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DIPLOMARBEIT

Fish diversity patterns and trophic relationships in different types of tropical seagrass meadows in the Spermonde Archipelago, South Sulawesi, Indonesia

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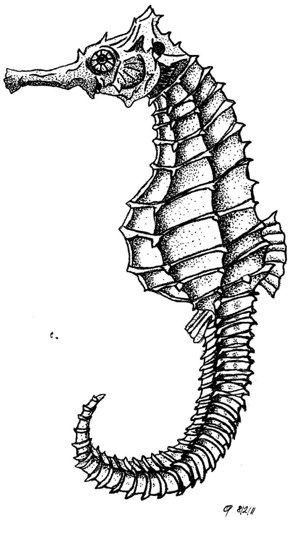
Here briefly, learning, one with nature. Memories swim ever gently.

Peter F. Sale



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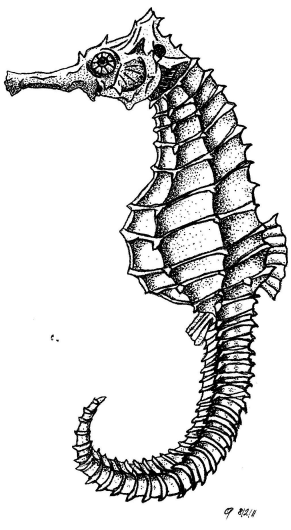

1. General introduction

1.1. The role of seagrass ecosystems

Tropical seagrass beds are nutrient-poor habitats (Vonk et al., 2008) that support high a floral and faunal biomass, biodiversity and productivity (Parrish, 1989; Gullström et al., 2002; Duffy, 2006; MacArthur & Hyndes, 2007). All over the world, seagrass beds contribute substantially to shallow coastal marine and estuarine areas (Gullström et al., 2002; Nakamura et al., 2003; Gillanders, 2006), making them among the most widespread coastal ecosystems (Duffy, 2006). In the tropics, they are often located adjacent to coral reefs (Nakamura & Sano, 2003). Since they are structurally highly complex, they provide shelter from predation and important feeding grounds for both invertebrates and fish (Dorenbosch et al., 2005; Nakamura et al., 2003; Unsworth et al., 2007b; Vonk et al., 2008), but also for higher vertebrates such as mammals and reptiles (e.g. Parrish, 1989; Baelde, 1990; Edgar & Shaw, 1995; Duarte & Chiscano, 1999; Beck et al., 2001; Gullström et al., 2002). Furthermore, seagrass beds interact strongly with adjoining coral reefs, mangroves or sandy sea bottoms, for example via animal migrations for foraging, spawning or related to ontogenetics (Ogden & Buckman, 1973; Ogden & Quinn, 1984; Pollard, 1989; de la Morinière et al., 2002; Dorenbosch et al., 2006; Verwej et al., 2006).

South-East Asia is a biodiversity hotspot due to its enormous species richness and exceptionally high number of endemic organisms (Sodhi et al., 2004). Indonesian coasts, at the heart of the so-called ′coral triangle′, harbor an exceptionally high fish diversity. Nonetheless, scientific work on seagrass ecosystems and their fish assemblages has focussed mostly on the Caribbean (summarized by Unsworth et al., 2007). Few studies

studies have examined the fish assemblages of Indo-Pacific seagrass beds (Erftemeijer & Allen, 1993; Hutomo & Martosewojo 1977; Pet-Soede et al., 2001; Nakamura & Sano, 2004; Unsworth et al., 2007; Vonk et al., 2010). Most of the few publications on Indonesian seagrass beds suggest a high number of around 80 species of fish in the associated fish assemblages (Hutomo & Martosewojo, 1977; Kuriandewa et al., 2003; Unsworth et al., 2007a). The inconsistent methodology, however, suggests that many more species are present. The Spermonde Archipelago in the Indonesian province South Sulawesi (Sulawesi Selatan) has intensively studied in the last decades, with the focus on a variety of invertebrate taxa such as corals (Cleary et al., 2005; Knittweis et al., 2009), sponges (Cleary et al., 2005; de Voogd et al., 2006), foraminiferans (Cleary et al., 2005) or holothurians (Massin, 1999). Publications on fish assemblages in seagrass beds are scarce (Erftemeijer & Allen, 1993; Pet-Soede et al., 2001; Vonk et al., 2008, 2010).

1.2. The Indonesian Spermonde Archipelago

The Spermonde Archipelago is situated along the west coast of the Indonesian province South Sulawesi (Sulawesi Selatan) and consists of a number of small coral islands on the shelf area (Fig. 1). It is 200 km long and 40 km wide. The distance of the islands from Makassar ranges between 2 km (Laelae) and about 60 km (Kapoposang). The islands chosen for the present study were Barrang Lompo and Bone Batang (14 and 15 km off Makassar). The island of Barrang Lompo is easily accessible by ferry boat (daily); this island is about 0.5 km² in size and has a population of 5000 people. The human impact on the surrounding seagrass beds and coral reefs is high due to exploitation of marine resources, invasive fishing techniques (blast fishing, cyanide fishing, gill nets) and sewage water, which is released directly into the sea. Bone Batang consists only of a small emerged sandbank surrounded by a vast reef flat and inter- and subtidal seagrass beds and macroalgae field. To the west, there is a small coral reef and intertidal reef flat with a seagrass bed, algae patch and rubble zone; the east consists of a subtidal sandy area. The seagrass beds on both islands are multiple-species stands with varying proportions of the different seagrass species and thus different canopy architecture; each seagrass bed is comprised by three to six species (Hydrocharitaceae: *Enhalus acoroides, Thalassia hemprichii, Halophila ovalis*; Cymodoceaceae: *Cymodocea rotundata, Halodule uninervis, Syringodium isoetifolium*).

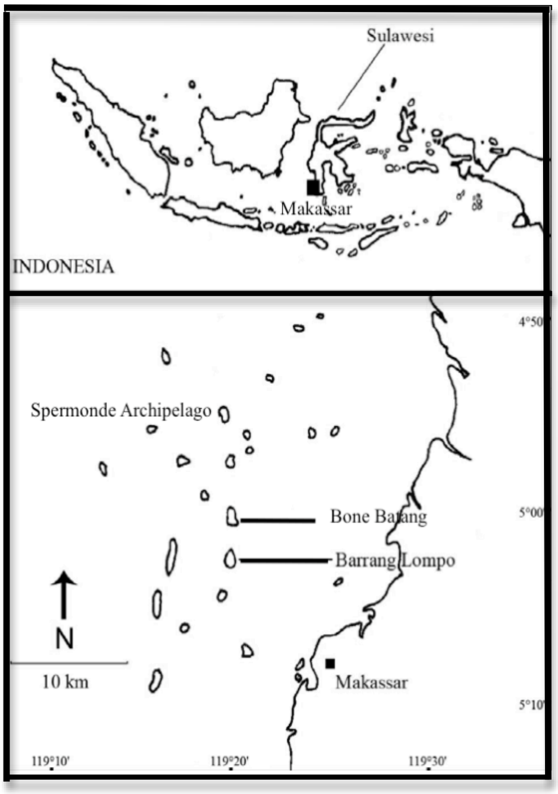

Fig. 1. Location of Sulawesi and the city of Makassar in Indonesia (above) and of the two coral islands in the Spermonde Archipelago off South Sulawesi (adapted from Liu et al., 2008).

1.3. Fish assemblages in different types of seagrass beds

Worldwide, most studies comparing fish assemblages in different seagrass beds focussed on monospecific stands (Middleton et al., 1984; Rotherham & West, 2002; Hyndes et al., 2003; Nakamura & Sano, 2004a,b). Nonetheless, many studies emphasize that fish abundance increases with increasing seagrass bed complexity (e.g. Heck & Orth, 1980; Bell & Westoby, 1986; Nakamura & Sano, 2004b) and that multiple-species seagrass beds might support enormous fish diversity. Only a few authors focussed on mixed-species seagrass habitat (e.g. Martin & Cooper, 1981; Blaber et al., 1992). Most of those studies focussing on differences between fish assemblages in different types of seagrass meadows reported highly differing effects of canopy structure on fish assemblages depending on seagrass bed (Martin & Cooper, 1981; Kiswara et al., 1991; MacArthur & Hyndes, 2001; Nakamura & Sano, 2004b; Unsworth et al., 2010; Vonk et al., 2010). A smaller number of studies do not find significant differences for total fish abundance between seagrass beds (Middleton et al., 1984, Loneragan, 1998), but for the abundance of single fish species (e.g. Rooker & Holt, 1997). Blaber et al. (1992) did not find any differences for mixed tall dense and short seagrass beds.

Typical fish families in Indonesian seagrass beds are Apogonidae (e.g. *Apogon margaritiphorus*), Atherinidae, Labridae, Gerridae, Siganidae, Gobiidae, and Monacanthidae. Although seagrass beds can be extraordinarily species-rich, only a small number of fish species are considered to be permanent residents and typical for seagrass environments. These include *Syngnathoides biaculeatus* (Syngnathidae), *Novaculoides* spp. (Labridae), *Pervagor* spp. (Monacanthidae) and *Centrogenys vaigiensis* (Centrogenyidae). Other species that are quite common in seagrass beds can also be found in other habitats such as adjacent algal beds; these include the labrids *Halichoeres argus* and *Cheilio inermis* (Kuriandewa et al., 2003).

1.4. Trophic relationships in seagrass beds

1.4.1. Food web analysis

Although South-East Asian seagrass beds support a high fish diversity and many species are at least of local commercial interest, little information is available on fish assemblages and only a few studies on trophic relationships have been published (Unsworth et al., 2007b, Kneer et al., 2008; Vonk et al., 2008). Both the structure and functioning of a fish assemblage relies partially on the trophic status and relationships of the component species (Carassou et al., 2008). The trophic relationships of fish communities are fundamental tools for fisheries and ecosystem management (Blaber, 1997; Hajisamae & Ibrahim, 2008). Information on food webs can be gained by a range of methods. Two of the most common ones to describe food webs are gut content analysis and stable isotope analysis. Gut content analysis yields representative information on food items consumed at the time of sampling or a few hours earlier (Pinnegar & Polunin, 2000; Carassou et al., 2008); this represents a mere snapshot of the dietary spectrum of a species. The taxa resolution of food items, however, is high and can provide insights into the commonly preferred food species. Unfortunately, gut contents provide no information on what food items are digested and assimilated (Melville & Conolly, 2003; Lugendo et al., 2006). Nor can it be assumed that all food items are digested at the same rate (Pinnegar & Polunin, 2000). For example, zooplankton is digested much faster than other food items (Post, 2002). This also leads to interpretational problems in fish taxa that grind food items, such as labrids (Pinnegar & Polunin), or in herbivores, such as some partially or predominantly herbivorous members of the family Hemirhamphidae. Members of the latter, such as *Hyporhamphus* *melanochir* (cf. Klumpp & Nichols, 1983; Robertson & Klumpp, 1983) or *Hemirhamphus far* (pers. obs.), macerate plant food items.

In contrast, applying stable isotope analysis on consumers (e.g. fish species), primary producers (e.g. algae, phytoplankton or seagrass) and primary consumers yields information on food web-structure and long-term energy flow (Pinnegar & Polunin, 1999; Post, 2002; Carassou et al., 2008). The combination of stable or heavy carbon ($\delta^{13}C$) and stable or heavy nitrogen ($\delta^{15}N$) is a very common approach to modelling or describing food webs and the relationships within (Kruitwagen et al., 2010). Stable isotope analysis is based on the accumulation of stable carbon and nitrogen within the food web, i.e. on actual food assimilation of organisms (Davenport & Bax, 2002; Cocheret de la Morinière et al., 2003; Abed-Navandi & Dworschak, 2005; Vonk et al., 2008; Kruitwagen et al., 2010): stable isotope ratios are mainly determined by consumed and digested food items (Marguilier et al., 1997). Enrichment of stable nitrogen takes place at a rate of ~3.4 ‰ relative to dietary organisms, allowing an estimate of the trophic position of the consumer (Peterson & Fry, 1987; Pinnegar & Polunin, 2000; Post, 2002). Enrichment of stable carbon is much lower, with an average gain of about ~0.4 ‰ (maximum 1 ‰) per trophic level; thus, stable carbon values change little with trophic transfer. Nonetheless, since stable carbon values vary strongly among primary producers, depending on the photosynthetic pathway a plant uses (C3, C4, CAM), they are a powerful tool in determining the source of assimilated food items (Marguilier et al., 1997; Post, 2002; Layman, 2007). When there are significant differences between the primary producers of a seagrass bed, the contribution of each group of primary producers can be identified as a diet of a herbivore (Yamamuro, 1999; Vonk et al., 2008). In terrestrial systems, large-scale (e.g. continental) patterns of stable carbon can also indicate the geographic origin of migratory organisms (Hobson et al., 1999). Compared to gut content analysis, stable isotope analysis provides only an average estimate of preferred groups of food items (Peterson & Fry, 1987; Vonk et al., 2008). It cannot give a detailed picture of an organism's diet: the resolution on the food spectrum is low. Thus, temporal bias is reduced compared to gut content analysis, and food types such as detritus and epiphytes can be recognised as a food source in isotope signatures of the consumer. These sources are difficult to quantify by gut content analysis (Pinnegar & Polunin, 1999; Pinnegar & Polunin, 2000).

1.4.2. Herbivory in seagrass beds

Herbivory in seagrass beds was an early focus in marine ecology and was long considered to be of minor importance. However, in contrast to temperate seagrass beds, where fish herbivory on seagrasses is low (cf. Pollard, 1984; Pinnegar & Polunin, 2000; Heck & Valentine, 2006), in the tropics the consumption of seagrasses and their epiphytes by fishes can be substantial (e.g. Kirsch et al., 2002; MacArthur & Hyndes, 2007; Liu et al., 2008; Vonk et al., 2008). Some authors consider that the extent of herbivory in seagrass beds is still underestimated (Valentine & Duffy, 2006; Unsworth et al., 2007b).

1.5. Aims of the study

The present study has two central topics: the diversity of fish assemblages in different types of Indonesian seagrass beds, and trophic relationships within multiple-species seagrass beds. In the framework of the first topic, the following hypotheses are tested: (1) fish density is correlated with seagrass shoot density; (2) seagrass beds with different canopy structures do not differ significantly in fish diversity, species composition and abundance; (3) fish diversity is lowest at the most impacted sites. The second topic is designed to describe the food web of a multiple-species seagrass bed of the island of Barrang Lompo, and to compare the outcomes of stable isotope and food web analysis. This study also focuses on the distribution of feeding guilds of different types of seagrass beds at four sampling sites at the islands of Barrang Lompo and Bone Batang, based on visual census data.

2. References

Abed-Navandi, D. & Dworschak, P.C. 2005. Food sources of tropical thalassinidean shrimps: A stable-isotope study. Marine Ecology Progress Series 291, 159-168.

Baelde, P. 1990. Differences in the structures of fish assemblages in *Thalassia testudinum* beds in Guadeloupe, and their ecological significance. Marine Biology 105, 163-173.

Beck, M.W., Heck, K.L, Able, K.W., Childers, D.I., Eggleston, D.B., Gillanders, B.M., Halpern, B., Hays, C.G., Hoshino, K., Minello, T.J., Orth, R.J., Sheridan, P.F. & Weinstein, M.R. 2001. The identification, conservation and management of estuarine and marine nurseries for fish and invertebrates. BioScience 51, 633-661.

Bell, J.D. & Westoby, M. 1986. Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. Journal of Experimental Biology 104, 249-274.

Blaber, S.J.M., Brewer, D.T., Salini, J.P., Kerr, R.D. & Conacher, C. 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, northern Australia. Estuarine, Coastal and Shelf Science 35, 605-620.

Carassou, L., Kulbicki, M., Nicola, T.J.R. & Polunin, N.V.C. 2008. Assessment of fish trophic status and relationships by stable isotope data in the coral reef lagoon of New Caledonia, southwest Pacific. Aquatic Living Resources 21, 1-12.

Cleary, D.F.R., Becking, L.E., de Voogd, N.J., Renema, W., de Beer, M., van Soest, R.W.M., Hoeksema, B.W. 2005. Variation in the diversity and composition of benthic taxa as a function of distance offshore, depth and exposure in the

Spermonde Archipelago, Indonesia. Estuarine, Coastal and Shelf Science 65, 557-570.

Cocheret de la Morinière, E., Pollux, B.J.A., Nagelkerken, I., Hemminga, M.A., Huiskes, A.H.L. & van der Velde, G. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef-continuum: Stable isotopes and gut-content analysis. Marine Ecology Progress Series 246, 279-289.

Davenport, S.R. & Bax, N.J. 2002. A trophic study of a marine ecosystem off southeastern Australia using stable isotopes of carbon and nitrogen. Canadian Journal of Fisheries and Aquatic Science 59, 514-530.

de Voogd, N.J., Cleary, D.F.R., Hoeksema, B.W., Noor, A. & van Soest, R.W.M. 2006. Sponge beta diversity in the Spermonde Archipelago, SW Sulawesi, Indonesia. Marine Ecology Progress Series 309, 131-142.

Dorenbosch, M., Grol, M.G.G., Christianen, M.J.A., Nagelkerken, I. & van der Velde, G. 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. Marine Ecology Progress Series 302, 63-76.

Dorenbosch, M., Grol, M.G.G., Nagelkerken, I. & van der Velde, G. 2006. Different surrounding landscapes may result in different fish assemblages in East African seagrass beds. Hydrobiologia 563, 45-60.

Duarte, C.M. & Chiscano, C.L.1999. Seagrass biomass and production: A reassessment. Aquatic Botany 65, 159-174.

Duffy, J.E. 2006. Biodiversity and the functioning of seagrass ecosystems. Marine Ecology Progress Series 311, 233-250.

Edgar, G.J. & Shaw, C. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. I. Species richness, size-structure and production of fishes in Western Port, Victoria. Journal of Experimental Marine Biology and Ecology 194, 53-81.

Erftemeijer, P.L.A. & Allen, G.R. 1993. Fish fauna of seagrass beds in south Sulawesi, Indonesia. Records of the West Australian Museum 16, 269-277.

Gillanders, B.M. 2006. Seagrasses, fish, and fisheries. In: Larkum, A.W.D., Orth, R.J. & Duarte, C.M. (Eds.), Seagrasses: Biology, ecology and conservation. Springer, Dordrecht, The Netherlands, pp. 503-536.

Gullström, M., de la Torre Castro, M., Bandeira, S.O., Björk, M., Dahlberg, M., Kautsky, N., Rönnbäck, P. & Öhmann, M.C. 2002. Seagrass ecosystems in the western Indian Ocean. Ambio 31, 588-596.

Heck Jr., K.L. & Orth, R.J. 1980. Seagrass habitas: The roles of habitat complexity, competition and predation in structuring associated fish and mobile macroinvertebrate assemblages. In: Kennedy, V.S. (Ed.), Estuarine perspectives. Academic Press, New York, pp. 449-462.

Heck Jr., K.L. & Valentine, J.F. 2006. Plant-herbivore interactions in seagrass meadows. Journal of Experimental Marine Biology and Ecology 330, 420-436.

Hobson, K.A., Wassenaar, L.I. & Taylor, O.R. 1999. Stable isotopes (δD and $\delta^{13}C$) are geographic indicators of natal origins of monarch butterflies in eastern North America. Oecologia 120, 397-404.

Hutomo, M. & Martosewojo, S. 1977. The fishes of segrass communities on the west side of Burung Island (Pari Islands, Seribu Islands) and their variations in abundances. Marine Research in Indonesia 17, 147-172.

Hyndes, G.A., Kendrick, A.J., MacArthur, L.D. & Stewart, E. 2003. Differences in the species- and size-composition of fish assemblages in three distinct seagrass habitats with differing plant and meadow structure. Marine Biology 142, 1195-1206.

Khalaf, M.A. & Kochzius, M. 2002. Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea. Marine Ecology Progress Series 239, 287-299.

Kirsch, K.D., Valentine, J.F., Heck Jr., K.L. 2002. Parrotfish grazing on turtlegrass *Thalassia testudinum*: Evidence for the importance of seagrass consumption in food web dynamics of the Florida Keys National Marine Sanctuary. Marine Ecology Progress Series 227, 71-85.

Kiswara, W., Genisa, A.S., Arifin, A. & Purnomo, L.H. 1991. A preliminary study of the species composition, abundance and distribution of fishes in the seagrass beds of Banten Bay, West Java, Indonesia. In: Sasekumar, A. (Ed.), Mangrove fisheries and connections. ASEAN Australia Marine Science Project, Living Coastal Resources (Malaysia), pp. 183-213.

Klumpp, D.W. & Nichols, P.D. 1983. Nutrition of the Southern sea garfish *Hyporhamphus melanochir*: Gut passage rate and daily consumption of two food types and assimilation of seagrass components. Marine Ecology Progress Series 12, 207-216.

Kneer, D., Asmus, H. & Vonk, J.A. 2008. Seagrass as the main food source of *Neaxius* *acanthus* (Thalassinidea: Strahlaxiidae), its burrow associates, and of *Corallianassa coutieri* (Thalassinidea: Callianassidae). Estuarine, Coastal and Shelf Science 79, 620-630.

Knittweis, L., Jompa, J., Richter, C. & Wolff, M. 2009. Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde Archipelago, South Sulawesi, Indonesia. Coral Reefs 28, 793-804.

Kruitwagen, G., Nagelkerken, I., Lugendo, B.R., Mgaya, Y.D. & Wendelaar Bonga, S.E. 2010. Importance of different carbon sources for macroinvertebrates and fishes of an interlinked mangrove-mudflat ecosystem (Tanzania). Estuarine, Coastal and Shelf Science 88, 464-472.

Kuriandewa, T.E., Kiswara, W., Hutomo, M. & Soemodihardjo, S. 2003. The seagrasses of Indonesia. In: Green, E.P. & Short, F.T. (Eds.), World Atlas of Seagrasses. Prepared by the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley USA, pp. 171-182.

Layman, C.A. 2007. What can stable isotope ratios reveal about mangroves as a fish habitat? Bulletin of Marine Science 80, 513-527.

Liu, H.T.H., Kneer, D., Asmus, H. & Ahnelt, H. 2008. The feeding habits of *Austrolethops wardi*, a gobiid fish inhabiting burrows of the thalassinidean shrimp *Neaxius acanthus*. Estuarine, Coastal and Shelf Science 79, 764-767.

Loneragan, N.R., Kenyon, R.A., Staples, D.J., Poiner, I.R. & Conacher, C.A. 1998. The influence of seagrass type on the distribution and abundance of postlarval and juvenile tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) in the western

Gulf of Carpentaria, Australia. Journal of Experimental Marine Biology and Ecology 228, 175-195.

Lugendo, B.R., Nagelkerken, I., van der Velde, G. & Mgaya, M.D. 2006. The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas for juvenile fishes in Chwaka Bay, Zanzibar: Gut content and stable isotope analysis. Journal of Fish Biology 69, 1639-1661.

MacArthur, L.D. & Hyndes, G.A. 2007. Varying foraging strategies of Labridae in seagrass habitats: Herbivory in temperate seagrass meadows? Journal of Experimental Marine Biology and Ecology 340, 247-258.

Marguillier, S., van der Velde, G., Dehairs, F., Hemminga, M.A. & Rajagopal, S. 1997. Trophic relationships in an interlinked mangrove-seagrass ecosystem as traced by $\delta^{13}C$ and $\delta^{15}N$. Marine Ecology Progress Series 151, 115-121.

Martin, F.D. & Cooper, M. 1981. A comparison of fish faunas found in pure stands of two Atlantic seagrasses, *Thalassia testudinum* and *Syringodium filiforme*. Northeast Gulf Science 5, 31-37.

Massin, C. 1999. Reef-dwelling Holothuroidea (Echinodermata) of the Spermonde Archipelago (South-West Sulawesi, Indonesia). Zoologische Verhandelingen Leiden 329, 3-144.

Melville, A.J. & Connolly, R.M. 2003. Spatial analysis of stable isotope data to determine primary sources of nutrition for fish. Oecologia 136, 499-507.

Middleton, M.J., Bell, J.D., Burchmore, J.J., Pollard, D.A. & Pease, B.C. 1984. Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. Aquatic Botany 18, 89-109.

Moncreiff, C.A. & Sullivan, M.J. 2001. Trophic importance of epiphytic algae in subtropical seagrass beds: Evidence from multiple stable isotope analyses. Marine Ecology Progress Series 215, 93-106.

Nakamura, Y., Horinouchi, M., Nakai, T. & Sano, M. 2003. Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, Southern Japan. Ichthyological Research 50, 15-22.

Nakamura, Y. & Sano, M. 2004a. Comparison between community structures of fishes in *Enhalus acoroides*- and *Thalassia hemprichii*-dominated seagrass beds on fringing coral reefs in the Ryukyu Islands, Japan. Ichthyological Research 51, 38-45.

Nakamura, Y. & Sano, 2004b. Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: Importance of the seagrass bed as juvenile habitat. Fisheries Science 70, 788-803.

Ogden, J.C. & Buckman, N.S. 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54, 589-506.

Ogden, J.C. & Quinn, T.P. 1984. Migration in coral reef fishes: Ecological significance and orientation mechanisms. In: McCleave, J.D., Arnold, G.P., Dodson, J.J., Neill, W.H. (Eds.), Mechanisms of migration in fishes. Plenum, New York, pp. 293-308.

Parrish, J.D. 1989. Fish communities of interacting shallow-water habitats in tropical oceanic regions. Marine Ecology Progress Series 58, 143-160.

Peterson, B.J. & Fry, B. 1987. Stable isotopes in ecosystem studies. Annual Review of Ecology and Systematics 18, 293-320.

Pet-Soede, C., van Densen, W.L.T., Pet, J.S. & Machiels, M.A.M. 2001. Impact of Indonesian coral reef fisheries on fish community structure and the resultant catch composition. Fisheries Research 51, 35-51.

Pinnegar, J.K. & Polunin, N.V.C. 1999. Differential fractionation of δ^{13}C and δ^{15}N among fish tissues: Implications for the study of trophic interactions. Functional Ecology 13, 225-231.

Pinnegar, J.K & Polunin, N.V.C. 2000. Contributions of stable isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122, 399-409.

Pollard, D.A. 1984. A review of ecological studies of seagrass-fish communities, with particular reference to recent studies in Australia. Aquatic Botany 18, 3-42.

Post, D.M. 2002a. Using stable isotopes to estimate trophic position: Models, methods and assumptions. Ecology 83, 703-718.

Post, D.M. 2002b. The long and short of food-chain length. TRENDS in Ecology & Evolution 17, 269-277.

Post, D.M., Pace, M.L. & Hairston Jr., N.G. 2000. Ecosystem size determines food-chain length in lakes. Nature 405, 1047-1049.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. Studies in Tropical Oceanography 5, 666-847.

Robertson, A.I. & Klumpp, D.W. 1983. Feeding habits of the Southern Australian garfish *Hyporhamphus melanochir*: A diurnal herbivore and nocturnal carnivore. Marine Ecology Progress Series 10, 197-201.

Rooker, J.R. & Holt, S.A. 1997. Utilization of subtropical seagrass meadows by newly settled red drum *Sciaenops ocellatus*: Patterns of distribution and growth. Marine Ecology Progress Series 185, 139-149.

Rotherham, D. & West, R.J. 2002. Do different seagrass species support distinct fish communities in south-eastern Australia? Fisheries Management and Ecology 9, 235-248.

Sodhi, N.S., Koh, L.P., Brook, B.W., Ng, P.K.L. 2004. Southeast Asian biodiversity: An impending disaster. TRENDS in Ecology and Evolution 19, 655-660.

Thayer, G.W., Engel, D.W. & Bjorndal, K.A. 1982. Evidence for short-circuiting of the detritus cycle of seagrass beds by the green turtle, *Chelonya mydas* L. Journal of Experimental Marine Biology and Ecology 62, 173-183.

Unsworth, R.K.F., Wylie, E., Smith, D.J. & Bell, J.J. 2007a. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. Estuarine, Coastal and Shelf Science 74, 53-62.

Unsworth, R.K.F., Taylor, J.D., Powell, A., Bell, J.J. & Smith, D.J. 2007b. The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific. Estuarine, Coastal and Shelf Science 74, 53-62.

Valentine, J.F. & Heck Jr., K.L. 1999. Seagrass herbivory: Evidence for the continued grazing of marine grasses. Marine Ecology Progress Series 176, 291-302.

Valentine, J.F. & Duffy, J.E. 2006. The central role of grazing in seagrass ecology. In: Larkum, A.W.D., Orth, R.J. & Duarte, C.M. (Eds.), Seagrasses: Biology, ecology and conservation. Springer, Dordrecht, The Netherlands, pp. 463-501.

Verweij, M.C., Nagelkerken, I., Wartenbergh, S.L.J., Pen, I.R. & van der Velde, G. 2006. Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile

French grunts, *Haemulon flavolineatum*. Marine Biology 149, 1291-1299.

Vonk, J.A., Christianen, M.J.A. & Stapel, J. 2008. Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. Estuarine, Coastal and Shelf Science 79, 653-660.

Vonk, J.A., Christianen, M.J.A. & Stapel, J. 2010. Abundance, edge effect, and seasonality of fauna in mixed-species seagrass meadows in southwest Sulawesi, Indonesia. Marine Biology Research 6, 282-291.

Yamamuro, M. 1999. Importance of epiphytic cyanobacteria as food sources for heterotrophs in a tropical seagrass bed. Coral Reefs 18, 263-271.

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Fish assemblages in different types of tropical Indo-Pacific seagrass meadows

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Abstract. Seagrass meadows are known to support high abundances and diversity of fish assemblages. However, studies on the effects of seagrass beds with distinctly different plant canopy on associated fish fauna remain scarce. In the present study, fish assemblages were investigated by an underwater visual census at five study sites with varying seagrass species composition and shoot density at two small coral islands in the Spermonde Archipelago, Indonesia. The present study revealed that 1) fish abundance did not correlate with seagrass shoot density, 2) seagrass beds differ distinctly from each other by means of fish species composition and total diversity, although the basic composition of fish assemblages was similar and 3) fish diversity was highest at the most impacted site. There was no difference for total abundance between study sites, but for six common species. Species accumulation curves for local gamma diversity, each study site and the two most diverse fish families (Labridae, Pomacentridae) were not saturated, thus suggest high likelihood that local fish diversity might be much higher. Differences in fish assemblages might be due to the different canopy structures, water depth, and high proportions of single records due to spillover effects from adjacent coral reefs. The outcome of the present study gives implications for both socioeconomic and conservation issues.

Key words: seagrass; fish assemblages; visual census; Southeast Asia; Indonesia; Spermonde Archipelago.

1. Introduction

Seagrass beds support high floral and faunal diversity, abundance and biomass and are crucial habitats for economically important fish and invertebrate species (Parrish, 1989; Gullström et al., 2002; Duffy, 2006; MacArthur & Hyndes, 2007; Vonk et al., 2008). They are considered to be structural highly complex habitats, offering shelter from predation, nursery areas and feeding grounds for diverse fish assemblages (Parrish, 1989; Dorenbosch et al., 2005; Nakamura et al., 2003; Unsworth et al., 2007b; Vonk et al., 2010). Seagrass beds are widely open and dynamic habitats at different scales (Duffy, 2006; Duarte et al., 2006; Valentine & Duffy, 2006) and strongly interact with adjacent coral reefs and mangroves (reviewed by Parrish, 1989; Nakamura & Sano, 2004b;

Unsworth et al., 2007b; Unsworth et al., 2010), e.g. by different types of fish migration (Ogden & Quinn, 1984).

Southeast Asian coasts comprise the world's highest numbers of fish species, especially in the heart of the 'coral triangle' region, which is comprised by the Philippines, Indonesia and Papua New Guinea (Fenner, 2007). In Indonesia, seagrass beds cover a substantial part of coastline and off-shore islands, and harbour up to ten seagrass species (McKenzie et al., 2007) and around 80 or more fish species (Hutomo & Martosewoto, 1997; Unsworth et al., 2007b) within a single meadow. Playing a crucial role as a habitat for a high number of fish species, seagrass beds are of major interest for local fisheries. However, increasing human population and demands for food result in overexploitation of the seagrass beds, a serious threat for their fish communities (Duffy, 2006; Unsworth et al., 2010).

