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An ecological survey of the abundance and diversity of benthic macrofauna in Indonesian multispecific seagrass beds

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Abstract

Seagrasses are one of the most productive ecosystems in coastal areas and support a wide variety of associated fauna. The tropical Indo-Pacific region is considered to have the highest diversity of seagrass plant species and the largest distribution areas of seagrass, yet the seagrass macrofauna in this region are poorly understood. To help fill this gap in our knowledge, an ecological survey was conducted to describe the abundance and diversity of benthic macrofauna from tropical seagrass beds and to determine between-station variations within a transect and between-site variations in macrofaunal abundance, taxa richness and community structure. Benthic macrofaunal samples associated with seagrass beds were collected with a core sampler on the east coast of North Sulawesi in May 2014 and on the west coast in October 2015. A total of 149 species from 14 higher taxa was collected. The most species-rich groups were polychaetes (56 species, 26% of total individual numbers), decapods (20 species, 9% of total numbers) and amphipods (18 species, 35% of total numbers). Between-station variations within a transect displayed different patterns between the east coast and the west coast. On the east coast, there were marked variations in abundance between stations within a transect for the macrofauna and amphipod assemblages. Both taxa richness and abundance varied with station for the macrofauna and polychaete assemblages on the west coast, resulting from the heterogeneity of the substrate along a transect. One-way ANOSIM together with MDS ordination indicated that macrofaunal community structure in seagrasses differed significantly between the east coast and the west coast, corresponding with the division of seagrasses into two broad categories of habitats, i.e., mangrove-seagrass-reef continuum and seagrass-reef continuum. Compared with other studies in tropical areas, the abundance and diversity of benthic macrofauna in the present study were moderate. The reason for the two markedly distinct macrofaunal communities might be attributed to multiple factors, including sediment pattern, seagrass structure and temporal changes.

Key words: benthic macrofauna, diversity, abundance, community structure, seagrass bed, North Sulawesi

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1 Introduction

Seagrasses are marine flowering plants that are commonly found in shallow coastal waters around the world (Green and Short, 2003). Unlike mangroves and coral reefs with distribution restricted to tropical regions, seagrasses can extend their distribution from tropical regions to temperate regions, except Antarctica (den Hartog, 1970). Seagrasses exhibit low taxonomic diversity with only approximately 60 species worldwide (Saenger et al., 2013), and the highest diversity of seagrass plant species is centered in the tropical Indo-Pacific (Waycott et al., 2004). Despite their limited diversity, seagrasses are one of the most productive ecosystems (Duarte and Chiscano, 1999; Short et al., 2007) and have enormous ecological and economic values, including organic carbon export to adjacent ecosystems, food provision, habitat for associated fauna, sediment stabilization, shoreline protection, etc. (Fonseca, 1989; Eyre and Ferguson, 2002; Orth et al., 2006; Heck et al., 2008). Despite their importance, the scientific community now realizes that seagrasses are declining globally at an unprecedented rate, especially in the Indo-Pacific, due to increases in natural and anthropogenic disturbances (Orth et al., 2006; Waycott et al., 2009).

Seagrasses enhance biodiversity (Leopardas et al., 2014). A wide variety of benthic macrofauna are attracted to seagrass vegetated areas, including epifauna on the leaves of the seagrass and infauna in the surface sediments (Williams and Heck, 2001; Tanner, 2005; Klumpp and Kwak, 2005). Among all macrofaunal assemblages, polychaete worms, molluscs and crustaceans (mainly amphipods and decapods) are the dominant fauna, and echinoderms, sipunculids, and nemerteans are common (Adulyanukosol and Poovachiranon, 2006). Benthic macrofauna play an important ecological role in a detritus-based food web of seagrass, forming a trophic linkage between primary producers and higher trophic-level predators (Klumpp et al., 1989; Orth et al., 1984). They also affect the physical structure of seagrass habitats and growth of seagrass species through burrowing activity (Orth et al., 1984; Valentine et al., 1994). Analysis of benthic mac-

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rofauna is very important to facilitate future monitoring studies of seagrass beds, because the loss and deterioration of seagrasses will eventually lead to the alteration of macrofaunal communities. Quite a few studies have been conducted on the abundance, diversity and seasonality of seagrass macrofauna and the impact of seagrass structure (Orth et al., 1984; Mukai et al., 1999; Somerfield et al., 2002; Klumpp and Kwak, 2005), but most of the studies were focused on temperate seagrass beds instead of tropical (Klumpp and Kwak, 2005).

The coastal areas in North Sulawesi, Indonesia, are characterized by large seagrass beds, often constituted by multiple species. Little is known about seagrasses throughout the area, even the basic information, such as species composition of seagrass plants and the extent of seagrass beds. The seagrass beds here can be divided into the following two broad categories of habitats: seagrass+reef continuum on the east coast and mangrove+ seagrass+reef continuum on the west coast. Seagrass beds in the former habitat are located between the coastline and submerged reefs, while those in the latter are situated between mangroves and fringing reefs. The present study represents the first attempt to describe seagrass macrofauna in this area, also serves as part of a wider joint study aimed at understanding marine biodiversity and the environment in Indonesian tropical areas. The aims of this study were (1) to describe the diversity of seagrass macrofauna, (2) to determine whether the taxa richness and abundance of seagrass macrofauna vary with station within a transect and (3) to compare benthic macrofaunal communities between the two categories of seagrass beds.

