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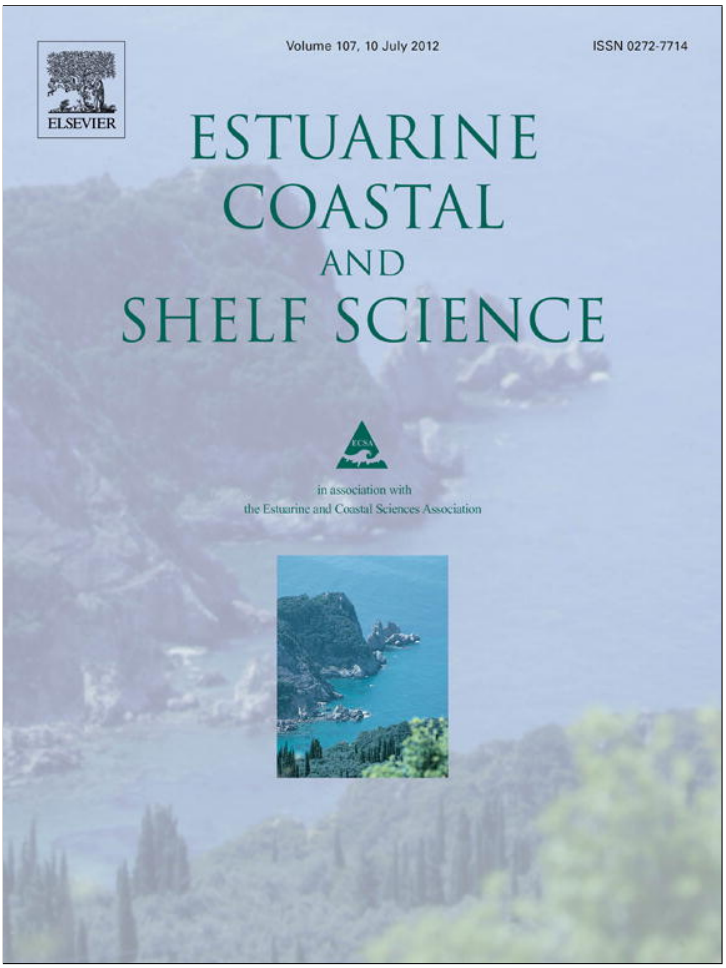

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The influence of canopy structure and tidal level on fish assemblages in tropical Southeast Asian seagrass meadows

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ABSTRACT

Seagrass meadows support abundant and diverse fish assemblages, but there are very few studies on the relation between seagrass beds with distinctly different plant canopies and their associated fish fauna. In the present study, fish assemblages were investigated by underwater visual census at intertidal and subtidal sites with varying seagrass species composition, shoot density, biomass, and leaf area index (LAI) on two small coral islands in the Spermonde Archipelago, Indonesia. We investigated (1) whether fish assemblages in distinctly different seagrass beds differ regarding community parameters, and (2) whether seagrass parameters affect fish abundances. Overall, more than 120 fish taxa were found. Bray–Curtis cluster analysis and non-Metric Multidimensional Scaling ordination (nMDS) showed site-specific similarities for fish assemblage structure with a distinct separation into subtidal and intertidal sites. Species accumulation curves for gamma diversity, single study sites, and the two most diverse fish families (Labridae, Pomacentridae), suggesting that species numbers are likely to increase with diel sampling. Total fish abundance and abundance for six out of the nine most common species varied distinctly among the study sites. The study indicates that seagrass beds with differing canopy parameters support distinct fish assemblages that differ with respect to species richness, dominant species, and the abundance of total and most common fish species. These differences are likely due to different canopy structures and water depth.

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1. Introduction

Seagrass beds support high species diversity, abundance and biomass, and are important habitats for economically important fish and invertebrates (Parrish, 1989; Gullström et al., 2002; Duffy, 2006; MacArthur and Hyndes, 2007). They are structurally highly complex habitats, offering shelter from predation, nursery areas and feeding grounds for diverse fish assemblages (Parrish, 1989; Nakamura et al., 2003; Dorenbosch et al., 2005). Seagrass beds are open and dynamic habitats at different spatial scales (Duffy, 2006; Duarte et al., 2006; Valentine and Duffy, 2006) and interact with adjacent coral reefs and mangroves (reviewed by Parrish, 1989; Nakamura and Sano, 2004; Unsworth et al., 2007).

Southeast Asian seas contain the world's highest numbers of fish species, especially in the heart of the coral triangle region, which is comprised of the Philippines, Indonesia and Papua New Guinea (Fenner, 2007). In Indonesia, seagrass beds cover substantial parts of coastlines and offshore islands, and can harbour up to ten seagrass species (McKenzie et al., 2007) and 80 or more fish species (Hutomo and Martosewojo, 1977; Unsworth et al., 2007) within a single meadow. They are important for fish species, and are therefore of interest for local fisheries. However, the increasing human population and demand for food result in an over-exploitation of seagrass beds, and pose a serious threat to associated fish communities (Duffy, 2006; Unsworth and Cullen, 2010).

Most studies investigating fish communities in seagrasses have been conducted in the Caribbean. Seagrass beds in Southeast Asia, however, have a distinctly higher faunal diversity (Unsworth et al., 2007), and may therefore differ in mechanisms influencing fish assemblages. Despite this, research on fish communities in Southeast Asian seagrass meadows is scarce (Nienhuis et al., 1989; Erftemeijer and Allen, 1993; Vonk et al., 2008, 2010). While the Indonesian Spermonde Archipelago is well investigated with respect to benthic invertebrates such as sponges (e.g. Cleary et al., 2005), foraminiferans (e.g. Cleary et al., 2005), holothurians (e.g. Massin, 1999), or corals (e.g. Cleary et al., 2005; Knittweis et al., 2009), few studies have focussed on fish assemblages (Pet-Soede et al., 2001; Vonk et al., 2008, 2010).

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Although earlier research suggested that fish density increases with seagrass canopy complexity (e.g. Bell and Westoby, 1986; Nakamura and Sano, 2004), and that variations in seagrass habitats influence associated fish assemblages (Heck and Orth, 1980), few studies have focused on the effect of mixed-species seagrass beds with complex canopies on fish assemblages (e.g. Blaber et al., 1992). The effects of seagrass species composition and bed structure on fish species composition can vary distinctly between seagrass beds (Kiswara et al., 1991; MacArthur and Hyndes, 2007; Nakamura and Sano, 2004; Vonk et al., 2010). Several studies did not find significantly different fish abundances among sites (Middleton et al., 1984; Loneragan et al., 1998). In contrast, abundances of single species more often show distinct variations between different seagrass beds (e.g. Rooker and Holt, 1997).

The present study investigated fish assemblages in five offshore seagrass beds with varying canopy architecture in the Spermonde Archipelago, Indonesia. The aim of this study was to assess 1) whether fish assemblages differ with regard to community parameters (species number, abundance, most common species), and 2) whether seagrass parameters (shoot density, biomass, leaf area index (LAI)) have an effect on total fish abundance.

2. Material and methods

2.1. Site description

All field work was conducted in the Spermonde Archipelago, Indonesia. The archipelago is about 200 km long and 40 km wide, and consists of numerous reef islands and submerged reefs along the continental shelf off the west coast of South Sulawesi (Fig. 1). It is subject to tropical climate, with an annual mean air and water temperature of 27 °C and 28 °C, respectively (Erftemeijer and Herman, 1994; Renema and Troelstra, 2001). May to October are considered as dry, November to April as wet season, although prolonged dry seasons extending to the end of November attributed to ENSO events are known (Erftemeijer and Herman, 1994). The tidal regime is predominantly semi-diurnal with a maximum tidal range at spring tide of 180 cm and an average tidal range of 80 cm (according to the tidal predictions for Makassar harbour). The islands Barrang Lompo (lat. 4°85′S, long. 119°20′E) and Bone Batang (lat. 4°90′S, long. 119°18′E) were chosen as study sites. The islands are situated 12 and 15 km off Makassar, respectively. Both islands are patch reefs crowned by a coral cay, and the reef flats support intertidal and shallow subtidal seagrass beds of different successional stages. Barrang Lompo is heavily populated, its local population lives mainly on marine resources using fishing techniques such as compressor diving, gill nets, blast and cyanide fishing. Sewage water and garbage are released directly into the sea. Even though Bone Batang is uninhabited, it is visited by several fishing vessels daily (unpubl. obs.). In total, five sampling sites were chosen for the survey: Bone Batang North (BBN), East (BBE), West (BBW) and South (BBS). Care was taken to choose seagrass meadows of different canopy structure and species composition. Subtidal sites at Barrang Lompo are subject to heavy boat traffic, so only one intertidal site was chosen at this island for safety reasons.