The majority of studies dealing with fish communities in seagrass meadows have been conducted in the Caribbean but seagrass beds in Southeast Asia have a distinctly higher faunal diversity (summarized in Unsworth et al., 2007b). Therefore processes influencing fish assemblages are possibly different. In spite of this fact, research on fish communities in Southeast Asian seagrass meadows is scarce (Nienhuis et al. 1989; Erftemeijer & Allen, 1993; Unsworth et al. 2007a,b; Vonk et al. 2008, 2010). The Southeast Asian Spermonde Archipelago is well investigated with respect to benthic organisms, such as sponges (e.g. Cleary et al., 2005; de Voogd et al., 2006), foraminiferans (e.g. Cleary et al., 2005), holothurians (e.g. Massin, 1999), or corals (e.g. Cleary et al., 2005; Knittweis et al., 2009), but few studies focussed on fish assemblages (Erftemeijer & Allen, 1993; Pet-Soede et al., 2001; Vonk et al., 2008, 2010).

Although earlier publications suggested increasing fish density with increasing complexity of seagrass beds (e.g. Heck & Orth, 1980; Bell & Westoby, 1986; Nakamura & Sano, 2004b), and that variations in seagrass habitats influence associated fish assemblages (Heck & Orth, 1980; Unsworth et al., 2007b), few studies emphasize the importance of mixed-species seagrass beds with most complex canopy structures on fish assemblages (e.g. Martin & Cooper, 1981; Blaber et al., 1992). Generally the effect of seagrass and seagrass bed structure on fish species composition may vary distinctly between seagrass beds (Martin & Cooper, 1981; Middleton et al., 1984; Kiswara et al., 1991; MacArthur & Hyndes, 2001; Nakamura and Sano, 2004b; Unsworth et al., 2010; Vonk et al., 2010), while several studies have found no significant differences for total fish abundance between different seagrass beds (Middleton et al., 1984; Loneragan et al., 1998), but for single species (e.g. Rooker & Holt, 1997). No such differences have been found for mixed tall dense and short seagrass beds by Blaber et al. (1992).

In the present study we investigated fish assemblages in five extremely diverse offshore seagrass beds with varying canopy architecture in the Spermonde archipelago, South Sulawesi, Southeast Asia. Following null hypotheses were tested: (1) fish density shows a correlation with seagrass shoot density; (2) seagrass beds with different canopy structures do not differ significantly in diversity, species composition and abundance of associated fish assemblages; (3) diversity is lowest at the most impacted sites. Results may reflect the importance of different types of seagrass beds for local fish populations, thus may have crucial implications for conservational and socioeconomical issues.

2. Material and methods

2.1. Site description

All fieldwork was conducted in the Spermonde Archipelago, Indonesia. The archipelago is about 200 km long and 400 km wide and comprised by numerous coral islands along the continental shelf off the west coast of South Sulawesi (Fig. 1). As study sites, 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. The islands are situated 14 and 15 km off the coast. Both islands consist of an intertidal sandbank, surrounded by reef flat and a small barrier reef, and are fringed by intertidal and subtidal seagrass beds comprised by different species of seagrass or seagrass communities. While Barrang Lompo is heavily populated, Bone Batang is uninhabited. Local population lives mainly of marine resources, using different fishing techniques (blast fishing, gill nets, cyanide fishing). Sewage water and garbage are released directly into the sea. For Bone Batang, limited anthropogenic impact can be assumed, though fishermen from Barrang Lompo and other places nearby fish around the island occasionally (pers. obs. C.P.). Overall, five study sites for the survey have been chosen: at Barrang Lompo South (BLS), at Bone Batang North (BBN), East (BBE), West (BBW) and South (BBS).

2.2. Seagrass densities

The seagrass meadows in the present study were comprised by *Enhalus acoroides, Thalassia hemprichii, Cymodocea rotundata, Halodule uninervis, Syringodium isoetifolium* and *Halophila ovalis* in varying shoot densities, indicating varying stages of succession. The different seagrass and canopy architectures displayed by each study site are shown in a scheme below (Fig. 2). At BLS and BBW, single small coral of the genera *Porites* and *Pocillopora* as well as various sponges were scattered scarcely across the seagrass beds.

To assess seagrass shoot densities, a frame with side length of 0.5 m was thrown to randomly choose patches within the transects to assess seagrass shoot density. The frame was subdivided into 16 smaller quadrates, each with a side length of 125 mm. Within the frame, all shoots of *E. acoroides* were counted; for other seagrass species, three quadrates of the grid within the frame were randomly chosen and for each species all shoots of all species within these three quadrates were counted.

2.3. Fish densities

Fish diversity and abundance were assessed during daytime hours by using a rapid visual census (Harvey et al., 2004) in belt transects. This technique was chosen because it is known as rapid, non-destructive and inexpensive; transects can be resurveyed over time and the data gained are highly comparable (Nagelkerken et al., 2000), since visual censi are widely applied for ecological fish studies (Khalaf & Kochzius, 2002). Transects were 25 m in length and 6 m in width, each transect covering an area of 150 m^2. Transects where apart at least 15 m and directed parallel to the shore line. Number of permanent transects per study sites was depending on the size of the seagrass beds (2 each for BBW and BBN; 5 each for BBE and BBS). For each site at Bone Batang, 30 replicates were conducted (= 120 transects in total). For BLS, four permanent transects were pegged out. Each was replicated 15 times (= 60 transects in total). All sites were within 200 m of a fringing reef.

To reduce differences in accuracy in estimation of numbers by the observers and to reduce attraction or repellence of fish, the survey has been conducted snorkelling by one single observer (C. P.). Care was taken not to count any fish twice moving into, within and out of the transect. Cryptobenthic species, such as gobies were recorded when observed, but it was not actively looked for them. After transect setup, the observer waited for at least five minutes to minimize fish disturbance, then slowly swam in a zigzag pattern along the transect line, recording data. Recorded data contained taxa and number per taxon as well as water depth. Observed fauna was identified up to species level. Other taxonomic units were used when identification up to species level was not possible. Surveys were conducted throughout the day from 05:30 to 16:30, randomized at different water depths to control for possible time or day effects (Gratwicke & Speight, 2005). Off Bone Batang, surveys were conducted at a minimum water depth of 0.4 m in the subtidal seagrass beds and at a minimum water depth of 0.2 m in the intertidal area. Off Barrang Lompo, the shallowest transects were conducted at a minimum water depth of 0.2 m. Visual census data on both islands were conducted during October and November 2009, a period of time which marks the transitional period between dry and wet season.

2.4. Data analysis

Seagrass shoot densities and fish abundances are presented as mean ± SD (m^{-2} for shoot densities and 100 m^{-2} for fish abundances). To test for a correlation between seagrass shoot density and fish abundance, a multiple regression was conducted. To test for significance between different habitats in terms of fish species and species abundance and the most abundant fish species found a non-parametric Kruskal-Wallis test were performed. All tests were conducted using Statistica 7.0 (StatSoft, Inc., 2007). To evaluate alpha diversity, Shannon Index (H') was calculated. To assess species heterogeneity of each study site, Pielou Evenness (J') was calculated (Magurran, 2004).

Analysis of differences in fish assemblage structure was conducted using multivariate non-Metric Multidimensional Scaling ordination (MDS) 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-weigh the influence of rare and extremely abundant species, and then converted into a MDS ordination and a cluster (Clarke, 1993). To assess global differences, SIMPROF analysis was applied. SIMPER analysis was used to determine the relative contribution of individual fish species to differences between groupings (Rotherham & West, 2002).

For analysis of species accumulation and saturation for habitats (Gamma diversity) as well as for selected fish families, data were entered into a spreadsheet program to obtain species x site matrices. Further analysis were conducted using the computer package EstimateS 7.5.2. (Colwell, 2006). As estimators of total species richness, the Incidence-Based Coverage Estimator (ACE) and the Chao 1 Estimator were used.

3. Results

3.1. Seagrass shoot densities

The following species of seagrass were found at the different study sites: *Enhalus acoroides, Thalassia hemprichii, Halophila ovalis, Halodule uninervis, Cymodocea rotundata, Syringodium isoetifolium*. With the exception of *E. acoroides* and *S. isoetifolium*, all species were observed at all study sites (*E. acoroides* lacking at BBE and BBN, *S. isoetifolium* lacking at BLS and BBN). Seagrass shoot density differed among the study sites and mean shoot density (± SD m^{-2}) ranged between 463 ± 639 at BLS and 1365 ± 474 (Table 1). Epiphyte growth was most remarkable on leaves of *E. acoroides* and *S. isoetifolium*, while it was observed only moderately on the other seagrasses.

3.2. Fish species

For the visual census, 180 transects have been conducted, 60 off Barrang Lompo and 30 for each site off Bone Batang. Allover, 39 families and 120 taxa from have been found at all study sites (Table 2), 30 families and 89 species off Barang Lompo and 36 families and 107 species off Bone Batang. The four study sites of Bone Batang reveal: About 27 families and 58 species of BBS, 26 families and 45 species off BBE, 16 families and 38 species of BBW and 15 families and 31 species off BBN.

The most speciose families were wrasses (Labridae; 20 species), damselfish (Pomacentridae; 17 species) and threadfin breams (Nemipteridae; 8 species), followed by gobies (Gobiidae; 6 species). Fish species that were more abundant than 10 individuals 100 m^{-2} at all or certain study sites were *Atherinomorus lacunosus* (Atherinidae), *Cheilio inermis, Halichoeres argus, H. chloropterus* (all Labridae), *Pentapodus bifasciatus, P.*

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,* Pomacentridae sp. 1 and *Tylosurus crocodilus* (Belonidae). 61 species were recorded on a single occasion or rarely (A.1), 25 additional taxa were found at study sites outside transects (A.2). The wrasse *H. argus* was the dominant species at BLS, BBN and BBW followed by *S. canaliculatus, A. lacunosus* and *D. 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 also 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).

There were no significant differences for fish abundance between study sites (Kruskal-Wallis test, H(4, N = 254) = 2.49556; p = 0.6454). There were significant differences for species composition between BLS and BB (Kruskal-Wallis test, H(4, N = 630) = 53.38589; p = 0.000; for BLS vs. BBE: p = 0.001358; for BLS vs. BBN: p = 0.000000; for BLS vs. BBS: p = 0.032441; for BLS vs. BBW: p = 0.000005), but no significant differences between the four different sites off BB (all p-values > 0.05).

Nevertheless for the most abundant eight fish species occurring at Barang Lompo and the different sites of Bone Batang, significant differences of abundance for six species were found: *H. far* (Kruskal-Wallis test, H (3, N = 53) = 18.33157; p = 0.0004), *C. inermis* (H (4, N = 112) = 68.45746; p = 0.0000), *H. argus* (H (4, n = 124) = 46.26580, p = 0.0000), *H. chloropterus* (H (4, N = 115) = 41.26183, p = 0.0000), *P. trivittatus* (H

(4, N = 123) = 42.63372, p = 0.0000) and *S. canaliculatus* (H (3, N = 90) = 15.08231, p = 0.0017), but not for *A. lacunosus* (H (3, N = 54) = 0.604691; p = 0.4567) and *T. crocodilus* (H (3, N = 29) = 2.005531; p = 0.5713). None of the tested fish species showed significant differences between all study sites, but for at least in one case (*S. canaliculatus*: BBS vs. BLS, p = 0.003473) up to seven cases (e.g. *C. inermis*; Table 3).

Both Shannon Index and Evenness were highest for BBN and BBW (H' = 2.45 each; J_{BBN}' = 0.71; J_{BBW}' = 0.67) and lowest for BBS (H' = 1.88; J' = 0.47).

There was no general correlation between seagrass shoot density and total fish abundance (Spearman correlation; R = 0.61729199; F(1,3) = 1.8469; $p < 0.26729$).

3.3. Site similarity

A cluster analysis of site similarity with abundance-based fish species data showed that the study sites are significantly different from each other (Fig. 3A). Two distinct groups with a similarity level of 34.5 % (SIMPROF; $\pi = 18.88$; $p < 0.1$) are apparent, the subtidal (BBE, BBS) and intertidal seagrass beds (BLS, BBW, BBN). BLS and BBW appear to be more similar to each other than to BBN. The MDS ordination plot clearly distinguished the different seagrass beds (Fig. 3B).

The cluster analysis based on the shoot density of each seagrass species shows the same groups as for the fish species abundance-based data (subtidal vs. intertidal), but the similarity level of 63.9 % ($\pi = 12.93$; p = 0.9) is much higher than for the fish abundance-based clusters, and there is no significant dissimilarity (all p-values ≥ 0.5). However, clusters show a trend towards dissimilarity for the clusters of intertidal seagrass beds (see below). Within the subtidal beds, BBW and BBN appear to be more similar to each other than to BLS (Fig. 4).

The SIMPER analysis revealed an average dissimilarity between intertidal and subtidal seagrass beds of 65.5 %. Average similarity for 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 *C. inermis* (7.8 %) as well as the pomacentrid *D. chrysopoecilus* (11.3 %) and the nemipterid *P. trivittatus* (9.2 %). For subtidal seagrass beds average similarity was 58.0 % and *C. inermis* (10.2 % contribution), *P. bifasciatus* (8.0 %) and *S. canaliculatus* (7.6 %) were the most representative species.

3.4. Species accumulation curves

All randomized species accumulation (S_{obs} MauTao, ACE, Chao 1 estimator) for gamma diversity across all study sites exhibit a strong increase and do not reach saturation. The picture does not change when splitting up the data set into the different study sites: species accumulation curves remain with a steep slope. Overall, most species were found at BLS, even at the smallest common sample size (n = 30). The lowest species number was recorded at BBN. The species number recorded for BBS, BBE and BBW was intermediate between the ones of the sites at BLS and BBN. This pattern was also found when comparing all five habitats at the smallest common sample size (30 transect counts) (Fig. 5A,B).

Species accumulation curves for the three most speciose families (Labridae, Pomacentridae, Nemipteridae) at all study sites still show a strong increase for both the

Labridae and the Pomacentridae. For the Nemipteridae the curve shows saturation: it does not exhibit any slope, and the upper and lower boundaries of the 95 % confidential interval are decreasing towards zero at a sample size of n = 160 (Fig 5C). For Labridae and Pomacentridae, the boundaries of the confidential interval do not behave that way. Species numbers for Labridae and Pomacentridae were similar (20 for Labridae and 17 for Pomacentridae), and lowest for Nemipteridae (8 species). The lower bound of 95 % confidential interval of the S_{obs} (MauTao) of Labridae is overlapping with the upper bound of the S_{obs} (MauTao) of Nemipteridae; the lower bound of the confidential interval of Pomacentridae is overlapping with the upper bound of the S_{obs} (MauTao) of Nemipteridae until up to 40 samples (Fig. 5C).

4. Discussion

The present study of five diverse seagrass beds showed no significant correlation of the investigated fish density with seagrass shoot density. Investigated types of seagrass beds dominated by different seagrass species harbour distinct fish assemblages: fish diversity and species composition are evidently different between all study sites, i.e. between the islands, intertidal and subtidal habitats and different types of seagrass beds. Total fish abundance differ between seagrass beds, except for a few common species. The site that is mostly impacted by human activity, BLS, has the highest species number of all sites observed, though both Shannon Index and Pielou Evenness are intermediate for this site.

4.1. Correlation of seagrass shoot densities and fish abundance

Seagrass shoot densities appear low in this study compared to recent literature (e.g. Erftemeijer & Herman, 1994; Loneragan et al., 1998; Gullström et al., 2002); Vonk et al., 2008, 2010). This may have two reasons: Erftemeijer & Herman (1994) found strong seasonal variation of both seagrass shoot densities and biomass, caused by emergence, during spring tides at noon from August to December and leading to ‘burning’ and massive die-off of more than 50 % of the seagrass. This effect may mask the correlation between seagrass shoot density and the abundance of associated fishes. Recently, Vonk et al. (2010) compared the fish fauna of an offshore mixed-species seagrass meadow at Bone Batang. They found that beds with significantly different seagrass shoot density and aboveground biomass had similar infauna densities between the two beds, but epifauna and fish abundance was significantly higher in the seagrass beds with higher seagrass density for most species. In addition due to a severe el Niño Southern Oscillation, the monsoon came late in the season during which the present study was conducted, not allowing the seagrasses to recover from insolation stress. This may also contribute to the lack of correlation between shoot densities and fish abundance.

4.2. Fish assemblages in different types of seagrass beds

In the present study, fish assemblages do not differ significantly by means of total fish abundance, but for few most common fish species and total species composition, because the seagrass beds are in different stages of succession. Further, it must be assumed that other parameters such as patch size, current, water depth or distance to adjacent coral reefs are factors affecting fish assemblages.

Most studies focussing on fish assemblages in seagrass beds focus on monospecific beds (e.g. Middleton et al., 1984; Rotherham & West, 2002; Hyndes et al. 2003; Nakamura & Sano, 2003). However, seagrass beds in the tropical Indo-Pacific often are comprised by multiple species. Altough earlier publications suggested increasing fish density with increasing complexity of seagrass beds (e.g. Heck & Orth, 1980; Bell & Westoby, 1986; Nakamura & Sano, 2003), and that variations in seagrass habitats influence associated fish assemblages (Heck & Orth, 1980; Unsworth et al., 2007), few studies emphasize the importance of multiple species seagrass beds with most complex canopy structures on fish assemblages (e.g. Martin & Cooper, 1981; Blaber et al., 1992), and even fewer studies focussed on fish fauna in different types of seagrass beds in the same region as the present study (e.g. Erftemeijer & Allen, 1993; Vonk et al., 2010). Earlier studies had mixed conclusions about the effect of seagrass and seagrass bed structure on fish assemblages, which might be due to differences in geographical latitude and/or the variety of applied methods (.Martin & Cooper 1981; Middleton et al. 1984; Blaber et al. 1992). Erftemeijer & Allen (1993) surveyed two different types of seagrass beds in South Sulawesi: one at Barrang Lompo, and the other at Gusung Tallang at the mouth of the Tallo river. Although the two beds did not differ in diversity, none of the recorded fish species were common at both study sites. The fish assemblages at Gusung Tallang was clearly typical for estuarine and brackish environments, while the assemblage at Barrang Lompo was similar to the present study, though not as diverse. Nakamura and Sano (2004) found significantly higher fish diversity and abundance in seagrass beds dominated by the large *Enhalus acoroides* than in the short *T. hemprichii*. The authors suggest that the more structured *Enhalus*-dominated seagrass bed is more attractive for fishes. This was confirmed in the present study where the most structured beds of BBS and BLS showed the highest number of fish species.

4.3. Habitat utilization

Cluster analysis showed a distinct grouping into intertidal and subtidal seagrass beds. Abundant species were either pelagic species (e.g. *A. lacunosus, T. crocodilus, H. far*) that might not necessarily respond to changes in seagrass bed architecture, or demersal species with high plasticity that not only can be found in all types of seagrasses, but even in other habitats, such as unvegetated area or reef environments (Labridae, Nemipteridae). An early assessment of fish assemblages at the island of Barrang Lompo by Erftemeijer & Allen (1993) accounted for fewer species than in the present study, which might be due to the applied methods (27 species from 15 families were collected with a chemical ichthyocide). However, despite differences in methodology, basic fish assemblags are similar: only a few of the recorded species in the present study can be considered typical residents of seagrass beds, for example the highly camouflaged *Acreichthys tomentosus* (Monacanthidae), *Syngnathoides biaculeatus* (Syngnathidae) or *Novaculoides macrolepidotus* (Labridae). However, according to Kuriandewa et al. (2003), permanent residents are defined by the presence of all life history stages within the seagrass bed. Juveniles were found for more than 32 taxa. Some of these species were found exclusively as juveniles (e.g. Chaetodontidae Haemulidae, *Platax teira* (Ephippidae)) of reef associated species that might utilize adjacent seagrass beds as a nursery, while for some abundant species, both adults and juveniles were regularly found in the seagrass environments (e.g. *C. inermis, H. argus, H. chloropterus, P. trivittatus,* *Apogon margaritiphorus,* Pomacentridae). The first group thus could be considered to be temporary residents, while the latter could be considered to be permanent residents, with the exception of *H. argus*, since this species is known to spawn outside seagrass habitats; the same applies to *S. biaculeatus* (Kuriandewa et al., 2003). However, not all species identified as residents were restricted to seagrass habitats. For example, some species can not only be found in seagrass beds, but in macrophyte stands and sandy sea bottoms, such as different species of wrasses (*H. chloropterus*, *H. scapularis*, *C. inermis* or *Cheilinus* spp.) or of pomacentrids (*D. chrysopoecilus, D. fasciatus, D. perspicillatus*, *P. tripunctatus*). Most taxa including single records are characteristic of reef environments, e.g. nemipterids, labrids (*H. melanurus, Thalassoma lunare*), pomacentrids (*Amphiprion ocellaris; Stegastes lividus; Abudefduf* spp.) and chaetodontids (*Chaetodon* spp.). More than half of the species in the present study are rare, which is a common pattern for many ecological communities (Magurran & Henderson, 2003 (fehlt in references); Unsworth et al., 2007b; Nakamura & Sano 2004b). These visitors can be referred to as occasional trespassing migrants from other habitats. Most of the remaining species do occur regularly, but not in high abundances, and can be referred to as temporary visitors.

The most abundant species in intertidal beds is *H. argus*, while *A. lacunosus* shows the highest abundances for subtidal sites. One reason for the distribution of *H. argus* might be the structurally extremely rich canopy architecture of BLS and BBW (short and long seagrasses intermingled forming various storeys) as well as the short vicinity to coral reefs, rubble and macroalgal zone (BBN). This species predominantly inhabitats highly structured phytal zones and reef flats (pers. obs. C.P.), and does not seem to prefer seagrass beds with either short and/or evenly long plant leaves, as at BBS (dense *Enhalus* bed) and BBE (dense bed of *Cymodocea* and *Halophila*), not allowing storeys, but a uniform canopy. For larger zoobenthivorous species, there was no clear sites preference. *Pentapodus bifasciatus* was found only at subtidal sites, while *H. chloropterus* was rare at these sites and showed higher abundances at subtidal sites. Vonk et al. (2010) found that zoobenthivores preferred seagrasses with open canopy (low seagrass leaf biomass), except for *C. inermis* preferring closed canopy (high seagrass leaf biomass). In the present study, leaf biomasses were not calculated to account for an "open" or "closed" canopy. However, the highest abundances of *C. inermis* were found at BBE, where leaves of *C. rotundata* form a dense bed like a lawn, and at BBS. This coincides with the study of Vonk et al. (2010). The common siganid *S. canaliculatus* is strongly abundant at BLS, BBE and BBS. This species can often be observed feeding on the dense epiphyte layer on the leaves of *E. acoroides* (Tomascik et al. 1997).

4.4. Influence of sites on fish diversity

A total of 120 fish taxa was recorded from seagrass beds of the islands of Barrang Lompo and Bone Batang in the Spermonde Archipelago. Generally it is expected that the less disturbed ecosystem is more species-rich. However, distinctly more species were found at BLS than at any of the other sites (89 species BLS, less than 60 for each of the Bone Batang sites), even at the smallest common sampling size (n = 30). This is surprising, since the densely inhabited island of Barrang Lompo and its surrounding marine environment is impacted stronger by human activities than the uninhabited island of Bone Batang. There might be several explanations for this outcome. First, the seagrass bed at BLS is in close vicinity to adjacent rubble zones and a coral reef, and thus might experience spill-over effects. Second, the moderate disturbance of an ecosystem or habitat might alter and even increase species diversity, since it can offer space and resources for "alien" species that do not occur or occur only rarely in the undisturbed habitat. Furthermore, BLS is not only impacted by exploitation by the local populations of the island, but also by sewage water and waste that may not have a negative affect on all species. This may add to the diet of many opportunistic organisms, thus possibly enhancing species richness. Third, the seagrass bed at BLS is highly structured by long *Enhalus*-leaves intermingled with shorter species. However, since this is also the case for BBW and BBS and the species richness is considerably lower, the enormous diversity at BLS might be more likely due to a combination of all factors mentioned.

Species numbers for BBN and BBW might occur low compared to other sites, but randomized species accumulation curves suggest a high likelihood that recorded fish diversity does not cover the total diversity: although the steep of the slope is lowest for BBN, none of the species accumulation curves is saturated, implicating that with higher sampling effort or enhanced methods more fish species might be recorded, especially for e.g. the Gobiidae, Labridae and Pomacentridae. Furthermore, the present study applied a daytime visual census. Unsworth et al. (2007b) recorded a similar species number (81 species) for a seagrass bed in the Wakatobi Marine National Park in Sulawesi, comparable to BLS, but with different methods and diurnal sampling. In their study, mean fish abundance increased by 45 % and diversity by 35 % from day to night. If the case is similar for BLS or BB, it can be assumed that with diurnal sampling methods up to a third more species could be yielded.

Most speciose fish families in the present study were Labridae, Pomacentridae and Nemipteridae. While randomized species accumulation curves for Labridae and Pomacentridae were strongly increasing, the curve for Nemipteridae showed saturation. It is not very likely to increase recorded species diversity for this family by increasing sampling effort, while it can be expected to yield more labrid and pomacentrid species. In the present study, most abundant fish species belonged to the Labridae, Siganidae, Atherinidae, Pomacentridae and Nemipteridae and varied for different study sites, with *H. argus* being most abundant species for intertidal and *A. lacunosus* the most abundant species for subtidal sites. In contrast, the most abundant familiy found by Unsworth et al. (2007b) were Apogonidae including four species, and the most abundant species was *A. lacunosus*, which might be due to the diurnal sampling method. Most abundant families found by Nakamura & Sano (2004b) in a seagrass bed simliar to BLS in the present study were Labridae, Gobiidae and Scaridae.

5. Conclusion

Seagrass beds at small coral islands in the Indonesian Spermonde Archipelago with different canopy architecture harbor distinct fish assemblages and have high fish diversity at very small scale. Species numbers found in the present study are similar to (e.g. Nakamura & Sano, 2004b; Unsworth et al., 2007b) or higher than in recent studies (cf. Erftemeijer & Allen, 1993; Vonk et al., 2008, 2010). Fish abundance did not correlate with shoot density of seagrasses, but different types of seagrass beds showed different fish assemblages and species composition. The species richness was highest at the most impacted site, probably due to a combination of the habitat heterogeneity and the higher nutrient loading by human sewage. However, diurnal sampling methods may improve the recording of actual species numbers. Additionally, a long-term monitoring might increase our knowledge of seasonal fluctuations in fish abundance and species composition. Considering small patch size of the study site, high diversity, distinct variability of fish assemblages and value for indigenous fishery, there is need for conservational efforts to maintain or enhance fish diversity to assure a sustainable and rich socioeconomic use and preserve marine diversity.

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References

Bell, J.D., Westoby, M. 1986. Importance of local changes in leaf height and density to fish and decapods associated with seagrasses. Journal of Experimental Biology 104, 249-274.

Blaber, S.J.M., Brewer, D. T., Salini, J. P., Kerr, R. D., Conacher, C. 1992. Species composition and biomasses of fishes in tropical seagrasses at Groote Eylandt, northern Australia. Estuarine, Coastal and Shelf Science 35, 605-620.

Clarke, K. R. 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18, 117-143.

Clarke, K.R. & Warwick, R.M. 1994. Changes in marine communities: an approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth, UK. Natural Environment Research Council. 144 pp.

Cleary, D.F.R., Becking, L.E,, de Voogd, N.J., Renema, W., de Beer, M., van Soest, R. W.M., Hoeksema, B.W. 2005. Variation in the diversity and composition of benthic taxa as a function of distance offshore, depth and exposure in the Spermonde Archipelago, Indonesia. Estuarine, Coastal and Shelf Science 65, 557-570.

Colwell, R.K. 2006. EstimateS: statistical estimation of species richness and shared species from samples, Version 8.0. Available at persistent URL http://viceroy.eeb.uconn.edu/estimates (last accessed 15 March 2010).

de Voogd, N.J., Cleary, D.F.R., Hoeksema, B.W., Noor, A. & van Soest, R.W.M. 2006. Sponge beta diversity in the Spermonde Archipelago, SW Sulawesi, Indonesia. Marine Ecology Progress Series 309, 131-142.

Dorenbosch, M., Grol, M.G.G., Christianen, M.J.A., Nagelkerken, I. & van der Velde, G. 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. Marine Ecology Progress Series 302, 63-76.

Duarte, C.M., Forqurean, J.W., Krause-Jensen, D. & Olesen, B. 2006. Dynamics of seagrass stability and change. In: Larkum, A.W.D., Orth, R.J. & Duarte, C.M. (Eds.), Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, The Netherlands, pp. 271-294.

Duffy, J. E. 2006. Biodiversity and the functioning of seagrass ecosystems. Marine

Ecology Progress Series 311, 233-250.

Edgar, G.J. & Shaw, C. 1995. The production and trophic ecology of shallow-water fish assemblages in southern Australia. I. Species richness, size-structure and production of fishes in Western Port, Victoria. Journal of Experimental Marine Biology and Ecology 194, 53-81.

Erftemeijer, P.L.A. & Herman, P.M.J. 1994. Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. Oecologia 99, 45-59.

Erftemeijer, P.L.A. & Allen, G.R. 1993. Fish fauna of seagrass beds in south Sulawesi, Indonesia. Records of the West Australian Museum 16, 269-277.

Fenner, D. 2007. The Ecology of Papuan Coral Reefs. In: Marshall, A.J. & Beehler, B.M. (Eds.), The Ecology of Papua. Part Two. Periplus Editions (Hk) Ltd., pp. 771-800.

Gratwicke, B. & Speight, M.R. 2005. The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. Journal of Fish Biology 66, 650-667.

Gullström, M., de la Torre Castro, M., Bandeira, S.O., Björk, M., Dahlberg, M., Kautsky, N., Rönnbäck, P. & Öhman, M. C. 2002. Seagrass ecosystems in the Western Indian Ocean. Ambio 31, 588-596.

Harvey, E., Fletcher, D., Shortis, M.R. & Kendrick, G.A. 2004. A comparison of underwater visual distance estimates made by scuba divers and a stereo-video system: implications for underwater visual census of reef fish abundance. Marine and Freshwater Research 55, 573-580.

Heck, K.L.Jr., Orth, R.J. 1980. Seagrass habitats: the roles of habitat complexity, competition and predation in structuring associated fish and mobile macroinvertebrate assemblages. In: Kennedy, V.S. (Ed.), Estuarine perspectives. Academic Press, New York, pp. 449-462.

Hutomo, M. & Peristiwady, T. 1996. Diversity, abundance and diet of fish in the seagrass beds of Lombok island, Indonesia. Seagrass Biology: Proceedings of an international workshop, Rottnest Island, Western Australia, 25 - 29 January 1996, pp. 205-212.

Hutomo, M. & Martosewojo, S. 1977. The fishes of seagrass community on the west side of Burung Island (Pari Islands, Seribu Islands) and their variations in abundances. Marine Research in Indonesia 17, 147-172.

Hyndes, G.A., Kendrick, A.J., MacArthur, L.D., Stewart, E. 2003. Differences in the species- and size-composition of fish assemblages in three distinct seagrass habitats with differing plant and meadow structure. Marine Biology 142, 1195-1206.

Khalaf, M.A. & Kochzius, M. 2002. Changes in trophic communitiy structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea. Marine Ecology Progress Series 239, 287-299.

Kiswara, W., Genisa, A.S., Arifin, A. & Purnomo, L.H. 1991. A Preliminary study of the species composition, abundance and distribution of fishes in the seagrass beds of Banten Bay, West Java, Indonesia. In: Sasekumar, A. (Ed.), Mangrove Fisheries and Connections. ASEAN Australia Marine Science Project, Living Coastal Resources (Malaysia), pp. 183-213.

Knittweis, L., Jompa, J., Richter, C. & Wolff, M. 2009. Population dynamics of the mushroom coral *Heliofungia actiniformis* in the Spermonde Archipelago, South Sulawesi, Indonesia. Coral Reefs 28, 793-804.

Kuriandewa, T.E., Kiswara, W., Hutomo, M. & Soemodihardjo, S. 2003. The seagrasses of Indonesia. In: Green, E.P. & Short, F.T. (Eds.), World atlas of seagrasses. Pepared by the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley USA, pp. 171-182.

Loneragan, N.R., Kenyon, R.A., Staples, D.J., Poiner, I.R. & Conacher, C.A. 1998. The influence of seagrass type on the distribution and abundance of postlarval and juvenile tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) in the western Gulf of Carpentaria, Australia. Journal of Experimental Marine Biology and Ecology 228, 175-195.

MacArthur, L.D. & Hyndes, G.A. 2007. Varying foraging strategies of Labridae in seagrass habitats: herbivory in temperate seagrass meadows? Journal of Experimental Marine Biology and Ecology 340, 247-258.

Magurran, A.E. 2004. Measuring biological diversity. Blackwell Science Ltd, Oxford, UK, 256 pp.

Magurran, A.E. & Henderson, P.A. 2003. Explaining the excess of rare species in natural species abundance distributions. Nature 422, 714-716.