2 Materials and methods

2.1 *Study area*

The survey area was located in North Sulawesi (Fig. 1) and supports diverse coastal ecosystems, including mangroves, coral reefs and seagrasses. The tidal range in this region was approximately 1.5 m based on personal observation. Fieldwork on seagrasses was carried out at Site 2 (on the east coast of North Sulawesi) in May 2014 and at Site 1 (on the west coast) in October 2015. We sampled two transects (SGT1 and SGT3) on the east coast, with an inshore station and an offshore station along one transect (an extra station was located between the inshore station and offshore station at the SGT3 transect). Fine sand dominated the seagrass bed. There were eight seagrass species, dominated by *Thalassia hemprichii*, *Halodule pinifolia* and *Cymodocea rotundata*. In the seagrass bed along the west coast, we established three transects with two sampling stations within each transect. Inshore stations were located near the edge of the mangroves while offshore stations were approximately 20 m from the edge of the reef. The substrate here is heterogeneous. Inshore stations are influenced by mangrove detritus while small coral rubble is scattered around seagrass beds at offshore stations. Seagrass beds along the west coast consisted of six species, dominated by *Syringodium isoetifolium* and *Thalassia hemprichii*.

2.2 *Collection and measurement of benthic macrofauna*

All field sampling was conducted at low tide. Four or five replicate core samples of sediment were collected randomly within a chosen 10 m×10 m quadrat at each station, using a PVC core sampler with an inner diameter of 10 cm (78.54 cm^2 surface area for each core sample). The core sampler was pushed into the sediment to a depth of 30 cm. Next, the sediment samples were sieved through 0.5 mm mesh screen in the field, and specimens retained on the sieve were preserved in 7% diluted seawater formalin for further analysis. In the laboratory, living organisms were extracted under a microscope, identified to the lowest possible taxon and counted. In the present study, macrofaunal abundance was reported as the number of individuals per square meter, and taxa richness was expressed as the number of species occurring in one core sample.

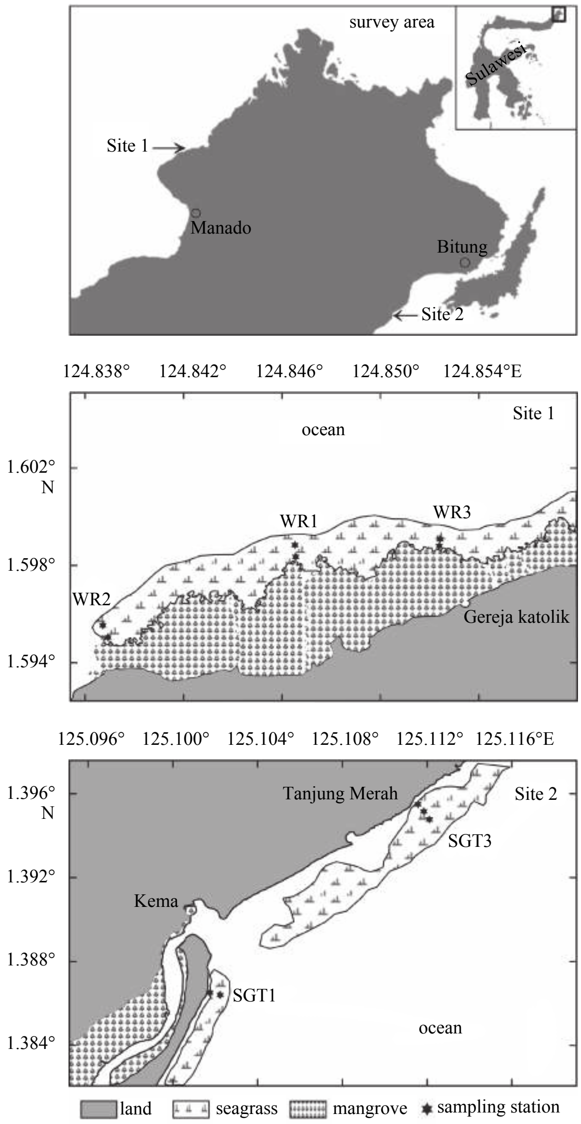

Fig. 1. Map of the sampling stations on the east and west coasts of North Sulawesi, Indonesia.