2.2. Seagrass parameters and water depth

To assess seagrass shoot densities, a quadrat (0.25 m^2) was thrown into randomly selected patches along the transects (see 2.3.) for the visual census. At each site except BBE, the frame was thrown seven times per transect ($n = 14$ for BBN, BBS, BBW, and $n = 28$ for BLS). At BBE, the frame was thrown 21 times per transect to reduce observer bias, since this site had the most difficult sampling conditions for a snorkelling observer (greatest water depth, highest shoot densities). The frame was subdivided into 25 smaller sub-quadrats, each with a side length of 0.1 m. For shoots of *Enhalus acoroides*, the whole area of the frame was counted. For other seagrass species, all shoots per species within three sub-quadrats were counted.

Shoot densities were converted into leaf area index (LAI) and aboveground biomass by multiplying the number of shoots per species counted in the present study with the single sided leaf area per shoot and the leaf biomass per shoot measured in a separate study on the identical sites exactly one year later (Kneer et al. unpublished data).

2.3. Fish community parameters

Fish diversity and abundance were assessed during daylight using a rapid visual census (Harvey et al., 2004) in belt transects. This technique was chosen because it is rapid, non-destructive and inexpensive. Transects can be resurveyed over time and the data gained are highly comparable (Nagelkerken et al., 2000) since visual censuses are widely applied for ecological fish studies (Khalaf and Kochzius, 2002). Transects were not permanent and were set

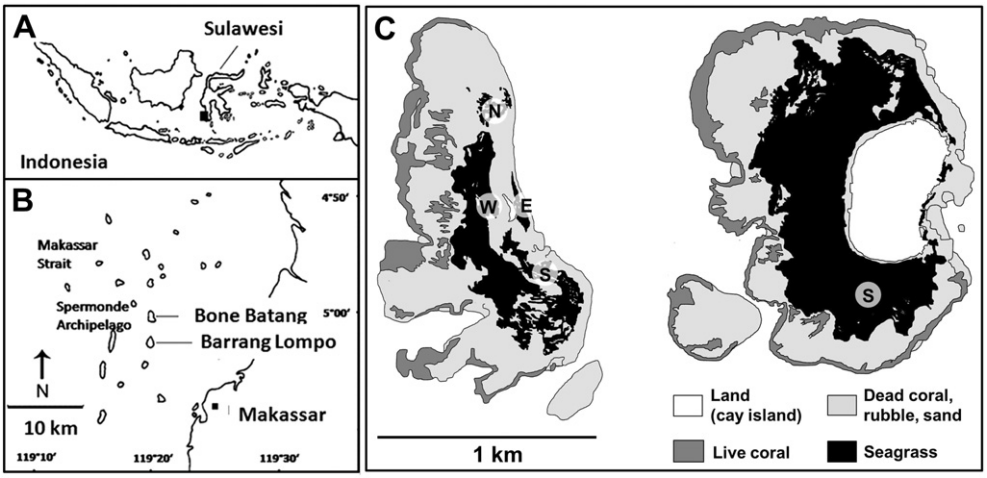

Fig. 1. Study area showing (A) The location within Indonesia, (B) The islands of the. Spermonde archipelago (both adapted from Liu et al., 2008), and overviews of the islands (C) Bone Batang (left, lat. 4°90′S, long. 119°18′E) and Barrang Lompo (right, lat. 4°85′S, long. 119°20′E). Letters indicate transect positions. The areal extent of surface features (island, seagrass, live coral, dead coral, rubble and sand) is shown.

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up prior to fish counting. They were 25 m in length and 6 m in width, covering an area of 150 m^2. Transects were separated by at least 15 m in each direction and were directed parallel to the shore line. Start and end points of transects were marked with buoys. The number of permanent transects per study site was two for each of the Bone Batang sites and four for the Barrang Lompo site. Each transect was resurveyed 15 times.

To reduce observer bias as well as the attraction or repellence of fish, all surveys were conducted by snorkelling by one single observer (C. P.). Care was taken not to count any fish that was moving into, within, or out of transects twice. Cryptobenthic species were recorded when observed, but were not actively searched for. After transect setup, the observer waited for at least 5 min to minimize fish disturbance, and then slowly swam along the transect line transect in a zigzag pattern in order to maximize the number of fishes seen. Data recorded included taxa observed and number per taxon, as well as water depth (assessed with a measuring rod prior to the census). Fishes were identified to the highest possible taxonomic separation, usually species level. Surveys were conducted throughout the day from 06:30 AM to 04:00 PM, and randomized at different water depths to control for possible time or day effects (Gratwicke and Speight, 2005). Visual census data were collected in 2009 from October until November.

2.4. Data analysis

Seagrass shoot densities and fish abundances are presented as means ± SD (m^{-2} for seagrass parameters and 100 m^{-2} for fish abundances). Since assumptions for parametric testing could not be met, a non-parametrical Kruskal–Wallis test and post-hoc Mann–Whitney *U*-test were performed to test for differences in fish community parameters, seagrass parameters, and water depth among habitats. All tests were conducted using the software package R 2.13.2 (R Development Core Team, 2011). Site-specific similarities for fish assemblage structure were analysed using multivariate non-Metric Multidimensional Scaling ordination (nMDS) and Bray–Curtis cluster analysis using the computer package PRIMER 6 (Clarke and Warwick, 1994). The Bray–Curtis similarity index was applied on square root transformed data to down-weight the influence of rare and highly abundant species, and then converted into nMDS ordination and cluster analysis (Clarke, 1993). SIMPROF analysis was applied to assess global differences between study sites, while SIMPER analysis was used to determine the relative contribution of individual fish species to differences between groupings (Rotherham and West, 2002). To test for the effects of water depth and seagrass parameters on total fish abundance and abundance of the most common species, a simple generalized linear model (GLM) was performed with standardized data in the gam package in R (Hastie, 2011). The R syntax for the GLM was model $\leq$ glm($y \sim x_1 + x_2 + x_3 + \ldots x_n$), y being the predicted variables and x_n the predictors.

For the analysis of habitat saturation (gamma diversity), and saturation of most diverse fish families, data were arranged into species x site matrices and analysed using the software EstimateS 7.5.2 (Colwell, 2006). The Abundance-Based Coverage Estimator (ACE) and the Chao 1 Estimator were used as estimators of total species richness.

3. Results

3.1. Seagrass parameters and water depth

The seagrass beds were composed of *Enhalus acoroides*, *Thalassia hemprichii*, *Cymodocea rotundata*, *Halodule uninervis*, *Syringodium isoetifolium* and *Halophila ovalis*. If present, *E. acoroides* formed an upper canopy, and smaller species together formed a lower canopy. Consequently, in the absence of *E. acoroides* the canopy was generally uniform. At BBN, there was a patchwork of dense *T. hemprichii* and recently eroded areas (blowouts sensu Patriquin, 1975) being recolonized mainly by *H. ovalis*. The intertidal sites BBW and BLS were dominated by well established *E. acoroides* and *T. hemprichii*, and single small colonies of the coral genera *Porites* and *Pocillopora* as well as sponges were scattered infrequently across the seagrass beds. Other conspicuous features of these two sites were sand patches and expulsion mounds created by the burrowing activity of alpheid and callianassid shrimp. The subtidal site BBE was covered by a dense short vegetation dominated by *C. rotundata* and *H. uninervis*. At BBS, there was an upper canopy of dense *E. acoroides* and a lower canopy dominated by *H. uninervis* in terms of shoot number but by *T. hemprichii* in terms of LAI and biomass. Schematic canopy architectures for each study site are shown below (Fig. 2). With the exception of *E. acoroides* (lacking at BBE and BBN) and *S. isoetifolium* (lacking at BLS and BBN), all seagrass species were observed in variable densities at all study sites. Mean total shoot density (±SD; shoots m^{-2}) ranged from 647.4 ± 348.5 at BLS to 2156.4 ± 550.1 at BBE. Mean leaf biomass (g m^{-2}) was highest at BBS, while BBW was ranked second (107.2 ± 47.7 and 49.5 ± 18.8, respectively). Lowest mean seagrass biomasses were found at BBE (29.8 ± 11.8) and BBN (31.8 ± 12.3). Mean total LAI ranged from 0.88 ± 0.34 (BLS) to 2.19 ± 0.94 (BBS) (Table 1). Seagrass shoot density, biomass and LAI differed significantly (Kruskal–Wallis Test, $p < 0.05$) among study sites (Table 2). Epiphyte growth was most notable on leaves of *E. acoroides* and *S. isoetifolium* but was observed only moderately on the other seagrass species. Mean values and ranges of water depth are given in Table 1.