Martin, F.D. & Cooper, M. 1981. A comparison of fish faunas found in pure stands of two Atlantic seagrasses, *Thalassia testudinum* and *Syringodium filiforme*. Northeast Gulf Science 5, 31-37.

Massin, C. 1999. Reef-dwelling Holothuroidea (Echinodermata) of the Spermonde

Archipelago (South-West Sulawesi, Indonesia). Zoologische Verhandelingen Leiden 329, 3-144.

McKenzie, L., Coles, R. & Erftemeijer, P. 2007. Seagrass ecosystems of Papua. In: Marshall, A.J. & Beehler, B.M. (Eds.), The Ecology of Papua. Part Two. Periplus Editions (Hk) Ltd., pp. 800-823.

Middleton, M.J., Bell., J.D., Burchmore, J.J., Pollard, D.A. & Pease, B.C. 1984. Structural differences in the fish communities of *Zostera capricorni* and *Posidonia australis* seagrass meadows in Botany Bay, New South Wales. Aquatic Botany 18, 89-109.

Nagelkerken, I., van der Velde, G., Gorissen, M.W., Meijer, G.J., van't Hof, T. & den Hartog, C. 2000. Importance of mangroves, seagrass beds, and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. Estuarine, Coastal and Shelf Science 51, 31-44.

Nakamura, Y., Horinouchi, M., Nakai, T. & Sano, M. 2003. Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, Southern Japan. Ichthyological Research 50, 15-22.

Nakamura, Y. & Sano, M. 2004a. Comparison between community structures of fishes in *Enhalus acoroides*- and *Thalassia hemprichii*-dominated seagrass beds on fringing coral reefs in the Ryukyu Islands, Japan. Ichthyological Research 51, 38-45.

Nakamura, Y. & Sano, M. 2004b. Overlaps in habitat use of fishes between a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan: Importance of the seagrass bed as juvenile habitat. Fisheries Science 70, 788-803.

Nelson, J. S. 2006. Fishes of the world. Hoboken New Jersey: John Wiles & Sons, Inc. 601 pp.

Nienhuis, P.H., Coosen, J., Kiswara, W. 1989. Community structure and biomass distribution of seagrasses and macrofauna in the Flores Sea. Netherlands Journal of Sea Research 23, 197-214.

Ogden, J.C. & Quinn, T.P. 1984. Migration in Coral Reef Fishes: Ecological Significance and Orientation Mechanisms. In: McCLeave, J.D., Arnold, G.P., Dodson, J.J., Neill, W.H. (Eds.), Mechanisms of Migration in Fishes. Plenum, New York, pp. 293-308.

Parrish, J.D. 1989. Fish communities of interating shallow-water habitats in tropical oceanic regions. Marine Ecology Progress Series 58, 143-160.

Pet-Soede, C., van Densen, W.L.T., Pet, J.S. & Machiels, M.A.M. 2001. Impact of Indonesian coral reef fisheries on fish community structure and the resultant catch composition. Fisheries Research 51, 35-51.

Pollard, D.A. 1984. A review of ecological studies on seagrass-fish communities, with particular reference to recent studies in Australia. Aquatic Botany 18, 3-42.

Rooker, J.R. & Holt, S.A. 1997. Utilization of subtropical seagrass meadows by newly settled red drum *Sciaenops ocellatus*: Patterns of distribution and growth. Marine Ecology Progress Series 158, 139-149.

Rotherham, D. & West, R.J. 2002. Do different seagrass species support distinct fish communities in south-eastern Australia? Fisheries Management and Ecology 9, 235-248.

StatSoft, Inc. 2007. STATISTICA (Data Analysis Software System), version 7.0.

www.statsoft.com.

Tomascik, T., Mah A.J., Nontji A. & Moosa N.K. 1997. The Ecology of the Indonesian Seas, Part II, Chapter 18, Seagrasses, Dallhousie University, Oxford University Press, pp. 829-906.

Unsworth, R.K.F., Cullen, L. C. 2010. Recognising the necessity for Indo-Pacific seagrass conservation. Conservation Letters 3, 63-73.

Unsworth, R.K.F., Bell, J.J. & Smith, D.J. 2007a. Tidal fish connectivity of reef and sea grass habitats in the Indo-Pacific. Journal of the Marine Biology Association of the U.K. 87, 1287-1296.

Unsworth, R.K.F., Wylie, E., Smith, D.J. & Bell, J.L. 2007b. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. Estuarine, Coastal and Shelf Science 72, 81-88.

Valentine, J.F. & Duffy, J.E. 2006. Grazing in Seagrass Ecosystems. In: Larkum, A.W.D., Orth, R.J. & Duarte, C.M. (Eds.) 2006. Seagrasses: Biology, Ecology and Conservation. Springer, Dordrecht, The Netherlands, pp. 463-501.

Vonk, J.A., Christianen, M.J.A. & Stapel, J. 2008. Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. Estuarine, Coastal and Shelf Science 79, 653-660.

Vonk, J.A., Christianen, M.J.A. & Stapel, J. 2010. Abundance, edge effect, and seasonality of fauna in mixed-species seagrass meadows in southwest Sulawesi, Indonesia. Marine Biology Research 6, 282-291.

Figures

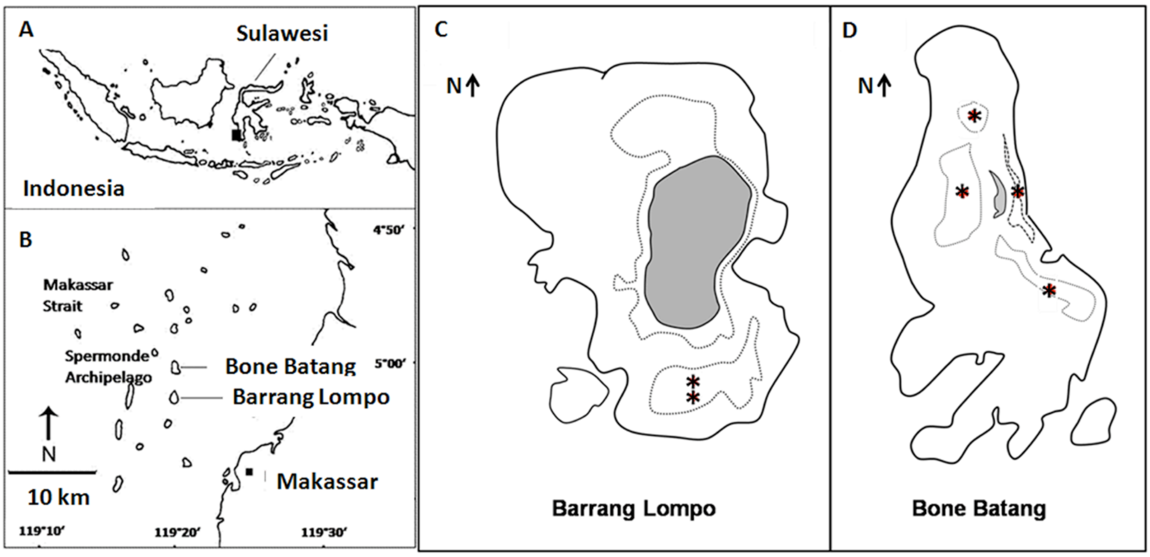

Fig. 1.

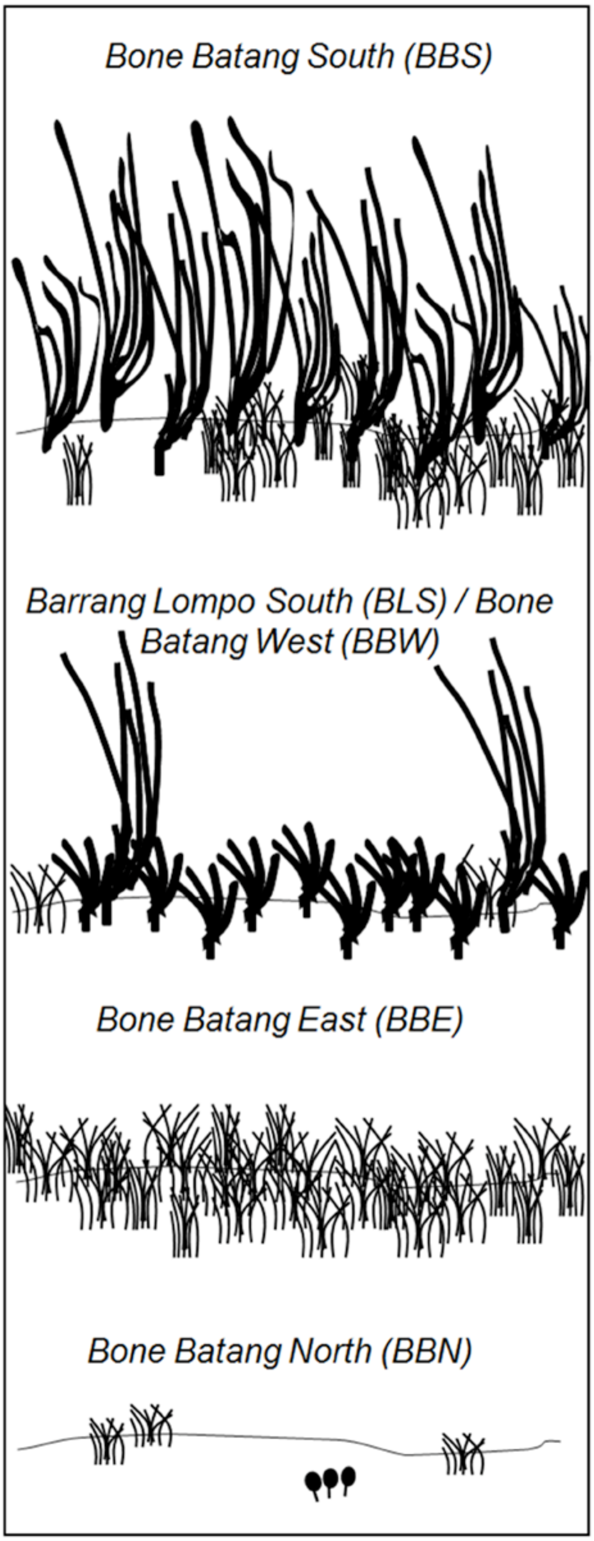
Bone Batang South (BBS)
Barrang Lompo South (BLS) / Bone Batang West (BBW)
Bone Batang East (BBE)
Bone Batang North (BBN)

Fig. 2.

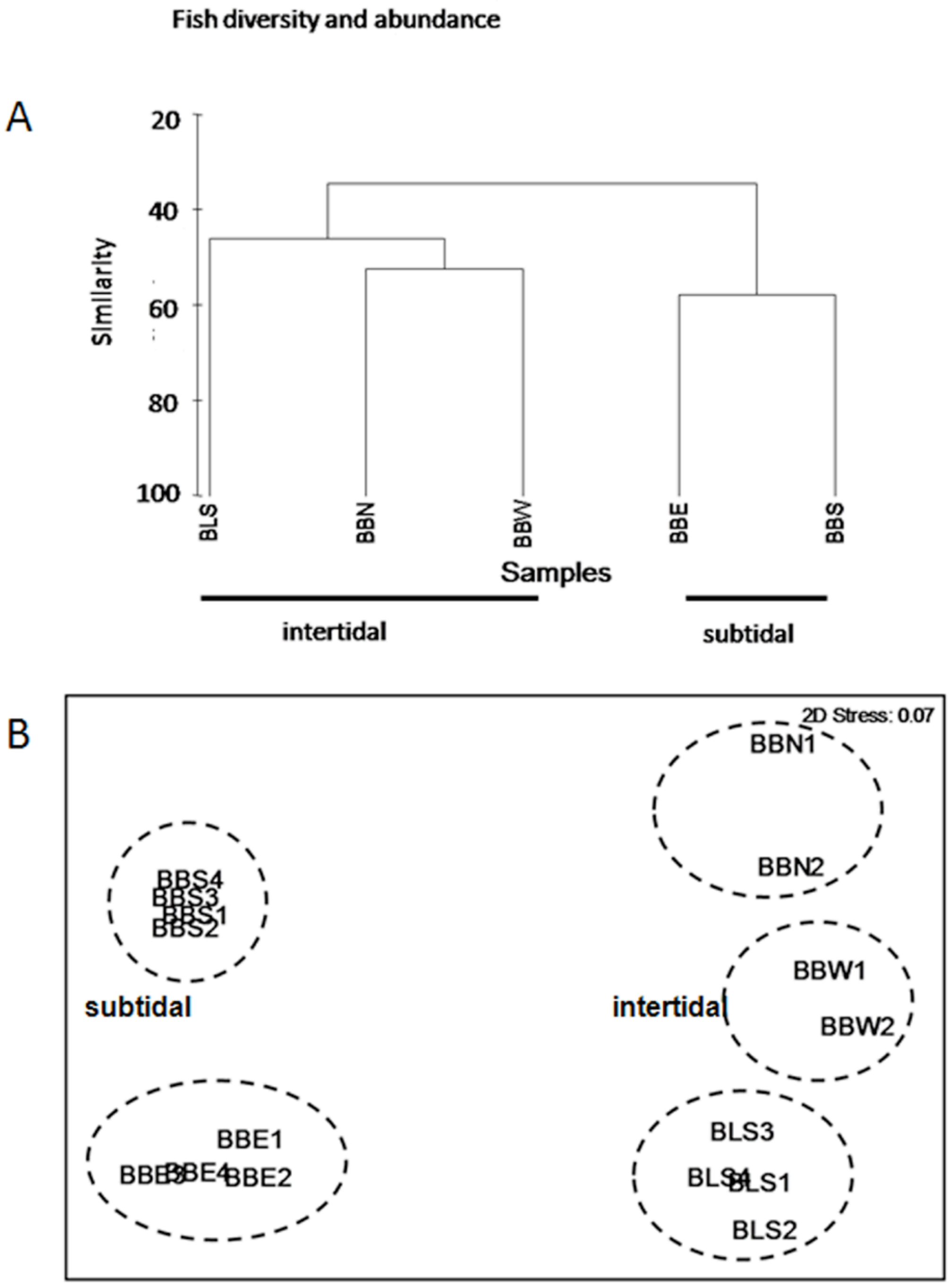
Fish diversity and abundance
A
20
40
60
80
100
Similarity
BLS
BBN
BBW
BBE
BBS
Samples
intertidal
subtidal
B
2D Stress: 0.07
BBN1
BBN2
BBS4
BBS3
BBS1
BBS2
subtidal
intertidal
BBW1
BBW2
BBE1
BBE3
BBE4
BBE2
BLS3
BLS4
BLS1
BLS2

Fig. 3.

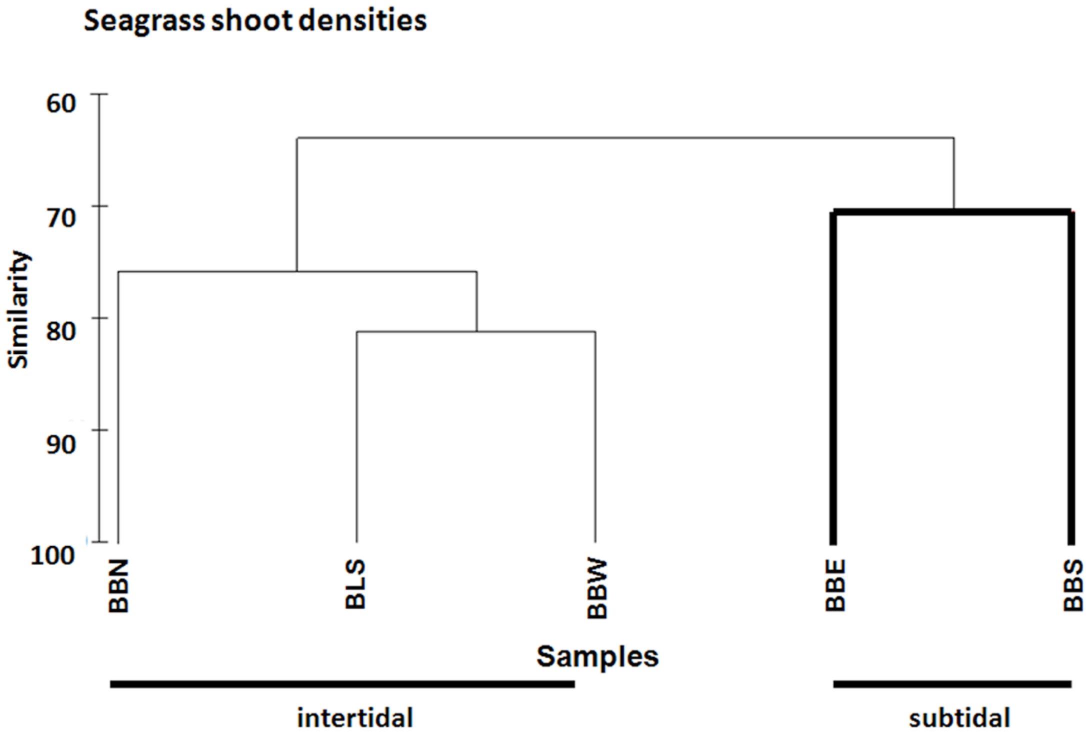
Seagrass shoot densities
Similarity
60
70
80
90
100
BBN
BLS
BBW
BBE
BBS
Samples
intertidal
subtidal

Fig. 4.

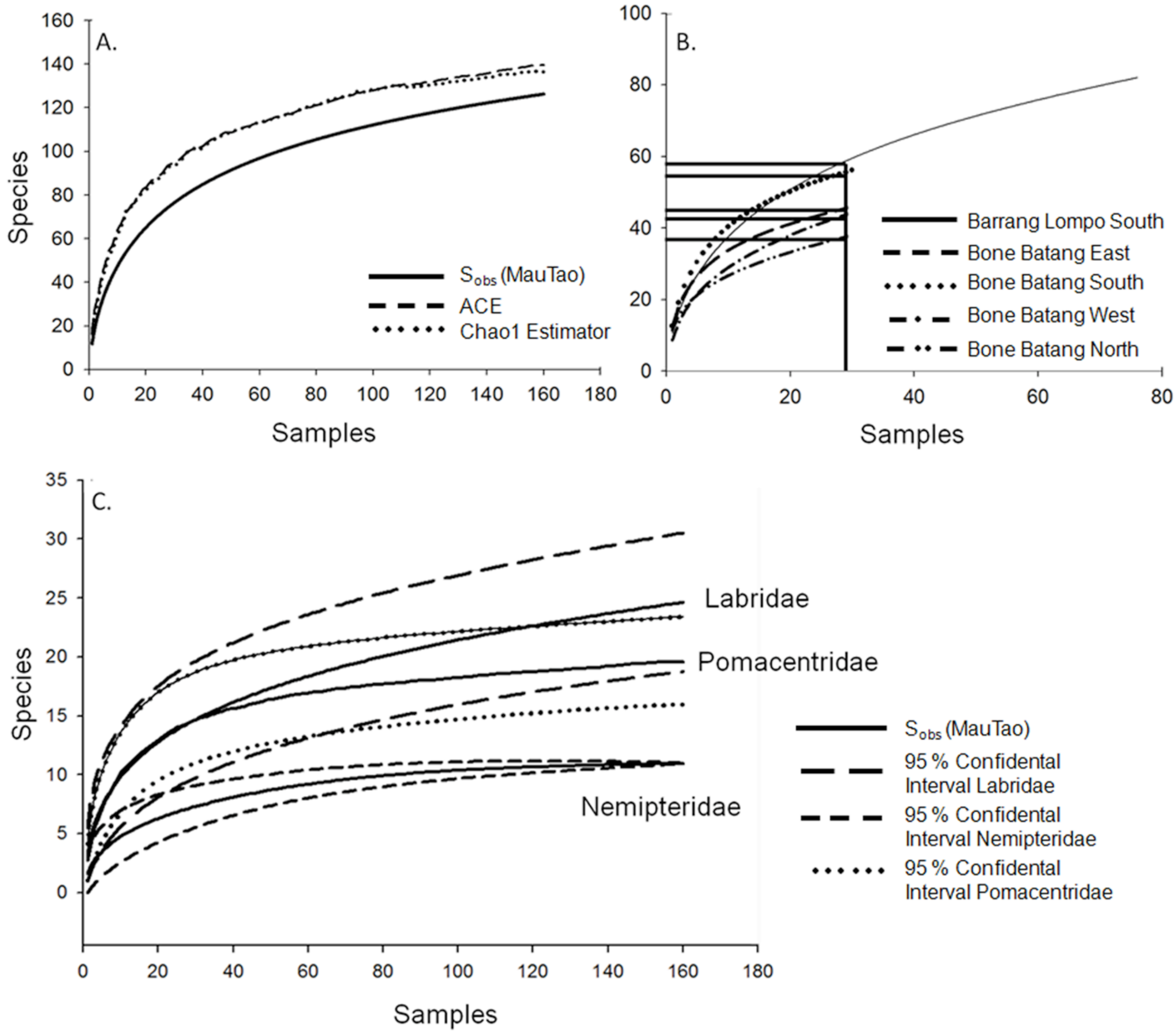
A.
Species
160
140
120
100
80
60
40
20
0
0
20
40
60
80
100
120
140
160
180
Samples
S_{obs} (MauTao)
ACE
Chao1 Estimator
B.
100
80
60
40
20
0
0
20
40
60
80
Samples
Barrang Lompo South
Bone Batang East
Bone Batang South
Bone Batang West
Bone Batang North
C.
Species
35
30
25
20
15
10
5
0
0
20
40
60
80
100
120
140
160
180
Samples
Labridae
Pomacentridae
Nemipteridae
S_{obs} (MauTao)
95 % Confidental Interval Labridae
95 % Confidental Interval Nemipteridae
95 % Confidental Interval Pomacentridae

Fig. 5.

Figure captions

Fig.1. Study area, showing the location within Indonesia (A) and the islands of the Spermonde Archipelago (B) (both adapted from Liu et al., 2008) and overviews of the islands Barrang Lompo (lat. 4°85'S, long. 119°20'E) (C) and Bone Batang (lat. 4°90'S, long. 119°18'E) (D). Asterisks indicate transect positions. C) Grey shaded area indicates the island; solid line indicates sand and reef flat; dotted lines refer to the ranges of seagrass meadows. D) Grey shaded area indicates intertidal sand; solid line indicates reef flat and coral; dotted lines refer to the ranges of the seagrass meadows.

Fig.2. Schematic diagram showing the different seagrass and meadow structures of the selected study sites. Bone Batang South (BBS) is dominated by *Enhalus acoroides* and *Cymodocea rotundata*; Barrang Lompo South (BLS) and Bone Batang West (BBW) are dominated by *Enhalus acoroides* and *Thalassia hemprichii*; Bone Batang East (BBE) consists mostly of the smaller seagrasses *Halodule uninervis* and *Cymodocea rotundata*; Bone Batang North (BBN) was still in an early stage of succession, with mainly *Halophila ovalis*.

Fig.3. Similarity of the 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; BLS = Barrang Lompo South. A. Cluster analysis with SIMPROF (S17 Bray Curtis similarity). All study sites are

distinctly different from each other and can be divided into two groups (intertidal and subtidal seagrass beds). B. Non-metric scale ordination (MDS) of permanent transects per study site. Both transects and study sites form distinct groupings that do not overlap. The same clustering into intertidal and subtidal seagrass beds as in A. are evident.

Fig.4. Similarity of the study sites based on seagrass shoot densities (data square root transformed). Cluster analysis with SIMPROF (S17 Bray Curtis similarity). Study sites can be divided into intertidal and subtidal seagrass beds. Intertidal seagrass beds differ distinctly from each other, while subtidal seagrass beds are significantly similar to each other (bold cluster). BBE = Bone Batang East; BBN = Bone Batang North; BBS = Bone Batang South; BBW = Bone Batang West; BLS = Barrang Lompo South.

Fig.5. Fish species accumulation curves for study area. A. Randomized species accumulation curve of all fish species and for all 5 sampling sites (Gamma diversity). The solid line shows the sum of all species observed (S_{obs} (Mau Tao)) the dashed line shows the Abundance-Based Coverage Estimator (ACE), and the dotted line the Chao 1 estimator of total expected species richness. B. Randomized species accumulation curves for the five sampled habitats indicating the S_{obs} (Mao Tau) for all species: Solid curve Barrang Lompo South; dotted curve Bone Batang South; dashed curve Bone Batang East; dashed curve interrupted by single dots Bone Batang West; dashed curve interrupted by double dots Bone Batang North. C. Randomized species accumulation curves (S_{obs} (Mao Tau)) for fish species of the families Labridae, Pomacentridae and Nemipteridae for all

habitats. Solid curves indicate accumulated observed species numbers (S_{obs} (MaoTau)), long-dashed curves indicate upper and lower boundaries of 95 % confidential intervals of Labridae, dotted curves indicate upper and lower bounds of the 95 % confidential interval of Pomacentridae, and short-dashed curves indicate upper and lower boundaries of 95 % confidential intervals of Nemipteridae. Nemipteridae are saturated, while curves for Labridae and Pomacentridae are still increasing.

Tables

Table 1

	BBE	BBS	BLS	BBN	BBW
Enhalus acoroides	0 ± 0	10 ± 17	19 ± 9	0 ± 0	5 ± 6
Thalassia hemprichii	49 ± 60	178 ± 148	315 ± 161	498 ± 308	334 ± 148
Halophila ovalis	686 ± 624	333 ± 216	49 ± 133	196 ± 203	35 ± 69
Halodule uninervis	32 ± 70	27 ± 39	11 ± 41	108 ± 330	15 ± 26
Cymodocea rotundata	540 ± 551	10 ± 24	69 ± 187	61 ± 116	242 ± 309
Syringodium isoetifolium	59 ± 192	61 ± 99	0 ± 0	0 ± 0	21 ± 80
Total	1365 ± 474	610 ± 140	463 ± 639	863 ± 301	652 ± 173

Table 2

				Abundance		
Family	Species	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
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

Table 3

	BBE	BBN	BBS	BBW	BLS
BBE					
Hemirhamphus far		**0.002893**	0.896084		**0.013300**
Cheilio inermis		**0.000001**	**0.002681**	**0.000000**	**0.000000**
Halichoeres argus		1.000000	1.000000	**0.001820**	**0.000203**
Halichoeres chloropterus		**0.035467**	1.000000	**0.000935**	0.523417
Pentapodus trivittatus		**0.005661**	0.414988	0.639148	**0.025802**
Siganus canaliculatus			1.000000	1.000000	0.186681
BBN					
Hemirhamphus far	**0.002893**		1.000000		1.000000
Cheilio inermis	**0.000001**		**0.043093**	1.000000	1.000000
Halichoeres argus	1.000000		0.729544	**0.014465**	**0.000951**
Halichoeres chloropterus	**0.035467**		**0.000349**	1.000000	0.509301
Pentapodus trivittatus	**0.005661**		1.000000	**0.000004**	1.000000
Siganus canaliculatus					
BBS					
Hemirhamphus far	0.896084	1.000000			1.000000
Cheilio inermis	**0.002681**	**0.043093**		**0.035100**	**0.034257**
Halichoeres argus	1.000000	0.729544		**0.000125**	**0.000008**
Halichoeres chloropterus	1.000000	**0.000349**		**0.000001**	**0.021614**
Pentapodus trivittatus	0.414988	1.000000		**0.007233**	1.000000
Siganus canaliculatus	1.000000			1.000000	**0.003473**
BBW					
Hemirhamphus far					
Cheilio inermis	**0.000000**	1.000000	**0.035100**		1.000000
Halichoeres argus	**0.001820**	**0.014465**	**0.000125**		1.000000
Halichoeres chloropterus	**0.000935**	1.000000	**0.000001**		**0.001236**
Pentapodus trivittatus	0.639148	**0.000004**	**0.007233**		**0.000002**
Siganus canaliculatus	1.000000		1.000000		0.073112
BLS					
Hemirhamphus far	**0.013300**	1.000000	1.000000		
Cheilio inermis	**0.000000**	1.000000	**0.034257**	1.000000	
Halichoeres argus	**0.000203**	**0.000951**	**0.000008**	1.000000	
Halichoeres chloropterus	0.523417	0.509301	**0.021614**	**0.001236**	
Pentapodus trivittatus	**0.025802**	1.000000	1.000000	**0.000002**	
Siganus canaliculatus	0.186681		**0.003473**	0.073112	

Table captions

Table 1. Seagrass shoot densities (mean ± SD, m^{-2}) for all species and total at all study sites. Abbreviations for study sites: BBE = Bone Batang East; BBN = Bone Batang North; BBS = Bone Batang South; BBW = Bone Batang West; BLS = Barrang Lompo South.

Table 2. List of all fish species observed during visual census at study sites. Abundance is individual counts 100 m-2. All values are mean ± SD. BBE = Bone Batang East; BBN = Bone Batang North; BBS = Bone Batang South; BBW = Bone Batang West; BLS = Barrang Lompo South.

Table 3. Differences in abundance between study sites of six abundant fish species common at all or most study sites. Values in bold numbers refer to significant differences between two sites (Kruskal-Wallis-Test, $p < 0.05$).

Appendix

A.1.

Family	Species	Site	Family	Species	Site
Apogonidae	*Apogon margaritiphorus*	BLS	Nemipteridae	*Scolopsis bilineatus*	BLS
	Apogon angustatus	BBS		*Scolopsis monogramma*	BBE
Belonidae	*Strongylura incisa*	BLS		*Scolopsis taeniopterus*	BBE
Blenniidae	*Ecsenius* sp.	BBN		*Scolopsis trilineata*	BLS
Callionymidae	*Callionymidae* Gen. sp.	BBN	Ostraciidae	*Lactoria cornuta*	BBE
Chaetodontidae	*Chaetodon melannotus*	BLS	Pinguipedidae	*Parapercis cylindrica*	BBN
	Chaetodon sp. 1	BLS		*Parapercis* sp. 1	BBN
	Chaetodon rafflesi	BLS	Platycephalidae	*Cymbacephalus beauforti*	BLS
	Chaetodon vagabundus	BLS	Plotosidae	*Plotosus lineatus*	BBE
Ephippidae	*Platax teira*	BBS	Pomacentridae	*Abudefduf lorenzi*	BLS
Gobiesocidae	*Diademichthys lineatus*	BBS		*Abudefduf vaigiensis*	BLS
Gobiidae	*Amblygobius bynoensis*	BBN		*Amphiprion polymnus*	BBS
	Amblygobius phalaena	BBE		*Chromis analis*	BLS
	Valenciennea muralis	BBN		*Dascyllus aruanus*	BBS
Haemulidae	*Plectorhinchus vittatus*	BLS		Pomacentridae Gen. Sp. 3	BBS
Labridae	*Coris pictoides*	BBS	Pseudochromidae	*Congrogadus subducens*	BLS
	Halichoeres nigrescens	BBE		*Manonichthys paranox*	BLS
	Labridae Gen. sp. 1	BBE	Scaridae	*Hipposcarus* sp.	BLS
	Pteragogus enneacanthus	BBS		Scaridae sp.	BLS
	Stegastes lividus	BLS		*Scarus ghobban*	BBN
	Stethojulis interrupta	BBS	Serranidae	*Cephalopholis cyanostigma*	BLS
	Stethojulis sp. 1	BBN		*Cromileptes altivelis*	BBN
	Stethojulis sp. 2	BBN		*Epinephelus argus*	BLS
	Wetmorella albofasciata	BLS		*Epinephelus bontoides*	BBN
Lutjanidae	*Lutjanus decussatus*	BLS		*Epinephelus ongus*	BLS
	Lutjanus ehrenbergi	BLS	Siganidae	*Siganus spinus*	BLS
Monacanthidae	*Aluterus scriptus*	BLS		*Siganus virgatus*	BLS
Mullidae	*Parupeneus indicus*	BBE	Sphyraenidae	*Sphyraena obtusata*	BBS
Muraenidae	*Siderea picta*	BLS	Tetraodontidae	*Canthigaster compressa*	BLS
	Uropterygius macrocephalus	BLS		*Canthigaster* sp.	BLS

A.2.