2.3 *Statistical analyses*

To characterize the functional composition of the fauna, each macrofaunal species was assigned to a microhabitat category and feeding guild using information from the literatures. Habitat categories (Rainer and Fitzhardinge, 1981; Klumpp and Kwak, 2005) were as follows: (1) infaunal tubicolous, (2) infaunal burrower, (3) infaunal commensal, (4) epifaunal domicolous and (5) epifaunal free-living. All fauna were divided into five feeding guilds (Boaventura et al., 1999), i.e., (1) carnivorous group, (2) omnivorous group, (3) detritivorous group, (4) phytophagous group and (5) planktophagous group.

To test between-station variations within a transect in the abundance and taxa richness of the macrofauna and major groups, nested ANOVA was applied. The analysis was also carried out to detect the difference in abundance and taxa richness of macrofauna between the two sampling sites. Prior to the ANOVA, data were $\log_{10}(X+1)$-transformed if they did not meet the assumptions of normality and homogeneity required for the ANOVA test.

The community structure of seagrass macrofauna was analyzed by means of PRIMER 6.0 software, using cluster analysis and non-metric multidimensional scaling (MDS). The cluster analysis was based on the Bray-Curtis similarity index (Bray and Curtis, 1957) and used the group average method. The similarity matrix was based on square-root transformed abundance. The ANOSIM routine (Clarke and Warwick, 1994) based on average abundances was used to analyze the between-site variation. Macrofaunal species responsible for the observed patterns were identified by means of the SIMPER routine (Clarke and Warwick, 1994).

3 Results

3.1 *Macrofaunal diversity*

In total, 824 specimens of benthic macrofauna representing 149 species were collected from the seagrass beds of North Sulawesi (Table 1). Of these, 14 higher taxa were identified as follows: Polychaeta, Bivalvia, Gastropoda, Tanaidacea, Amphipoda, Decapoda, Ophiuroidea, Echinoidea, Holothuroidea, Porifera, Cnidaria, Nemertinea, Sipuncula and Chordata. The major macrofaunal groups ranked by species numbers were polychaetes (38%), decapods (13%) and amphipods (12%); however, ranking by the number of individuals, the order was amphipods (35%), polychaetes (26%) and tanaids (17%).

Polychaetes showed the highest species diversity in the survey area, represented by 56 species, of which the most abundant species in decreasing order were *Ceratonereis mirabilis*, *Linopherus* cf. *hirsute* and *Dasybranchus caducus*. Decapods (20 species) were the next richest group, and the most abundant species were *Callianassa* sp. and *Eualus* sp. Amphipods were the most abundant group with 18 species, among which the most abundant were *Ampelisca miharaensis*, *Melita longidactyla*, *Grandidierella* sp.1 and *Photis hawaiensis*. Although only two species of tanaids were recorded, the paratanaid species *Chondrochelia dubia* was found in great number.

In the case of microhabitat type, 43 species (29%) of benthic macrofauna were categorized as epifaunal free-living, 50 species (34%) as epifaunal domicolous and 42 species (28%) as infaunal burrower. Polychaetes consisted of 54% epifaunal domicolous and 29% infaunal burrower. Eighty-five percent of decapods were categorized as epifaunal free-living, and most amphipods were composed of 50% epifaunal domicolous and 28% infaunal burrower. For feeding guild, 55 species (36.9%) had a diet of invertebrates, 42 species (28.2%) were detritivorous, 19 species (12.8%) were planktivorous, 19 species (12.8%) were omnivorous, and 14 species were found to be phytophagous. Hence, most of the benthic macrofaunal species feed on invertebrates and organic debris on the sediment. For the major groups occurring in the seagrass, most polychaetes were composed of carnivores and detritivores, amphipod species mainly fed on plankton, and decapod species were mainly classified as either carnivore or omnivore.

3.2 *Abundance and taxa richness of macrofauna*

In the seagrass bed along the west coast of North Sulawesi, the taxa richness of benthic macrofauna varied with sampling station (nested ANOVA, F=10.805, P<0.001), which tended to be higher at offshore stations than at inshore stations along each transect (Fig. 2, Table 2). There was also significant variation between transects (nested ANOVA, F=5.068, P=0.018). Further analysis of the major groups revealed that the taxa richness of the polychaete assemblage differed significantly between stations within a transect (nested ANOVA, F=7.269, P=0.002). Variation in macrofaunal abundance was statistically significant between stations within a transect (nested ANOVA, F=3.401, P=0.04), with abundance usually higher at offshore stations except at the WR1 transect. However, macrofaunal abundance did not differ between transects. Further analysis of the major groups showed that there were marked variations in polychaete abundance between stations within a transect (nested ANOVA, F=5.646, P=0.007) and in amphipod abundance between transects (nested ANOVA, F=3.768, P=0.043).

Compared with the seagrass bed on the west coast, benthic macrofauna displayed a different distribution pattern in the seagrass bed along the east coast. There was no marked difference in the taxa richness of macrofauna between transects and between stations within a transect. However, the taxa richness of the amphipod assemblage differed significantly between transects (nested ANOVA, F=12.398, P=0.003). The nested ANOVA revealed that macrofaunal abundance varied with transect (nested ANOVA, F=8.345, P=0.01) and station (nested ANOVA, F=3.776, P=0.03). Higher macrofaunal abundance occurred at the inshore station than at the offshore station at the SGT1 transect, although this trend was opposite at the SGT3 transect, where abundance was higher at the offshore station. Further analysis of the major groups indicated that there were significant differences in amphipod abundance between transects and between stations within a transect, but not in polychaete abundance (Table 2).