3.2. Fish community parameters and environmental effects

A total of 180 individual visual censuses were conducted: 60 off Barrang Lompo (4 transects) and 30 for each of the BB sites (2 transects each). Over all sites, 120 taxa from 39 families were recorded (Table 2). Thirty families and 89 species were found off Barang Lompo, and 36 families and 107 species were found off Bone Batang (27 families and 58 species off BBS, 26 families and 45 species off BBE, 16 families and 38 species off BBW and 15 families and 31 species off BBN).

The most species rich families were Labridae (20 species), Pomacentridae (17 species), Nemipteridae (8 species), and Gobiidae (6 species). Mean abundance per species (mean ± SD 100 m^{-2}) ranged from 0.94 ± 2.1 (BBN) to 4.5 ± 14.4 (BBE) (Table 2). Fish species occurring in an abundance of more than 10 individuals 100 m^{-2} at all or specific study sites were *Atherinomorus lacunosus* (Atherinidae), *Cheilio inermis*, *Halichoeres argus*, *Halichoeres chloropterus* (all Labridae), *Pentapodus bifasciatus*, *Pentapodus trivittatus* (both Nemipteridae) and *Siganus canaliculatus* (Siganidae). Fish species occurring at all study sites were *A. lacunosus*, *C. inermis*, *H. argus*, *H. chloropterus*, *P. trivittatus*, pomacentrid sp. 1 and *Tylosurus crocodilus* (Belonidae). Sixty-one species were recorded on a single or few occasions (A.1), and 25 additional taxa were found at the study sites but outside the observation period (A.2). The wrasse *H. argus* was the dominant species at BLS, BBN and BBW, followed by *S. canaliculatus*, *A. lacunosus* and *Dischistodus chrysopoecilus* at BLS and *H. chloropterus* at BBN and BBW where *D. chrysopoecilus* (BBN) or *P. trivittatus* (BBW) occupied the third rank. At BBE and BBS *A. lacunosus* was the most abundant species followed by *Lethrinus obsoletus* at BBE and *Sphyraena obtusata* at BBS. At BBE, *C. inermis*, *S. canaliculatus* and *P. bifasciatus* were found in abundances higher than 10 individuals 100 m^{-2}, while at BBS the latter two species were found in abundances higher than 6 individuals 100 m^{-2} (Table 2).

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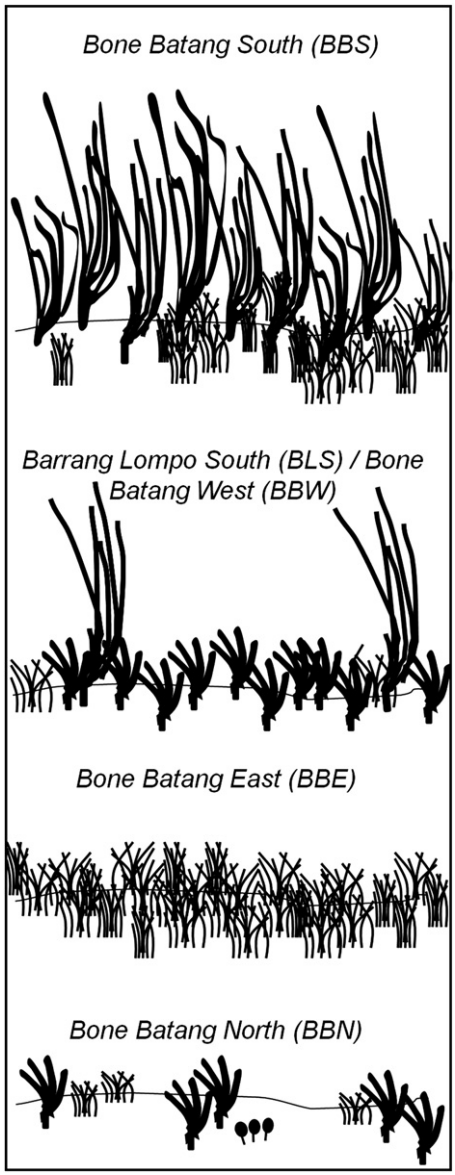

Fig. 2. Schematic diagram showing different seagrass architectures of the selected study sites. Bone Batang south (BBS) is dominated by *Enhalus acoroides* and *Halodule uninervis*, Barrang Lompo south (BLS) and Bone Batang west (BBW) are dominated by *E. acoroides* and *Thalassia hemprichii*, Bone Batang East (BBE) consists mostly of the smaller seagrasses *H. uninervis* and *Cymodocea rotundata*, and Bone Batang North (BBN) is a patchwork of areas with established *T. hemprichii*, and areas where ephemeral *Halophila ovalis* expands on bare sands where the vegetation was recently eroded.

SIMPER analysis of fish abundances revealed an average similarity between intertidal and subtidal seagrass beds of 65.5%. Average similarity among intertidal seagrass beds was 48.2%. The most representative fish species of intertidal seagrass beds were the labrids *H. chloropterus* (13.4% contribution), *H. argus* (11.9%) and *Cheilio inermis* (7.8%), as well as the pomacentrid *Dischistodus chrysopoecilus* (11.3%) and the nemipterid *P. trivittatus* (9.2%). Average similarity for subtidal seagrass beds was 58.0%, with *C. inermis* (10.2% contribution), *Pentapodus bifasciatus* (8.0%) and *Siganus canaliculatus* (7.6%) being the most representative fish species.

Study sites showed significant differences regarding total fish diversity and abundance (Kruskal–Wallis test; df = 4, both $p < 0.0005$) (for detailed post-hoc comparisons, see Table 3). For six out of nine most abundant fish species, there were significant differences in abundance (Table 3). Only for *Halichoeres chloropterus*, post-hoc comparisons showed significant differences among all sites (Table 3).

The GLM found significant effects on fish abundances regarding water depth at BBE ($p = 0.00156$) and shoot density at BBE ($p = 0.04312$) and BBN ($p = 0.00734$) (AIC = 401.28). In other sites, no significant effects of water depth and seagrass shoot density were found. No effects of seagrass biomass and LAI on the whole fish assemblages were found in any site. Regarding abundances of most common fish species, significant effects were found for LAI at BBS ($p = 0.01902$), for seagrass biomass at BBN ($p = 0.01306$), and for water depth at BBE ($p = 0.02856$) and BBN ($p = 0.00957$) (AIC = 717.95).

Cluster analysis of site similarity using abundance-based fish species data showed that study sites differed significantly from each other (Fig. 3A). With a similarity level of 34.5% (SIMPROF; $\pi = 18.88$; $p < 0.1$), study sites grouped distinctly into subtidal (BBE, BBS) and intertidal seagrass beds (BLS, BBW, BBN). The sites BLS and BBW appear to be more similar to each other than to BBN. The nMDS ordination plot clearly distinguished the different seagrass beds (Fig. 3B).

Cluster analysis based on shoot density of each seagrass species showed the same groupings as the fish species abundance-based data (subtidal vs. intertidal), but the similarity level of 63.9% ($\pi = 12.93$; $p = 0.9$) was higher than that of the fish abundance-based clusters, and there was no significant dissimilarity (all p-values ≥ 0.5). However, clusters showed a trend towards dissimilarity regarding groupings of intertidal sites. Within intertidal sites, BBW and BBN are more similar to each other than to BLS (Fig. 4).