	Species	**Site**
Balistidae	Balistidae Gen. sp.	BLS
Blenniidae	*Cirripectes castaneus*	BLS
	Ecsenius axelrodi	BLS
	Petroscirtes variabilis	BLS
Callionymidae	*Synchiropus ocellatus*	BLS; BBE
Carcharhinidae	*Carcharhinus melanopterus*	BLS; BBE
Centrogenyidae	*Centrogenys vaigiensis*	BLS; BBW
Dasyatidae	*Neotrygon kuhlii*	BLS
Diodontidae	*Diodon holacanthus*	BLS
Fistulariidae	*Fistularia commersonii*	BLS
Gobiidae	*Austrolethops wardi*	BLS
Haemulidae	*Plectorhinchus albovittatus*	BLS
Hemirhamphidae	*Hyporhamphus dussumieri*	BLS
Labridae	*Leptojulis cyanopleura*	BBW
	Stethojulis trilineatus	BLS
	Stethojulis sp. 2	BLS
Lutjanidae	*Lutjanus Sargassum*	BLS
Ophichthidae	*Leiuranus versicolor*	BLS
Platycephalidae	*Cymbacephalus beauforti*	BLS
Pomacentridae	*Abudefduf bengalensis*	BLS
	Dischistodus melanotus	BLS
Scaridae	*Scarus ghobban*	BLS
	Scaridae sp.	BLS
Serranidae	*Epinephelus quoyanus*	BLS
Siganidae	*Siganus spinus*	BLS
Solenostomidae	*Solenostomus* sp.	BLS
Syngnathidae	*Syngnathoides biaculeatus*	BLS

Appendix Captions

A.1. List of single records and rare fish taxa observed at study sites. BBE = Bone Batang East; BBN = Bone Batang North; BBS = Bone Batang South; BLS = Barrang Lompo South.

A.2. List of additional fish species observed outside transects or not during surveys at study sites. BBE = Bone Batang East; BBW = Bone Batang West; BLS = Barrang Lompo South.

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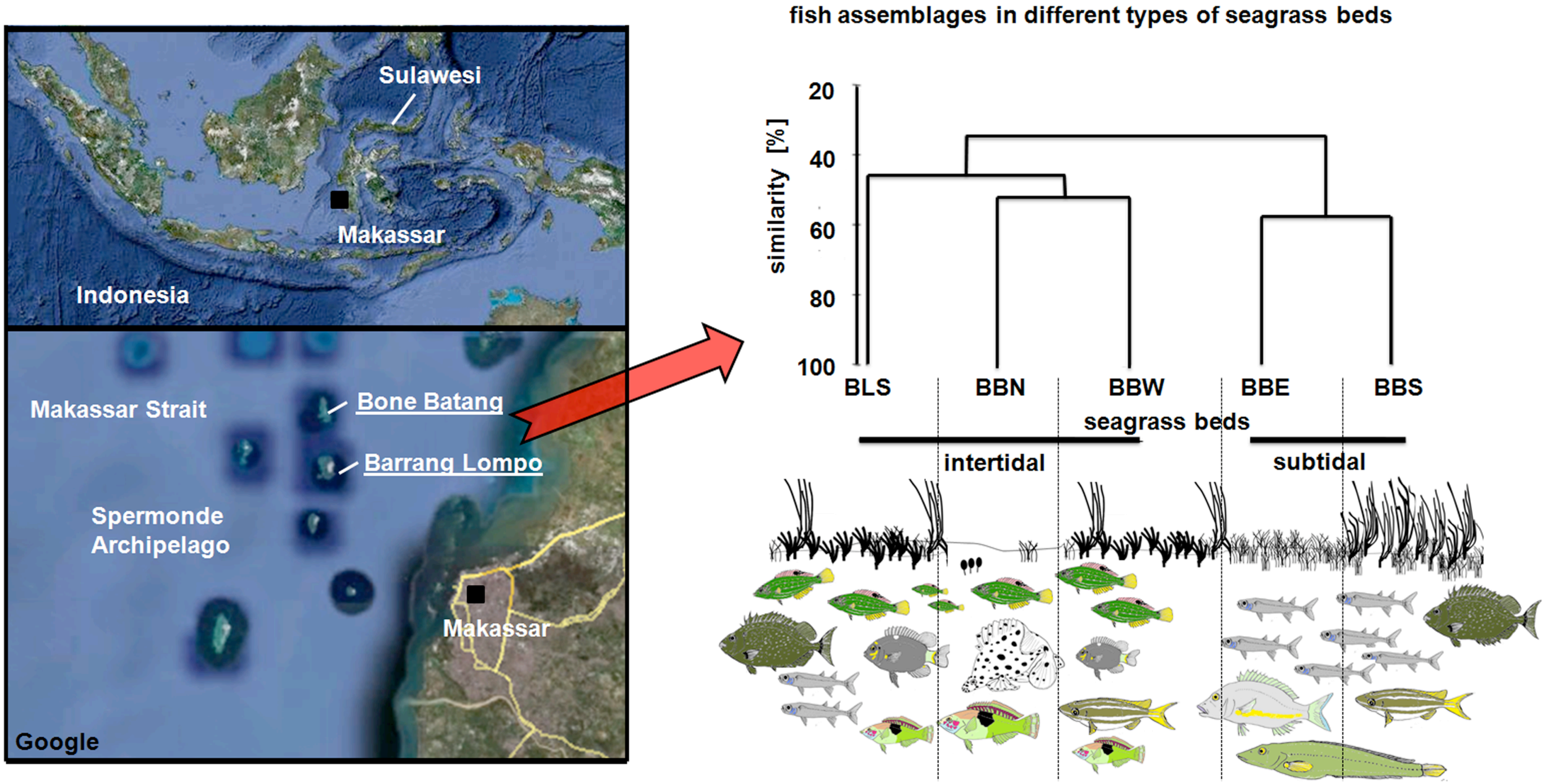

III. Food web relations of fishes in mixed-species tropical seagrass beds in the Spermonde Archipelago, South Sulawesi, Indonesia, as revealed by stable isotope analysis and gut-content analysis

1. Introduction

Seagrass beds are crucial habitats for many animals. Due to their structural complexity, seagrass ecosystems provide shelter from predation and represent important feeding grounds for a range of organisms, including invertebrates (e.g. amphipods, isopods or sea urchins and fish), but also higher vertebrates such as dugongs and green turtles, and birds such as waterfowl (Thayer et al., 1982; Heck & Valentine, 2006). Many studies in the higher latitudes have shown that both intake and assimilation of seagrass material by heterotrophs is of low significance in seagrass beds (Moncreiff & Sullivan, 2001). This was previously explained by the low nutrient value (Klumpp & Nichols, 1983; Valentine & Heck, 1999), high fibre content (Vonk et al., 2008) and high content of tannine and phenolic substances (Liu et al., 2008).

Furthermore, many studies – not only restricted to temperate regions – concluded that most fish species found in seagrass meadows are omnivores or predators (Unsworth et al., 2007b), and that only a small number of fish is truly or predominantly herbivorous and feeds directly on seagrass plants. Some trophic studies conducted in the lower latitudes, however, were contradictory to food web results from temperate regions (Heck & Valentine, 2006). For example, in contrast to the higher latitudes, tropical seagrass beds experience considerable grazing, with both direct and indirect utilization (i.e. feeding on seagrass epiphytes) (Vonk et al., 2008; Yamamuro, 1999). Grazing fish species have been reported from the families Scaridae, Labridae and Siganidae from the Mediterranean and Indo-Pacific (Randall, 1967; Pollard, 1984; Valentine & Heck, 1999; Khalaf & Kochzius, 2002; Unsworth et al., 2007c) Members of the omnivorous family Hemirhamphidae (Randall, 1967) include *Hyporhamphus* *melanochir*, a species feeding on seagrass during daytime and on amphipods during night time (Klumpp & Nichols, 1983; Robertson & Klumpp, 1983), and *Hemirhamphus far*,feeding on seagrass leaves floating freely in the water column (pers. obs. C.P.). From the Caribbean, Scaridae and Acanthuridae are known to ingest seagrasses (Valentine & Heck, 1999; summarized by Liu et al., 2008).

A food web describes trophic interactions between organisms within ecosystems. To describe food webs, different methods have been established in the last decades. The present study provides the results from combined gut-content and stable isotope analysis. Gut-content analysis yields high-resolution information on the food spectrum of an organism, although such contents represent restricted periods of time immediately before killing the examined organism (Pinnegar & Polunin, 2000; Carassou et al., 2008). Moreover, it is not possible to distinguish between food items that are actually digested and assimiliated and those that are merely ingested (Lugendo et al., 2006). In contrast, stable isotope analysis is based on the enrichment of stable isotopes, such as stable carbon or nitrogen, between trophic levels (e.g. Cocheret de la Morinière et al., 2003). This approach allows to average the assimilated diet of an organism over a longer period of time (days to months, depending on the type of tissue used) (Pinnegar & Polunin, 1999; Post, 2002), but with low resolution. It is not possible to identify species or genera; only the trophic level is revealed (e.g., herbivore or top-predator), provided that there is a baseline isotopic signature (i.e., isotopic composition of primary producers or primary consumers). For stable nitrogen ($\delta^{15}N$) and stable carbon ($\delta^{13}C$), different rates of accumulation between trophic level are apparent: while the enrichment of stable nitrogen from one trophic level to another averages 3.4 ‰ (Post et al., 2000), the enrichment of stable carbon is much lower and variable, ranging on average from 0.4 ‰ to 1 ‰.

This study is the first in the Indo-Pacific region to combine stable isotope and gut-content analysis to describe the food web of a highly diverse mixed-species seagrass community. One aim is to describe the food web of a seagrass bed of the small coral cay Barrang Lompo in the Indonesian Spermonde Archipelago, and to compare the outcomes of applying stable isotope and gut-content analysis. A further focus is on comparing the contribution of trophic guilds of four seagrass beds at the small coral cays Barrang Lompo and Bone Batang, another small coral island; this is based on visual census data presented in the manuscript that is part of this thesis (Pogoreutz et al., submitted).

2. Material and methods

2.1. Site description

Sampling took place at two small coral cays in the Spermonde Archipelago. The archipelago is about 200 km long and about 40 km wide and consists mainly of coral islands and submerged coral reefs (Vonk et al., 2008; Fig. 1). Two islands that were easily accessible from the city Makassar were chosen for the study: the island of Barrang Lompo (lat. 4°85’S, long. 119°20’E) and Bone Batang (lat. 4°90´S, long. 119°18´E). The islands are situated 14 and 15 km off Makassar, respectively. Barrang Lompo measures 0.5 km² and is densely populated. Local residents live mainly on marine resources, while waste and sewage water is released directly into the sea. Thus, the anthropogenic impact on surrounding marine ecosystems is high. Bone Batang is considerably smaller and uninhabited. The human impact with respect to nutrient enrichment is lower compared to Barrang Lompo, but there is a considerable amount of artisanal fishery. Both islands are surrounded by an extensive intertidal reef flat and a coral reef. Seagrass beds around the islands are distinctly differening from each other, multiple-species stands with varying shoot densities and dominating species. They are composed of seagrass species of the families Hydrocharitaceae (*Thalassia hemprichii*, *Enhalus acoroides*, *Halophila ovalis*) and Cymodoceaceae (*Cymodocea* *rotundata*, *Halodule uninervis*, *Syringodium isoetifolium*). Each of the seagrass beds is within 200 m of a coral reef and a rubble zone. Small single coral colonies of the genera *Pocillopora* and *Porites* as well as unidentified sponges are loosely scattered all across the seagrass beds at Barrang Lompo and Bone Batang. One study site was chosen at Barrang Lompo in the south of the island (BLS), and four sites in the cardinal points of Bone Batang: Bone Batang North (BBN), Bone Batang East (BBE), Bone Batang South (BBS), Bone Batang West (BBW). All food web and biomass sampling was conducted at BLS exclusively, whereas visual fish censuses were conducted at all study sites. The fish census was conducted in Octobre and November 2009, the food web sampling was done in November and December 2009.

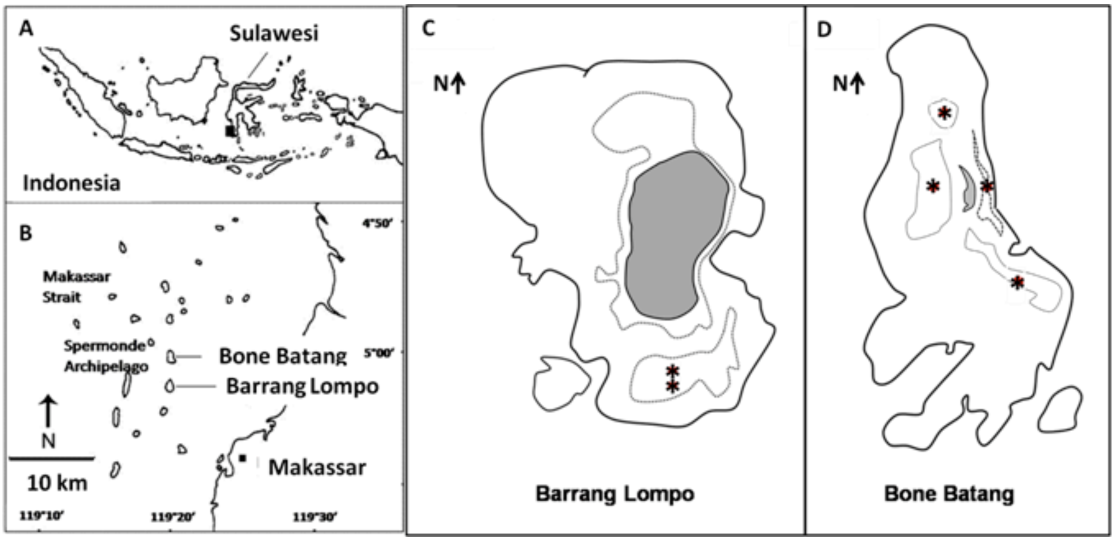

Fig. 1 Study area showing (A) the location within Indonesia, (B) the islands of the Spermonde Archipelago (both adapted from Liu et al., 2008), and overviews of the islands (C) Barrang Lompo (lat. 4°85'S, long. 119°20'E) and (D) Bone Batang (lat. 4°90'S, long. 119°18'E). Asterisks indicate positions of transects and food web sampling (Barrang Lompo only). Dotted lines refer to the ranges of seagrass meadows.

2.2. Macrophyte and fish densities

Seagrass shoot densities were assessed by throwing a frame with 0.5 m side length at random. This frame was subdivided into 16 quadrats with a side length of 125 mm each. All shoots of *E. acoroides* were counted within the frame. For other seagrasses, three quadrats of the grid within the frame were randomly chosen. All shoots of all seagrasses were counted within these quadrats and extrapolated.

To assess fish densities, daytime visual censuses were conducted. One observer experienced with fish censuses surveyed fish assemblages whilst snorkelling along transects. There were four permanent belt-transects deployed at BLS, two each at BBW and BBN and five each at BBS and BBE. The dimensions of each transect were 25 x 6 m (covering an area of 150 m^2 per transect). Transects were parallel to each other and to the shoreline and at least 15 m apart. The distance from the edge of the seagrass bed exceeded 5 m for each transect. Visual fish censuses were conducted during October and November 2009.

2.3. Sampling procedures

Sample collection took place in November and December 2009. The main primary producers were collected (the seagrasses *E. acoroides*, *T. hemprichii*, *C. rotundata* and *H. uninervis*; algae; phytoplankton). For the seagrasses, samples from living plants, freely floating seagrass leaves and dead accumulated seagrass detritus from the surface of the sediment were taken.

Practical considerations prohibited including all the fauna species in the food web, so selected invertebrate (epifauna, infauna) and fish species were collected based on observed abundance and presumed roles in the seagrass meadow based on the literature (Randall, 1967; Nienhuis et al., 1989; Khalaf & Kochzius, 2002; Nakamura et al., 2003; Lugendo et al., 2006; Vonk et al., 2008; Benstead et al., 2006; Froese and Pauly, 2010). Care was taken to include all fauna species and representatives of functional groups assumed to be of importance in the food web of the meadow.

Zooplankton was collected during daytime using fine mesh nets (200 µm and 50 µm). Those fish species to be included into the food web were chosen by abundance assessed during visual census and in catches with gill net (100 m x 0.5 m, mesh size 30 x 20 mm) and beach seine (opening 2 x 3 m; mesh size 2 x 2 mm). Fish were caught during daytime at high tide. After catching, total length (TL) and standard length (SL) of all specimens was measured to the nearest millimetre.

Invertebrates were sampled by deploying three plastic foils (3 x 3 m) on the sediment. All epibenthos (sponges, bivalves of the genus *Pinna*) was collected before deploying the foil. All infauna trying to escape to the sediment surface due to oxygen depletion was collected 24, 48 and 72 h after deploying the foils. To collect the infauna, the foil was removed carefully and all dead and living animals collected. Cryptobenthic fish (e.g. gobies, moray eels) were also collected when available. Additionally, 18 sediment cores (15.7 cm in diameter, 30 cm deep) were taken parallel to each other. The contents of the cores were washed over a 1 mm sieve and all fauna visible with the naked eye collected. Invertebrate sampling and identification was done by experienced invertebrate biologists (D. Kneer and D. Priasombodo).

For stable isotope analysis of organic matter in the sediment, six cores (6 cm in diameter, 20 cm deep) were taken from the seagrass meadow. A 1-cm-thick layer from one centimetre depth from each core was taken for analysis; the rest was discarded. All living seagrass parts were removed from the surface samples and discarded. Subsamples of the rest were suspended in a bucket of filtered seawater and the resuspendible sediment fraction washed over a 1 mm sieve first to gain sediment particulate organic matter (sPOM > 1 mm) and afterwards washed over a Whatman GF-F filter (sPOM < 1 mm). This procedure yielded samples for the sediment, rough detritus from the sediment and fine detritus from the sediment.

Zooplankton was sampled with a 200 µm and 55 µm sieve, phytoplankton (POC) with Niskin canisters (volume 5 l). Of each, four replicates were collected. Zooplankton and POC were filtered and washed down with de-ionized water to remove salt and then dried at 60 °C to constant weight.

2.4. Preparation of stable isotope samples

Seagrass was rinsed in freshwater to remove salt and then carefully cleaned of epiphytes. Epiphytes were rinsed and filtered through G/F Whatman filters. From fish, a small amount of muscle tissue from the dorsal white muscle was taken for stable isotope analysis. For *Acreichthys tomentosus* and smaller labrids, it was necessary to add white muscle from other parts of the body, such as the pygostyle. For juvenile *Atherinomorus lacunosus*, whole gutted specimens were used. For invertebrates, care was taken to use muscle tissue for analysis; otherwise whole specimens were used. All samples (fish, invertebrates, plankton, epiphytes and seagrasses) were dried at 60 °C until constant weight. The samples were then ground to fine powder. If necessary, samples were treated with hydrochloric acid to remove inorganic carbon. If available, three separate samples or three pooled samples per species were subjected to stable isotope analysis.

Stable isotope analysis was conducted at the Humboldt University Natural History Museum, Berlin, Germany. Analysis of stable nitrogen and stable carbon as well as concentration measurements were performed simultaneously with an isotope ratio mass spectrometer (THERMO/Finnigan MAT V), coupled to a THERMO Flash EA 1112 elemental analyzer. Carbon and nitrogen isotope ratios are expressed in δ per mil notation relative to Vienna PDB (Vienna PeeDee Belemnite standard) and atmospheric N_2. All isotope values are expressed as either enriched or depleted in $\delta^{13}C$ and $\delta^{15}N$, respectively. Average reproducibility based on replicate measurements of stable carbon and nitrogen isotopes are usually about 0.15 ‰ (Mariotti et al., 1984; Vonk et al., 2008).

2.5. Gut-content analysis

Fish guts were fixed with 4 % seawater buffered formalin immediately after sampling. Fixed guts were dissected under a stereomicroscope and all food items identified to at least class level, and, if possible, further. All food items contained in one gut were recorded. After dissection, all food items were dried at 60 °C until constant weight to gain values of gravimetric proportions. Empty stomachs or those containing parasiters were recorded. Gut-content analysis was conducted at the Waddensea Station of the Alfred-Wegener-Institute at the island of Sylt, Germany.

2.6. Biomass calculations

Data on dry weight were gained during preparation for stable isotope analysis after drying samples at 60 °C to constant weight. The remainders of samples (fish, invertebrates, seagrasses) were burned for 5 h at 450 °C. Ash-free dry weight (AFDW) was determined by subtracting the weight of burned samples from dry weight.

2.7. Data analysis

Seagrass biomass, fauna density, isotopes and isotope ratio-values are presented as mean ± SD. Differences in isotopic signatures between seagrasses, their epiphytes and phytoplankton (POC) were tested using a one-way ANOVA and post-hoc Tukey's b-test using the package Statistica 7.0 (Statsoft, 2007). Evaluation of trophic level (TL) of each species was done after Schaal et al. (2008) based on their mean $\delta^{15}N$, because this ratio has previously been suggested to comprise a valuable indicator of trophic position (Post, 2002). Mean stable isotope values for primary consumers (e.g. *Pinna muricata*, *Tapes literatus*, *Antigona puerpera*, *Gafrarium pectinatum*, *Vasticardium* sp.) were calculated. The following formula was used to calculate TL (Schaal et al., 2008):

$$TL_i = [(\delta^{15}N_i - \delta^{15}N_{PC}/3.4] + 2$$

Where TL_i is the average trophic level of species *i*, $\Delta^{15}N_i$ is the average $\delta^{15}N$ of species *i*, $\delta^{15}N_{PC}$ is the average $\delta^{15}N$ of primary consumers the value 3.4 is the mean $\delta^{15}N$ trophic enrichment occurring from primary consumers.

To analyse differences between trophic structures of fishes, proportions of gravimetric food items and differences between trophic distribution of fish assemblages between study sites, data were subjected to multivariate non-metric Multidimensional scaling ordination (MDS) and/or Bray-Curtis cluster analysis using the PRIMER v6 package (Clarke and Warwick, 1994). The Bray-Curtis similarity index was applied on square-root transformed data and then converted into MDS ordination and cluster (Clarke, 1993). To determine the relative contribution of proportions of trophic categories to differences between groupings, SIMPER analysis was applied. To assess the width of dietary niches of fish species, Levins Index of niche width was applied (Levins, 1968; Feinsinger et al. 1981). The Schoener Index of niche overlap was applied to evaluate dietary niche overlap (Hurlbert et al. 1978, Leitaõ et al. 2005).

Information on the trophic status of each fish species was drawn from a number of sources including Randall (1969), Khalaf & Kochzius (2002), Nakamura et al. (2002), Unsworth et al. (2007), Vonk et al. (2008) and field observations by the author.

3. Results

3.1. Macrophyte and fauna densities

At BLS, six seagrass species were found: *E. acoroides*, *T. hemprichii*, *H. ovalis*, *H. uninervis*, *C. rotundata* and *S. isoetifolium*. The last species was restricted to very small patches within the meadow and was never counted within the frame. Seagrass shoot density was low compared to literature values for this area (cf. Erftemeijer & Herman, 1993; Vonk et al., 2008). Total shoot density was about 463 ± 639 m^{-2}, ranging from 19 ± 9 shoots for *E. acoroides* to 315 ± 161 shoots for *T. hemprichii* (Table 1). Large proportions of seagrass leaves suffered from severe burning due to insolation. Epiphytes were found on all seagrass species, but were most abundant on the large *E. acoroides* leaves.

Table 1. Shoot densities of seagrass species (shoots m^{-2}) in the bed at Barrang Lompo South.

Seagrass species	shoots
Enhalus acoroides	19 ± 9
Thalassia hemprichii	315 ± 161
Halophila ovalis	49 ± 133
Halodule uninervis	11 ± 41
Cymodocea rotundata	69 ± 187
Syringodium isoetifolium	0 ± 0
Total	463 ± 639

The three most abundant fish species in the investigated seagrass bed were the omnivorous wrasse *Halichoeres argus* (21.9 ± 24.6 individuals 100 m^{-2}), the predominantly herbivorous siganid *Siganus canaliculatus* (18.6 ± 37.8 individuals 100 m^{-2}) and juveniles of the planktivorous atherinid *Atherinomorus lacunosus* (16.6 ± 48.2 individuals 100 m^{-2}; A.1).

3.2. Stable isotope analysis

3.2.1. Primary producers

Primary producers differed significantly in stable carbon (ANOVA: $F_{2,34} = 380.17$, $p = 0.0000$) and stable nitrogen (ANOVA: $F_{2,34} = 4.0412$, $p = 0.02663$) signatures. A post-hoc Tukey’s b-test showed significant differences between seagrasses (including floating seagrass leaves and dead leaves from the sea bottom) and POC (MS = 1.8596, df = 34, $p = 0.049341$) with respect to stable nitrogen. It also showed significant differences among all groups of primary producers with respect to stable carbon (MS = 1.0664, df = 34; seagrasses vs epiphytes: $p = 0.012976$; seagrasses vs POC: $p = 0.000125$; epiphytes vs POC: $p = 0.000125$). Among living seagrass leaves, *E. acoroides* had the least depleted $\delta^{13}C$ values, while *H. uninervis* was the most depleted. The other two seagrasses (*C. rotundata* and *T. hemprichii*) were intermediate between *E. acoroides* and *H. uninervis*. Seagrass leaves that were either collected floating in the water column or from the sandy sea bottom were similarly depleted as the seagrass *T. hemprichii*. Epiphytes were clearly less depleted than seagrasses, though the differences for *E. acoroides* and its epiphytes were minor (Table 2).

Table 2. Primary food sources $\delta^{13}C$, $\delta^{15}N$, C and N concentration and C:N ratio mean values ± SD in the seagrass bed (n = 3 each).

Primary food sources	**code**	**$\delta^{13}C$**	**$\delta^{15}N$**	**% C**	**% N**	**C:N ratio**
macrophytes						
Enhalus acoroides	Ea	-4.88±0.13	3.94±0.89	38.21±4.31	2±0.23	19.25±3.1
Thalassia hemprichii	Th	-6.39±0.23	2.18±0.51	41.9±1.23	2.07±0.13	20.29±0.69
C.rotundata	Cr	-5.95±1.01	1.86±0.69	36.13±13.53	1.69±0.7	21.7±1.81
Halodule uninervis	Hu	-7.04±0.31	2.74±0.41	44.9±0.51	2.23±0.03	20.13±0.31
seagrass floating	fls	-6.79±0.19	2.94±0.69	40.7±0.82	1.48±0.22	27.84±3.42
seagrass detritus	dts	-6.95±0.18	3.17±0.6	40.65±1.26	1.31±0.15	31.22±2.8
Epiphytes *Enhalus*	Eea	-4.27±0.26	5.54±2.3	22.34±1.13	1.03±0.15	21.98±1.94
Epiph. *Thalassia*	Eth	-4.37±1.48	4.31±0.23	16.07±1.46	0.87±0.22	18.97±3.14
Epiph. *Cymodocea*	Ecr	-4.99	2.71	22.63	1.16	19.,57
Epiph. *Halodule*	Ehu	-5.42±0.6	1.91±0.45	22.5±1.66	1.28±0.11	17.6±0.28
Epiph.floating	Efls	-5.28±0.29	3.42±1.54	20.06±0.23	1.02±0.06	19.8±1.05
Epiph. detritus	Edts	-6.86±0.09	3.83±1.78	21.17±1.26	0.96±0.12	22.12±1.46
Chlorophyta	Chl	-10.62	2.71	20.23	0.98	20.56
other						
sPOM > 1 mm	sPl	-5.71	3.12	16.36	0.85	19.27
sPOM < 1mm	SPs	-5.01	6.48	18.02	1.3	27.21
Phytoplankton	POM	-20.51±1.1	4.47±0.83	0.62±0.08	0.09±0.01	6.9±0.44

3.2.2. Fauna

A total of 66 fishes from 18 species were subjected to stable isotope analysis. The $\delta^{13}C$ values of fish species ranged from -8.32 ‰ (*Gymnothorax* sp., Muraenidae) to -15.87 ‰ (*Tylosurus crocodilus*, Belonidae). The $\delta^{15}N$ values of fish ranged from 4.88 ‰ (*Siganus virgatus*, Siganidae) to 10.95 ‰ (*Sphyraena barracuda*, Sphyraenidae) (Table 3). Abundances and lengths (mean ± SD) of all fish species recorded during visual census are shown in the appendix (A.1). Additionally, a total of 81 individuals of 45 taxa plus a total of nine zooplankton samples (five samples for zooplankton up to 55µm and four samples for zooplankton up to 200µm) were subjected to stable isotope analysis. The range of invertebrate $\delta^{13}C$ values was broader than for fish: invertebrate values ranged from -4.43 ‰ (Ophiuroidea sp. “striped“) to -28.53 ‰ (*Eucalliax* sp.). Invertebrate $\delta^{15}N$ values had a similar range, but overall were at lower nitrogen levels than fish: they ranged from -7.53 ‰ (*Eucalliax* sp.) to 8.68 ‰ (Ophiuroidea sp. “sponge“) (Table 4). Highest $\delta^{15}N$ values for animals were found for the two fish *S. barracuda* ($\delta^{15}N$ = 10.94 ‰) and *T. crocodilus* ($\delta^{15}N$ = 10.26 ‰).The lowest $\delta^{15}N$ and $\delta^{13}C$ values were determined for three species of bivalves (*Solemya pusilla*, *Codakia tigerina*, *Fimbria* sp.) and two species of crustaceans (*Eucalliax panglaoensis* and *Calliaxina* sp.) (Fig. 2).

Table 3. Fish densities (individuals 100 m^{-2}) and mean size ± SD (cm) of the species counted in the seagrass meadow using a rapid visual census. For the food web, mean δ^{13}C and δ^{15}N values (‰) are shown (± SD). Trophic category is given according to Vonk et al. (2008): herbivorous (H), piscivorous (P), omnivorous (O), zoobenthivorous (ZB), and planktivorous (ZP).

(b) teleosts	**Species**	**density**	**size**	**trophic category**	**code**	**n**	**δ^{13}C**	**δ^{15}N**
Atherinidae	*Atherinomorus lacunosus*	16.60±48.2	2.37±0.90	ZP	Al	3	-15.58±0.27	7.12±0.02
Belonidae	*Strongylura incisa*	2.32±11.07	30.00±0.00	P	Si	3	-9.64±0.07	7.2±0.1
	Tylosurus crocodilus			P	Tc	3	-15.87±0.26	10.26±0.63
Blenniidae	*Petroscirtes variabilis*			H	Pv	2	-13.97	5.95
Gobiidae	*Cryptocentrus* sp.	0.00±0.19	2.67±0.58	H	Csp	1	-9.96	8.14
Hemirhamphidae	*Hemirhamphus far*	0.09±0.19	24.00±6.52	H	Hf	3	-11.99±2.31	8.71±0.49
Labridae	*Cheilinus chlorourus*	0.91±1.79	6.11±5.29	ZB	Cc	3	-9.37±0.37	7.77±0.12
	Cheilio inermis	1.01±1.70	17.72±7.44	ZB	Ci	3	-10.82±0.82	7.42±0.68
	Choerodon anchorago	0.29±0.70	12.83±6.39	O	Ca	3	-9.09±0.07	8.1±0.16
	Halichoeres argus	21.79±24.56	4.11±1.54	O	Ha	3	-8.97±0.24	7.01±0.31
	Halichoeres chloropterus	3.40±4.21	9.69±3.74	ZB	Hc	3	-10.07±1.3	7.78±0.53
	Halichoeres scapularis	0.19±0.79	6.33±4.93	ZB	Hs	1	-9.03	7.87
	Stethojulis trilineatus	0.20±1.00	7.00±3.39	O	St	3	-9.64±0.07	7.2±0.1
Lethrinidae	*Lethrinus obsoletus*	0.30±1.30	9.89±3.72	ZB	Lo	2	-8.9	8.5
Monacanthidae	*Acreichthys tomentosus*	0.10±0.30	7.39±0.55	O	At	3	-8.63±0.35	7.83±0.68
Mullidae	*Upeneus tragula*	0.10±040	20.63±3.20	ZB	Ut	2	-9.33	8.11
Muraenidae	*Gymnothorax* sp.			ZB, P	Gsp	1	-8.32	9.03
Nemipteridae	*Pentapodus trivittatus*	2.32±2.79	11.52±2.42	ZB	Pt	3	-9.07±0.24	8.79±0.43
	P. trivittatus juv.				Ptj	3	-9.08±0.3	5.96±0.3
	Scolopsis margaritifera	0.30±0.80	8.63±1.61	ZB	Sm	1	-9.75	8.51
Pomacentridae	*Dischistodus chrysopoecilus*	7.21±7.60	4.37±2.33	H	Dc	3	-13.47±0.07	6.94±0.16
	Dischistodus fasciatus	0.00±0.10	8.00±0.00	H	Df	1	-12.16	6.62
	D. perspicillatus	0.40±1.20	4.77±1.82	H	Dp	1	-13.14	6.78
Scaridae	Scaridae sp.	0.40±1.20	2.00±0.00	H	Ssp	3	-11.1±0.1	5.25±0.25

Siganidae	*Siganus canaliculatus*	18.61±37.80	10.63±2.32	H	Sc	3	-11.28±0.9	6.81±0.63
	Siganus spinus	0.00±0.40	8.00±0.00	H	Ss	1	-12.17	6.65
	Siganus virgatus	0.00±0.19	10.00±0.00	H	Sv	1	-12.09	4.88
Sphyraenidae	*Sphyraena barracuda*	0.00±0.19	33.33±7.64	P	Sb	1	-9.94	10.94
Syngnathidae	*Syngnathoides biaculeatus*			ZP	Syb	3	-13.74±2.82	7.51±0.56

Table 4. Sample sizes and isotopic signatures of invertebrates subjected to stable isotope analysis, collected from the seagrass meadow. Values are given as mean (± SD).