Comparison of the taxa richness and abundance of benthic macrofauna between the two study sites is shown in Fig. 3. The taxa richness of benthic macrofauna in seagrass beds was from (8.1±3.9) to (9.5±4.8) species/core on the east coast while (5.9±3.0) to (12.3±7.6) species/core on the west coast. Macrofaunal abundance ranged between (1 602±784) ind./m^2 and (2 725±1 357) ind./m^2 on the east coast and between (2 228±2 136) ind./m^2 and (2 722±1 603) ind./m^2 on the west coast. The nested ANOVA revealed that neither taxa richness (nested ANOVA, F=0.002, P=0.961) nor macrofaunal abundance (nested ANOVA, F=0.362, P=0.551) differed significantly between the two study sites.

3.3 *Macrofaunal community structure*

Superimposed Bray-Curtis clusters on the MDS ordination (Fig. 4) showed that all the sampling stations can be divided into two groups at a similarity level of 20%, in agreement with the division of the two broad categories of seagrass habitats, i.e., one habitat on the east coast and the other on the west coast. ANOSIM confirmed the differences in community structure between the two habitats to be significant (global R=0.944, P=0.002). The SIMPER analysis showed the highest dissimilarity (>2% dissimilarity contribution) to be as result of *Ampelisca miharaensis*, *Chondrochelia dubia*, *Melita longidactyla*, *Ampelisca bocki*, *Photis hawaiensis*, *Paraphoxus tomiokaensis* and *Grandidierella* sp.1. These species were from the amphipod and tanaid assemblages. Furthermore, the classification of the sampling stations varied between the two study sites at a similarity level of 30%, as shown in Fig. 4. Macrofaunal communities were more similar between stations within the same transect on the east coast. However, it was not the case on the west coast, where sampling stations at the same position (inshore stations or