3.3. Species accumulation curves

Randomized species accumulation curves (Sobs MauTao, ACE, Chao 1 Estimator) for gamma diversity across all study sites exhibited a strong increase without reaching saturation. Species accumulation curves for single study sites also maintained a steep slope. Most species were found at BLS, even at the smallest common sample size ($n = 30$). The lowest species number was recorded at BBN. The number of species recorded for BBS, BBE and BBW was intermediate compared to those at BLS and BBN. This pattern was also apparent when comparing all five sites at the smallest common sample size (Fig. 5A,B).

Species accumulation curves for the three most diverse families (Labridae, Pomacentridae, Nemipteridae) at all sites showed a strong increase for Labridae and Pomacentridae. For Nemipteridae, the curve showed saturation, and the 95% confidence intervals decreased towards zero at a sample size of $n = 160$ (Fig. 5C). For Labridae and Pomacentridae, saturation was not reached. Species numbers were similar for Labridae and Pomacentridae (20 for Labridae and 17 for Pomacentridae), and lowest for Nemipteridae (8 species). The lower boundary of the 95% confidence interval of the Sobs (MauTao) of Labridae overlapped with the upper boundary of the Sobs (MauTao) of Nemipteridae, and the lower boundary of the confidence interval of Pomacentridae overlapped with the upper boundary of the Sobs (MauTao) of Nemipteridae until up to 40 samples (Fig. 5C).

4. Discussion

The present study investigated whether fish assemblages in seagrass beds with significantly different seagrass parameters differ with respect to community parameters. Fish diversity, species composition and abundance are significantly different between all

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Table 1
Seagrass and water variables. (a) Shoot densities (shoots m^{-2}), (b) Seagrass biomasses (g m^{-2}), (c) leaf area index (LAI), (d) Water depth. Abbreviations for study sites: BBE = Bone Batang East, BBN = Bone Batang North, BBS = Bone Batang south, BBW = Bone Batang west, BLS = Barrang Lompo South. Abbreviations for seagrass names: *Enhalus acoroides* (Ea), *Thalassia hemprichii* (Th), *Cymodocea rotundata* (Cr), *Halodule uninervis* (Hu), *Syringodium isoetifolium* (Si), *Halophila ovalis* (Ho). Values are presented as mean ± SD, if not stated otherwise.

	Ea	Th	Cr	Hu	Si	Ho	Sum	n
(a) seagrass shoot densities (m^{-2}, mean ± SD)								
BBE	0.0	76.2 ± 93.8	859.5 ± 851.7	1072.2 ± 974.5	92.1 ± 300.4	56.3 ± 111.8	2156.3 ± 550.1	42
BBN	0.0	807.1 ± 460.4	95.2 ± 181.1	354.8 ± 321.5	0.0	169.0 ± 515.8	1426.2 ± 401.3	14
BBS	95.4 ± 53.3	281.8 ± 110.0	19.0 ± 42.8	628.6 ± 338.4	142.9 ± 172.2	61.9 ± 67.8	1229.6 ± 295.7	14
BBW	18.3 ± 23.1	521.4 ± 231.9	381.0 ± 481.0	54.8 ± 107.5	33.3 ± 124.7	38.1 ± 67.8	1046.9 ± 525.6	14
BLS	76.7 ± 34.6	479.0 ± 246.5	2.8 ± 8.4	71.6 ± 243.7	0.0	17.3 ± 65.6	647.4 ± 348.5	28
(b) Seagrass biomasses (gm^{-2}, mean ± SD)								
BBE	0.0	3.7 ± 4.6	17.3 ± 17.2	8.5 ± 7.7	0.0	0.3 ± 0.6	29.8 ± 11.8	
BBN	0.0	25.4 ± 14.5	1.0 ± 1.9	4.3 ± 3.9	0.0	1.1 ± 3.4	31.8 ± 12.3	
BBS	75.2 ± 42.0	13.9 ± 5.4	0.1 ± 0.3	4.7 ± 2.5	12.9 ± 15.5	0.3 ± 0.4	107.2 ± 47.7	
BBW	6.9 ± 8.7	35.7 ± 15.9	5.5 ± 6.9	0.9 ± 1.7	0.2 ± 0.8	0.4 ± 0.6	49.5 ± 8.8	
BLS	20.3 ± 9.1	14.9 ± 7.7	0.1 ± 0.2	1.9 ± 6.4	0.0	0.0	37.1 ± 12.5	
(c) LAI (leaf area m^{-2}, mean ± SD)								
BBE	0.0	0.11 ± 0.13	0.58 ± 0.57	0.34 ± 0.31	0.0	0.02 ± 0.03	1.05 ± 0.37	
BBN	0.0	0.80 ± 0.46	0.04 ± 0.07	0.18 ± 0.16	0.0	0.07 ± 0.21	1.08 ± 0.35	
BBS	1.56 ± 0.87	0.42 ± 0.16	0.00 ± 0.05	0.08 ± 0.05	0.11 ± 0.13	0.01 ± 0.02	2.19 ± 0.94	
BBW	0.13 ± 0.17	1.13 ± 0.50	0.21 ± 0.27	0.03 ± 0.06	0.00 ± 0.01	0.01 ± 0.02	1.53 ± 0.54	
BLS	0.31 ± 0.14	0.50 ± 0.26	0.00 ± 0.01	0.07 ± 0.22	0.0	0.0	0.88 ± 0.34	

(d) *Water depth (m) while counting transects*				*Water depth (m) relative to chart datum*			
	Mean ± SD	Min	Max	Mean ± SD	Min	Max	n
BBE	1.3 ± 0.2	1.0	1.7	−0.5 ± 0.2	−0.9	−0.3	28
BBN	0.6 ± 0.2	0.4	0.8	0.1 ± 0.1	−0.1	0.2	28
BBS	0.7 ± 0.2	0.4	1.2	−0.4 ± 0.2	−1.0	0.0	30
BBW	0.5 ± 0.1	0.4	0.8	−0.1 ± 0.1	−0.3	0.2	28
BLS	0.6 ± 0.2	0.2	1.4	0.0 ± 0.1	−0.2	0.3	55

study sites, i.e. between two islands, between intertidal and subtidal sites, and among different seagrass beds. Although some sites have smaller species numbers than others, none of the sites show saturated species accumulation curves and seagrass parameters and water depth influence total fish abundances.

4.1. Seagrass parameters

The seagrass meadows examined represented different successional stages. BBE was dominated by the small seagrasses *Cymodocea rotundata* and *Halodule uninervis*. This subtidal meadow was unvegetated up to 14 years before the present study was carried out (vegetation probably cleared by a moving sandbar, Kneer unpublished data). The other subtidal meadow, BBS, has been undisturbed for much longer and is dominated by *Enhalus acoroides* and *Thalassia hemprichii* in terms of LAI and biomass, even though *H. uninervis* has the highest shoot number. *H. uninervis* seems to perform much better in subtidal areas, and can resist replacement by *T. hemprichii* for much longer compared to intertidal areas (Kneer unpublished data). Of the intertidal meadows, BBN is a patchwork of recently devegetated areas with abundant *Halophila ovalis* and *H. uninervis*, and older areas dominated by *T. hemprichii*. This is caused by blowouts which frequently erode the established vegetation due to the high water movement in this area. In contrast, BBW and BLS have probably been undisturbed for decades just like BBS, and the vegetation is composed almost exclusively of *E. acoroides* and *T. hemprichii*.

4.2. Fish diversity and community composition among sites

A total of 120 fish taxa were recorded in seagrass beds off the two small islands in the Spermonde Archipelago. Even though species numbers for BBE, BBS and BLS are high compared to BBN (lowest slope), the accumulation curves for total fish diversity do not show site-specific saturation. This suggests that recorded fish diversity does not represent the actual total diversity. Higher sampling efforts might yield higher species numbers, especially for Gobiidae, Labridae and Pomacentridae. Unsworth et al. (2007) recorded a similar species number (81 species) in a seagrass bed comparable to BLS, using beach seine netting and diel sampling. In their study, they found that during the night, mean fish abundance and diversity showed an increase of 45% and 35%, respectively, relative to daytime. Although a part of the transects counted in the present study were conducted before 9 AM, and thus may include diurnal-nocturnal changeover periods of fish (English et al., 1997), it is likely that additional night sampling efforts may yield even more species at BLS or BB.