(a) **Invertebrates**	**species**	**code**	**n**	**δ^{13}C**	**δ^{15}N**
Crustaceans					
	Alpheus sp.	Alp	1	-5.86±0.15	6.19±0.07
	Amphipoda	Am	1	-7.72	4.12
	Mysidae	My	3	-11.46±0.04	6.51±0.01
	Cirripedia	Cir	3	-5.59±0.58	4.03±0.27
	Corallianassa coutieri	Cog	2	-4.80±0.13	2.79±0.42
	Corallianassa assimilis	Coy	1	-8.85	4.25
	Callianida typa	Cal	3	-9.16±0.32	7.19±0.42
	Eucalliax panglaoensis	Eu	1	-28.53	-7.53
	Calliaxina novaebritanniae	Cax	1	-25.72	-3.38
	Glypturus armatus	Gly	1	-8.02	3.25
Molluscs					
Bivalvia	*Tapes* sp.	Ta	3	-13.25±0.22	6.35±0.36
	Tellina sp.	Te	1	-14.51	4.12
	Gafrarium sp.	Ga	1	-13.73	4.45
	Vasticardium sp.	Va	1	-13.5	5.83
	Scutarcopagia sp.	Scu	1	-8.71	5.12
	Antigona sp.	Ans	1	-10.93	4.62
	Antigona lamellaris	Al	1	-11.73±0.00	7.17±0.00
	Pinna muricata	Pim	3	-13.23±0.18	4.69±0.28
	Pitar sp.	Pit	1	-13.45	5.8
	Fimbria sp.	Fsp	1	-21.54	3.07
	Codakia tigerina	Ct	1	-23.48	-0.94
	Solemya pusilla	Ssp	1	-26.59	2.36
	Tellina staurella	Ts	1	-8.24	5.11

	Antigona puerpera	Ap	3	-12.75±0.48	8.07±0.75
	Mactra maculata	Mm	1	-11.91	4.18
	Anodontia edentula	Ae	1	-13.32	5.68
	Anadara antiquata	Aa	1	-12.41	6.74
Gastropoda	*Zeacolpus pagodus*	Ze	1	-10.7	6.99
	Strombus urceus	Str	1	-9.32	3.47
	Polinices flemingianus	Pf	1	-13.65	6.22
	Polinices melanostomus	Pm	1	-18.61	4.57
	Conus virgatus	Cv	1	-8.48	6.7
	Cymbiola sp.	Cy	1	-7.88	7.17
Echinoderms					
Asteroidea	*Archaster typicus*	Art	3	-6.32±0.21	4.86±1.01
Holothuroidea	*Holothuria* sp.	Hsp	3	-9.46±0.6	6.05±1.2
	Holothuroidea sp.	Hol	1	-6.04	5.25
Ophiuroidea	ophiurid sponge	Op1	1	-5.34	8.68
	ophiurid stripes	Op2	3	-4.43±0.44	6.13±0.49
	ophiurid black	Op3	3	-5.05±1.09	7.16±1.31
	ophiurid	Op4	1	5.62	-6.34
other invertebrates					
Cnidaria	Actinia large	Ac1	3	-6.77±1.29	7.78±0.36
	Actinia small	Ac2	3	-7.42±0.55	7.08±0.43
Porifera	dark brown sponge	dbs	3	-12.24±0.09	4.01±0.36
	sponge brown tips	sbt	3	-10.51±1.88	4.26±0.62
	sponge yellow body	sy	3	-11.41±0.57	5.04±0.44
	mossy sponge	ms	1	-15.14	4.89
Zooplankton	zooplankton 55µm	Z55	5	-12.47±3.73	5.17±0.94
	zooplankton 200µm	Z200	4	-12.37±0.89	5.53±1.04

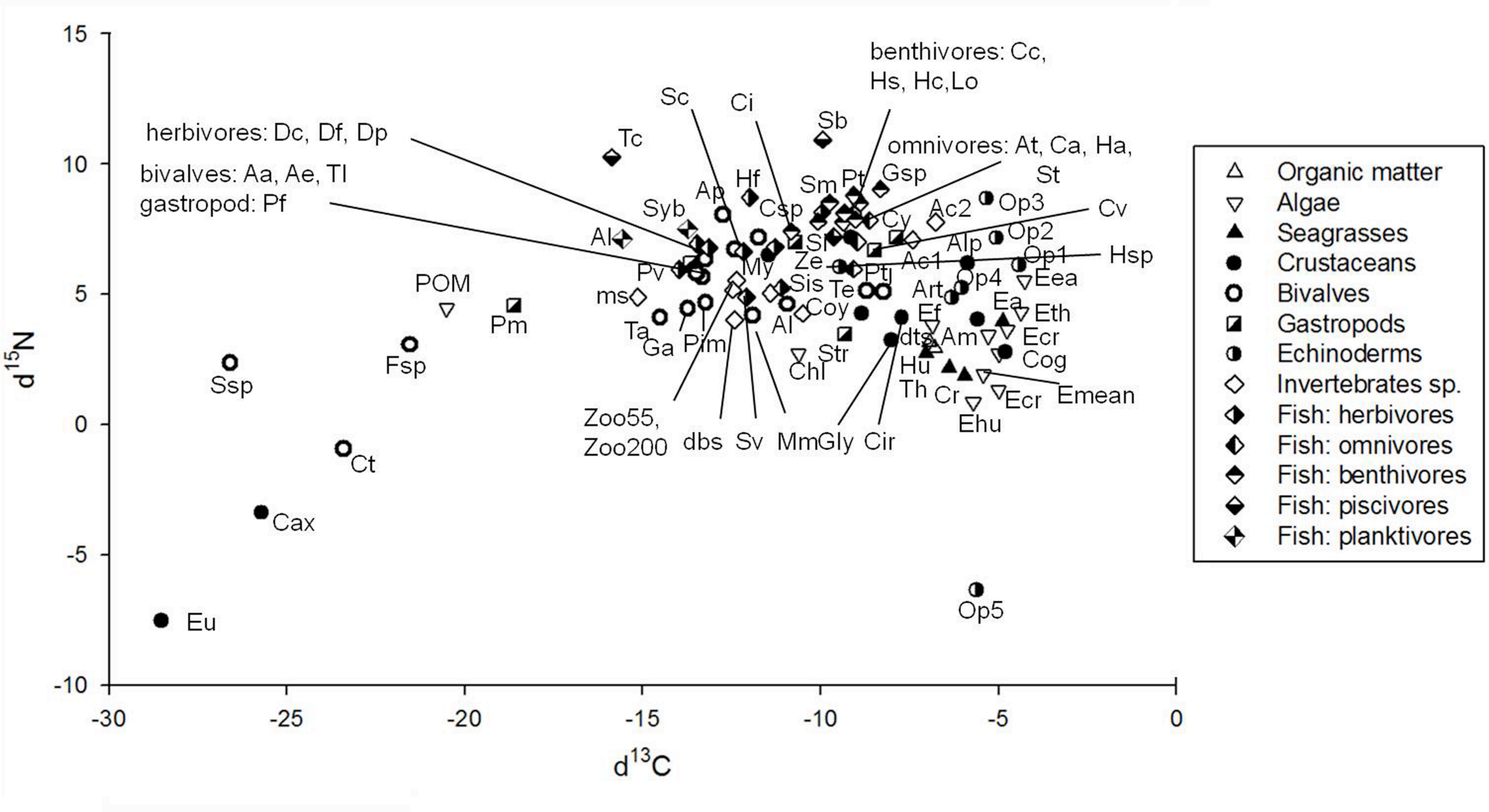

Fig. 2. δ^{15}N and δ^{13}C of algae, microphytobenthos, plants, plankton, benthic invertebrates and fishes. Abbreviations follow tables 2, 3, 4.

3.2.3 Determination of fish trophic level

The highest trophic levels were found for the three piscivores *S. barracuda*, *S. incisa* and *T. crocodilus*, followed by the macrozoobenthivores *Gymnothorax* sp. and adult *P. trivittatus*. The predominantly seagrass-feeding herbivore *H. far* displayed a considerably high trophic level and was ranked well before most zoobenthivorous species. Such a high trophic level for this species is not represented by gut-content analysis. Other herbivorous species occupied lowest trophic levels (≤ 2.51). Most zoobenthivores occupied a trophic level between 3.00 and 2.53. The planktivorous *A. lacunosus* and the omnivorous *H. argus* do not differ much from herbivorous species with respect to trophic level (Table 5).

Table 5. Trophic level of the investigated fish taxa of the mixed-species seagrass bed off Barrang Lompo South.

Species	**Trophic level**
Sphyraena barracuda	3.69
Strongylura incisa	3.49
Tylosurus crocodilus	3.44
Gymnothorax sp.	3.13
Pentapodus trivittatus	3.06
Hemirhamphus far	3.03
Scolopsis margaritifer	2.97
Lethrinus obsoletus	2.97
Choerodon anchorago	2.90
Cryptocentrus sp.	2.87
Halichoeres scapularis	2.78
Acreichthys tomentosus	2.77
Halichoeres chloropterus	2.76
Cheilinus sp.	2.76
Syngnathoides biaculeatus	2.68
Cheilio inermis	2.65
Stethojulis trilineatus	2.59
Atherinomorus lacunosus	2.57
Halichoeres argus	2.53
Dischistodus chrysopoecilus	2.51
Siganus canaliculatus	2.47
Dischistodus perspicillatus	2.46
Siganus spinus	2.43
Dischistodus fasciatus	2.42
Pentapodus trivittatus juv.	2.22
Petroscirtes variabilis	2.22
Scaridae sp.	2.01
Siganus virgatus	1.91

3.3. Gut-content analysis

3.3.1. Feeding guilds

Overall, the guts of 182 individuals from 27 fish species were analysed. All of these species were assigned to one of the following four feeding guilds: herbivorous, omnivorous, (macro)zoobenthivorous and piscivorous. For the nemipterid *Pentapodus trivittatus*, two different ontogenetic classes were used: juveniles (total length ranging from 37 mm to 58 mm) and adults (TL 120 mm to 250 mm).

Bray-Curtis Hierarchical Cluster analysis and non-dimensional MDS were able to clearly distinguish between herbivores, piscivores, and a large group comprising omnivores and zoobenthivores (Fig. 3 A, B).

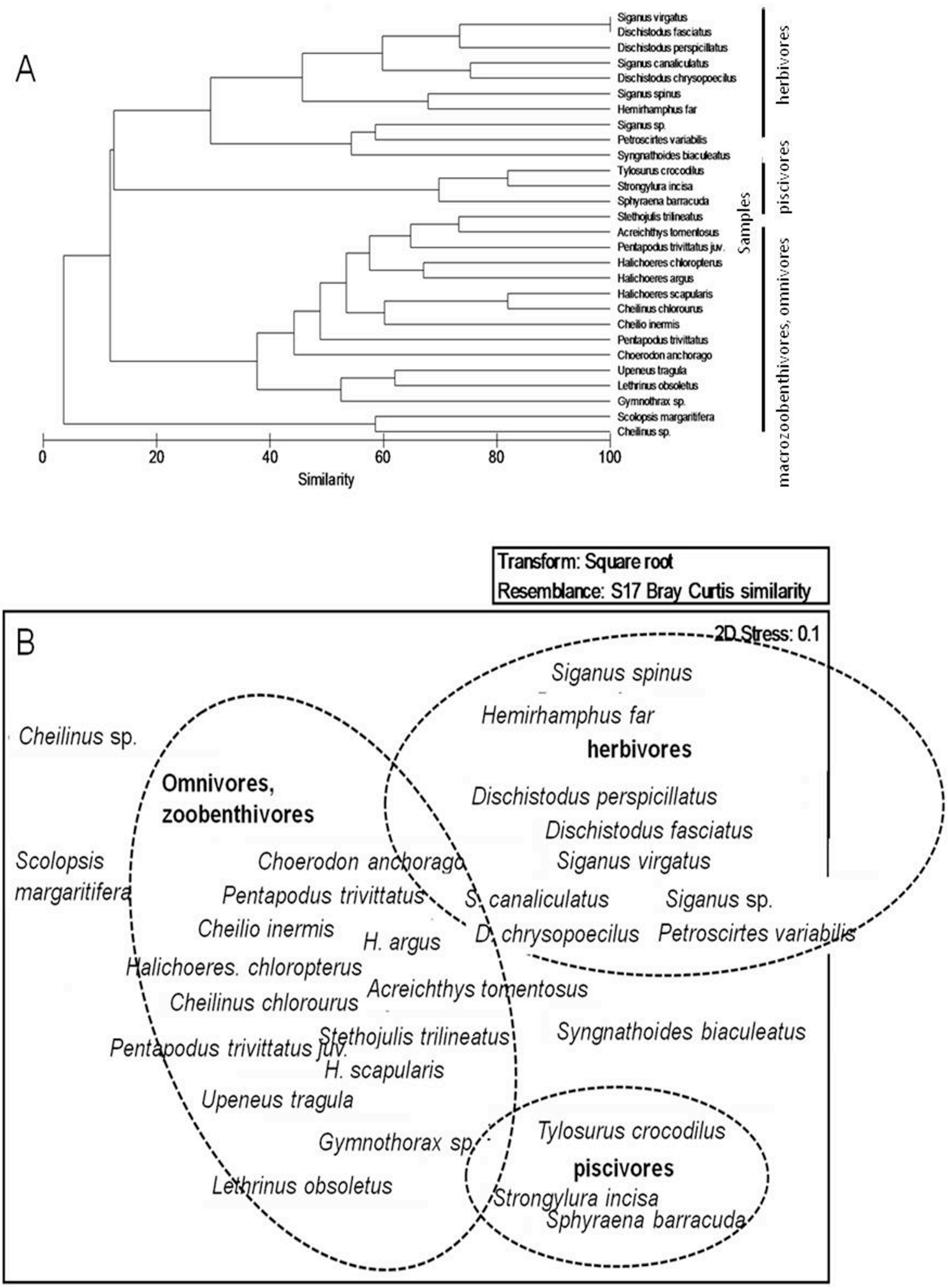

Fig. 3. Analysis of fish feeding guilds based on gravimetric gut-content data. A. Bray-Curtis Cluster analysis of fish feeding guilds based on gravimetric gut-content data. B. Non-dimensional MDS.

3.3.2. Prey items

Altogether, a total of 4436 prey items (macerated seagrass and algae excluded) from 23 major prey categories were identified (Table 6). Highest numbers of prey items were found in macrozoobenthivores (herbivores mostly excluded from this calculation): for the labrids *C. inermis*, 361 prey items from 10 major categories and for the nemipterid *P. trivittatus* (adults only), 356 items from 18 categories were found, followed by the labrid *S. trilineatus* with 169 items and the omnivorous monacanthid *A. tomentosus* with 165 prey items from five major food item categories each. The lowest numbers of prey items were found in piscivores and herbivores, with the exception of two specimens of *H. far*, which had a gut filled with macerated seagrasses and several hundred of seagrass-associated foraminiferans. The average dietary spectrum of omnivores and zoobenthivores was considerably broader than that of herbivores or piscivores.

Intestinal parasites were found in three species: several specimens of the belonid species *Tylosurus crocodilus* and *Strongylura incisa* were strongly infected by tapeworms (Cestoda), and in one specimen of the half-beak *Hemirhamphus far*, a mild infection with spiny-headed worms (Acanthocephala) was found.

Table 6. Vacuity Index (VI) of empty fish guts and Frequency of Occurrence Index (FO; both %) of dietary categories for fish species subjected to gut-content analysis. For abbreviations of fish species see Table 2. Species for which less than 4 specimens were subjected to gut-content analysis were neglected for calculating indices. Bold numbers at the top of the table refer to dietary category. Bold numbers within table refer to FO (%) found in more than one third of all guts. 1 = algae; 2 = Alpheidae; 3 = Amphipoda; 4 = Annelida; 5 = Anomura; 6 = Bivalvia; 7 = Brachyura; 8 = Crustacea (unidentified); 9 = Echinodermata; 10 = fish; 11 = fish eggs; 12 = Foraminifera; 13 = Gastropoda; 14 = Hydrozoa; 15 = Molluska (unidentified); 16 = Nematoda; 17 = Oligochaeta; 18 = Ostracoda; 19 = Pantopoda; 20 = Polychaeta; 21 = seagrass; 22 = shrimps; 23 = Sipunculida.

			FO																						
fish	**n**	**VI**	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**
At	11	**36.36**	0.00	0.00	**42.86**	0.00	0.00	0.00	0.00	**42.86**	0.00	0.00	0.00	0.00	14.29	0.00	0.00	0.00	0.00	0.00	0.00	14.29	14.29	0.00	0.00
Ci	18	0.00	0.00	0.00	11.11	0.00	0.00	22.22	5.56	**66.67**	**38.89**	16.67	0.00	5.56	**66.67**	0.00	5.56	0.00	0.00	0.00	0.00	5.56	5.56	0.00	0.00
Ca	4	0.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	**100.00**	25.00	0.00	0.00	25.00	**100.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Dc	10	0.00	**100.00**	0.00	0.00	10.00	0.00	0.00	0.00	30.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**80.00**	0.00	0.00
Ha	24	12.50	8.00	0.00	24.00	0.00	0.00	0.00	0.00	**56.00**	0.00	0.00	0.00	4.00	**44.00**	8.00	4.00	16.00	4.00	16.00	4.00	12.00	0.00	12.00	0.00
Hc	11	0.00	0.00	0.00	18.18	0.00	0.00	0.00	0.00	**90.90**	9.09	0.00	0.00	18.10	**63.63**	0.00	18.18	9.10	0.00	9.10	0.00	0.00	0.00	0.00	0.00
Hf	13	0.00	0.00	0.00	7.69	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	23.08	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**100.00**	0.00	0.00
Pt	23	0.00	0.00	26.09	**47.82**	4.34	8.70	8.70	21.74	**69.57**	8.69	8.69	8.69	0.00	13.04	0.00	4.34	4.34	8.69	0.00	0.00	**56.52**	13.04	0.00	4.34
Ptj	12	0.00	7.69	0.00	23.07	0.00	0.00	0.00	0.00	**100.00**	0.00	0.00	15.38	0.00	15.38	0.00	15.38	0.00	0.00	7.69	0.00	23.07	0.00	23.07	0.00
Sc	15	0.00	**66.67**	0.00	0.00	0.00	0.00	0.00	6.67	33.33	0.00	0.00	0.00	13.33	33.33	0.00	0.00	0.00	0.00	0.00	0.00	0.00	80.00	0.00	0.00
St	13	0.00	0.00	0.00	23.08	0.00	0.00	0.00	0.00	**92.31**	0.00	7.69	0.00	0.00	**46.15**	0.00	0.00	0.00	0.00	0.00	0.00	7.69	0.00	0.00	0.00
Si	8	50.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**100.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Syb	4	0.00	25.00	0.00	25.00	0.00	0.00	0.00	0.00	25.00	0.00	25.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Tc	10	27.27	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	**100.00**	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

3.3.3. Diet composition

Over all guts sampled, crustaceans were the most common food items (in 58 % of all guts, where unidentified specimens were found in 48.2 % and amphipods in 15.8 % of all guts), followed by gastropods (FO = 26.5 %) and seagrass (FO = 24.5 %). A considerable contribution to unidentified crustaceans were detached carapaces, appendages and other body parts of microcrustaceans. It was not possible to determine whether these were parts of benthic or pelagic life forms.

The Vacuity Index (VI) of all guts was 7.3 %. Empty guts were found only for the belonids *T. crocodilus* (VI = 27.3 %) and *S. incisa* (VI = 50 %), the monacanthid *A. tomentosus* (VI = 36.4 %) and the labrid *H. argus* (VI = 12.5 %). For the macrozoobenthivorous labrid *C. inermis*, gastropods and crustaceans were dominant food items found in an equal number of guts (in 66.7 % of all guts investigated), followed by echinoderms and bivalves (38.9 and 22.2 % of all guts). For both belonid species, fish was the only food item; they were found in 100 % of all non-empty guts. For the labrids *H. chloropterus* and *S. trilineatus*, the frequency of occurrence (FO) was highest for unidentified crustaceans (FO = 90.9 % and FO = 92.31 %), followed by gastropods (FO = 63.6 % and 46.5 %), and furthermore, for *H. chloropterus* amphipods (FO = 18.2 %) and alpheid shrimps for *S. trilineatus* (FO = 26.08 %). In the labrid *H. argus*, small unidentified crustaceans were found in about half of all guts (FO = 56.0 %), followed by gastropods (FO = 44 %), amphipods (FO = 24 %) and nematodes (FO = 16.0 %). In all guts of dissected *C. anchorago* (n = 4), unidentified crustaceans and gastropods, and in half of the specimens, echinoderms were found. For adult *P. trivittatus*, unidentified crustaceans were again the food source found in most guts (FO = 69.6 %), followed by polychaete worms (FO = 56.5 %), amphipods (FO = 47.8 %), alpheid shrimps (FO = 26.1 %) and unidentified brachyurids (FO = 21.7 %). For juvenile *P. trivittatus*, tiny unidentified crustaceans were present in all guts (FO = 100 %), while shrimps, polychaete worms and amphipods were each found in the same proportions of guts (FO = 23.1 %). In less than half of all guts of *A. tomentosus*, amphipods and unidentified crustaceans were found (each FO = 42.9 %), followed by polychaetes, gastropods and seagrass (each FO = 14.3 %). In the syngnathid *S. biaculeatus*, macroalgae, amphipods and other crustaceans were present in equal proportions (each FO = 25.5 %). In the herbivorous hemirhamphid *H. far*, all guts contained seagrass (FO = 100 %); seagrass-associated foraminiferans were found in about one quarter of all guts (FO = 23.08 %). A few *H. far* guts contained amphipods (FO = 7.7 %). In all guts of the pomacentrid *D. chrysopoecilus*, epiphytic algae were found (FO = 100 %). Seagrass (FO = 80 %) and crustaceans (FO = 30 %) were present in fewer guts. For the predominantly herbivorous *S. canaliculatus*, plant material was found in most guts (for seagrass FO = 80 % and epiphytic algae FO = 66.7 %), and about one third of all guts contained gastropods and unidentified crustaceans (FO = 33.33 % each; Table 8).

3.3.4. Dietary niche overlap and niche breadth

Overall, 30 cases of significant niche overlap, indicated by the Schoener Index (SI), occurred between fish species. This ranged from a low degree of overlap (e.g. for *D. chrysopoecilus* and *D. fasciatus* SI = 0.60*) up to complete overlap (e.g. for *S. incisa* and *S. barracuda* SI = 1.00*) (Table 8). Many overlaps occurred between macrozoobenthivores and/or omnivores. The omnivores *A. tomentosus* (Monacanthidae) and *C. chlorourus* (Labridae) had a dietary spectrum of similar composition and proportion of food items, with small and medium-sized crustaceans dominating (SI = 0.69*). Macrozoobenthivorous labrids that already grouped together in Hierarchical Cluster analysis showed significant niche overlap (e.g *C. inermis* and *C. anchorago,* SI = 0.66*; *C. chlorourus* and *H. chloropterus*, SI = 0.78*; *H. chloropterus* and *C. inermis*, SI = 0.62*; *H. chloropterus* and *C. anchorago*, SI = 0.68*, *H. scapularis* and *C. inermis*, SI = 0.66*; *S. trilineata* and *H. argus*, SI = 0.81*), due to a mutual preference of benthic invertebrates such as crustaceans, gastropods and echinoderms. High overlap in the zoobenthivore/omnivore fraction was found between *L. obsoletus* (Lethrinidae) and *H. argus* (Labridae; SI = 0.99*), *U. tragula* (Mullidae) and juvenile *P. trivittatus* (Nemipteridae; SI = 0.84*) and *L. obsoletus* and *Gymnothorax* sp. (Muraenidae). Note, however, that the sample size for the latter two was very small (n = 1 each). Although adult *P. trivittatus* were grouped with other macrozoobenthivores in the cluster analysis, there was no significant niche overlap either with any of the other fish species or with juvenile *P. trivittatus*. Another species showing no significant overlap was *S. margaritifera* (Nemipteridae), which did not overlap with any other species except for *P. trivittatus* (SI = 0.50); the gut-content of only one specimen was examined during this study.

For the (predominantly) herbivorous feeding guild, there was significant overlap for the three species of *Dischistodus* (Pomacentridae; *D. chrysopoecilus* and *D. fasciatus*, SI = 0.60*; *D. chrysopoecilus* and *D. perspicillatus*, SI = 0.86*), based on a diet of mainly epiphytic algae and seagrasses and a small amount of microcrustaceans (mainly copepods). There was a partially highly significant overlap between the seagrass-feeding *H. far* (Hemirhamphidae) and several species of siganids that ingest seagrasses and their epiphytes (*H. far* and *S. canaliculatus*, SI = 0.77*; *H. far* and *S. spinus*, SI = 0.99*; *H. far* and *S. virgatus*, SI = 0.92*), as well as for all of the siganids (*S. canaliculatus* and *S. spinus*, SI = 0.76*; *S. canaliculatus* and *S. virgatus*, SI = 0.84*; *S. spinus* and *S. virgatus*, SI = 0.92*) and between the pomacentrid *D. fasciatus* and the siganids *S. canaliculatus* (SI = 0.76*) and *S. virgatus* (SI = 0.64*). In the cluster analysis, *P. variabilis* (Blenniidae) and *S. biaculeatus* (Syngnathidae) were grouped together with the herbivores. While the former showed significant overlap with the herbivorous pomacentrids mentioned above (SI for *P. variabilis* and *D. chrysopoecilus* SI = 0.77* and for *P. variabilis* and *D. perspicillatus* = 0.76*), the latter overlapped significantly with omnivorous or zoobenthivorous species, such as *H. argus* (SI = 0.89*), *L. obsoletus* (SI = 0.89*) and *S. trilineatus* (SI = 0.81). The syngnathid *S.*

biaculeatus is generally not known as a herbivore, but rather as being zooplanktivorous or zoobenthivorous.

Concerning the piscivorous guild, all three species were grouped together in cluster analysis and had highly significant niche overlap (for *Sphyraena barracuda* and *Strongylura incisa* SI = 1.00*; for *S. barracuda* and *Tylosurus crocodilus* = 0.96*; for *S. incisa* and *T. crocodilus* SI = 0.96*) (Table 7).

Levins Index for niche breadth was highest for adult *P. trivittatus* (R_B = 4.39); ranks two and three are occupied by *C. chlorourus* (R_B = 3.69) and *C. inermis* (R_B = 3.00). About 50 % of the studied species (13 out of 26) had a Levins Index value < 1.50. Smallest niche breadth values were found for *S. barracuda*, *S. spinus*, *L. obsoletus* and *Gymnothorax* sp. (R_B = 1.00 each) (Table 8).

Table 7. Schoener Index values (SI) of trophic niche overlap between (25) fish species of the mixed-species seagrass bed off the island of Barrang Lompo. Asterisks indicate significant overlap of trophic niches (≥ 0.6*). For abbreviations of fish names see Table 2. Ptj refers to juvenile *P. trivittatus*.

	At	*Ct*	*Ci*	*Ca*	*Dc*	*Df*	*Dp*	*Gsp*	*Ha*	*Hc*	*Hs*	*Hf*	*Lo*	*Pt*	*Ptj*	*Pv*	*Sm*	*Sc*	*Ss*	*Sv*	*Sb*	*St*	*Si*	*Syb*	*Tc*	*Ut*
At	-	**0.69***	0.10	0.15	0.02	0.00	0.00	0.35	0.36	0.42	0.18	0.10	0.35	0.26	0.45	0.09	0.14	0.11	0.10	0.10	0.09	0.45	0.10	0.35	0.10	0.36
Ct	**0.69***	-	0.41	0.39	0.20	0.19	0.19	0.42	0.55	**0.78***	0.39	0.19	0.42	0.31	0.50	0.19	0.19	0.20	0.19	0.23	0.19	0.53	0.19	0.42	0.19	0.42
Ci	0.10	0.41	-	**0.66***	0.01	0.00	0.00	0.08	0.09	**0.62***	**0.66***	0.00	0.50	0.24	0.11	0.00	0.09	0.02	0.00	0.04	0.04	0.21	0.05	0.08	0.05	0.08
Ca	0.15	0.39	**0.66***	-	0.02	0.01	0.02	0.13	0.13	**0.68***	0.38	0.00	0.13	0.20	0.16	0.01	0.10	0.02	0.00	0.01	0.00	0.25	0.00	0.15	0.00	0.13
Dc	0.02	0.20	0.01	0.02	-	**0.60***	**0.86***	0.01	0.01	0.03	0.05	0.16	0.01	0.02	0.03	**0.77***	0.01	0.35	0.16	0.24	0.01	0.02	0.01	0.12	0.05	0.01
Df	0.00	0.19	0.00	0.01	**0.60***	-	0.46	0.00	0.00	0.02	0.04	0.56	0.00	0.01	0.02	0.44	0.00	**0.76***	0.56	**0.64***	0.00	0.01	0.00	0.11	0.04	0.00
Dp	0.00	0.19	0.00	0.02	**0.86***	0.46	-	0.00	0.00	0.03	0.04	0.02	0.00	0.01	0.02	**0.76***	0.00	0.21	0.50	0.10	0.00	0.01	0.00	0.29	0.02	0.00
Gsp	0.35	0.42	0.08	0.13	0.01	0.00	0.00	-	0.00	0.28	0.07	0.00	**1.00***	0.50	0.47	0.00	0.00	0.01	0.00	0.00	0.00	**0.81***	0.00	0.00	0.02	0.50
Ha	0.36	0.55	0.09	0.13	0.01	0.00	0.00	0.00	-	0.28	0.07	0.00	**0.99***	0.11	0.47	0.00	0.00	0.01	0.00	0.00	0.01	**0.81***	0.00	**0.89***	0.01	0.50
Hc	0.42	**0.78***	0.09	**0.68***	0.03	0.02	0.03	0.28	0.28	-	0.41	0.03	0.28	0.26	0.32	0.02	0.04	0.03	0.02	0.02	0.02	0.42	0.02	0.28	0.03	0.28
Hs	0.18	0.39	**0.62***	0.38	0.05	0.04	0.04	0.07	0.07	0.41	-	0.04	0.07	0.08	0.09	0.04	0.04	0.05	0.04	0.50	0.04	0.18	0.04	0.07	0.04	0.07
Hf	0.10	0.19	**0.66***	0.00	0.16	0.56	0.02	0.00	0.00	0.03	0.04	-	0.00	0.01	0.02	0.49	0.00	**0.77***	**0.99***	**0.92***	0.00	0.01	0.00	0.00	0.04	0.00
Lo	0.35	0.42	0.00	0.13	0.01	0.00	0.00	**1.00***	**0.99***	0.28	0.07	0.00	-	0.10	0.47	0.00	0.00	0.01	0.00	0.00	0.00	**0.81***	0.00	**0.89***	0.00	0.50
Pt	0.26	0.31	0.50	0.20	0.02	0.01	0.01	0.50	0.11	0.26	0.08	0.01	0.10	-	0.16	0.00	0.50	0.05	0.01	0.01	0.05	0.16	0.06	0.10	0.06	0.11
Ptj	0.45	0.50	0.11	0.16	0.03	0.02	0.02	0.47	0.47	0.32	0.09	0.02	0.47	0.16	-	0.02	0.04	0.03	0.02	0.02	0.02	0.54	0.02	0.47	0.02	**0.84***
Pv	0.09	0.19	0.00	0.01	**0.77***	0.44	**0.76***	0.00	0.00	0.02	0.04	0.49	0.00	0.00	0.02	-	0.00	0.32	0.00	0.08	0.00	0.01	0.00	0.11	0.00	0.00
Sm	0.14	0.19	0.09	0.10	0.01	0.00	0.00	0.00	0.00	0.04	0.04	0.00	0.00	0.50	0.04	0.00		0.01	0.00	0.00	0.00	0.03	0.00	0.00	0.00	0.00
Sc	0.11	0.20	0.02	0.02	0.35	**0.76***	0.21	0.01	0.01	0.03	0.05	**0.77***	0.01	0.05	0.03	0.32	0.01	-	**0.76***	**0.84***	0.01	0.11	0.01	0.12	0.05	0.01
Ss	0.10	0.19	0.00	0.00	0.16	0.56	0.50	0.00	0.00	0.02	0.04	**0.99***	0.00	0.01	0.02	0.00	0.00	**0.76***	-	**0.92***	0.00	0.01	0.00	0.00	0.04	0.00
Sv	0.10	0.23	0.04	0.01	0.24	**0.64***	0.10	0.00	0.00	0.02	0.50	**0.92***	0.00	0.01	0.02	0.08	0.00	**0.84***	**0.92***	-	0.00	0.01	0.00	0.08	0.04	0.00
Sb	0.09	0.19	0.04	0.00	0.01	0.00	0.00	0.00	0.01	0.02	0.04	0.00	0.00	0.05	0.02	0.00	0.00	0.01	0.00	0.00	-	0.02	**1.00***	0.00	**0.96***	0.00
St	0.45	0.53	0.21	0.25	0.02	0.01	0.01	**0.81***	**0.81***	0.42	0.18	0.01	**0.81***	0.16	0.54	0.01	0.03	0.11	0.01	0.01	0.02	-	0.02	**0.81***	0.03	0.51
Si	0.10	0.19	0.05	0.00	0.01	0.00	0.00	0.00	0.00	0.02	0.04	0.00	0.00	0.06	0.02	0.00	0.00	0.01	0.00	0.00	**1.00***	0.02	-	0.00	**0.96***	0.00
Syb	0.35	0.42	0.08	0.15	0.12	0.11	0.29	0.00	**0.89***	0.28	0.07	0.00	**0.89***	0.10	0.47	0.11	0.00	0.12	0.00	0.08	0.00	**0.81***	0.00	-	0.00	0.50
Tc	0.10	0.19	0.05	0.00	0.05	0.04	0.02	0.02	0.01	0.03	0.04	0.04	0.00	0.06	0.02	0.00	0.00	0.05	0.04	0.04	**0.96**	0.03	**0.96**	0.00	-	0.00
Ut	0.36	0.42	0.08	0.13	0.01	0.00	0.00	0.50	0.50	0.28	0.07	0.00	0.50	0.11	**0.84**	0.00	0.00	0.01	0.00	0.00	0.00	0.51	0.00	0.50	0.00	-

Table 8. Levins Index of dietary niche breadth (R_B) for 26 fish species of the mixed-species seagrass bed off the island of Barrang Lompo.