Table 1. Benthic macrofauna occurring in the seagrass beds of North Sulawesi

Species	*n*	Percentage/%	H.T.	F.G.
Polychaeta				
Acoetes melanonota	1	0.1	Ed	C
Armandia intermedia	7	0.8	Ib	D
Armandia sp.	1	0.1	Ib	D
Branchiosyllis exilis	1	0.1	Ed	C
Cabira pilargiformis	1	0.1	Ed	C
Capitella capitata	3	0.4	Ib	D
Ceratonereis mirabilis	22	2.7	Ed	O
Chrysopetalum debile	2	0.2	Ed	C
Dasybranchus caducus	17	2.1	Ib	D
Euclymene sp.	6	0.7	It	D
Eunice indica	9	1.1	It	C
Eunice sp.	1	0.1	It	C
Eurysyllis sp.	1	0.1	Ed	C
Glycera capitata	2	0.2	Ed	C
Glycera chirori	2	0.2	Ed	C
Glycera rouxii	3	0.4	Ed	C
Glycera tesselata	2	0.2	Ed	C
Harmothoe sp.	1	0.1	Ed	C
Hesione splendida	1	0.1	Ed	C
Hesionidae und.	2	0.2	Ed	C
Hyboscolex sp.	1	0.1	Ib	D
Linopherus cf. *hirsute*	19	2.3	Ib	D
Linopherus sp.	1	0.1	Ib	D
Lumbrinerides sp.	1	0.1	Ib	C
Lumbrineris sp.	11	1.3	Ib	C
Lysidice ninetta	1	0.1	It	C
Lysidice unicornis	11	1.3	It	C
Malacoceros indicus	1	0.1	Ed	O
Maldanidae und.	1	0.1	It	D
Mesochaetopterus sp.	1	0.1	It	O
Micronephthys sp.	5	0.6	Ed	C
Neanthes sp.	4	0.5	Ed	O
Nephtys sp.	1	0.1	Ed	C
Notomastus aberans	6	0.7	Ib	D
Notomastus polyodon	8	1	Ib	D
Orbinidae und.	1	0.1	It	O
Parheteromastus sp.	4	0.5	Ib	D
Phyllodoce malmgreni	1	0.1	Ed	C
Phyllodoce sp.	5	0.6	Ed	C
Platynereis dumerilii	8	1	Ed	O
Podarkeopsis sp.	4	0.5	Ed	C
Polydora sp.	1	0.1	Ed	O
Polynoidae und.	2	0.2	Ed	C
Prionospio membranacea	9	1.1	Ed	O
Promastobranchus sp.	1	0.1	Ib	D
Sabellidae und.	3	0.4	It	Pl
Samythella sp.	1	0.1	Ib	D
Scolelepis (Scolelepis) squamata	1	0.1	Ed	O
Scoloplos cf. *armiger*	1	0.1	It	O
Syllis hyaliyna	1	0.1	Ed	C
Syllis setoensis	1	0.1	Ed	C
Terebella plagiostoma	1	0.1	Ib	D
Terebellides stroemii	2	0.2	Ib	D
Typosyllis maculata	2	0.2	Ed	C
Typosyllis regulata	6	0.7	Ed	C
Typosyllis sp.	6	0.7	Ed	C
Subtotal	218	26.5		
Bivalvia				
Anodontia edentula	4	0.5	Ib	D
Anodontia stearnsiana	4	0.5	Ib	D
Atrina penna	1	0.1	Ib	Pl
Epicodakia divergens	1	0.1	Ib	D
Jitlada philippinarum	1	0.1	Ib	O
Mactra antecedens	1	0.1	Ib	Pl
Merisca sp.	1	0.1	Ib	O
Myrtina sp.	1	0.1	Ib	D
Plicatula sp.	1	0.1	Ib	Pl
Pseudopythina sp.	2	0.2	Ib	Pl
Subtotal	17	2.1		
Gastropoda				
Acteocina decorata	1	0.1	Ef	C
Assiminea sp.	1	0.1	Ef	Ph
Canarium microurceus	1	0.1	Ef	Ph
Cerithium vulgatum	1	0.1	Ef	Ph
Clithon oualaniense	3	0.4	Ef	Ph
Epitonium sp.	1	0.1	Ef	C
Euplica scripta	1	0.1	Ef	Ph
Mammilla sebae	2	0.2	Ef	C
Miniaceoliva tremulina	1	0.1	Ef	C
Nassarius sp.	1	0.1	Ef	C
Neptunea sp.	2	0.2	Ef	C
Peronia verruculatum	1	0.1	Ef	Ph
Peristernia nassatula	1	0.1	Ef	Ph
Retusa borneensis	2	0.2	Ef	Ph
Trivirostra oryza	2	0.2	Ef	Ph
Umbonium thomasi	6	0.7	Ef	Ph
Vexillum sp.	2	0.2	Ef	Ph
Subtotal	29	3.5		
Tanaidacea				
Chondrochelia dubia	130	15.8	Ed	D
Pseudosphyrapus anomalus	9	1.1	Ed	D
Subtotal	139	16.9		
Amphipoda				
Ampelisca bocki	21	2.5	It	Pl
Ampelisca miharaensis	102	12.4	It	Pl
Amphitoe sp.	2	0.2	Ed	Ph
Gammaropsis sp.	12	1.5	Ib	Pl
Grandidierella gilesi	1	0.1	Ib	Pl
Grandidierella sp.1	30	3.6	Ib	Pl
Hippomedon sp.	1	0.1	It	Ph
Leucothoe alata	3	0.4	Ic	Pl
Liljeborgia sp.	1	0.1	Ed	Pl
Melita longidactyla	36	4.4	Ed	D
Paraphoxus tomiokaensis	25	3	Ed	C
Parelasmopus echo	2	0.2	Ed	D
Parelasmopus sp.1	13	1.6	Ed	D
Parelasmopus sp.2	3	0.4	Ed	D
Photis hawaiensis	30	3.6	Ib	Pl
Photis sp.	1	0.1	Ib	Pl
Sinoediceros homopalmatus	1	0.1	Ed	C
Stenothoe gallensis	1	0.1	Ed	C