The most diverse fish families in the present study were Labridae, Pomacentridae and Nemipteridae. While species accumulation curves for Labridae and Pomacentridae were increasing, the curve for Nemipteridae was saturated. It is therefore considered likely that increased sampling effort would lead to additional labrid and pomacentrid species, but not nemipterids. Labridae and Pomacentridae are taxonomically diverse, while Nemipteridae are relatively species-poor (Nelson, 2006). In the present study, the most abundant fish species were from the families Labridae, Siganidae, Atherinidae, Pomacentridae and Nemipteridae, with variations between the study sites. *Halichoeres argus* was the most abundant species at intertidal sites, and *A. lacunosus* at subtidal sites. Similarly, Labridae, Gobiidae and Scaridae comprised the most abundant families in a Japanese seagrass bed comparable to BLS (Nakamura and Sano, 2004). In contrast, the most abundant family found by Unsworth et al. (2007) in a seagrass bed at Wakatobi was Apogonidae, and the most abundant species was *A. lacunosus*. These differing results might be due to the diel sampling methods applied by Unsworth et al. (2007), or may be site-specific.

Intertidal and subtidal sites differed regarding fish species composition. Abundant species were either pelagic species (*Atherinomorus lacunosus*, *Tylosurus crocodilus*, *Hemirhamphus far*) not

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Table 2
List of all fish species observed during visual censi at the 5 study sites. Abundance represents counts of individuals 100 m^{-2}. All values are mean ± SD. Abbreviations for site names as in Table 1.

Family	Species	Abundance				
		BBE	BBN	BBS	BBW	BLS
Apogonidae	*Apogon angustatus*			0.0 ± 0.2		
	Apogon chrysopomus	2.7 ± 8.7				0.0 ± 0.1
	Apogon margaritiphorus					0.1 ± 0.6
	Cheilodipterus quinquelineatus			0.1 ± 0.7	0.1 ± 0.7	0.0 ± 0.1
	Cheilodipterus sp. 1	1.9 ± 10.2				0.0 ± 0.2
Atherinidae	Atherinidae Gen. sp. 1	97.2 ± 226.1	1.9 ± 7.3	66.1 ± 80.2		16.6 ± 48.2
Balistidae	*Balistoides viridescens*	0.1 ± 0.2	0.1 ± 0.2			0.1 ± 0.1
	Rhinecanthus verrucosus	0.1 ± 0.2	0.1 ± 0.3	0.0 ± 0.2		0.1 ± 0.3
Belonidae	*Strongylura incisa*					2.32 ± 11.07
	Tylosurus crocodilus	2.8 ± 6.2	0.0 ± 0.2	0.8 ± 1.3	0.0 ± 0.3	
Blenniidae	*Salarias fasciatus*		0.2 ± 0.5			0.0 ± 0.1
Callionymidae	*Synchiropus ocellatus*					0.0 ± 0.1
Centriscidae	*Aeoliscus strigatus*	1.3 ± 2.5		0.1 ± 0.3		
Chaetodontidae	*Chaetodon melannotus*					0.1 ± 0.3
	Chaetodon rafflesi					0.0 ± 0.1
	Chaetodon vagabundus					0.0 ± 0.2
	Chaetodon sp.					0.0 ± 0.1
Dasyatidae	*Taeniura lymma*	0.0 ± 0.2	0.1 ± 0.2	0.0 ± 0.2		0.0 ± 0.1
Diodontidae	*Diodon holocanthus*	0.2 ± 0.4		0.1 ± 0.2		
Ephippidae	*Platax teira*			0.1 ± 0.2		
Gerreidae	*Gerres oyena*	2.0 ± 6.1		1.6 ± 3.1		0.2 ± 1.8
Gobiesocidae	*Diademichthys lineatus*			0.2 ± 0.4		
Gobiidae	*Amblygobius phalaena*	0.0 ± 0.2				
	Cryptocentrus cinctus			0.2 ± 0.8		0.1 ± 0.3
	Cryptocentrus sp.	0.0 ± 0.2		0.4 ± 0.9	0.5 ± 0.7	0.0 ± 0.2
	Amblygobius bynoensis		0.7 ± 1.2			
	Asterropteryx striatus		0.2 ± 0.6		0.4 ± 0.8	
	Valenciennea muralis		0.1 ± 0.3			
Haemulidae	*Plectorhinchus vittatus*	0.1 ± 0.2				
	Plectorhinchus lessoni				0.1 ± 0.3	0.1 ± 0.2
Hemirhamphidae	*Hemirhamphus far*	5.2 ± 7.2	0.3 ± 0.6	4.3 ± 7.7		0.1 ± 0.3
Labridae	*Cheilinus chlorourus*	0.1 ± 0.3			0.1 ± 0.2	0.1 ± 0.4
	Cheilinus trilobatus		0.2 ± 0.4	0.2 ± 0.4	0.8 ± 0.9	0.9 ± 1.8
	Cheilio inermis	15.4 ± 8.6	0.4 ± 0.7	4.9 ± 4.7	1.6 ± 2.0	1.0 ± 1.7
	Choerodon anchorago			0.1 ± 0.2		0.3 ± 0.7
	Coris pictoides			0.1 ± 0.4		
	Halichoeres argus	1.7 ± 3.0	6.8 ± 7.4	1.0 ± 1.7	17.6 ± 8.3	21.8 ± 24.6
	Halichoeres chloropterus	0.4 ± 0.8	6.7 ± 6.5	0.4 ± 0.6	9.6 ± 6.1	3.4 ± 4.2
	Halichoeres melanurus				0.0 ± 0.2	0.0 ± 0.2
	Halichoeres nigrescens					0.0 ± 0.2
	Halichoeres scapularis		1.2 ± 3.1	0.1 ± 0.3	0.2 ± 0.9	0.2 ± 0.8
	Stethojulis bandanensis		0.3 ± 0.4	0.3 ± 0.4		1.3 ± 3.7
	Stethojulis interrupta			0.1 ± 0.2		
	Stethojulis strigiventer			0.6 ± 1.3	5.7 ± 5.2	0.0 ± 0.1
	Stethojulis sp.		0.9 ± 1.7			0.0 ± 0.2
	Stethojulis trilineata		0.0 ± 0.2		0.0 ± 0.2	0.2 ± 1.0
	Labridae Gen. sp. 1	0.0 ± 0.2				
	Novaculichthys macrolepidotus	0.1 ± 0.2		0.1 ± 0.2		
	Pteragogus enneacanthus			0.1 ± 0.2		
	Thalassoma lunare	0.2 ± 0.5		0.2 ± 0.4		
	Wetmorella albofasciata					0.0 ± 0.1
Lethrinidae	*Lethrinus harak*			0.1 ± 0.3		0.2 ± 0.8
	Lethrinus obsoletus	24.6 ± 21.5		0.3 ± 0.5		0.3 ± 1.3
	Lethrinus variegatus	2.1 ± 3.7				1.1 ± 2.8
Lutjanidae	*Lutjanus ehrenbergi*	0.1 ± 0.7				0.0 ± 0.1
	Lutjanus decussatus					0.1 ± 0.4
Monacanthidae	*Acreichthys tomentosus*			0.0 ± 0.2	0.0 ± 0.2	0.1 ± 0.3
	Aluterus scriptus					0.0 ± 0.1
Mugilidae	Mugilidae Gen. sp.			0.1 ± 0.6		0.1 ± 0.4
Mullidae	*Parupeneus barberinoides*	0.3 ± 0.5		0.1 ± 0.3		
	Parupeneus barberinus	0.2 ± 0.7		0.1 ± 0.2	0.0 ± 0.2	0.6 ± 1.5
	Parupeneus indicus	0.1 ± 0.3				
	Upeneus tragula	0.9 ± 1.7		0.1 ± 0.2		0.1 ± 0.4
Muraenidae	*Siderea picta*					0.0 ± 0.1
Nemipteridae	*Pentapodus bifasciatus*	10.3 ± 7.9		6.3 ± 4.2		0.2 ± 0.7
	Pentapodus paradiseus			0.1 ± 0.4	0.0 ± 0.2	
	Pentapodus trivittatus	7.7 ± 9.3	0.9 ± 1.3	0.8 ± 1.5	8.6 ± 3.9	2.3 ± 2.8
	Scolopsis affinis	0.6 ± 1.6		0.0 ± 0.2		
	Scolopsis bilineatus					0.0 ± 0.2
	Scolopsis margaritifer	0.0 ± 0.2			0.0 ± 0.2	0.3 ± 0.8
	Scolopsis monogramma	4.2 ± 7.1				
	Scolopsis trilineata					0.1 ± 0.5

