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Restored seagrass beds support Macroalgae and Sea Urchin communities

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Abstract. Seagrass decline and loss have been reported worldwide. Restoration is an increasingly popular approach to improving ecosystem services and may become a mitigation measure for seagrass habitat loss. However, in Indonesia seagrass restoration is still at a trial stage and small scale. This study aimed to compare the seaweeds and sea urchin communities in restored seagrass beds and in control areas (natural seagrass beds) around Barrang Lompo Island, Indonesia. Sea urchin and seaweed community structure was compared using non-metric multidimensional scaling and Bray-Curtis cluster analysis, while (as an indicator of ecosystem service provision) species contribution to the difference in sea urchin and seaweed community structure was analysed using SIMPER (similarity of percentages); both analyses were implemented in PRIMER v7. Regression analysis in SPSS v25 was applied to evaluate the correlations between sea urchin and seaweed density, sea urchin and seagrass density, seaweed and seagrass density. The results indicate that, although the ability to harbour associated organisms differed, restored seagrass beds can provide habitat for associated organisms and improve ecosystem services.

1. Introduction

Seagrasses, submerged aquatic vascular plants, are known to support marine biodiversity; in particular, they provide vital habitat for fishes [1–4] and invertebrates [5,6] as well as threatened "charismatic megafauna" such as turtles and dugongs [7–9]. Seagrass ecosystems support fisheries production, especially for small scale fisheries [10], and consequently provide potential economic value from the standing stock of seagrass-associated fishes [11]. However, there is no denying that degradation and even loss of seagrasses meadows continues to this day around the world [12–18]. Several seagrass species are considered at risk of extinction under the Criteria of the International Union for the Conservation of Nature (IUCN) Red List of Threatened Species [19]. Inevitably, the decline and loss of seagrasses will reduce the quality and quantity of seagrass ecosystem services.

Efforts to maintain or improve seagrass ecosystem services and avoid or reverse further seagrass habitat loss include various rehabilitation and restoration trials. A variety of techniques have been used, and seagrass restoration has become more popular in recent years. Examples include large scale

restoration through the transplanting of seagrasses (*Thalassia testudinum*, *Halodule wrightii*, *Syringodium filiforme*) in a degraded estuary in Biscayne Bay, south-eastern Florida [20]; large-scale seagrass restoration using eelgrass seed [21]; seagrass rehabilitation using hessian bags [22]; seagrass restoration trials off the Adelaide metropolitan coast, Australia [23]; rehabilitation in Tamil, Nadu, India [24]; seagrass transplantation in Whangarei Harbour, New Zealand [25]; restoration off the Swedish west coast [26], and multi-species seagrass restoration in Indonesia [27,28].

A small-scale restoration trial was conducted in 2013 (Rohani Ambo-Rappe, pers.com.) on bare substrate off the west coast of Barrang Lompo Island in the Spermonde Archipelago, South Sulawesi Province, Indonesia. This restoration trial was not monitored regularly, so there are no quantitative observational data to measure the early impact of the restoration, but anectodatal information indicated that the restoration was at least partially successful. Two years later (in 2015) the seagrass cover in the restored area was reported as in poor to moderate condition [29] and the percentage cover is still within this category (20 to 50%) (Nadiarti, pers. obs. 2019). The most likely reasons for the partial success of the restoration are activities of the island community which can reduce seagrass cover. These include boat anchoring and propeller damage [30], human trampling [31], and a habit (common among local people) of cutting off the seagrass leaves to clear access lanes for their boats. According to [32], the more extensive and denser the seagrass meadow, the greater the capacity to provide ecosystem services. Nonetheless, even though the restored seagrass beds are relatively sparsely vegetated, they visibly support marine biodiversity. Macroalgae and sea-urchins are the most visible associated biota, and are readily observed during low tide.

Seagrass ecosystems are complex ecological communities with food webs involving many interacting taxonomic and functional groups of organisms [7]. Two of these are the sea urchins and the seaweeds or macroalgae. Seagrass-associated sea urchins are generally considered as belonging to the guild of herbivores [33,34] although some taxa have been reported as (mostly primarily herbivorous) omnivorous [33,35,36]. The dietary habits of many taxa are opportunistic [33,34], and can include detrivory [33], and even carnivory [37–40]. Macroalgae are primary producers at the base of the seagrass food web, consumed by many herbivorous and omnivorous fish and invertebrates [7]. Sea urchins commonly found in seagrass ecosystems include the genera *Diadema* [41–43], *Tripneustes* [6,7,43] and *Mespilia* [43–45], There is some evidence that diadematid urchins [46], in particular *Diadema setosum* [47,48], as well as *Mespilia globulus* [43], tend to consume macroalgae in preference to seagrasses. Therefore it is possible there could be some correlation between the sea urchin and macroalgal communities in seagrass ecosystems.

The aims of this study were to compare the seaweed and sea-urchin species present in the sparsely vegetated restored seagrass beds and in nearby dense (natural) seagrass beds, in particular in terms of density, community structure, and the correlation between these two taxonomic and functional groups.