Species	**R_B**
Pentapodus trivittatus	**4.39**
Cheilinus chlorourus	**3.69**
Cheilio inermis	**3.00**
Halichoeres chloropterus	**2.95**
Acreichthys tomentosus	**2.92**
Pentapodus trivittatus juv.	2.90
Halichoeres scapularis	2.28
Upeneus tragula	2.03
Dischistodus fasciatus	1.97
Choerodon anchorago	1.71
Siganus canaliculatus	1.63
Petroscirtes variabilis	1.57
Stethojulis trilineatus	1.52
Scolopsis margaritifera	1.42
Dischistodus chrysopoecilus	1.39
Syngnathoides biaculeatus	1.25
Siganus virgatus	1.17
Tylosurus crocodilus	1.10
Dischistodus perspicillatus	1.05
Halichoeres argus	1.02
Hemirhamphus far	1.02
Strongylura incisa	1.01
Gymnothorax sp.	1.00
Lethrinus obsoletus	1.00
Siganus spinus	1.00
Sphyraena barracuda	1.00

3.4. Fish biomasses

Biomass or ash-free dry weight (ASDW) was calculated for 24 fish taxa. Overall, 179 specimens were used. Ash-free dry weight ranged from 0.24 ± 18 (juvenile *P. trivittatus*) to 32.12 ± 0.68g (*S. barracuda*). Total length of specimens ranged from 44.64 ± 6.42 (juvenile *P. trivittatus*) to 414.33 ± 167.73mm (*T. crocodilus*; Table 9).

Table 9. Sample size (n), total length (TL), dry weight (DW) and ash-free dry weight (ASDW) of the most common fish species from seagrass beds off Barrang Lompo South. All values are presented as mean ± SD.

species	**n**	**TL [mm]**	**DW [g]**	**ASDW [g]**
Acreichthys tomentosus	11	88.45±3.96	3.66±1.19	2.38±1.01
Cheilinus trilobatus	3	97.00±52.33	12.64	9.85
Cheilio inermis	12	280.00±19.77	31.89±8.05	24.15±6.63
Choerodon anchorago	4	116.50±4.36	8.59±0.67	6.6±0.61
Dischistodus chrysopoecilus	12	117.08±8.67	9.41±2.97	6.83±2.37
Dischistodus perspicillatus	1	105.00	5.20	3.90
Halichoeres argus	24	52.40±5.58	0.46±0.13	0.35±0.09
Halichoeres chloropterus	14	150.00±9.70	10.65±2.94	9.00±2.13
Halichoeres scapularis	1	145.00	13.86	4.71
Hemirhamphus far	17	320.75±30.34	27.54±6.13	21.97±5.15
Lethrinus obsoletus	2	130.00±7.07	6.47±1.02	4.87±0.72
Gymnothorax sp.	1	380.00	6.29	4.66
Pentapodus trivittatus	23	169.87±31.91	16.84±7.51	13.14±6.16
Pentapodus trivittatus juv.	14	44.64±6.42	0.34±0.15	0.24±0.18
Siganus canaliculatus	14	187.64±46.63	21.24±14.21	17.27±12.02
Siganus spinus	1	105.00	3.83	3.03
Siganus virgatus	1	130.00	5.41	5.41
Sphyraena barracuda	2	327.00±9.9	41.97±0.96	32.12±0.68
Stethojulis trilineatus	12	131.25±8.38	9.52±2.44	7.09±1.89
Strongylura incisa	11	374.36±56.02	36.97±5.18	29.72±3.68
Syngnathoides biaculeatus	3	171.33±18.04	1.16±0.10	0.85±0.3
Tylosurus crocodilus	7	414.33±167.73	39.31±4.86	31.68±4.17
Upeneus tragula	2	222.00±2.83	29.05±1.28	22.02±1.39

3.5. Differences in trophic composition between study sites

The trophic status of fish species was determined based on the literature (A.1.). The study sites varied in proportions with respect to the trophic distribution of both individuals and taxa. With respect to taxon numbers, zoobenthivorous species made up the largest proportions over all study sites (range: 32.9 - 71.1 %), with the lowest values for corallivores (exclusively found at BLS: 0.2 %), piscivores (3.2 - 5.3 %) and zooplanktivores (3.2 - 8.3 %; Table 10). With respect to individual counts, zooplanktivores dominated at the intertidal sites (52.4 % for BBE and 55.9 % for BBS), omnivores at BLS (50.3 %) and zoobenthivores at BBN (36.8 %) and BBW (39.8 %). Herbivores showed the lowest relative abundance at the subtidal sites at 2.7 % for BBE and 4.2 % for BBS (Table 11), followed by piscivores (0.1 % to 2.8 %), while corallivores accounted for the lowest individual counts (again found only at BLS, 0.2 %).

A Simprof test on the trophic composition of fish assemblages over all study sites showed two distinct groupings with a similarity of 64.2 % ($\pi = 4.55$): the intertidal seagrass beds BLS, BBN and BBW with a similarity of 79.8 % ($\pi = 4.21$) versus the subtidal seagrass beds BBE and BBS with a similarity of 81.0 %. Within the groups, BBE vs BBS and BBN vs BBW are not distinctly different from each other (BBE vs BBS: 85.5 % similarity, $\pi = 0.00$; BBN vs BBW: 96.4 % similarity, $\pi = 0.00$; Fig. 4).

Table 10. Proportions of taxa (%) per trophic fraction for each study site. Numbers in brackets show proportion of total amount of zoobenthivorous taxa feeding on a diet including fish. BBE = Bone Batang East; BBN = Bone Batang North; BBS = Bone Batang South; BBW = Bone Batang West; BLS = Barrang Lompo South. C = corallivores; H = herbivores; O = omnivores; P = piscivores; ZB = zoobenthivores; ZP = zooplanktivores.

	C	**H**	**O**	**P**	**ZB**	**ZP**
BBE	0.00	7.89	10.53	5.26	71.05 (28.95)	5.26
BBN	0.00	20.83	16.67	4.17	50.00 (16.67)	8.33
BBS	0.00	8.70	26.09	4.35	54.35 (13.04)	6.52
BBW	0.00	20.83	25.00	4.17	45.83 (8.33)	4.17
BLS	0.03	14.52	22.58	3.23	32.90 (2.26)	3.23

Table 11. Proportions of individual counts (%) per trophic fraction for each study site. Numbers in brackets show proportion of total amount of individuals of zoobenthivorous taxa feeding on a diet including fish. For abbreviations, see Table 5.

	C	**H**	**O**	**P**	**ZB**	**ZP**
BBE	0.00	2.70	6.31	1.41	37.17 (8.39)	52.42
BBN	0.00	19.10	29.56	0.11	37.78 (0.96)	13.45
BBS	0.00	4.18	6.96	0.63	32.34 (25.36)	55.89
BBW	0.00	17.91	31.57	0.08	40.16 (0.33)	10.28
BLS	0.18	12.90	50.29	2.78	14.10 (2.43)	19.74

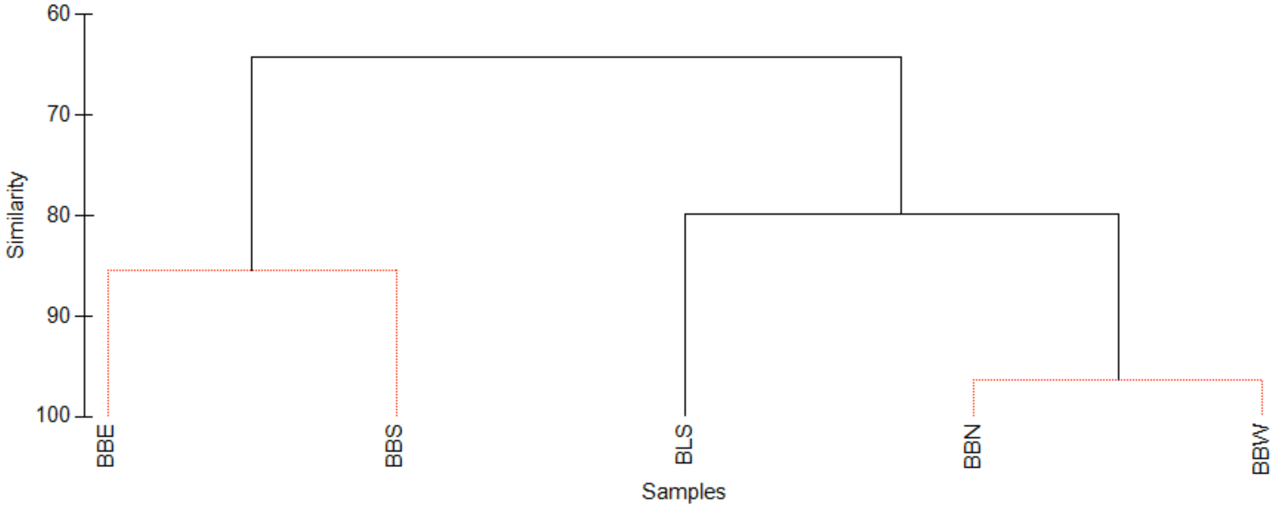

Fig. 4. Results of Hierarchical Cluster anaysis and Simprof test on trophic composition of fish assemblages over all study sites. Two major groupings into subtidal (BBE, BBS) and intertidal seagrass beds (BLS, BBN, BBW) are apparent.

SIMPER analysis of trophic distributions of fish assemblages based on individuals showed high similarity between inter- and subtidal seagrass beds (35.79 %). Subtidal seagrass beds were dominated by zooplanktivorous species (40.84 %

contribution), followed by zoobenthivores (31.24 %). Omnivores and herbivores were less similar within subtidal beds (14.17 and 9.25 %). In intertidal seagrass beds the largest trophic fraction contributing to similarity were the omnivores (30.55 %), followed by the zoobenthivores and the herbivores (24.03 and 21.18 %, respectively). Zooplanktivores comprise a smaller fraction (18.65 %). Piscivores did not account for similarity in either intertidal or subtidal seagrass beds.

4. Discussion

4.1. Seagrass shoot densities and fish abundances

Seagrass shoot densities are low compared to values in the recent literature both for the area and globally (e.g. Erftemeijer & Herman, 1994; Loneragan et al., 1998; Vonk et al., 2008, 2010). One reason might be strong seasonal fluctuations in shoot densities as mentioned by Erftemeijer & Herman (1994), which can be a result of full exposure to air and insolation. Another potential explanation is that seagrass shoot densities were affected by the strong El Niño Southern Oscillation during the study period: in this year, the rain season came late (in January 2010 instead of November or December 2009). This might have caused insolation stress and stress from elevated water temperatures, resulting in low shoot densities.

The three most abundant fish species are the labrid *H. argus*, the siganid *S. canaliculatus* and the atherinid *A. lacunosus*. *Halichoeres argus* is a small species that inhabits not only seagrass beds but also other habitats (Kuriandewa et al., 2003) such as coral rubble. It typically forms larger schools of at least 10 individuals rather than small groups or solitary individuals. Many such schools occurred in the seagrass bed at Barrang

Lompo South (BLS) and they apparently represented scattered aggregations with regular interactions between the schools (pers. obs.). Field observations suggest that this species prefers habitats with high structural complexity such as the mixed-species seagrass beds at BLS, where long leaves of the seagrass *E. acoroides* are intermingled with shorter seagrasses. In seagrass beds with a less differentiated canopy structure, e.g. predominantly short species or monospecific stands of *E. acoroides*, *H. argus* is much less abundant (Pogoreutz et al., submitted). The species appears to prefer closed canopy meadows. The other two most abundant species have a patchy distribution, with larger aggregations containing up to several hundred individuals. *Atherinomorus lacunosus* is a typical schooling fish. This species is zooplanktivorous, might not be dependent on the benthic food web (Khalaf & Kochzius, 2002) and might utilize the seagrass meadow as shelter from predation or a spawning area rather than as a feeding area. During censussing, schools of *A. lacunosus* never were observed feeding (pers. obs), which supports this interpretation.

The other abundant species, *S. canaliculatus*, is predominantly herbivorous, foraging in the seagrass bed and feeding on leaves of the seagrass *E. acoroides* and its epiphytes. The high densities of *S. canaliculatus* and *A. lacunosus* in the complex seagrass canopy at BLS might also be due to lower predation pressure here (Vonk et al., 2010). Vonk et al. (2008) found a different ranking for the most abundant species in a seagrass bed at Bone Batang, Indonesia, with *A. lacunosus* being by far the most abundant, followed by unidentified clupeids. The third rank is occupied by the labrid *Cheilio inermis*. Unsworth et al. (2007b) found that, in a comparable seagrass bed in the Wakatobi Marine National Park in southeast Sulawesi, *A. lacunosus* and three species of apogonids were the most abundant species. Such differences in similar habitats might reflect different canopy structure of seagrass beds (Vonk et al., 2008), different sampling methodology (e.g. diurnal sampling; Unsworth et al., 2007b), or different levels of exploitation of living marine resources.

4.2. Stable isotope analysis

In the present study different types of primary producers and organic matter were distinguished as food sources based on significantly different $\delta^{13}C$ signatures: seagrasses (including floating detached seagrass leaves and dead leaves, i.e. detritus), seagrass epiphytes, and POM (phytoplankton). Phytoplankton signatures were within the range of earlier studies in this region, and temperate habitats (Moncreiff & Sullivan, 2001; Vonk et al., 2008). Values for sPOM where enriched compared to the literature. Note, however, that in the present study these were single samples, and the amounts were too small to treat them with acid; thus, a contamination with inorganic carbon must be assumed. Signatures of $\delta^{13}C$ for seagrasses were in the range of recent literature values (Hemminga & Mateo, 1996), but enriched by about 3 ‰ compared to an earlier study at the neighbouring island of Bone Batang in the Spermonde Archipelago (Vonk et al., 2008). Hemminga & Mateo (1996) mention intraspecific and interspecific variability of stable isotope signatures within seagrasses. With respect to $\delta^{15}N$ signature, the seagrasses *T. hemprichii* and *H. uninervis* are depleted by about 1 ‰ compared to the study by Vonk et al. (2008), whereas the signatures of *E. acoroides* and *C. rotundata* do not differ. The nitrogen signature indicates no human impact on the investigated seagrass meadow in terms of nutrient input (i.e. eutrophication). This was unexpected because the island of

Barrang Lompo is densely inhabited (population density of about 5000 on an area of 0.5 km²?). Values of around 8 ‰ would indicate strong human impact (sewage water, waste etc.) (Grice et al., 1996; Vonk et al., 2008), but such levels were not found in this study. Moreover, high amounts of nitrogen fixation by cyanobacteria can be excluded in the present seagrass beds: strong fixation would be reflected by $\delta^{15}N$ signatures of around 0 ‰ (Yamamuro, 1999). Epiphytes of single seagrass species were enriched in $\delta^{15}N$ compared to their substrate, except for *H. uninervis*, where epiphytes were slightly more depleted. Stable carbon signatures for epiphytes were significantly different from seagrasses, but strongly enriched compared to other studies (Moncreiff & Sullivan, 2001; Vonk et al., 2008), while $\delta^{15}N$ signatures were in range of other studies. One possible explanation for strongly enriched $\delta^{13}C$ values is contamination with inorganic carbon, which is a component of seagrass epiphytes such as encrusting calcareous algae or seagrass-associated foraminiferans. In the present study, epiphytes were treated with hydrochloric acid to remove inorganic carbon contents in epiphytes. However, not all inorganic carbon may have been removed by the treatment, and remnants mask the actual organic $\delta^{13}C$ from the epiphytes. This is surprising because the acid treatment is usually sufficient to remove all inorganic carbon.

Numerous studies show that the stable carbon signature helps trace the potential food sources of a consumer species; this is based on the assumption that stable carbon values of a consumer are enriched less than 1 ‰ compared to their diet (e.g. Marguillier et al., 1997; Pinnegar & Polunin, 1999; Post, 2002; Benstead, 2006; Carassou et al., 2008). In this study, no organism was found to rely predominantly or exclusively on phytoplankton. Most species were much more enriched in stable carbon, with the belonid

Tylosurus crocodilus and the zoobenthivorous atherinid *A. lacunosus* being the most depleted fish (stable carbon of -15.8 and -15.6 ‰, respectively). Values for zooplankton were enriched compared to *A. lacunosus* (-12.47 and -12.37 ‰ for size fractions of 55 and 200µm, respectively), which is an unexpected result. Signatures of planktonic resources may vary largely with time, while the signatures of animal tissue reflect their diet of the last days up to months (Vonk et al., 2008). Discrepancies in isotopic signatures between consumer and possible food source are known. The gastropod *Polinices melanostomus* was enriched in stable carbon by about 2 ‰ compared to phytoplankton, indicating that it might at least partially rely on planktonic food sources. However, species of *Polinices* and other naticid gastropods are known to be predators (e.g. *P. duplicatus* feeding on the bivalve *Mya arenaria*; Edwards & Hubner, 1977). Thus, this gastropod probably relies indirectly on phytoplankton by foraging on filter-feeding prey, such as bivalves.

Some of the organisms subjected to stable isotope analysis had depleted stable carbon values compared to phytoplankton: the two callianassidean crustaceans *Eucalliax panglaoensis* and *Calliaxina novaebritannicae* (-28.53 and -25.72 ‰) and the bivalves *Fimbria* sp., *Codakia tigerina* and *Solemya pusilla* (-21.54, -23.48 and -26.59 ‰) are clearly depleted in $\delta^{13}C$. This suggests that they do not utilize photosynthetic carbon but rely rather on chemoautotrophic symbionts (Powell & Somero, 1985; Conway et al., 1992; Gros et al., 1996; Stewart & Cavanaugh, 2006; Taylor & Glover, 2006). Such invertebrate-bacteria symbioses are known from sulfur- and methane-rich hydrothermal vents in the deep-sea (Polz & Cavanaugh, 1995; Polz et al., 1998; Gebruk et al., 2000), but there are also examples from shallow coastal habitats in the photic zone. *Codakia* *tigerina* and *S. pusilla* belong to the bivalve families Lucinidae and Solemyidae, respectively. Both bivalve families are known for their symbiosis with intracellular chemoautotrophic, sulfur-oxidizing bacteria located in the gills of the host (e.g. Conway et al., 1992; Gros et al., 1996); this symbiosis covers substantial amounts of both the carbon and nitrogen requirements of their host bivalves. In the well-studied solemyid *Solemya velum*, about 98 % of the carbon and 100 % of the nitrogen required by the host was contributed by its symbionts (Stewart & Cavanaugh, 2006). For a species closely related to *C. tigerina, C. orbicularis*, symbiosis with chemoautotrophs located in the gills is known (Frenkiel & Mouëza, 1995). The fimbriid bivalve *F. fimbriata* may also have a symbiotic relationship with autotrophic bacteria based on its gill histology (Reid, 1990), although this remains to be confirmed. The present study is the first to show that a member of the bivalve genus *Fimbria* appears to utilize carbon fixed in a chemoautotrophic symbiosis.

For the crustaceans *Eucalliax panglaoensis* and *Calliaxina novaebritannicae*, chemoautotrophic symbionts were assumed earlier, based on stable isotope studies (Kneer, unpublished data). Symbioses of crustaceans with either epibiotic bacteria located on anterior body appendages and/or in the gut are known from several studies on the trophic relations of hydrothermal vent communities in the deep sea (e.g. Polz et al., 1998; Gebruk et al., 2000), where sulfur is available in high amounts. Since 1) the two crustacean taxa investigated in this study are known to live in burrows inside the sediments, 2) marine sediments are known to contain elevated levels of sulphide (Johns et al., 1997) and 3) $\delta^{13}C$ signatures do not suggest a nutrition based on fixed carbon from photosynthetic sources, these taxa might meet their carbon requirements with the help of chemoautotrophic symbiotic bacteria.

Vonk et al. (2008) found a considerable number of species with carbon signatures similar to those of epiphytes, which is consistent with previous studies (e.g. Yamamuro, 1999; Moncreiff & Sullivan, 2001; Smit et al., 2005, 2006). The mean value of stable carbon for seagrass epiphytes (-13 ‰) in Vonk et al. (2008) was in the range of previous studies but is much more depleted than in the present study (mean for all seagrass epiphytes around -4.7 ‰). Moncreiff & Sullivan (2001) reported even more depleted mean $\delta^{13}C$ values for epiphytes of the seagrass *Halodule wrightii* (-17.5 ‰). In the present study, only one organism had a stable carbon signature matching that of epiphytes, which is not consistent with previous studies. The present study showed similar, but slightly enriched (by 3 ‰) seagrass stable carbon signatures compared to values measured by Vonk et al. (2008). If we assume that the highly enriched $\delta^{13}C$ for epiphytes in this study reflect a contamination with inorganic carbon, despite sample acidification, then these values clearly do not reflect the natural abundance of organic carbon in the seagrass epiphytes. If we further assume for the present study similar values (i.e. between -12.9 and -17.5 ‰) for epiphytes as described in Vonk et al. (2008) or Moncreiff & Sullivan (2001), considerably more organisms of various guilds have a carbon signature similar to seagrass epiphytes. This would be consistent with previous studies. Comparable $\delta^{13}C$ values were found in the top predator *T. crocodilus*, the omnivorous blenny *P. variabilis*, the seagrass-ingesting herbivores *H. far*, *D. chrysopoecilus*, *D. fasciatus*, *D. perspicillatus*, *S. canaliculatus*, *S. spinus*, *S. virgatus*, and in the pipefish *S. biaculeatus*. Most zoobenthivores are clearly enriched in heavy carbon compared to epiphytes. For invertebrates, mysid shrimps and several gastropods reflect epiphytic signatures similar to those reported in Vonk et al. (2008) and Moncreiff & Sullivan (2001). In this case, it is possible to identify gastropods that are known as herbivores, such as *Strombus* spp. (Klumpp et al., 1992; Stoner et al., 1995; Alyakrinskaya, 2005), or possible detritus feeders, such as the turritellid *Zeacolpus* sp. Similar values were also found in the gastropod *Polinices flemingianus*. As discussed earlier, this species is probably a predator, and carbon values might reflect an indirect consumption of epiphytes by prey organisms.

Using the $\delta^{13}C$ values of epiphytes measured by Vonk et al. (2008) as a baseline, epiphytes seem to be an important carbon source in the trophic web of the studied meadow. This would coincide with numerous previous food web studies in seagrass beds (e.g., Yamamuro, 1999; Moncreiff & Sullivan, 2001; Smit et al., 2005, 2006; Vonk et al., 2008). Stable carbon signatures of seagrass leaves ranged from -4.88 (*E. acoroides*) to -7.04 ‰ (*H. uninervis*). The smallest species (*H. uninervis*) was most depleted, followed by *C. rotundata* and *T. hemprichii*. *Enhalus acoroides*, the largest species, showed the least depletion. The same pattern was found by Vonk et al. (2008). In the present study, no fish had a $\delta^{13}C$ signature that would reflect the exclusive assimilation of seagrass leaves. Even the hemirhamphid *H. far*, assumed to be a herbivore predominantly feeding on seagrasses, is more depleted in $\delta^{13}C$ compared to seagrasses in the present study (-11.99 ‰). This suggests that this fish is not assimilating the ingested seagrasses, but rather seagrass epiphytes. This contradicts previous findings (e.g. Vonk et al., 2008). Among the crustaceans, *Alpheus* sp., amphipods, and the thalassinidean shrimp *Corallianassa coutieri* exhibit a $\delta^{13}C$ signature comparable to seagrasses; the signature of

Alpheus sp., however, might reflect not only a seagrass diet, but also the more depleted seagrass detritus. The large burrowing shrimp *C. coutieri* is known to rely on a diet mainly based on seagrass (Kneer et al., 2008). For the related *C. assimilis* and *Callianida typa*, $\delta^{13}C$ values were more depleted than seagrasses in the present study, suggesting a diet not exclusively based on seagrasses, but perhaps also on epiphytes. Assimilation of seagrass material by alpheids and amphipods has been described in previous studies (e.g. Vonk et al., 2008). In the present study, also an unidentified holothurian, the starfish *A. typicus* and several ophiurids had $\delta^{13}C$ signatures similar to seagrasses and detritus. The starfish *A. typicus* was previously identified as a carnivore (Pinto, 1982). Based on the data in the present study, this starfish preys upon organisms that feed on seagrasses. The holothurian is assumed to be a detritus feeder rather than a seagrass consumer. Various feeding strategies are known for ophiurids in general, for example predation, suspension-feeding and deposit-feeding (Harris et al., 2009).

Previous studies drew contradictory conclusions on the importance of seagrass matter as a food source in a seagrass ecosystem. While Vonk et al. (2008) found that seagrass is utilized widely by a broad range of organisms, other studies did not corroborate this result (e.g. Yamamuro, 1999; Lepoint et al., 2000; Smit et al., 2005). Seagrass material does not appear to make a major contribution to the food web of the investigated seagrass bed. This supports the finding that seagrasses contribute mostly to the food web via the detritus food chain. The sampled fish fauna, for example, is not dependent on feeding exclusively within the seagrass bed and probably moves for feeding to adjacent habitats, for example sand flats or coral reefs (Lugendo et al., 2006; Verweij et al., 2006; Vonk et al., 2008), as was occassionally observed for *H. argus*, *C. inermis* and *P. trivittatus*. Food items ingested during excursions to neighbouring ecosystems may not depend on seagrass as a food source at all and therefore might not be reflected in the analyses (Vonk et al., 2008). In the present study, mangroves can be excluded as a potential foraging habitat for fish in the investigated seagrass bed because the bed is located on the reef flat of an off-shore island.

Highest $\delta^{15}N$ levels in the present food web were found for the two piscivores *S. barracuda* ($\delta^{15}N$ = 10.94 ‰) and *T. crocodilus* ($\delta^{15}N$ = 10.26 ‰). These species are top predators: with increasing trophic level, their $\delta^{15}N$ enrichment increases. Thus, top predators show the highest enrichment within a food web. Rank number two is occupied by *Gymnothorax* sp., a carnivorous muraenid ($\delta^{15}N$ = 9.03 ‰). High values (8.79 to 8.10 ‰) were also recorded in several zoobenthivores and omnivores (*P. trivittatus*, *S. margaritifera*, *L. obsoletus*, *U. tragula*, *C. anchorago*) and in two predominantly herbivorous species (*H. far* and *Cryptocentrus* sp.). Surprisingly, another piscivore, *S. incisa*, is depleted compared to all these species, and is ranked between other zoobenthivores and omnivores. Since the mean size of the examined specimens was similar to that of *T. crocodilus* (400 mm mean TL for *T. crocodilus,* 370 mm mean TL for *S. incisa*), an age effect on the $\delta^{15}N$ signature can be excluded. One potential explanation for the low $\delta^{15}N$ value of *S. incisa* is that this species was found at the sampling site only very briefly, in a large school of about more than 100 individuals, and was never observed again. If this species migrates between habitats, it is possible that the specimens subjected to stable isotope analysis fed in areas with less nutrient input and might thus be less enriched in $\delta^{15}N$. Moreover, this species is not as piscivorous as previous studies have shown, but may also feed on more nitrogen-depleted prey.

Lowest $\delta^{15}N$ enrichment (< 7 ‰) was found in herbivores and juvenile *P. trivittatus*. Low values for herbivores are common because they feed on primary producers, which are not as enriched in $\delta^{15}N$ as higher trophic levels (various levels of non-primary consumers). Low values in juvenile *P. trivittatus* can be explained by ontogeny: stable nitrogen was found to accumulate with age (Vander Zanden et al., 1998; Overman & Parrish, 2001).

Among the invertebrates, the highest $\delta^{15}N$ enrichment (> 8 ‰) was found in sponge-associated ophiurids and the bivalve *Antigona puerpera*. For the latter, both $\delta^{13}C$ and $\delta^{15}N$ values suggest a diet based on zooplankton. Lowest (negative) values were found for the thalassinieans *E. panglaoensis* and *C. novaebritannicae* and the bivalve *C. tigerina*. As discussed above, these organisms are suggested to have a symbiotic relationship with chemoautotrophic bacteria, as found in some species of shrimps from hydrothermal vents (Polz et al., 1998; Gebruk et al., 2000) and bivalves from both deep-sea and coastal habitats (Powell & Somero, 1985; Conway et al., 1992; Stewart & Cavanaugh, 2006). Such bacteria provide them with a substantial amount of the carbon and nitrogen they require for growth and living.