(*continued on next page*)

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Table 2 (*continued*)

Family	Species	Abundance				
		BBE	BBN	BBS	BBW	BLS
Ophichthidae	*Leiuranus versicolor*	0.0 ± 0.2	0.0 ± 0.2			
Ostraciidae	*Lactoria cornuta*	0.1 ± 0.2				
Pinguipedidae	*Parapercis cylindrica*		0.6 ± 1.2			
	Parapercis sp. 1		0.0 ± 0.2			
Platycephalidae	*Sunagocia carbunculus*		0.1 ± 0.2			0.0 ± 0.1
	Cymbacephalus beauforti					0.0 ± 0.1
Plotosidae	*Plotosus lineatus*	6.2 ± 16.4				
Pomacentridae	*Abudefduf lorenzi*					0.0 ± 0.1
	Abudefduf sexfasciatus					0.1 ± 0.6
	Abudefduf vaigiensis					0.0 ± 0.2
	Amblypomacentrus clarus	0.2 ± 0.6	0.7 ± 1.4			
	Amphiprion clarkii	0.3 ± 0.8		0.1 ± 0.4		
	Amphiprion ocellaris				0.0 ± 0.2	0.1 ± 0.6
	Amphiprion polymnus			0.2 ± 0.8		
	Pomacentridae Gen. sp. 1	1.4 ± 1.9	0.8 ± 1.2	1.6 ± 1.6	2.8 ± 2.4	0.7 ± 2.6
	Pomacentridae Gen. sp. 2			1.2 ± 2.2	0.7 ± 2.0	
	Chromis analis					0.2 ± 0.6
	Dascyllus aruanus			0.2 ± 0.4		
	Dischistodus chrysopoecilus		2.8 ± 3.3		5.0 ± 4.1	7.2 ± 7.6
	Dischistodus fasciatus		1.6 ± 1.5		1.0 ± 1.5	0.0 ± 0.1
	Dischistodus perspicillatus				0.1 ± 0.4	0.4 ± 1.2
	Pomacentrus simsiang		0.1 ± 0.3	0.2 ± 0.5		0.6 ± 1.3
	Pomacentrus tripunctatus			0.0 ± 0.2	4.5 ± 3.8	2.8 ± 3.3
	Stegastes lividus					0.1 ± 0.5
Pseudochromidae	*Congrogadus subducens*					0.0 ± 0.1
	Manonichthys paranox					0.1 ± 0.2
Scaridae	*Hipposcarus* sp.					0.1 ± 0.7
	Leptoscarus vaigiensis	0.2 ± 0.5		1.0 ± 1.3	0.9 ± 2.2	0.1 ± 0.7
	Scarus ghobban		0.1 ± 0.3			
	Scarus sp.					0.4 ± 1.9
Scorpaenidae	*Dendrochirus zebra*		0.0 ± 0.2		0.1 ± 0.3	
	Parascorpaena picta					0.0 ± 0.1
Serranidae	*Cephalopholis cyanostigma*					0.0 ± 0.1
	Epinephelus argus					0.0 ± 0.1
	Epinephelus ongus					0.2 ± 0.5
	Epinephelus quoianus	0.0 ± 0.2	0.1 ± 0.2	0.1 ± 0.4		
	Epinephelus sp.			0.2 ± 0.3		0.04 ± 0.18
Siganidae	*Siganus canaliculatus*	10.5 ± 10.0		6.8 ± 6.7		18.6 ± 37.8
	Siganus doliatus	0.1 ± 0.3		0.2 ± 0.5		
	Siganus spinus					0.0 ± 0.4
	Siganus virgatus					0.0 ± 0.2
Sphyraenidae	*Sphyraena barracuda*	0.0 ± 0.2				0.0 ± 0.2
	Sphyraena obtusata			26.4 ± 47.2		
Synanceiidae	*Synanceia horrida*			0.0 ± 0.1		0.0 ± 0.1
Synodontidae	*Synodus dermatogenys*	0.0 ± 0.2		0.1 ± 0.2		
Tetraodontidae	*Arothron manilensis*	0.3 ± 0.5		0.2 ± 0.4	0.1 ± 0.2	
	Canthigaster compressa					0.0 ± 0.1
	Canthigaster sp.					0.0 ± 0.1
total		4.5 ± 14.4	0.9 ± 2.1	2.4 ± 12.5	1.9 ± 3.1	1.0 ± 7.2

necessarily responding to changes in seagrass bed architecture, or demersal habitat generalists that were also observed in unvegetated areas or reef environments (some Labridae, Nemipteridae). An earlier assessment of fish assemblages at the island of Barrang Lompo by Erftemeijer and Allen (1993) accounted for fewer species than the present study, which might be due to different sizes of sampling plots, or sampling duration. Despite methodological differences, basic fish assemblages are similar in the two studies. Some of the recorded species in the present study are typical residents of seagrass beds, e.g. *Acreichthys tomentosus* (Monacanthidae), *Syngnathoides biaculeatus* (Syngnathidae) or *Novaculoides macrolepidotus* (Labridae). According to Kuriandewa et al. (2003), permanent residents are defined by the presence of all life history stages within the habitat. In the present study, juveniles of 32 taxa were recorded. Some common species (*Cheilio inermis*, *Halichoeres argus*, *Halichoeres chloropterus*, *Pentapodus trivittatus*, *Apogon margaritiphorus*, Pomacentridae) were found regularly as both adults and juveniles in the seagrass beds while other species were found exclusively as juveniles of reef-associated families that might utilize adjacent seagrass beds as nurseries (e.g., Chaetodontidae, Haemulidae, Ephippidae). The first group can be considered permanent residents, with the exception of *H. argus* and *S. biaculeatus*, which are known to spawn outside seagrass habitats (Kuriandewa et al., 2003), while the latter are temporary residents as juveniles. However, not all permanently residential species are restricted to seagrass habitats. Some labrid species move to macroalgal stands and unvegetated areas, for example for spawning or foraging (Kuriandewa et al., 2003). Many taxa recorded in this study, including single records, are characteristic of reef environments, e.g. nemipterids, labrids (*Halichoeres melanurus*, *Thalassoma lunare*), pomacentrids (*Amphiprion ocellaris*; *Stegastes lividus*; *Abudefduf* spp.) and chaetodontids. More than half of the species in the present study were rare, which is common in many ecological communities (Magurran and Henderson, 2003; Unsworth et al., 2007; Nakamura and Sano, 2004). These species can be referred to as occasional trespassers (visitors) from other habitats. Most of the remaining species occur regularly but not in high abundances, and can be referred to as temporary visitors.

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Table 3
Summary of non-parametric comparisons of sites using Kruskal–Wallis tests for general comparison and Wilcoxon's rank sum tests with continuity correction as post-hoc tests. Differences in fish species number and abundance, seagrass shoot density and biomass, LAI, water depth, and abundance of eight most abundant fishes were assessed at five sites in the Spermonde Archipelago: Bone Batang north, east, west and south (BBN, BBE, BBW, BBS) and Barrang Lompo south (BLS). Comparisons of post-hoc are significant at $p < 0.01$ or smaller, except for comparison of BBN and BBS concerning abundance of *H. far* and BBW and BLS concerning abundance of *S. canaliculatus* (indicated by parentheses).