to be continued

Continued from Table 1

Species	*n*	Percentage/%	H.T.	F.G.
Subtotal	285	34.6		
Decapoda				
Alpheus brevicristatus	3	0.4	Ib	O
Alpheus hoplocheles	4	0.5	Ib	O
Alpheus sp.	2	0.2	Ib	O
Callianassa sp.	13	1.6	Ef	D
Calocaris sp.	1	0.1	Ef	C
Etisus electra	5	0.6	Ef	C
Eualus sp.	10	1.2	Ef	C
Galathea orientalis	1	0.1	Ef	C
Gomeza bicornis	1	0.1	Ef	C
Hayashidonus japonicus	5	0.6	Ef	C
Hippolysmata sp.	7	0.8	Ef	C
Nihonotrypaea japonica	6	0.7	Ef	D
Parapanope euagora	1	0.1	Ef	C
Pilumnus sp.	1	0.1	Ef	O
Pseudoliomera sp.	1	0.1	Ef	C
Sicyonia sp.	1	0.1	Ef	C
Thalamita sp.	4	0.5	Ef	C
Tylocarcinus styx	1	0.1	Ef	O
Typhlocarcinops canaliculatus	2	0.2	Ef	O
Typhlocarcinops denticarpus	2	0.2	Ef	O
Subtotal	71	8.6		
Ophiuroidea				
Amphioplus (Lymanella) depressus	7	0.8	Ef	D
Amphioplus sp.	2	0.2	Ef	D
Amphiura sp.	3	0.4	Ef	D
Macrophiothrix longipeda	1	0.1	Ef	D
Macrophiothrix sp.	3	0.4	Ef	D
Ophiarachna sp.	1	0.1	Ef	D
Subtotal	17	2.1		
Holothuroidea				
Holothuria impatiens	1	0.1	Ef	D
Subtotal	1	0.1		
Echinoidea				
Temnopleurus sp.	1	0.1	Ef	D
Subtotal	1	0.1		
Porifera				
Axinella sp.	–	–	Ed	Pl
Callyspongia sp.	–	–	Ed	Pl
Haliclona sp.	–	–	Ed	Pl
Halichondria sp.	–	–	Ed	Pl
Pofifer und.	–	–	Ed	Pl
Subtotal	–	–		
Cnidaria				
Cerianthus sp.	2	0.2	Ed	C
Edwardsia sp.	5	0.6	Ed	C
Gorgonacea und.	–	–	Ed	C
Phellia gausapata	2	0.2	Ed	C
Subtotal	9	1.1		
Nemertinea				
Cerebratulus sp.	1	0.1	Ib	C
Nemertinea und.	2	0.2	Ib	C
Subtotal	3	0.4		
Sipuncula				
Apionsoma (Apionsoma) trichocephalus	7	0.80	Ib	D
Aspidosiphon (Paraspidosiphon) grandis	10	1.2	Ib	D
Aspidosiphon sp.	3	0.4	Ib	D
Phascolosoma (Phascolosoma) arcuatum	1	0.1	Ib	D
Phascolosoma sp.	1	0.1	Ib	D
Phascolosoma sp.1	7	0.8	Ib	D
Subtotal	29	3.5		
Chordata				
Asymmetronys lucayanum	5	0.6	Ef	Pl
Subtotal	5	0.6		
Total	824	100		

Note: Individual numbers of macrofauna are summed across all the samples. The character "–" in the second column respresents no statistics of individual number for corresponding species, as they are impossible to be counted. *n* is individual number. H.T. (microhabitat type): It represents infaunal tubicolous, Ib infaunal burrower, Ic infaunal commensal, Ed epifaunal domicolous, and Ef epifaunal free-living. F.G. (feeding guild): C represents carnivorous, O omnivorous, D detritivorous, Ph phytophagous, and Pl planktophagous.

offshore stations) clustered together.

4 Discussion and conclusions

4.1 *Macrofaunal diversity and abundance*

Although seagrasses are widely distributed in the shallow coastal waters of North Sulawesi, our knowledge of the seagrasses and associated fauna in this area remains poor, because no research papers were available in the database. Considering that the survey area is known for its high biodiversity, the finding that 149 species from 14 higher taxa were collected from seagrass beds of North Sulawesi indicated that the diversity of benthic macrofauna in the present study is moderate. The overall species diversity recorded in this study was greater than that reported for other areas in the tropical Indo-Pacific. For example, Klumpp and Kwak (2005) recorded 110 species in the Cockle Bay, North Queensland, Australia. Nakaoka (2001) found 61 species in an intertidal flat in Thailand. Forty-five species were recorded at Lopez Jaena, southern Philippines (Leopardas et al., 2014). However, the other studies cited above all referred to one site, which is in contrast to the two sites included in our study. The most speciose group of the present study was polychaetes, followed by decapods and amphipods. Some or all of these groups also dominate seagrass beds in other areas of the Indo-West Pacific. For example, polychaetes, amphipods and mollusks are the dominant groups in the Princess Royal Harbour, Albany, Western Australia (Hutchings et al., 1991); polychaetes and amphipods in the Western Port, Thomas Bay, Western Australia (Mukai et al., 1999); polychaetes and mollusks in the Haad Chao Mai National Park, Thailand (Nakaoka, 2001); polychaetes and amphipods in the Cockle Bay, Australia (Klumpp and Kwak, 2005); and polychaetes and mollusks, at Lopez Jaena, southern Philippines (Leopardas et al., 2014). In the present study, mollusks are the second most speciose group when bivalves (10 species) and gastropods (17 species) are considered together.