4.2.1. Determination of trophic level

The highest trophic levels were attributed to three piscivorous fish. The highest level was occupied by *S. barracuda* (3.69), followed by two large belonids *S. incisa* (3.49) and *T. crocodilus* (3.44). These species are top predators in the investigated seagrass ecosystem and are comparable to top predators found in previous studies (e.g. Vonk et al., 2008). Gut-content analysis showed an exclusive fish diet (see also 4.4). These three piscivorous pelagic species were followed by the benthic macrozoobenthivores *Gymnothorax* sp. and adult *P. trivittatus*. Interestingly, the predominantly herbivorous *H. far* occupies the sixth rank (trophic level of 3.03); it is not followed by other herbivores but by zoobenthivorous species. Although amphipods were occasionally found in gut-content analyses (see 4.4), the results suggested an herbivorous diet for this species, in agreement with previous studies (Vonk et al., 2008). Talwar (1962) also mentions the occasional ingestion of polychaetes, which were not identified in the present study. Note that the present specimens were all caught during daytime. Other hemirhamphid species, such as the temperate *Hyporhamphus melanochir*, are known to show a clear diurnal shift in diet. These fish are herbivores only during daytime hours, while they feed on small hyperbenthic invertebrates, predominantly amphipods, during the night (Klumpp & Nichols, 1983; Robertson & Klumpp, 1983; Earl et al., 2011) and occasionally consume insects and polychaetes (Earl et al., 2011). Waltham & Connolly (2006) reported a similar pattern for the hemirhamphid *Arrhamphus sclerolepis*, a species feeding on macroalgae during the day and on different amounts of various invertebrates (depending on the habitat) during the night. Generally, the beloniform family Hemirhamphidae is considered to be omnivorous, (e.g. Randall, 1962; Waltham & Connolly, 2006), with a considerable amount of herbivory in some species (e.g. Carseldine & Tibbets, 2005). Some species undergo considerable ontogenetic shifts in diet, e.g. *Arrhamphus sclerolepis krefftii* (Tibbetts & Carseldine, 2005), *Hyporhamphus quoyi* (Talwar, 1962; Tibbets & Carseldine, 2005), or *Hyporhamphus regularis ardelio* (Carseldine & Tibbetts, 2005; Tibbetts & Carseldine, 2005). Juveniles of the above species are carnivorous, feeding on zooplankton, which is common in many marine fishes. The juveniles of most species are non-herbivores due to two reasons. First, young fish have to meet an elevated nitrogen demand due to high growth rates and critical stages of development, thus requiring protein-rich food (animal tissue). Second, gut development is age dependent (Day et al., 2011a). However, a recent study by Day et al. (2011a) suggests that young *H. regularis ardelio* are limited not by the availability of digestive enzymes, but by mechanisms of mechanically processing plant matter. The pharyngeal mill, an important tool in macerating plant tissue in hemirhamphids (e.g., Carseldine & Tibbetts, 2005; Manjakasy et al., 2009; Day et al., 2011b), is incapable of processing such matter up until a certain body size (Day et al., 2011a). For *H. far*, this ontogenetic issue has not been described yet. The present specimens, however, were of intermediate body length (about 24 cm) and some had fully developed gonads. They were therefore clearly beyond such physiological thresholds. Diurnal sampling methods may be necessary to reveal possible diurnal effects on the diet of *H. far* and to determine whether this species is an obligate herbivore. Other herbivores in the present study belong to the families Siganidae, Pomacentridae, Scaridae and Blenniidae. These species occupied lowest trophic levels (below 2.51), which is consistent with expectations. Most zoobenthivores occupied trophic levels between those of *H. far* and other herbivores, with the exception of the muraenid *Gymnothorax* sp. and adult *P. trivittatus* sp. Juvenile *P. trivittatus* occupied a very low rank, characterizing them as herbivores. This is not consistent with gut-content analysis, which revealed a diet primarily based on microcrustaceans. Nonetheless, the shift in trophic level from juvenile (2.22) to adult *P. trivittatus* (3.06) is obvious and not surprising, considering that most young fish begin their lives feeding on microfauna (e.g. zooplankton).

4.3. Gut-content analysis

4.3.1. Feeding guilds

Four feeding guilds were revealed by gut-content analysis: herbivores, omnivores, (macro)zoobenthivores and piscivores. It was not possible to identify planktonic organisms within the microcrustaceans. In most samples, the presence of only appendages, carapaces and other partially digested body parts did not allow the distinction between benthic or pelagic life forms. Better-preserved gut-contents (e.g. not strongly digested) might have revealed a zooplanktivorous fish feeding guild.

Bray-Curtis Cluster analysis identified all four feeding guilds identified in the gut-content analysis. In this cluster, all siganids and pomacentrids subjected to gut-content analysis cluster together. The small sample size for five out of seven species did not enable distinguishing the two families. Furthermore, the herbivorous blenny *Petroscirtes variabilis* and the syngnathid *Syngnathoides biaculeatus* cluster together with the herbivore clade. In the present study, filamentous algae and unidentifiable microcrustaceans were found in the gut of *P. variabilis*. This partially agrees with Nakamura et al. (2003), who found not only algae but also debris and fish eggs in the guts. Froese & Pauly (2010) also mention fish scales and microcrustaceans. The present study was not able to identify the microcrustaceans, though they may have been forms living on and within colonies of filamentous algae. For *S. biaculeatus*, filamentous algae, amphipods, unidentified crustaceans and fish scales were found, which is consistent with Nakamura et al. (2003), except for the algae, which might have been ingested accidentally. For *P. variabilis* and *S. biaculeatus*, sample sizes were small (n = 2 for *P.*

variabilis and n = 4 for *S. biaculeatus*) and an increased sample size would probably provide a more detailed picture.

Bray-Curtis Cluster analysis further shows a grouping of the three top-predators *S. barracuda*, *S. incisa* and *T. crocodilus*; within this cluster, the two belonid species are more similar to each other than to the barracuda. Interestingly, the analysis suggests that herbivores and piscivores cluster together. This similarity, however, is very small (< 15 %), and may well be an analytical artifact of the software, based not on the food items per se but rather on the low variety of different food items for the two specialised guilds of herbivores and piscivores. In comparison, the omnivores and macrozoobenthivores feed on a broader spectrum.

The status of omnivores and macrozoobenthivores is less distinct in the Bray-Curtis Cluster analysis. The omnivores and the macrozoobenthivores are mixed and not clearly distinguishable, although there might be a transitional “grey zone“ between those two feeding guilds. Plant material can be accidentally ingested by zoobenthivorous species that actually do not rely on plant matter as a diet, and omnivores might not necessarily rely substantially on plant matter when they can meet their nitrogen requirement by predominantly feeding on animal matter. This can mask the results. Furthermore, the sampling sizes for some omnivorous and zoobenthivorous species were possibly too small for definitive results. For example, some omnivores (*A. tomentosus*, *H. argus*, *C. chlorourus* and juvenile *P. trivittatus*) cluster with macrozoobenthivorous (*H. chloropterus* and *H. scapularis)* as well as with zoobenthivorous species *(C. inermis* and adult *P. trivittatus)*. All of them cluster with the omnivore *C. anchorago*. In contrast, the macrozoobenthivorous *U. tragula*, *L. obsoletus and Gymnothorax* sp. cluster together.

All of these omnivores and zoobenthivores cluster together and share a similarity of about 38 %. The two zoobenthivores *S. margaritifera* and *Cheilinus* sp. cluster together and are not similar with any of the other groups, probably again reflecting small sample size.

A non-dimensional MDS shows herbivores and piscivores forming distinct groups, whereas omnivores and zoobenthivores are indistinguishable. *Syngnathoides biaculeatus*, *S. margaritifera* and *Cheilinus* sp. do not group with any other group.

4.3.2. Prey items

Many of the prey items identified were benthic. This includes epifauna (echinoderms such as brittle stars, sea stars and sea urchins, along with gastropods, large crustaceans, hydrozoans) and infauna (polychaetes, alpheids, gastropods, bivalves, sipunculids). Foraminifera in the guts were forms associated with seagrasses. Some fish species relied on microcrustaceans as a food source. This study did not distinguish between planktonic and benthic microcrustaceans.

Crustaceans were major prey items. They were found in almost 60 % of all guts investigated. Other studies report that crustaceans of all size fractions are a major component of seagrass food webs (Khalaf & Kochzius, 2002; Nakamura et al., 2003; Gillanders, 2006; Unsworth et al., 2007b). Gastropods were the second most important prey item, followed by seagrass (each of them found in about one quarter of all guts). Like crustaceans, both gastropods and seagrasses are highly abundant in seagrass beds. In the case of *H. far*, however, it was not possible to distinguish seagrass matter from algae. This is because hemirhamphids macerate plant food with their pharyngeal mill

(Carseldine & Tibbetts, 2005; Manjakasy et al., 2009; Day et al., 2011b). In Siganidae and Pomacentridae, pieces of seagrass and algae – presumably seagrass epiphytes – dominated gut-contents. It remains unknown, however, whether such plant matter is only ingested, or also digested and assimilated – a well-known drawback in gut-content analysis (Lugendo et al., 2006). Earlier studies do, however, show that seagrass epiphytes are typically a more important direct food source for consumers than seagrasses (e.g. Yamamuro, 1999; Moncreiff & Sullivan, 2001; Smit et al., 2005, 2006; Liu et al., 2008; Vonk et al., 2008). At least for tropical systems, seagrasses are a more significant food source than previously assumed (Valentine & Heck, 1999; Vonk et al., 2008).

The highest numbers of prey items were found in macrozoobenthivores, and the average prey spectrum was considerably wider in benthivores and omnivores compared to more specialised guilds such as the piscivores and herbivores. The four species containing highest numbers of food items were the zoobenthivores *C. inermis*, *P. trivittatus*, *S. trilineatus* and the omnivorous *A. tomentosus*. The nemipterid *P. trivittatus* showed not only a broad dietary spectrum, but also a considerable variability of ingested food items in individual fish: some specimens contained exclusively or predominantly large polychaetes, large decapod crustaceans, amphipods, echinoderms, or fish scales. An intraspecific variability of food selection was also found in *C. inermis*, although less distinct than in *P. trivittatus*. Such differences in prey selection among individuals of a given species within a given population can be of the same order of magnitude as interspecific differences. The ecological consequences can also be similar. This has been described as trophic polymorphism (Ehlinger & Wilson, 1988). Trophic polymorphism probably reflects a behavioral adjustment of individuals to a variety of circumstances (e.g. different habitats) to maximize foraging success (Ehlinger & Wilson, 1988; Ehlinger, 1990). Three of the four fishes mentioned above (*C. inermis*, *P. trivittatus*, *S. trilineatus)* do not occupy seagrass beds exclusively, but also move to adjacent sandy and rubble areas as well as to algal patches and coral reefs. Especially *P. trivittatus* was very abundant on coral reefs and rubble zones (pers. obs.). These fish not only move to habitats adjacent to seagrass beds but probably also forage there Switching between habitats might modify foraging behaviour and thus increase intraspecific variation (Ehlinger & Wilson, 1988; Ehlinger, 1990). In bluegill sunfish, such a "specialisation" of generalistic feeders is associated with phenotypic-limited feeding efficiency and differences in morphology (e.g. longer pectoral fins in individuals that prefer foraging in vegetated habitats) (Ehlinger, 1990). Whether such phentotypic variatons occur in *C. inermis* or *P. trivittatus* needs to be examined to get a better understanding of trophic polymorphism in these species. Since Labridae (to which *C. inermis* and several other investigated species belong) are amongst the most morphologically and ecologically diverse fish families (Westneat et al., 2005): the likelihood of both inter- and intraspecific variation of food selection is high.

4.3.3. Diet composition

Overall, the investigated fish species fed on a broad spectrum of food items. Since most of the items were in a quite processed condition, it was not possible to identify them to a low taxon level (e.g., genus or species), which would have yielded a more detailed picture of the food spectrum. In 182 guts of 27 species, a few empty guts were found in four species (two top predators, two omnivores). The top predators, in contrast to the herbivores, probably did not feeding all day long, but only during a certain day- or night time. This might yield a considerable number of individuals with empty guts, which is the case for about one third of *T. crocodilus* and one half of *S. incisa*. In the omnivore *A. tomentosus*, also about one third of all guts were empty, while the value was about 12.5 % in the omnivorous *H. argus*.

In both belonid species, *T. crocodilus* and *S. incisa*, fish was the single prey category (in one specimen, a single prey item was identified as small *Siganus* sp.). The order Beloniformes contains about six families that do not develop a stomach. Among those, the hemirhamphids comprise an omnivorous family with tendencies to herbivory. The other extreme are the Belonidae, which are carnivorous and highly piscivorous (Manjakasy et al., 2009). The belonid species investigated are no exceptions. They are known as predominantly piscivorous (Hiatt & Strasburg, 1960; Randall, 1967), though *T. crocodilus* might occassionally ingest crustaceans (Froese & Pauly, 2010).

Labridae comprise the second largest family of marine fishes and exhibit enormous morphological and ecological diversity in the tropics and subtropics. They occupy all major feeding guilds, feeding on a broad range of hard-shelled invertebrates, furthermore on fish, fish eggs, zooplankton, corals, ectoparasites, detritus and algal matter (Westneat et al., 2005). Here, the labrid *C. inermis* fed on a broad range of macrozoobenthos, with a clear preference for gastropods and crustaceans, which were ingested in about two thirds of all dissected specimens. Echinoderms were found in slightly more than one third, and bivalves in almost one quarter of all guts. This food spectrum is consistent with the literature (Froese & Pauly, 2010). In small amounts, small epibenthic crustaceans (e.g. amphipods), teleost fragments and other epibenthic invertebrates were found, which is consistent with Nakamura et al. (2003). *Halichoeres chloropterus* is another zoobenthivorous labrid that feeds predominantly on various crustaceans (unidentified crustaceans were found in more than 90 % of all individuals investigated), for example amphipods and alpheids, but also on other hard-shelled invertebrates such as gastropods. This appears to be typical not only for *H. chloropterus*, but also for other species of the genus *Halichoeres*, which is comprised by zoobenthivorous and omnivorous species (Hiatt & Strasburg, 1960; Westneat, 2001; Nakamura et al., 2003). *Halichoeres scapularis* apparently relies on a similar food spectrum, based on the one specimen whose gut content was analysed. In the present study, *Halichoeres argus* was omnivorous, predominantly feeding on miscellaneous tiny crustaceans, with a substantial contribution of amphipods, gastropods and nematodes. Occasionally, algae, hydrozoans, annelids and foraminiferans are ingested. This study is the first to reveal the feeding preferences of this small and highly abundant fish.

The labrid *S. trilineata* fed predominantly on unidentified large and small crustaceans, especially alpheid shrimps, and gastropods. According to the literature, this species is at least partially zooplanktivorous (Froese & Pauly, 2010). This is not in contrast to the present study, because the poor condition of the gut-contents (only appendages and pieces of carapace with no indication whether from benthic or pelagic life forms). Much of the fragmented planktonic organisms might well have been zooplankton, but had to be categorized as miscallaneous crustaceans. The same problem applies for the omnivorous labrid *C. anchorago*: many small and intermediate-sized crustaceans were found in almost all of the specimens. Nakamura et al. (2003), however, reported an exclusively benthic diet for this labrid. In the present study, filamentous algae, foraminifera, gastropods and echinoderms were found as additional food items for *C. anchorago*; this confirms the findings of Nakamura et al. (2003), except for the algae. Note, however, that accidental ingestion of plant matter might occasionally occur.

In the nemipterid *P. trivittatus*, two distinct fish size classes were considered in gut-content analysis: juveniles and adults. Adults clearly are generalists that feed on a broad range of macrozoobenthos. In the present study, unidentified large crustaceans and polychaetes were by far the predominant items in most guts, followed by amphipods, alpheids and brachyurid crabs. These results are confirmed by the literature (Russell, 1990). Interestingly, several individuals appeared to be "specialised" on a certain prey category, having ingested one type of organism exclusively: whole guts were filled either solely with polychaetes or crustaceans. In one specimen, the whole stomach was tightly filled with teleost scales. This species is thus another example of trophic polymorphism (Ehlinger & Wilson, 1988; Ehlinger, 1990).

The dietary spectrum of juvenile *P. trivittatus* does not differ from that of adults by prey taxa, but rather by size classes. All guts of juveniles contained unidentified tiny crustaceans. About one quarter of all guts contained small shrimps, polychaetes and amphipods (all < 1 cm), while the crustaceans and polychaetes in adult *P. trivittatus* were considerably larger. This reflects a shift in diet with respect to the prey size spectrum. As mentioned above, a substantial part of the unidentified microcrustaceans may have been comprised by zooplankton because young fish of many feeding uilds, even piscivores, begin life as planktivores (Mittelbach et al., 1988; Day et al., 2011). Such ontogenetic dietary shifts are often a consequence of changes in foraging ability, leading to more efficient feeding on different sizes or types of prey (Mittelbach et al., 1988). One constraint that may alter foraging ability is mouth gape size, which might explain the selection for smaller prey items in young *P. trivittatus*.

In contrast to the zoobenthivores mentioned above, the monacanthid *A. tomentosus* is a resident of seagrass beds. It is known to be omnivorous and to rely on a diet comprised primarily of gastropods, seagrasses, sponges, algae, amphipods and polychaetes (Peristiwady & Geistdorfer, 1991). In the present study, similar food items were identified: amphipods, unidentified crustaceans, gastropods, polychaetes and seagrasses, although most abundant items had a different ranking and the frequency of occurrence of single categories differed from the study of Peristiwady & Geistdorfer (1991). Note that the latter study had a considerably larger sample size (> 1000 specimens vs. 11).

The diet of the syngnathid *S. biaculeatus* consisted of algae, fish fragments, amphipods and unidentified crustaceans. Nakamura et al. (2003) mention shrimps and zooplankton, adding to the diet of this cryptobenthic species.

All guts of the hemirhamphid *H. far* contained macerated seagrass matter. This species appeared to be predominantly herbivorous, with occasional amphipods and foraminiferans found in a few guts. Ingestion of animal matter is not uncommon in the Hemirhamphidae. Many previous studies have shown that a number of hemirhamphid species display a sharp diurnal shift in their feeding patterns, with a preference for plant food during daytime hours and for invertebrates during the night (e.g. Talwar, 1962; Klumpp & Nichols, 1983; Robertson & Klumpp, 1983; Waltham & Connolly, 2006; Earl et al., 2011). Earl et al. (2011) also mention the occasional ingestion of polychaetes and insects during the day. In the present study, two specimens ingested extremely high numbers of foraminiferans (approximately 600 per gut). Most of them were seagrass-associated forms. The distribution of benthic foraminiferans depends strongly on various environmental factors, for example organic matter content of the sediment, oxygen, sediment grain size or current regime (Matera & Lee, 1962; Murray, 2000). This can lead to patchy distributions. Accordingly, the two specimens with high numbers of foraminifera in their guts probably fed on seagrass from a different patch than the other specimens, or they fed on detached floating seagrass leaves that were imported into the sampling area during flood tide.

Gut-content analysis of the pomacentrid *D. chrysopoecilus* revealed seagrass fragments in about 80 % and algae in 100 % of all guts. The latter are assumed to be seagrass epiphytes. One third of all examined guts contained microcrustaceans (predominantly benthic copepods), perhaps epifauna on seagrasses or epiphytes. Interestingly, in 20 % of all *D. chrysopoecilus* guts, no seagrass, but algae were found. Since it is unlikely that seagrasses are digested faster than the epiphytes, this may well represent another, milder example of trophic polymorphism. One interpretation is that specimens that solely ingested epiphytes were able to browse algae without biting off fragments of seagrass leaves, while the other 80 % of the examined specimens removes seagrass tissue while browsing the algae. Masuda & Allen (1993) mention that this species feeds predominantly on epibenthic algae. Whether *D. chrysopoecilus* assimilates the seagrass matter needs to be elucidated with stable-isotope analysis.

Gut-content analysis of the siganid *S. canaliculatus* revealed that plant matter dominates the diet. Seagrasses were found in 80 % of all guts, and epiphytes in more than two thirds of all guts. One third of all guts contained tiny gastropods and unidentified microcrustaceans (copepods, isopods, tanaids), potentially epifauna on seagrasses and epiphytes. Occassionally, larger crustaceans (brachyurids) were found. In *S. canaliculatus*, seagrasses were more abundant food items than epiphytes. This leads to two potential conclusions. First, some specimens bit off fragments of younger leaves that still lacked epiphytes; second, the epiphytes have a shorter digestion rate than the seagrasses and were already processed. The second scenario is more likely because the seagrass leaf matter here seemed to be affected by digestive processes. Generally, the family Siganidae is considered to be predominantly herbivorous, and siganids can contribute substantially to the herbivorous guild either in terms of abundance or biomass in some locations (Bryan, 1975; Fox et al., 2009). Previous studies, however, found that *S. canaliculatus* belongs to the omnivorous rather than to the herbivorous guild. Hajisamae (2009) reported that this species feeds mainly on polychaetes, and Froese & Pauly (2010) summarize that *S. canaliculatus* does feed on seagrasses and algae, but also on zoobenthos such as crustaceans, bryozoans, echinoderms, and detritus. In the present study, this fish did not consume such a broad spectrum of invertebrate prey. One reason might be the high abundances of the large seagrass *E. acoroides* and the dense epiphyte growth on the leaves of this species at the sampling site at the island of Barrang Lompo. Plant food may have been overabundant during the sampling period, so that the siganid met its nitrogen requirements by an exclusively herbivorous diet. *Siganus canaliculatus* was observed feeding mainly on stands of *E. acoroides* (pers. obs.). Salita et al. (2003) reported that in the herbivorous siganid *S. fuscescens*, adults prefer seagrasses and juveniles seagrass epiphytes.

4.3.4. Trophic niche overlap and dietary niche breadth

Thirty cases of significant trophic niche overlap (SI ≥ 0.60*) between fish species were found in the present study. Dietary overlap does not automatically cause resource competition, but is often related with high abundances and/or high diversity of prey items (Macpherson, 1981). Moreover, additional parameters such as prey type, prey size, depth distribution or guilds allow species with similar diet (i.e. dietary niche overlap) to coexist. The actual degree of overlap between species might also be reduced by species with seasonal or diel patterns of resource partitioning, using resources (i.e. prey items) at different times or in different situations. Thus, calculated overlap values might overestimate the direct competition between species (Macpherson, 1981).

Thirteen cases of overlap are smaller than SI = 0.80* and are thus considered as being moderate. Seventeen cases exceed SI = 0.80*, and in six cases, species exhibited a dietary niche overlap of SI ≥ 0.96*, which is very high or total. There is no significant overlap of dietary niches between species from different guilds, except for omnivores and zoobenthivores. The piscivorous guild in the present study was comprised by two belonid species and *S. barracuda*, which are top predators in the investigated food web. All three species show very high to complete dietary overlap. Within the herbivorous guild, most cases of overlap were moderate, especially when comparing *H. far* with other herbivores. No overlap was recorded between this species and any of the herbivorous pomacentrids, and only moderate overlap occurred between *H. far* and *S. canaliculatus*. Note, however, that it was not possible to identify any algae (e.g. epiphytes) in the macerated gut-contents of *H. far*. Otherwise, overlap might be higher. Overlap might be high or even complete if data for seagrasses and algae are pooled without discriminating between both different food sources. There was, however, a high overlap for *H. far* with each of the siganids *S. virgatus* and *S. spinus*, and between *S. canaliculatus* and *S. virgatus* and between *S. spinus* and *S. virgatus*. Sample sizes for the latter two species were small, limiting interpretability.

Degrees of overlap vary within the group of omnivorous/macrozoobenthivorous fish. Overlap is present, but low among the larger labrid species (C. *inermis*, *C. trilobatus*, *C. anchorago*, *H. chloropterus*, *H. scapularis*), which is unsurprising considering the high morphological and ecological diversification of labrids (Westneat et al., 2006). This is reflected in dietary preferences, and thus in niches. The small *H. argus*, however, has quite substantial overlap with other members of the guild, such as *S. biaculeatus*, *L. obsoletus* and *S. trilineata.* This might be indicated by a small mouth gape size of all these taxa compared to other zoobenthivores, i.e. they select prey items of smaller size classes (*L. obsoletus* examined here were young fish with small standard lengths, thus also small mouth gapes). Total overlap occurred between *L. obsoletus* and *Gymnothorax* sp., though this result should be interpreted with caution due to low sampling sizes in both taxa. High overlap also occurred between *S. trilineata* and *S. biaculeatus.*

Interestingly, there is no significant overlap for adults of the generalist *P. trivittatus*, despite the broad food spectrum. With a calculated dietary niche breadth of $R_B = 4.39$, *P. trivittatus* has by far the broadest dietary spectrum of all fish species investigated in the present study. In general, the species occupying the highest ranks of dietary niche breadth belong either to the zoobenthivorous (*P. trivittatus*, *C. chlorourus*, *C. inermis*, *H. chloropterus*) or omnivorous guild (*A. tomentosus*), whereas the smallest dietary niche breadth is found in specialists, such as the piscivores and some of the predominantly herbivorous species (*S. barracuda*, *S. incisa*; *H. far*, *S. spinus*), respectively. Narrow dietary niches were also found for *L. obsoletus* and *Gymnothorax* sp., although this no doubt reflects bias due to small sampling size. Sampling more individuals would probably have increased the food spectrum and broadened the dietary niche breadth. However, if we consider all values of dietary niche breadth where $R_B \leq 2.00$, all herbivores, all piscivores and all species from other feeding guilds where sampling size is smaller than n = 5 can be considered narrow in the present study.?habe ich das richtig verstanden? Surprisingly, the small labrid *H. argus* has a very narrow dietary niche breadth ($R_B = 1.02$) considering that it is an omivorous species.

There appears to be a general trend that with increasing dietary niche breadth, dietary niche overlap decreases. The nemipterid *P. trivittatus* as well as certain larger labrids – *C. chlorourus*, *C. inermis and H. chloropterus* – and the monacanthid *A. tomentosus* have large to very large calculated dietary niches, but either no or no significant niche overlap with any of the other species, or (in the labrids) only moderate dietary niche overlap (< 0.8*). This is surprising because one might expect that niche overlap would increase with increasing food spectra, which is clearly not the case. In contrast, specialised feeding guilds, such as the herbivores and the piscivores, have a very small food spectrum. Their niches overlap strongly or even completely with each other in some cases, which is logical because they belong to one feeding guild. As dietary niche breadth increases, trophic niche overlap decreases, especially in tropical environments, where a broad range of potential food items is available.

4.4. Differences in trophic composition between study sites

With respect to taxon numbers, zoobenthivorous fish accounted for largest proportions at all study sites (up to 71.1 % at BBE). This is unsurprising because seagrass beds are known to host an enormous diversity not only of fish, but also of invertebrates (e.g. Dorenbosch et al., 2005; Nakamura et al., 2003; Unsworth et al., 2007c; Vonk et al., 2008). Especially small benthic and/or epibenthic crustaceans exhibit both high species numbers and abundances; this makes them key prey items in seagrass habitats and in many other ecosystems (e.g. Khalaf & Kochzius, 2002; Nakamura et al., 2003; Nakamura & Sano, 2005; Gillanders, 2006; Unsworth et al., 2007b). They comprise a major component of marine foodwebs by linking trophic levels (Matheson et al., 1999; Unsworth et al., 2007a). Corallivores accounted for the smallest feeding guild, found at only one site in the present study. They are strongly associated with live stony corals (Khalaf & Kochzius, 2002), which are limited in seagrass beds. The corallivorous species were juveniles of several species of the family Chaetodontidae, typical residents of coral reef environments. It is not unusual to find juveniles of coral reef species in seagrass beds, which are hypothesized as being nursery habitats for early ontogenetic stages of reef fish and invertebrates (e.g. Ogden & Buckman, 1973; Ogden & Quinn, 1984; Pollard, 1989; de la Morinière et al., 2002; Dorenbosch et al., 2006; Verwej et al., 2006). In the present study, corallivores were found only at BLS, which provided the largest seagrass bed, the bed of highest structural complexity, and highest fish diversity. With respect to taxon numbers, piscivores (up to 5.26 %) and zooplanktivores (up to 8.33 %) were the smallest feeding guilds. Schools of zooplanktivorous fish contained only small individuals.

With respect to individual numbers, zooplanktivores were the dominating feeding guild at subtidal sites (BBE and BBS). This is due to large schools (up to several hundred individuals) of *A. lacunosus* (Atherinidae) that were counted along transects in irregular intervals. Such large aggregations of planktivores are possible due to their independence from the benthic substrate in respect to food availability (Khalaf & Kochzius, 2002). Atherinids were also recorded in lower abundance and in smaller schools at the intertidal sites. At BLS, omnivores, and at BBN and BBW, zoobenthivores were the dominant feeding guild. This might reflect the high structural complexity that the seagrass beds at BLS and BBW offer to both prey and small predators. At these sites the canopy consisted of the large species *E. acoroides* intermingled with several intermediate and short species. Furthermore, the seagrass beds at BBN and BBW are in very close to algal patches and coral reefs, which might enhance the species richness of zoobenthos. Again, corallivores accounted for very few individual counts, and only at BLS. Perhaps the other seagrass beds are too small to offer sufficient living space or shelter for juvenile corallivores from the neighbouring coral reefs. With respect to individual counts, piscivores made up the second-smallest guild, which is not surprising. Generally, top predators are present in considerably fewer numbers than their prey in all ecosystems. This does not contradict earlier studies that suggest that the major component of fishes in seagrass beds are predators (Unsworth et al., 2007b), because zoobenthivores are predators as well. Despite their lower trophic level, they contribute considerably to both species richness and abundance in the present study. Herbivorous fish comprise a small guild with respect to individual counts (ranging from 2.7 % at BBE to 4.2 % at BBS). One potential explanation is anthropogenic impact in form of overfishing. For example, Siganidae, especially the schooling species *S. canaliculatus*, as well as the hemirhamphid *S. far* and mugilids, are commonly caught for human consumption. The same applies to piscivores such as sphyraenids and belonids, as well as to elasmobranchs (the dasyatids *Taeniura lymma* and *Dasyatis kuhlii* as well as small carcharhinid sharks that are occassionally seen in the seagrass beds at Bone Batang and Barrang Lompo), which can be found at local fish markets (pers. obs.).

Omnivores, whilst not being the dominant feeding guild with regard to abundance or taxa, still contribute substantially to the fish fauna in intertidal seagrass beds (BLS, BBN and BBW). The BLS site has the strongest anthropogenic impact due to the high human population density on the island of Barrang Lompo. The site BBN provides a small and moderately dense seagrass bed in an early stage of succession, with low fish densities and species richness; BBW has a canopy structure similar to that of BLS, but might be impacted from gillnet fishing within the seagrass bed and blast fishing along the coral reef in the west of the island of Bone Batang. All three of these seagrass beds can be characterised as habitats “under stress“, and all three of them are rich and abundant in omnivorous fish species. These fish species are non-specialised feeders that cope well with changes in their habitat, which might not be the case in piscivores or other specialists (Khalaf & Kochzius, 2002).

4.5. Conclusion

A food web analysis in a seagrass bed of a small coral island in the Spermonde Archipelago, Indonesia, South Sulawesi, was conducted based on two different methodological approaches. The food web based on stable isotope analysis shows that seagrass epiphytes contribute substantially to trophic relations of the seagrass bed, in agreement with previous studies (Yamamuro, 1999; Moncreiff & Sullivan, 2001; Smit et al., 2005, 2006; Vonk et al., 2008). Seagrasses do not appear to play a major role as a food source in the investigated seagrass bed, conflicting with the outcome of a study by Vonk et al. (2008) on an inhabited neighbouring island, where both seagrass epiphytes and seagrasses are widely utilized in the whole food web. Future work might need to include more components of the food web (e.g. more taxa, such as crustaceans, gastropods or echinoids). Based on gut-content analysis, trophic relations of the fish fauna were based on crustaceans, gastropods, seagrasses and their epiphytes. This study clearly shows that gut-content analysis is a useful tool to describe food webs, but this method yielded contrasting results to the stable isotope analysis, which indicated a minor role of seagrasses in the food web. This once again supports the common view that gut-content analysis provides a highly detailed but biased picture of a consumer's diet, because not all food ingested is actually assimilated (Lugendo et al., 2006).

The food web based on stable isotope analysis further revealed the existence of infauna within the seagrass bed that do not fully rely on photosynthetic carbon sources, but rather on symbioses with chemoautotrophic bacteria. Since such symbioses are based primarily on sulfur-oxidizing prokaryotes, and marine sediments may contain high amounts of sulphides, more as yet undescribed invertebrate-bacteria symbioses may be present.

Trophic relations of fish assemblages in a tropical multiple-species seagrass bed between habitats, based on visual census data, revealed six feeding guilds: herbivorous, corallivorous, zooplanktivorous, omnivorous, zoobenthivorous, and piscivorous. With respect to taxon numbers, zoobenthivores are the most diverse and dominate all study sites. Corallivores, piscivores and zooplanktivores account for the smallest guilds. With respect to individual counts, zooplanktivores dominate subtidal and omni-/zoobenthivores dominate intertidal sites, while corallivores, piscivores and herbivores make up the smallest feeding guilds. Differences between study sites may reflect varying canopy architecture of seagrass beds, which in turn may result in varying abundances of major prey items (e.g. crustaceans, gastropods). Seagrass canopies at intertidal sites are structurally more complex than at subtidal sites, yielding higher abundances of benthic invertebrates and zoobenthivores. Higher abundances of plankton feeders at subtidal sites can be explained by their independence of benthic food webs (Khalaf & Kochzius, 2002).

5. References

Alyakrinskaya, I.O. 2005. Morphological and biochemical adaptions to feeding in some herbivorous gastropods. Biology Bulletin 32, 57-64.

Benstead, J.P., March, J.G., Fry, B., Ewel, K.C. & Pringle, C.M. 2006. Testing IsoSource: Stable isotope analysis of a tropical fishery with diverse organic matter sources. Ecology 87, 326-333.

Bryan, P.G. 1975. Food habits, functional digestive morphology, and assimilation efficiency of the rabbitfish *Siganus spinus* (Pisces, Siganidae) on Guam. Pacific Science 29, 268-277.

Carassou, L., Kulbicki, M., Nicola, T.J.R. & Polunin, N.V.C. 2008. Assessment of fish trophic status and relationships by stable isotope data in the coral reef lagoon of New Caledonia, southwest Pacific. Aquatic Living Resources 21, 1-12.