Variables	General comparison	Differences between sites				
		BBE (1)	BBN (2)	BBS (3)	BBW (4)	BLS (5)
Fish species number	***					
Fish abundance (Ind 100 m^{-2})	***	2, 3, 4, 5	1, 4, 5	1, 4	1, 3	1, 2
Seagrass shoot density (shoots m^{-2})	***	3, 5	3	2, 4	5	1, 4
Seagrass biomass (g m^{-2})	***	2, 3, 4,	1, 3, 4, 5	1, 2, 5	1, 2	2, 3
LAI	NS	–	–	–	–	–
Water depth	***	2, 3, 4, 5	1, 3, 4, 5	1, 2, 4, 5	1, 2, 3, 5	1, 2, 3, 4
Abundance of single fish species						
A. lacunosus	NS	–	–	–	–	–
C. inermis	***	2,3,4,5	1,3,4	1,2,4	1,2,3	1,3
D. chrysopoecilus	NS	–	–	–	–	–
H. argus	***	2, 4, 5	1, 3	2, 5	1	1, 3
H. chloropterus	***	2, 4, 5	1, 3, 5	2, 5	1, 5	1, 2, 3, 4
H. far[a]	***	2, 3, 5	1, (3)	1, (2)	–	1
P. trivittatus	***	2, 3, 4, 5	1, 4	1, 4	1, 2, 3, 5	1, 4
S. canaliculatus[b]	***	5	–	5	(5)	1, 3, (4)
T. crocodylus	NS	–	–	–	–	–

*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.
Differences between sites indicated in parentheses were found significant at a level of $p = 0.041$ (*H. far*), and $p = 0.048$ (*S. canaliculatus*).
[a] BBW excluded from analysis due to lack of samples.
[b] BBN excluded from analysis due to lack of samples.

The most abundant species in intertidal beds was *Halichoeres argus*, while *Atherinomorus lacunosus* showed the highest abundances at subtidal sites. One reason for the distribution of *H. argus* might be the structurally rich canopy architecture of BLS and BBW (short and long seagrasses intermingled, forming various storeys) as well as the vicinity to coral reefs, rubble and macroalgal zones (BBN). This species predominantly inhabits highly structured phytal zones and reef flats (pers. obs. C.P.), and does not appear to prefer uniform seagrass canopies, like BBS (dense *Enhalus* bed) and BBE (dense bed of *Cymodocea* and *Halodule*). For larger zoobenthivores in general, there were no clear site preferences. *Pentapodus bifasciatus* was found only at subtidal sites, while *Halichoeres chloropterus* was rare at these sites and showed higher abundances at intertidal sites. Vonk et al. (2010) found that most zoobenthivores preferred seagrass beds with an open canopy (low seagrass leaf biomass), except for *Cheilio inermis*, which prefers closed canopy beds (high seagrass biomass). Highest abundances of *C. inermis* were found at BBE and BBS. This coincides with the results of Vonk et al. (2010). The common siganid *Siganus canaliculatus* was strongly abundant at BLS and BBS, where the shoot density of *Enhalus acoroides* was highest. This species can often be observed feeding on the dense epiphyte layer on the leaves of *E. acoroides* (Tomascik et al., 1997).

4.3. Effects of seagrass variables and water depth

The present study investigated fish assemblages in Indo-Pacific multi-species seagrass beds. Fish assemblages in seagrass beds at different water depths and with differing canopy structure defined by significantly different shoot density, biomass and LAI, differed significantly in terms of species number, total abundance, and abundance of most common species. The GLM revealed an effect of water depth and seagrass shoot density on total fish abundance and LAI, seagrass biomass and water depth affected the abundance of most common fish species. Water depth affected total fish assemblages and most common fish species at BBE (greatest mean water depth) and BBN (lowest mean water depth), respectively. It can be

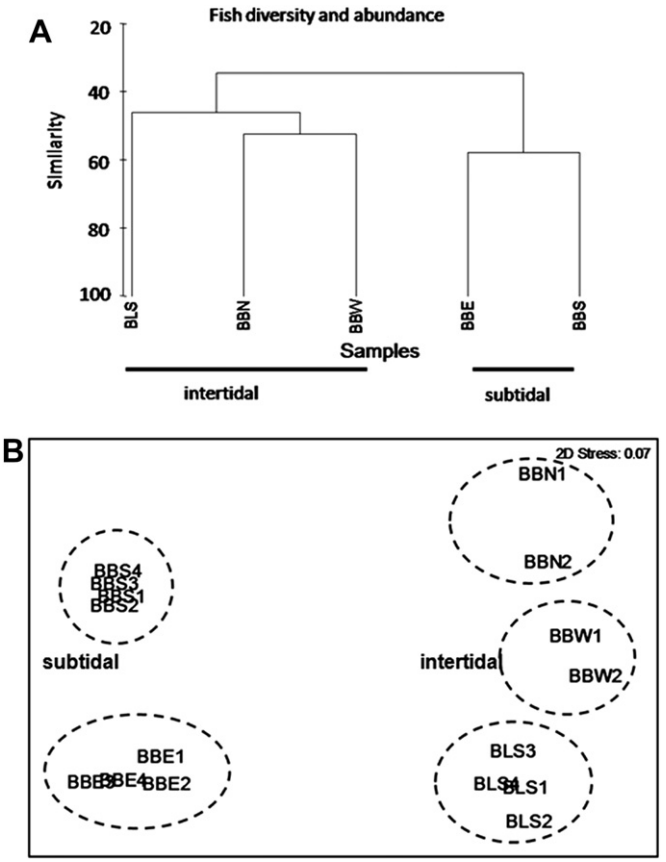

Fig. 3. Similarity of study sites based on fish abundance and fish species composition (data square root transformed). BBE = Bone Batang East, BBN = Bone Batang North, BBS = Bone Batang south, BBW = Bone Batang west, and BLS = Barrang Lompo south. (A) Cluster analysis (S17 Bray Curtis similarity). (B) Non-metric scale ordination (nMDS) of permanent transects at each study site.

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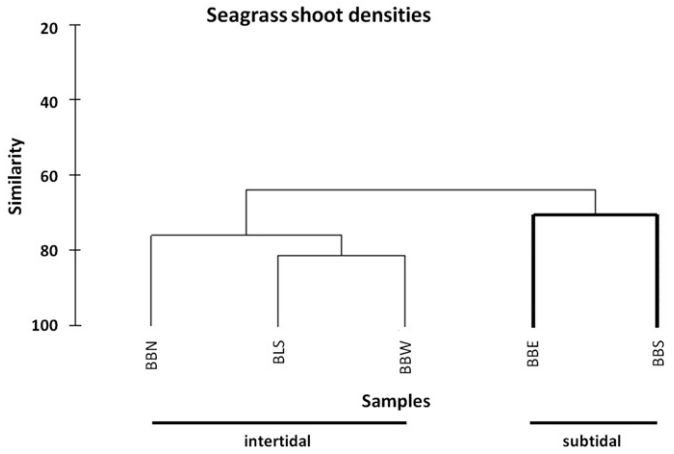

Fig. 4. Similarity of study sites based on seagrass shoot densities (shoots m^{-2}) based on cluster analysis (S17 Bray Curtis similarity with square root transformed data). Study sites can bedivided into intertidal and subtidal seagrass beds. Intertidal seagrass beds differ distinctly from each other, while subtidal seagrass beds do not (bold cluster). BBE = Bone Batang East, BBN = Bone Batang North, BBS = Bone Batang south, BBW = Bone Batang west, and BLS = Barrang Lompo south.

assumed that greater depths may support higher fish abundances, especially pelagic species and schooling fish. Thomas and Connolly (2001) found that species richness and abundances of fish in subtropical saltmarshes were positively correlated to seasonally high water levels.

It is generally accepted that structurally rich seagrass beds, i.e. beds with high shoot density and/or biomass, provide favourable conditions, such as increased habitat complexity and food availability, and reduced predation pressure (Hovel et al., 2002; Vonk et al., 2010). High fish abundances in relation to high seagrass shoot densities were encountered in previous studies (e.g. Gullström et al., 2002; Vonk et al., 2010). In the past, numerous studies have dealt with the effects of various seagrass and environmental variables on faunal community variables. The results of these studies were inconsistent, probably due to differences in geographical latitude, species-specific habitat requirements, scale-dependency of faunal responses to environmental variables, and/or applied methods (Martin and Cooper, 1981; Middleton et al., 1984; Blaber et al., 1992; Hovel et al., 2002). Hovel et al. (2002) found that of seven environmental variables tested, only seagrass biomass and relative wave exposure index had strong effects on macrofauna in North American seagrass beds. However, significant relationships between seagrass biomass and animal densities were only detected at high seagrass biomasses, which is in contradiction with the present study (BBE, BBN). Attrill et al. (2000) found positive relationships between seagrass biomass and macroinvertebrate abundances in subtidal *Zostera marina* beds. Conforming to the present study, overall faunal abundance in mixed-species seagrass beds off Bone Batang was found to be higher in beds with higher shoot densities and biomasses compared to beds with lower shoot densities, although certain taxa apparently preferred the less structured habitat (Vonk et al., 2010).