The mean abundance of seagrass macrofauna was 2 051

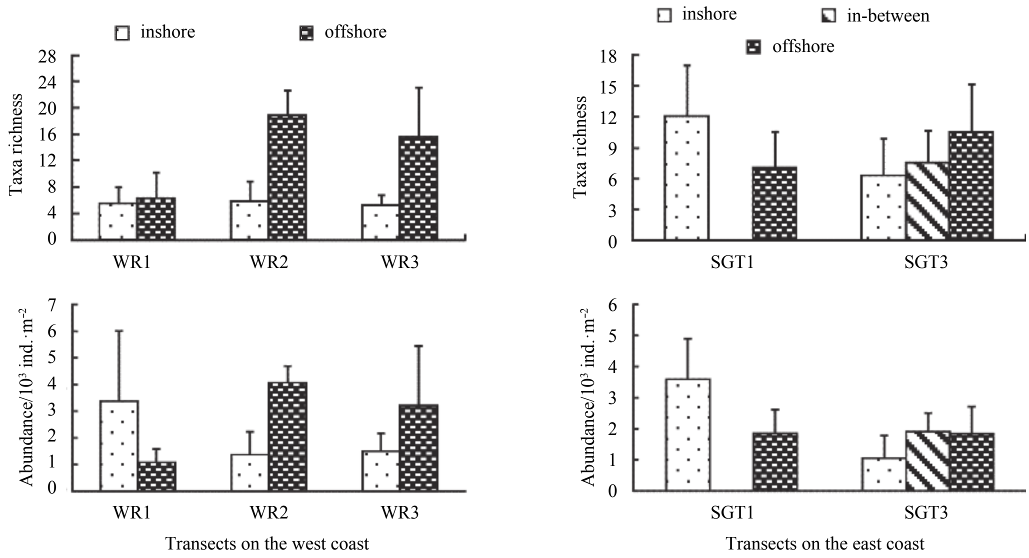

Fig. 2. Variation in the taxa richness and abundance of benthic macrofauna between transects and between stations within a transect in the seagrass beds of North Sulawesi.

Table 2. *F* values and level of significance for the nested ANOVA of the taxa richness and abundance of benthic macrofauna in the seagrass beds of North Sulawesi

Parameter		On the east coast				On the west coast			
		Between transects		Between stations		Between transects		Between stations	
		F	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Taxa richness	total	0.668	0.425	2.046	0.145	5.068	0.018$^{1)}$	10.805	0$^{3)}$
	polychaetes	1.302	0.27	1.51	0.248	2.199	0.14	7.269	0.002$^{2)}$
	amphipods	12.398	0.003$^{2)}$	2.393	0.104	2.105	0.151	1.21	0.335
Abundance	total	8.345	0.01$^{2)}$	3.776	0.03$^{1)}$	0.372	0.694	3.401	0.04$^{1)}$
	polychaetes	0.733	0.404	1.34	0.294	1.519	0.246	5.646	0.007$^{3)}$
	amphipods	23.476	0$^{3)}$	3.213	0.049$^{1)}$	3.768	0.043$^{1)}$	1.274	0.313

Note: Level of significance: $^{1)}$ 0.05; $^{2)}$ 0.01; $^{3)}$ 0.001.

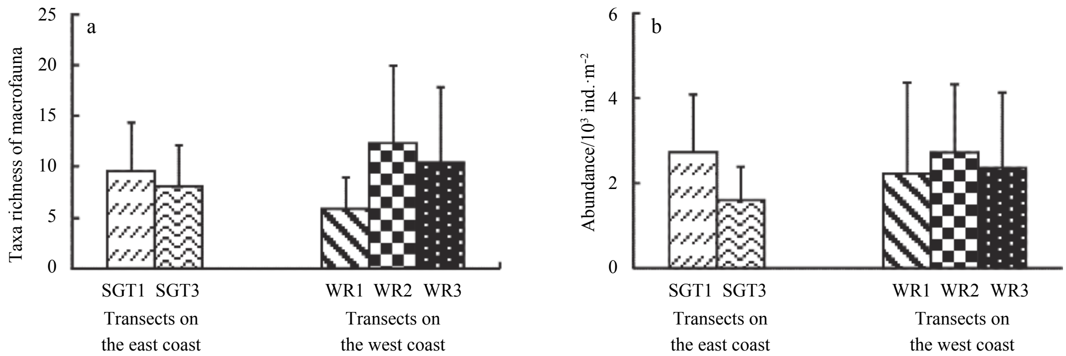

Fig. 3. Variations in the taxa richness (a) and abundance (b) of seagrass macrofauna between the two study sites in North Sulawesi.

ind./m^2 on the east coast and 2 435 ind./m^2 on the west coast. Compared with other tropical seagrass beds, the benthic macrofauna of the present study has considerably higher abundance, e.g., 654 ind./m^2 was recorded in the Apalachee Bay, Florida (Lewis III and Stoner, 1983), 31.8–64.7 ind./m^2 was observed at Lopez Jaena, southern Philippines (Leopardas et al., 2014) and 751–1 133 ind./m^2 was reported for southwest Sulawesi, Indonesia (Vonk et al., 2010), although values lower than 5 800–8 300 ind./m^2 observed in Kuraburi, Thailand (Whanpetch et al., 2007) and 28 148 ind./m^2 in the Cockly Bay of Australia (Klumpp and Kwak, 2005)

4.2 *Variations between stations within a transect*

Previous studies have reported the effect of seagrass structure on associated fauna, including seagrass biomass (Orth et al., 1984; Klumpp and Kwak, 2005), small-scale spatial heterogeneity of the seagrass vegetation (Nakaoka, 2001), seagrass meadows with different canopy structures (Vonk et al., 2010) and vegetation dominated by different seagrass species (Leopardas et al., 2014). However, sediment patterns in seagrass beds have been seldom mentioned in the literature. It is well known that sediment type plays an important role in macrofaunal community (Rhoads, 1975). In the present study, there was an important