Carseldine, L., & Tibbetts, I.R. 2005. Dietary analysis of the herbivorous hemirhamphid *Hyporhamphus regularis ardelio*: An isotopic approach. Journal of Fish Biology 66, 1589-1600.

Clarke, K.R. 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18, 117-143.

Clarke, K.R. & Warwick, R.M. 1994. Changes in marine communities: An approach to statistical analysis and interpretation. Plymouth Marine Laboratory, Plymouth, UK. Natural Environment Research Council. 144 pp.

Cocheret de la Morinière, E., Pollux, B.J.A., Nagelkerken, I., Hemminga, M.A., Huiskes, A.H.L. & van der Velde, G. 2003. Ontogenetic dietary changes of coral reef fishes in the mangrove-seagrass-reef-continuum: Stable isotopes and gut-content analysis. Marine Ecology Progress Series 246, 279-289.

Conway, N.M., Howes, B.L., McDowell Capuzzo, J.E., Turner, R.D. & Cavanauh, C.M. 1992. Characterizaton and site description of *Solemya borealis* (Bivalvia; Solemyidae), another bivalve-bacteria symbiosis. Marine Biology 112, 601-613.

Day, R.D., German, D.P. & Tibbetts, I.R. 2011a. Why can't young fish eat plants? Neither digestive enzymes nor gut development preclude herbivory in the young of a stomachless marine herbivorous fish. Comparative Biochemistry and Physiology 158, 23-29.

Day, R.D., Donovan, P., German, D.P., Manjakasy, J.M., Farr, I., Hansen, M.J. & Tibbetts, I.R. 2011b. Enzymatic digestion in stomachless fishes: How a simple gut accommodates both herbivory and carnivory. Journal of Comparative Physiology B. Online first, doi 10.1007/s00360-010-0546-y.

Dorenbosch, M., Grol, M.G.G., Christianen, M.J.A., Nagelkerken, I. & van der Velde, G. 2005. Indo-Pacific seagrass beds and mangroves contribute to fish density and diversity on adjacent coral reefs. Marine Ecology Progress Series 302, 63-76.

Earl, J., Fowler, A.J. & Dittmann, S. 2011. Temporal variation in feeding behaviour and trophic ecology of the temperate hemirhamphid, *Hyporhamphus melanochir*. Environmental Biology of Fishes 90, 71-83.

Edwards, D.C. & Hubner, J.D. 1977. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachussettes. Ecology 58, 1218-1236.

Ehlinger, T.J. 1990. Habitat choice and phenotype-limited feeding efficiency in bluegill: Individual differences and trophic polymorphism. Ecology 71, 886-896.

Ehlinger, T.J. & Wilson, D.S. 1988. Complex foraging polymorphism in bluegill sunfish. Proceedings of the National Academy of Sciences of the USA 85, 1878-1882.

Erftemeijer, P.L.A. & Herman, P.M.J. 1994. Seasonal changes in environmental variables, biomass, production and nutrient contents in two contrasting tropical intertidal seagrass beds in South Sulawesi, Indonesia. Oecologia 99, 45-59.

Feinsinger, R., Spears, E.E., Poole, R.W. 1981. A simple measure of niche breadth. Ecology 62, 27-32.

Fox, R.J., Sunderland, T.L., Hoey, A.S. & Bellwood, D.R. 2009. Estimating ecosystem function: Contrasting roles of closely related herbivorous rabbitfishes (Siganidae) on coral reefs. Marine Ecology Progress Series 385, 261-269.

Frenkiel, L. & Mouëza, M. 1995. Gill ultrastructure and symbiotic bacteria in *Codakia orbicularis* (Bivaliva, Lucinidae). Zoomorphology 115, 51-61.

Froese, R. & Pauly, D. (Eds.) 2010. Fishbase. World Wide Web electronic publication. www.fishbase.org version (11/2010). Last accessed on Feb 21, 1 PM.

Gebruk, A.V., Southward, E.C., Kennedy, H. & Southward, A.J. 2000. Food sources, behaviour, and distribution of hydrothermal vent shrimps at the Mid-Atlantic Ridge. Journal of the Marine Biology Association of the U.K. 80, 485-499.

Gillanders, B.M. 2006. Seagrasses, fish, and fisheries. In: Larkum, A.W.D., Orth, R.J. & Duarte, C.M. (Eds.), Seagrasses: Biology, ecology and conservation. Springer, Dordrecht, The Netherlands, pp. 503-536.

Gros, O., Darrasse, A., Durand, P., Frenkiel, L. & Mouëza, M. 1996. Environmental transmission of a Sulfur-oxidizing bacterial gill endosymbiont in the tropical lucinid bivalve *Codakia orbicularis*. Applied and Environmental Microbiology 62, 2324-2330.

Grice, A.M., Loneragan, N.R. & Dennison, W.C. 1996. Light intensity and the interactions between physiology, morphology and stable isotope ratios in five species of seagrass. Journal of Experimental Marine Biology and Ecology 195, 91-110.

Hajisamae, S. 2009. Trophic ecology of bottom fishes assemblage along coastal areas of Thailand. Estuarine, Coastal and Shelf Science 82, 503-514.

Harris, J.L., MacIsaac, K., Gilkinson, K.D., Kenchington, E.L. 2009. Feeding biology of *Ophiura sarsi* Lütken, 1855 on Banquereau bank and the effects of fishing. Marine Biology 156, 1891–1902.

Heck Jr., K.L. & Valentine, J.F. 2006. Plant-herbivore interactions in seagrass meadows. Journal of Experimental Marine Biology and Ecology 330, 420-436.

Hemminga, M.A. & Mateo, M.A. 1996. Stable carbon isotopes in seagrasses: Variability in ratios and use in ecological studies. Marine Ecology Progress Series 140, 285-298.

Hiatt, R.W. & Strasburg, D.W. 1960. Ecological relationships of the fish fauna on coral reefs of the Marshall Islands. Ecological Monographs 30, 65-127.

Hurlbert, S.H. 1978. The measurement of niche overlap and some relatives. Ecology 59, 67-77.

Johns, A.R., Taylor, A.C., Atkinson, R.J.A. & Grieshaber, M.K. 1997. Sulphide metabolism in thalassanidean crustacea. Journal of the Marine Biological Association of the U.K. 77, 127-144.

Khalaf, M.A. & Kochzius, M. 2002. Changes in trophic community structure of shore fishes at an industrial site in the Gulf of Aqaba, Red Sea. Marine Ecology Progress Series 239, 287-299.

Klumpp, D.W. & Nichols, P.D. 1983. Nutrition of the southern sea garfish *Hyporhamphus melanochir*: Gut passage rate and consumption of two food types and assimilation of seagrass components. Marine Ecology Progress Series 12, 207-216.

Klumpp, D.W., Salita-Espinosa, J.S. & Fortes, M.D. 1992. The role of epiphytic periphyton and macroinvertebrate grazers in the trophic flux of a tropical seagrass community. Aquatic Botany 43, 327-349.

Kneer, D., Asmus, H. & Vonk, J.A. 2008. Seagrass as the main food source of *Neaxius acanthus* (Thalassinidea: Strahlaxiidae), its burrow associates, and of *Corallianassa coutieri* (Thalassinidea: Callianassidae). Estuarine, Coastal and Shelf Science 79, 620-630.

Kuriandewa, T.E., Kiswara, W., Hutomo, M. & Soemodihardjo, S. 2003. The seagrasses of Indonesia. In: Green, E.P. & Short, F.T. (Eds.), World atlas of seagrasses. Pepared by the UNEP World Conservation Monitoring Centre. University of California Press, Berkeley USA, pp.171-182.

Leitão, R., Martinho, F., Neto, J.M., Cabral, H., Marques, J.C., Pardal, M.A., 2006.

Feeding ecology, population structure and distribution of *Pomatoschistus microps* (Krøver, 1838) and *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. Estuarine, Coastal and Shelf Science 66, 231-239.

Lepoint, G., Nyssen, F., Gobert, S., Dauby, P., Bouquegneau, J.-M. 2000. Relative impact of a seagrass bed and its adjacent epilithic algal community in consumer diets. Marine Biology 136, 513-518.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, New Jersey,132 pp.

Liu, H.T.H., Kneer, D., Asmus, H. & Ahnelt, H. 2008. The feeding habits of *Austrolethops wardi*, a gobiid fish inhabiting burrows of the thalassinidean shrimp *Neaxius acanthus*. Estuarine, Coastal and Shelf Science 79, 764-767.

Loneragan, N.R., Kenyon, R.A., Staples, D.J., Poiner, I.R. & Conacher, C.A. 1998. The influence of seagrass type on the distribution and abundance of postlarval and juvenile tiger prawns (*Penaeus esculentus* and *P. semisulcatus*) in the western Gulf of Carpentaria, Australia. Journal of Experimental Marine Biology and Ecology 228, 175-195.

Lugendo, B.R., Nagelkerken, I., van der Velde, G. & Mgaya, M.D. 2006. The importance of mangroves, mud and sand flats, and seagrass beds as feeding areas for juvenile fishes in Chwaka Bay, Zanzibar: Gut content and stable isotope analysis. Journal of Fish Biology 69, 1639-1661.

Macpherson, E. Resource partitioning in a Mediterranean demersal fish community. Marine Ecology Progress Series 4, 183-193.

Manjakasy, J.M., Day, R.D., Kemp, A. & Tibbetts, I.R. 2009. Functional morphology of digestion in the stomachless, piscivorous needlefishes *Tylosurus gavialoides* and *Strongylura leiura ferox* (Teleostei: Beloniformes). Journal of Morphology 270, 1155-1165.

Mariotti, A.1984. Atmospheric nitrogen is a reliable standard for natural ^{15}N abundance measurements. Nature 303, 685-687.

Marguillier, S., van der Velde, G., Dehairs, F., Hemminga, M.A., Rajagopal, S. 1997. Trophic relationships in an inter-linked mangrove-seagrass ecosystem as traced by δ^{13}C and δ^{15}N. Marine Ecology Progress Series 151, 115-112.

Masuda, H. & Allen, G.R. 1993. Meeresfische der Welt – Groß-Indopazifische Region. Tetra Verlag, Herrenteich, Melle. 528 pp.

Matera, N.J. & Lee, J.J. 1972. Environmental factors affecting standing crops of foraminifera of sublitoral and psammolitoral communities of a Long Island salt marsh. Marine Biology 14, 89-103.

Matheson, R.E., Camp, D.K., Sogard, S.M. & Bjorgo, K.A. 1999. Changes in seagrass-associated fish and crustacean communities on Florida Bay mud banks: The effects of recent ecosystem changes? Estuaries 22, 534-551.

Mittelbach, G.G., Osenberg, C.W. & Leibold, M.A. Trophic relations and ontogenetic niche shifts in aquatic ecosystems. In: Ebenman, B. & Persson, L. (Eds.), Size structured populations. Springer, Berlin, pp. 219-235.

Moncreiff, C.A. & Sullivan, M.J. 2001. Trophic importance of epiphytic algae in subtropical seagrass beds: Evidence from multiple stable isotope analyses. Marine Ecology Progress Series 215, 93-106.

Murray, J.W. 2000. The niche of benthic foraminifera, critical thresholds and proxies.

Marine Paleontology 41, 1-7.

Nakamura, Y. & Sano, M. 2005. Comparison of invertebrate abundance in a seagrass bed and adjacent coral and sand areas at Amitori Bay, Iriomote Island, Japan. Fisheries Science 71, 543-550.

Nakamura, Y., Horinouchi, M., Nakai, T. & Sano, M. 2003. Food habits of fishes in a seagrass bed on a fringing coral reef at Iriomote Island, Southern Japan. Ichthyological Research 50, 15-22.

Nienhuis, P.H., Coosen, J., Kiswara, W. 1989. Community structure and biomass distribution of seagrasses and macrofauna in the Flores Sea, Indonesia. Netherlands Journal of Sea Research 23, 197-214.

Ogden, J.C. & Buckman, N.S. 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). Ecology 54, 589-506.

Ogden, J.C. & Quinn, T.P. 1984. Migration in coral reef fishes: Ecological significance and orientation mechanisms. In: McCleave, J.D., Arnold, G.P., Dodson, J.J., Neill, W.H. (Eds.), Mechanisms of migration in fishes. Plenum, New York, pp. 293-308.

Overman, N.C. & Parrish, D.L. 2001. Stable isotope composition of walleye: ^{15}N accumulation with age and area-specific differences in d^{13}C. Canadian Journal of Fisheries and Aquatic Sciences 58, 1253-1260.

Peristiwady, T. & Geistdorfer, P. 1991. Biological aspects of *Monacanthus tomentosus* (Monacanthidae) in the seagrass beds of Kotania Bay, West Seram, Moluccas, Indonesia. Marine Biology 109, 135-139.

Pinnegar, J.K., Polunin, N.V.C. 1999. Differential fractionation of d^{13}C and d^{15}N among fish tissues: Implications for the study of trophic interactions. Functional Ecology 13, 225–231.

Pinnegar, J.K. & Polunin, N.V.C. 2000. Contributions of stable isotope data to elucidating food webs of Mediterranean rocky littoral fishes. Oecologia 122, 399-409.

Pinto, L. 1982. Gut content and food consumption of some echinoderms at Talin Bay, Batangas, Philippines. Philippine Journal of Biology 11, 302-308.

Pollard, D.A. 1984. A review of ecological studies of seagrass-fish communities, with particular reference to recent studies in Australia. Aquatic Botany 18, 3-42.

Polz, M.F. & Cavanaugh, C.M. 1995. Dominance of one bacterial phylotype at a Mid-Atlantic Ridge hydrothermal vent site. Proceedings of the National Academic of Sciences 92, 7232-7236.

Polz, M.F., Robinson, J.J. & Cavanaugh, C.M. 1998. Trophic ecology of massive shrimp aggregations at a Mid-Atlantic Ridge hydrothermal vent site. Limnology and Oceanography 43, 1631-1638.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: Models, methods and assumptions. Ecology 83, 703-718.

Powell, M.A. & Somero, G.N. 1985. Sulfide oxidation occurs in the animal tissue of the gutless clam, *Solemya reidi*. Biological Bulletin 169, 164-181.

Randall, J.E. 1967. Food habits of reef fishes of the West Indies. Studies in Tropical Oceanography 5, 666-847.

Reid, R.G.B. 1990. Evolutionary implications of sulphide-oxidizing symbioses in bivalves. In: Morton, B. (Ed.), The Bivalvia - Proceedings of a Memorial Symposium in Honour of Sir C. M. Yonge. Hong Kong University Press, Hong Kong p. 127–140.

Robertson, A.I., Klumpp, D.W. 1983. Feeding habits of the southern Australian garfish *Hyporhamphus melanochir*: A diurnal herbivore and nocturnal carnivore. Marine Ecology Progress Series 10, 197-201.

Russell, B.C. 1990. FAO Species Catalogue. Vol. 12. Nemipterid fishes of the world. (Threadfin breams, whiptail breams, monocle breams, dwarf monocle breams, and coral breams). Family Nemipteridae. An annotated and illustrated catalogue of nemipterid species known to date. FAO Fisheries Synopsis 12, 1-149.

Schaal, G., Riera, P., Leroux, C. 2008. Trophic coupling between two adjacent benthic food webs within a man-made intertidal area: A stable isotopes evidence. Estuarine, Coastal and Shelf Science 77, 523-534.

Smit, A.J., Brearley, A., Hyndes, G.A., Lavery P.S. & Walker, D.I. 2005. Carbon and nitrogen stable isotope analysis of an *Amphibolis griffithii* seagrass bed. Estuarine, Coastal and Shelf Science 65, 545–556.

Smit, A.J., Brearley, A., Hyndes, G.A., Lavery P.S. & Walker, D.I. 2006. δ^{15}N and δ^{13}C analysis of a *Posidonia sinuosa* seagrass bed. Aquatic Botany 84, 277–282.

StatSoft, Inc. 2007. STATISTICA (Data Analysis Software System), version 7.0. www.statsoft.com.

Stewart, F.J. & Cavanaugh, C.M. 2006. Bacterial endosymbioses in *Solemya* (Mollusca: Bivalvia)-Model systems for studies of symbiont-host adaptation. Antonie van Leuwenhoek 90, 343-360.

Stoner, A.W., Ray, M., Waite, J.M. 1995. Effects of a large herbivorous gastropod on macrofauna communities in tropical seagrass meadows. Marine Ecology Progress Series 121, 125-137.

Talwar, P.K. 1962. Studies on the food and feeding relationships of the halfbeak fishes (Hemirhamphidae) from the Gulf of Mannar and Palk Bay. Indian Journal of Fisheries 9, 1-9.

Taylor, J.D. & Glover, E.A. 2006. Lucinidae (Bivalvia) – the most diverse group of chemosymbiotic molluscs. Zoological Journal of the Linnean Society 148, 421-438.

Thayer, G.W., Engel, D.W. & Bjorndal, K.A. 1982. Evidence for short-circuiting of the detritus cycle of seagrass beds by the green turtle, *Chelonya mydas* L. Journal of Experimental Marine Biology and Ecology 62, 173-183.

Tibbetts, I.R. & Carseldine, L. 2005. Trophic shifts in three subtropical Australian halfbeaks (Teleostei : Hemirhamphidae). Marine and Freshwater Research 56, 925-932.

Unsworth, R.K.F., de Grave, S., Jompa, J., Smith, D.J. & Bell, J.J. 2007a. Faunal relationship with seagrass habitat structure: A case study using shrimp from the Indo-Pacific. Marine and Freshwater Research 58, 1008-1018.

Unsworth, R.K.F., Wylie, E., Smith, D.J., Bell, J.J. 2007b. Diel trophic structuring of seagrass bed fish assemblages in the Wakatobi Marine National Park, Indonesia. Estuarine, Coastal and Shelf Science 72, 81-88.

Unsworth, R.K.F., Taylor, J.D., Powell, A., Bell, J.J. & Smith, D.J. 2007c. The contribution of scarid herbivory to seagrass ecosystem dynamics in the Indo-Pacific. Estuarine, Coastal and Shelf Science 74, 53-62.

Valentine, J.F. & Heck Jr., K.L. 1999. Seagrass herbivory: Evidence for the continued grazing of marine grasses. Marine Ecology Progress Series 176, 291-302.

Vander Zanden, M.J., Hulsof, M., Ridgway, M.S. & Rasmussen, J.B. 1998. Application of stable isotope techniques to trophic studies of age-0 smallmouth bass. Transactions of the American Fisheries Society 127, 729-739.

Verweij, M.C., Nagelkerken, I., Wartenbergh, S.L.J., Pen, I.R. & van der Velde, G. 2006. Caribbean mangroves and seagrass beds as daytime feeding habitats for juvenile French grunts, *Haemulon flavolineatum*. Marine Biology 149, 1291-1299.

Vonk, J.A., Christianen, M.J.A. & Stapel, J. 2008. Redefining the trophic importance of seagrasses for fauna in tropical Indo-Pacific meadows. Estuarine, Coastal and Shelf Science 79, 653-660.

Vonk, J.A., Christianen, M.J.A. & Stapel, J. 2010. Abundance, edge effect, and seasonality of fauna in mixed-species seagrass meadows in southwest Sulawesi, Indonesia. Marine Biology Research 6, 282-291.

Waltham, N.J. & Connolly, R.M. 2006. Trophic strategies of garfish, *Arrhamphus sclerolepis*, in natural coastal wetlands and artificial urban waterways. Marine Biology 148, 1135-1141.

Westneat, M.W., Alfaro, M.E., Wainwright, P.C., Bellwood, D.R., Grubich, J.R., Fessler, J.L., Clements, K.D. & Smith, L.L. 2005. Local phylogenetic divergence and global evolutionary convergence of skull function in reef fishes of the family Labridae. Proceedings of the Royal Society B, 993-1000.

Yamamuro, M. 1999. Importance of epiphytic cyanobacteria as food sources for heterotrophs in a tropical seagrass bed. Coral Reefs 18, 263-271.

IV. Abstract

The present study investigated the nature and trophic relationships of fish assemblages in seagrass beds at small coral islands in the Indonesian Spermonde Archipelago. Total fish abundance did not correlate with seagrass shoot densities. Diversity and species composition of fish assemblages differed significantly among five examined seagrass beds, between intertidal and subtidal study sites, and between the two islands, while there was no significant difference for total fish abundance. Six common species, however, showed significant differences between study sites (Labridae: *Cheilio inermis, Halichoeres argus, H. chloropterus*; Hemirhamphidae: *Hemirhamphus far*; Siganidae: *Siganus canaliculatus*; Nemipteridae: *Pentapodus trivittatus*). Fish diversity was highest at the most impacted study site at Barrang Lompo South. Seagrass beds in a late stage of succession (high structural complexity) were more species-rich than seagrass beds in an early stage of succession (low structural complexity). Nonetheless, species-accumulation curves for total diversity did not show saturation for any of the study sites. For two of the most speciose fish families in the present study, the Labridae and Pomacentridae, species-accumulation curves did not exhibit saturation, whereas the curve for the third family, the Nemipteridae, clearly was saturated.

As expected, primary producers were more depleted in stable δ^{15}N and δ^{13}C isotope values than most animal taxa. Isotopic values of invertebrates had a broader range than those of fish, although the highest stable nitrogen enrichment was found for piscivorous fish. Lowest isotopic signatures for animals were recorded for bivalves and two taxa of crustaceans that are assumed to have bacterial symbionts. Trophic levels calculated based on stable isotopes show values of 3.69 and 3.44 for piscivorous fish such as barracuda *Sphyraena barracuda* and garfish *Tylosurus crocodilus*, respectively, whereas a herbivorous fish such as the rabbit fish *Siganus virgatus* feeds at a trophic level of only 1.91, characterizing it as a primary consumer. Neither seagrass nor phytoplankton was found to be utilized widely as a food source in the present seagrass bed. Seagrass epiphytes appear to play a major role in trophic relationship of the described food web.

Analysis of gut content revealed four major feeding guilds (zoobenthivores, omnivores, piscivores, herbivores). The most common food items over all guts sampled were crustaceans, gastropods and seagrass. The trophic composition of the fish assemblages differs distinctly between intertidal and subtidal study sites. In contrast to gut content analysis, the trophic contribution of fish assemblages based on visual census data revealed six feeding guilds in the seagrass beds (herbivorous, zooplanktivorous, corallivores, omnivorous, zoobenthivorous, piscivorous). This difference to gut-content analysis might be due to the fact that not all fish species could be included into the analysis (no zooplanktivores and corallivores). With respect to taxon numbers, zoobenthivores dominate over all study sites, and corallivores, piscivores and zooplanktivores accounted for the smallest proportions. With respect to individual counts, zooplanktivores dominated intertidal sites and omnivores and zoobenthivores dominated subtidal sites; again, corallivores, piscivores and herbivores accounted for smallest trophic guilds.

V. Zusammenfassung

In dieser Studie wurden Biodiversität und trophische Beziehungen von Fischgemeinschaften in Seegraswiesen von kleinen Koralleninseln im indonesischen Spermonde-Archipel untersucht. Die gesamte Fischabundanz korrellierte nicht mit der Seegras-Sproßdichte. Diversität und Artenzusammensetzung der Fischgemeinschaften unterschied sich signifikant zwischen einzelnen Seegraswiesen, intertidalen und subtidalen Seegraswiesen und den beiden Inseln. Für die Gesamtabundanz von Fischen gab es keine signifikanten Unterschiede zwischen den Seegraswiesen. Für die sechs häufigsten Fischarten kamen signifikante Unterschiede zwischen Standorten zu tragen (Labridae: *Cheilio inermis, Halichoeres argus, H. chloropterus*; Hemirhamphidae: *Hemirhamphus far*; Siganidae: *Siganus canaliculatus*; Nemipteridae: *Pentapodus trivittatus*). Die Fischdiversität war an dem Standort mit dem stärksten anthropogenen Einfluss am höchsten. Seegraswiesen in einem späten Sukzessionsstadium (hohe strukturelle Komplexität) waren artenreicher als Seegraswiesen in frühen Stadien (niedrige Komplexität). Art-Akummulationskurven zeigten dennoch für keinen der beprobten Standorte Sättigung. Für zwei der drei artenreichsten Fischfamilien, den Labriden (Lippfischen) und den Pomacentriden (Riffbarschen), erreichten Art-Akummulationskurven keine Saturierung, während die Kurve für die dritt-artenreichste Familie, den Nemipteriden (Scheinschnappern) Sättigung erreicht.

Wie erwartet zeigte die Stabile Isotopen-Analyse, dass Primärproduzenten eine geringere Anreicherung an δ^{15}N und δ^{13}C aufweisen als die meisten Tier-Taxa. Die Isotopen-Signaturen der Evertebraten hatten einen größeren Umfang als die der Fische, allerdings war die stärkste Anreicherung für schweren Stickstoff in der piscivoren

Fischgilde zu finden. Die niedrigsten Isotopen-Signaturen für Tiere wurden bei drei Arten von Muscheln (*Codakia tigerina, Solemya pusilla, Fimbria* sp.) und bei zwei Krebs-Arten (*Eucalliax panglaoensis* und *Calliaxina* sp.) gefunden. Es wird vermutet, dass diese Taxa eine Symbiose mit chemoautotrophen Bakterien pflegen und dass aus dieser Symbiose der für diese Organismen notwendige Kohlenstoff und Stickstoff für Wachstum und Entwicklung stammt. Die höchsten trophischen Stufen basierend auf Stickstoffwerten aus der Stabilen Isotopen-Analyse waren 3.69 und 3.44 für zwei piscivore Fische, den Großen Barrakuda (*Sphyraena barracuda*) und den Krokodils-Hornhecht (*Tylosurus crocodilus*). Herbivore Fische finden sich dagegen auf der niedrigsten Stufe wieder: der Kaninchenfisch *Siganus virgatus* belegt eine trophische Stufe von lediglich 1.91 und kann dadurch als Primärkonsument identifiziert werden. Weder Seegras noch Phytoplankton konnte in der Isotopen-Analyse als wichtige Nahrungsquelle in der untersuchten Seegraswiese identifiziert werden, der Algenaufwuchs auf den Seegräsern dürfte jedoch eine große Rolle im beschriebenen Nahrungsnetz spielen.

Darm-Inhalts-Analysen zeigten vier Nahrungsgilden (Zoobenthivore, Omnivore, Piscivore, Herbivore). Die Nahrungskategorien, die in den meisten Mägen oder Därmen gefunden wurden, waren die der Crustaceen, der Gastropoden und der Seegräser.

Die trophische Zusammensetzung von Fischgemeinschaften in unterschiedlichen Seegraswiesen zeigt distinkte Muster zwischen intertidalen und subtidalen Standorten. Die Gilden-Zusammensetzung basierend auf Daten aus einem visuellen Fisch-Zensus enthüllte sechs Nahrungsgilden in den Seegraswiesen: Herbivore, Zooplanktivore, Corallivore, Omnivore, Zoobenthivore und Piscivore. Unterschiede zu den Ergebnissen der Darm-Inhalts-Analyse werden damit erklärt, dass nicht alle Fischarten in die Analyse miteinbezogen werden konnten. Die zoobenthivore Gilde weist die höchsten Taxon-Zahlen an allen Standorten auf. Die artenmäßig kleinsten Gilden sind die Corallivoren, Piscivoren und Zooplanktivoren. Die höchsten Abundanzen sind an den intertidalen Standorten für die Zooplanktivoren und für die subtidalen Standorte für die Omnivoren und Zoobenthivoren zu finden. Corallivore, Piscivore und Herbivore sind an allen Standorten nur in geringen Abundanzen anzutreffen.

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Additionally, I would like to thank Dr. Lisa Shama and Dr. Michael Stachowitsch for proofreading the manuscripts.

I would also like to thank my dear friend, mentor and fellow marine biologist Dr. Robert Hofrichter for being supportive and believing in my skills, and of course for giving me the opportunity to join the wonderful trip to Raja Ampat, one of the last pristine oceanic realms at the centre of the coral triangle and thus the very heart of biodiversity. It was a great experience for a young marine tropical ecologist, thanks a lot!

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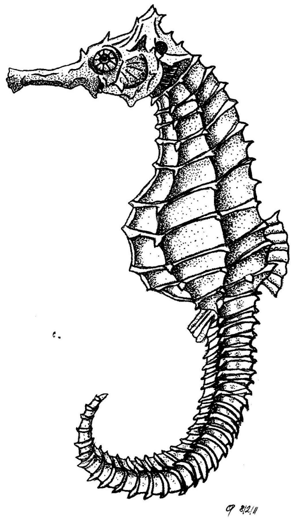

VII. Curriculum Vitae

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Education

Since 2006	Studies of Zoology/ Marine Biology at the **University of Vienna**
Since Jul 2006	First Diploma in General Biology
2004 – 2006	Studies of Biology at the **University of Vienna**
1996 - 2004	Grammar School, **Bundesgymnasium Kufstein**
1992 - 1996	Primary School, **Kufstein**

Experiences abroad

Feb.-Jul 2008	**Joint-study Program:** Exchange semester at the **Macquarie University,** Sydney, Australia

Research Experience

Dec. 2010	**Stable Isotope Tracing in Ecology: Food Web Analysis** (Practical), University of Vienna
Aug. 2010	**Aquatic Biocoenoses** (Field Course in Limnology), Lunz am See, Austria
July 2010	**Course** in **Food Web Analysis** the AWI Waddensea Station at the island of Sylt, Germany
June 2010	**Field Course in Fish Ecology** at Nationalpark Donauauen, Orth a. d. Donau, Austria
Feb. – June 2010	**Lab work / data acquisition for Diploma thesis** in Germany
Oct. 2009 – Jan. 2010	**Field and lab work / data acquisition for Diploma thesis** in Indonesia
Sept. 2009	**Summer School on Changing Sandy Coasts** at the AWI Waddensea Station, Island of Sylt, Germany
Aug. 2009	**Field course in Tropical Ecology** to the Krakatau Archipelago, Indonesia
Jul. – Sept. 2008	**Volunteer at the RSEC** (Red Sea Environmental Centre) in el Quseir, Egypt
Jul. – Sept. 2008	**el Quseir Fish Census 2008** at the RSEC in el Quseir,

	Egypt
Mar. – May 2008	**Marine Science Project:** at Macquarie University, Sydney: Microhabitat choice of wobbegong sharks
Apr. 2008	**Coral Reef Ecology Field Trip to Heron Island**, Great Barrier Reef, Australia
Nov. 2007	**Coral Reef Course and terrestrial Excursion** in Dahab, Egypt
Sept. 2007	**Marine Ecology Course at STARESO** (Station de Rechèrche Océanographiques et sous-marines) at Calvi, France.
Jul. – Aug. 2007	**Volunteer at the RSEC** (Red Sea Environmental Centre) in Dahab, Egypt
Aug. 2007	Participation at the **Dahab Reef Monitoring of the RSEC** (Red Sea Environmental Center) in Dahab, Egypt
May 2007	**Waddensea Field Course** at the AWI Waddensea Station at the island of Sylt, Germany
July 2006	**Marine Biology Field Course** of the University of Vienna in Rovinj, Croatia

Other skills

Feb. 2011	Course in **Scientific drawing techniques**
Oct. – Feb. 2008	Practical in **bioacoustic methods**
Sept. 2007	**SSI Master Diver** (>250 scuba dives)
Apr. 07 – Feb. 08	**Aquarium keeper** at the **Aqua Terra Zoo Haus des Meeres**, Vienna (marine section)
Mar. 2007	**Internship as aquarium keeper** at the **Aqua Terra Zoo Haus des Meeres**, Vienna (marine section)

Scholarships

- **Scholarship for a semester abroad (SS 2008)**
- **Scholarship for the study year 2006/7**
- **Scholarship for the study year 2008/9**

Publications

Articles

Schwaha, P., Heinzl, R., Mach, G., Pogoreutz, C., Fister, S. & Selberherr, S. 2007. A high performance webapplication for an electro-biological problem. Proceedings of the 21th ECMS 2007, Prague, Czech Republic.

Pogoreutz, C., Asmus, H., Ahnelt, H., submitted. Fish assemblages in different types of tropical Indo-Pacific seagrass meadows.

Abstract:

Pogoreutz, C., Asmus, H., Ahnelt, H. 2010. Fish diversity patterns in different types of tropical seagrass meadows in the Spermonde archipelago, Indonesia. In: The Wadden Sea: Changes and Challenges in a World Heritage Site. ECSA Conference 46, AWI-Wadden Sea Station Sylt, List, Germany, 3 – 6 May 2010

Poster Presentation at the **ECSA Conference 46** at the AWI Wadden Sea Station at the Island of Sylt, Germany, 3- 6 May 2010

Languages

German	Mother tounge
English	fluent (spoken and written)
Indonesian	basic
French	basic