Different species compositions among study sites are attributed to species-specific habitat preferences (Hyndes et al., 2003). The GLM showed that abundances of most common fishes were influenced by LAI, seagrass biomass, and water depth at certain sites. Differences in seagrass leaf surface area were found to be important for zoobenthos and thus zoobenthivores. Large leaf surfaces/unit biomass ratios provide better shelter from predation than leaves of lower ratios but conversely they facilitate predation for zoobenthivores (Stoner, 1982). In the present study, most recorded species

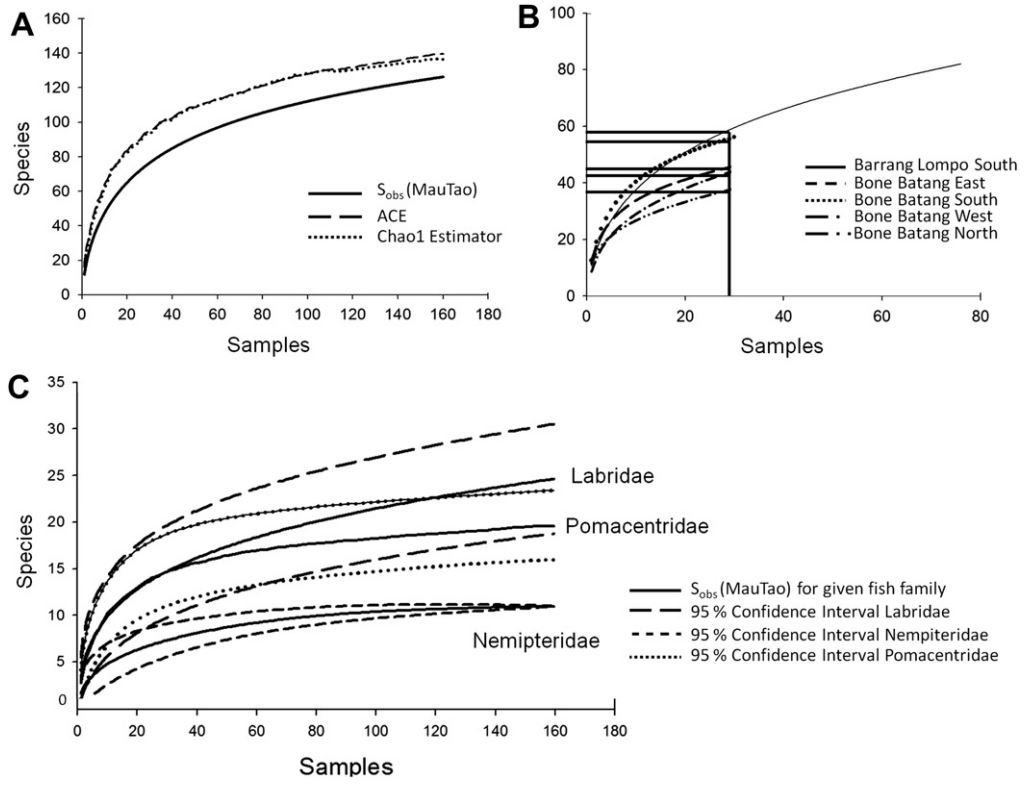

Fig. 5. Fish species accumulation curves for the study area. (A) Randomized species accumulation curve of all fish species over all 5 sampling sites (gamma diversity). (B) Randomized species accumulation curves for the five sampled habitats indicating Sobs(Mao Tau) for all species (C) Randomized species accumulation curves (Sobs (Mao Tau)) for fish species of the families Labridae, Pomacentridae and Nemipteridae summed overall habitats. Dashed lines refer to upper and lower boundaries of the 95% confidence interval.

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and four out of nine of the dominating species were zoobenthivores, which is comparable to other Indo-Pacific seagrass beds (Unsworth et al., 2007; Vonk et al., 2008, 2010). Vonk et al. (2010) found that this trophic guild often prefers open (low biomass) canopies, which is probably related to enhanced foraging efficiency in such habitats (Orth et al., 1984; Jackson et al., 2006). As an exception to this rule, Vonk et al. (2010) mention the cigar wrasse *Cheilio inermis*, which preferred habitats with higher seagrass shoot densities. These findings coincide with the present study. Cigar wrasse were found in highest abundances at BBS and BBE (high plant biomass and shoot density, respectively), while other abundant labrids and the nemipterid *Pentapodus trivittatus* were observed in greater abundances in seagrass beds of lower shoot densities.

Most studies on fish assemblages in seagrass beds focus on monospecific beds (e.g. Middleton et al., 1984; Rotherham and West, 2002; Hyndes et al., 2003). For the tropical Indo-Pacific, however, highly diverse mixed-species seagrass meadows are characteristic. Still, few studies emphasize the importance of these habitats. Vonk et al. (2010) have done so to a certain extent by distinguishing mixed-species seagrass beds with open (low biomass) and closed (high biomass) canopy structure, although both of the seagrass beds consisted of the same seagrass species. Nakamura and Sano (2004) found significantly higher fish diversity and abundance in seagrass beds dominated by the large *Enhalus acoroides* compared to beds dominated by shorter species. In the present study, the highest fish diversity was found at a site where large *Enhalus* shoots are intermingled with other species (BLS, BBW), while fish abundances were highest at sites with highest biomass (BBS) or highest shoot densities (BBE). Although the dataset did not allow applying a GLM to a single species, modelling of total abundance of the most common species showed effects of seagrass LAI, biomass and water depth. The outcomes suggest that fish diversity may rather be a correlate of seagrass diversity than of seagrass density, while it appears to be vice versa for fish abundances. This study shows clearly that seagrass variables have an impact on fish both on assemblage and species level, and that seagrass beds differing in seagrass shoot density, biomass and LAI have the capacity to support distinctly different fish assemblages, even at small patch sizes. The outcomes of this study underline the urgency for the management of seagrass beds at small scales in order to preserve habitat diversity, and thus biodiversity and ecosystem services at a landscape scale. However, the influence of environmental variables on faunal densities can differ considerably between seasons and years (Hovel et al., 2002), thus long-term studies and additional variables such as patchiness of seagrass beds or hydrodynamic setting may be necessary to fully comprehend seagrass parameters and their influences on faunal assemblages.

5. Conclusions

Seagrass beds with different canopy architecture on small tropical islands in the Indonesian Spermonde Archipelago harbour distinct and highly diverse fish assemblages at small spatial scales. Overall fish abundance and diversity and biotic (seagrass shoot density, biomass, LAI) and abiotic factors (water depth) differed with respect to study site. Cluster analyses suggest a distinct grouping into subtidal and intertidal sites with respect to fish and seagrass densities and species composition. Species numbers found in the present study are similar to (Nakamura and Sano, 2004) or higher than those found in other recent studies (Erftemeijer and Allen, 1993; Vonk et al., 2008, 2010). Additionally, higher sampling efforts (night-time sampling) may even increase species numbers, as species accumulation did not reach saturation for the two most speciose families and total fish diversities. A proportion of temporary residents was found in all seagrass beds, confirming the value of such habitats to reef fish. Also, effects of seagrass parameters and water depth on fish abundances were revealed. Further, a long-term study might enhance our knowledge of seasonal fluctuations in fish community parameters, or influences of seagrass parameters on fish assemblages. Considering species richness, distinct variability of fish assemblages and seagrass parameters at such small scale, the value for indigenous fishery, and globally high rates of habitat degradation in seagrass beds, there is a need for conservation efforts to maintain or enhance fish diversity, and to assure sustainable and rich socioeconomic use.

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Appendix A. Supplementary material

Supplementary data related to this article can be found online at doi:10.1016/j.ecss.2012.04.022.

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