria scabra</i> | Sipuncula | |
| Ophiactidae | <i>Ophiactis savignyi</i> | Golfingiidae | <i>Golfingia</i> sp. |
| Oreasteridae | <i>Protoreaster nodosus</i> | Sipunculidae | <i>Sipunculus nudus</i> |
| Mollusca | | | |
| Angariidae | <i>Angaria delphinus</i> | | |
| Buccinidae | <i>Polia</i> sp. | | |
| Bullidae | <i>Bulla ampulla</i> | | |
| Cerithiidae | <i>Cerithium atratum</i> | | |
| Columbellidae | <i>Euplica scripta</i> | | |
| Conidae | <i>Conus eburneus</i> | | |
| Cypraeidae | <i>Monetaria annulus</i> | | |
| | <i>Monetaria moneta</i> | | |
| Mitridae | <i>Mitra luctuosa</i> | | |
| Nassariidae | <i>Nassarius limnaeiformis</i> | | |
| Family 1 | Unknown nudibranch | | |
| Strombidae | <i>Canarium</i> sp. | | |
| | <i>Canarium urceus</i> | | |
| Turridae | <i>Turris crispa</i> | | |

Table 4

AIC, difference in AIC ($AIC_i - AIC_{min}$), df and Akaike weight values of each candidate model as summary results of zero-inflated Generalized Linear Mixed Models (GLMMs) using negative binomial distribution for macrofaunal abundance and species richness accounting the effect of seagrass vegetation structures.

| Response variable | Model | AIC | dAIC | df | weight |
|----------------------------|--------------|--------------|------|------|--------|
| Epifaunal abundance | Null-model | 234.7 | 0.0 | 4.0 | 0.996 |
| | Full-model 1 | 246.0 | 11.3 | 6.0 | 0.004 |
| | Full-model 2 | 251.6 | 16.9 | 10.0 | <0.001 |
| | Full-model 3 | 251.6 | 16.9 | 10.0 | <0.001 |
| | Full-model 4 | 255.6 | 20.9 | 12.0 | <0.001 |
| Epifaunal species richness | Null-model | 187.7 | 0.0 | 4.0 | 0.861 |
| | Full-model 1 | 191.4 | 3.7 | 6.0 | 0.133 |
| | Full-model 2 | 199.1 | 11.4 | 10.0 | 0.003 |
| | Full-model 3 | 199.1 | 11.4 | 10.0 | 0.003 |
| Infaunal abundance | Null-model | 156.6 | 0.0 | 4.0 | 0.851 |
| | Full-model 1 | 160.3 | 3.8 | 6.0 | 0.129 |
| | Full-model 2 | 167.0 | 8.3 | 10.0 | 0.014 |
| | Full-model 3 | 164.8 | 10.4 | 10.0 | 0.005 |
| | Full-model 4 | 168.8 | 12.3 | 12.0 | 0.002 |
| Infaunal species richness | Null-model | 134.1 | 0.0 | 4.0 | 0.547 |
| | Full-model 1 | 134.6 | 0.5 | 6.0 | 0.423 |
| | Full-model 2 | 142.2 | 6.8 | 10.0 | 0.019 |
| | Full-model 3 | 140.9 | 8.1 | 10.0 | 0.010 |
| | Full-model 4 | 144.9 | 10.8 | 12.0 | 0.003 |

Table 5

Results of permutational multivariate analysis of variance (PERMANOVA) using Bray-Curtis distance matrix for multivariate species composition of benthic macrofaunal assemblage based on 9999 permutations.

| Response variable | Source | df | SS | MS | F | R ² | P(>F) |
|---------------------|-----------|----|-------|-------|-------|----------------|--------------|
| Epifaunal abundance | Seagrass | 2 | 0.581 | 0.291 | 1.528 | 0.200 | 0.062 |
| | Site | 2 | 0.906 | 0.453 | 2.382 | 0.311 | 0.001 |
| | Month | 1 | 0.282 | 0.282 | 1.482 | 0.097 | 0.111 |
| | Residuals | 6 | 1.141 | 0.190 | | 0.392 | |
| | Total | 11 | 2.910 | | | 1.000 | |
| Infaunal abundance | Seagrass | 2 | 0.634 | 0.317 | 0.950 | 0.192 | 0.524 |
| | Site | 2 | 0.842 | 0.421 | 1.262 | 0.255 | 0.247 |
| | Month | 1 | 0.497 | 0.497 | 1.489 | 0.150 | 0.183 |
| | Residuals | 4 | 1.334 | 0.333 | | 0.404 | |
| | Total | 9 | 3.306 | | | 1.000 | |

Table 6

Summary results of the Canonical Correspondence Analysis (CCA) in assessing the importance of seagrass vegetation structures to benthic epifauna- and infaunal assemblages. Response variables are average values of epifauna and infaunal abundance for each vegetation types, sites, and months (log x+1 transformed), while environmental variables include average values of shoot density, aboveground biomass, belowground biomass (all log-transformed), and surrounding sediment silt-clay content (arcsin-transformed).

| CCA measures | Epifauna | | | | Infauna | | | |
|-----------------------|-------------|--------------|-------|--------------|-------------|--------------|-------|--------------|
| | Eigenvalues | Variance (%) | F | P(>F) | Eigenvalues | Variance (%) | F | P(>F) |
| <i>General</i> | | | | | | | | |
| Total | 2.90 | 100.00 | | | 2.97 | 100.00 | | |
| Constrained | 1.20 | 41.37 | | | 1.02 | 34.51 | | |
| Unconstrained | 1.70 | 58.63 | | | 1.94 | 65.49 | | |
| <i>Canonical axes</i> | | | | | | | | |
| CCA1 | 0.51 | 42.68 | 2.409 | 0.015 | 0.73 | 71.27 | 2.254 | 0.030 |
| CCA2 | 0.35 | 29.43 | 1.661 | 0.130 | 0.18 | 17.12 | 0.541 | 0.750 |
| CCA3 | 0.33 | 27.89 | 1.575 | 0.190 | 0.12 | 11.61 | 0.367 | 0.920 |
| Residual | 1.70 | | | | 1.94 | | | |
| <i>Constraints</i> | | | | | | | | |
| Shoot density | 0.37 | 31.07 | 1.754 | 0.110 | 0.29 | 28.07 | 0.884 | 0.640 |
| Above-ground biomass | 0.47 | 38.98 | 2.200 | 0.010 | nd | | | |
| Below-ground biomass | nd | | | | 0.55 | 54.28 | 1.709 | 0.140 |
| Silt-clay | 0.36 | 29.95 | 1.691 | 0.130 | 0.18 | 18.04 | 0.570 | 0.850 |
| Residual | 1.20 | | | | 1.94 | | | |