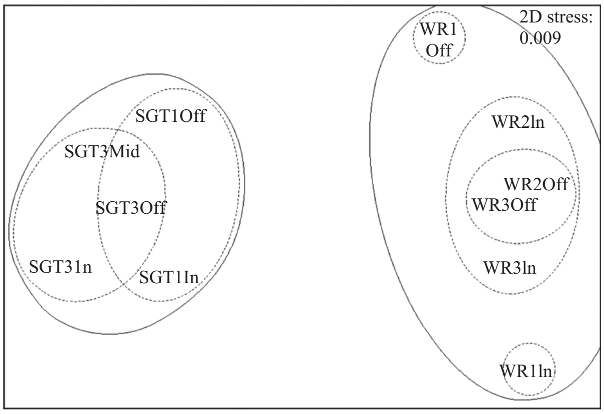

Fig. 4. MDS ordination of seagrass macrofauna at 11 sampling stations in North Sulawesi, Indonesia. Ordination is superimposed with Bray-Curtis similarity clusters at the 20% (solid lines) and 30% (dotted lines) level. The sampling station code is expressed as transect + position of the station along a transect.

finding that spatial variations in seagrass macrofauna displayed distinctly different patterns across the two study sites, which might be related to the different sediment patterns in the seagrass beds. On the east coast, the substrate was consistent throughout the study area. The vast beach extends from the coastline to the subtidal area along the investigated transect, and seagrasses grow in a sediment composed of fine sand. The homogenous substrate and similar species composition of seagrasses resulted in comparable communities between the stations within a transect. Additionally, the nested ANOVA showed that no variations in abundance and taxa richness between stations within a transect were found in the surface sediment-inhabiting polychaete assemblage, which could also be explained by the homogenous sediment pattern. We also observed that amphipod abundance varied with transect and with station within a transect. The great number of amphipods at the inshore station of the SGT1 transect might explain the spatial variation that was recorded on the east coast. Amphipods were small opportunistic species and they were usually recorded in large numbers at random stations where abundant food was available.

However, on the west coast, seagrasses were influenced by nearby habitats such as mangroves and coral reefs. A heterogeneous sediment pattern was formed along a transect with coral rubber scattered at offshore stations. Therefore, the communities of benthic macrofauna were less similar between stations within a transect than between stations at the same position, as revealed by the MDS ordination. At inshore stations near mangroves, mangrove detritus covered the nearby seagrass beds, which might reduce the water transparency. Consequently, the epiphytes on the leaves of seagrass and the seagrass itself were not able to fully photosynthesize, and food supply was limited for associated fauna. In contrast, at offshore stations in reef flats, the presence of coral rubble in the sediment increases the complexity of the benthic environment and provides more microhabitats and shelters for benthic fauna, especially for polychaete assemblages. This might explain the higher abundance and taxa richness of polychaetes at offshore stations.

4.3 *Variations between the two study sites*

In the present study, all the sampling stations can be divided into two groups at a similarity level of 20%. The division was in agreement with the following two broad categories of habitats: reef+seagrass continuum on the east coast and reef+seagrass+mangrove continuum on the west coast. Although there were no marked variations between the two study sites in terms of the abundance and taxa richness of benthic macrofauna, the difference in community structure was confirmed by the ANOSIM to be significant (P=0.002). The difference in macrofaunal community structure between the two study sites might be attributed to multiple reasons. First, there is a marked difference in sediment pattern. The complex substrate on the west coast is a combination of mangrove detritus, coral rubble and sand, which is different from the fine sand on the east coast. Previous studies have shown that sediment characteristics have a great impact on the benthic fauna living in the sediment (Rhoads, 1975; Snelgrove and Butman, 1994). Second, the species composition of seagrass varied between the two sites. The seagrass vegetation was dominated by *Thalassia hemprichii*, *Halodule pinifolia* and *Cymodocea rotundata* on the east coast, while *Syringodium isoetifolium* and *Thalassia hemprichii* dominated the west coast. Klumpp and Kwak (2005) found that the relative proportion of dominant amphipods differed among the three most abundant seagrass species, and tanaids and isopods with stout bodies tended to be abundant on the wide-bladed seagrass. However, Leopardas et al. (2014) observed that the species composition of macrofauna did not vary significantly by vegetation type. Third, temporal changes in seagrass macrofauna may exist. Our fieldwork on the east coast was conducted in October 2014, while on the west coast, we worked in May 2015. Temporal changes in macrofauna have been recorded in other studies. Bos et al. (2008) observed a lower abundance of the sea star *Protoreaster nodosus* during certain months of the year. Klumpp and Kwak (2005) found that the temporal pattern of macrofaunal abundance correlated with temporal variations in seagrass biomass in the Cockle Bay. The present study showed that there was significant difference between the two categories of seagrass habitats in the benthic macrofaunal community and biological environment. More studies are needed to analyze how nearby habitats such as mangroves and coral reef affect biodiversity in seagrass.

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