2. Methods

This study took place from September to October 2017 in the seagrass beds around Barrang Lompo Island in the Spermonde Archipelago, South Sulawesi, Indonesia. Barrang Lompo Island is located at about 14 km from the main land (Makassar City). The sampling site comprised areas of natural and restored seagrass beds on the extensive shallow shelf around the coast of Barrang Lompo Island (Figure 1). The restored seagrass beds along the north-west coast (5°02'45.15"S, 119°19'54.72"E) were visibly sparser than the natural seagrass beds along the south-west coast (5°02'53.09", 119°19'36.92"E).

Ten quadrats (10 x 10 m^2 = 100m^2 area) were placed randomly along 300 m stretches in each seagrass type (restored and natural) at distances determined using a Random Integer Generator (RIG). Observations (density and species identification) of the seagrasses, macro-algae and sea urchins were made during low tide. The seagrass percentage (%) cover and density were estimated using a standard photography-based method following [49] and [50]. Seagrasses and macro-algae were identified based on [51]. Sea-urchins found at the observation sites were identified following [52].

The variation in seaweed and sea-urchin community structure at each sampling site was analysed using non-metric multidimensional scaling (nMDS) and Bray-Curtis cluster analysis. Species that contributed most to the differences in seaweed and sea-urchin community structure were analysed using the SIMPER (similarity of percentage) routine. These statistical analyses were conducted in PRIMER version 7. Linear regression analysis was implemented in GraphPad PRISM version 5 to evaluate the significance of the relationship between seagrasses and macroalgae, between seagrasses and sea-urchins, and between macroalgae and sea-urchins. Statistical significance was evaluated at the 95% confidence level (α=0.05).

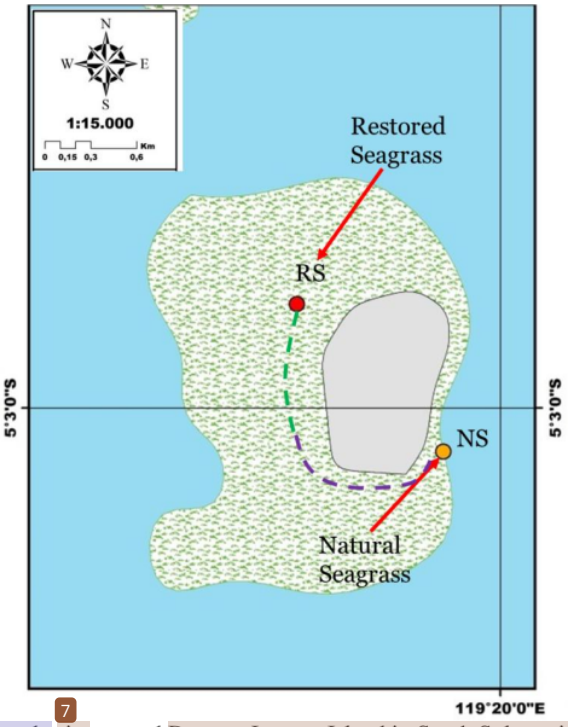

Figure 1. The study site around Barrang Lompo Island in South Sulawesi, Indonesia.

3. Results

Overall, five seagrass species were present at each of the study sites (natural and restored seagrass beds). Four species (*Enhalus acoroides, Thalassia hemprichii, Cymodocea rotundata,* and *Syringodium isoetifolium*) were present at both sites, while *Halophila ovalis* was only found in the restored seagrass beds, and *Halodule uninervis* was only found in the natural seagrass beds. Seagrass density was 281 ± 15.40 shoots·m^{-2} at the dense site and 60 ± 7.76 shoots·m^{-2} at the sparse site.

Five sea urchin species were also identified. Three species were present in both restored and natural seagrass beds: the black long-spined sea urchin *Diadema setosum* and the banded or double-spined sea urchin *Echinothrix calamaris*, both in the Family Diadematidae, and the globular sea urchin *Mespilia globulus*, Family Temnopleuridae. A further three species were only present in the denser natural seagrass beds: the collector urchins *Tripneustes gratilla* and *T. ventricosus* and the green or variegated sea urchin *Lytechinus variegatus*, all belonging to the Family Toxopneustidae. Mean sea urchin density was higher in the restored seagrass beds (25.42 ind·m^{-2}) compared to the natural seagrass beds (12.3 ind·m^{-2}).

Nine species of macroalgae were identified. The species richness (diversity) of macroalgae was higher in the natural than the restored seagrass beds (Table 1).

Table 1. Macroalgae identified in natural and restored seagrass beds, Barrang Lompo Island.

No	Species	Natural	Restored	No	Species	Natural	Restored
1	*Dictyota ciliata*	X	X	6	*Sargassum* sp.	X	
2	*Boodlea composita*	X		7	*Sargassum cristaefolium*	X	X
3	*Hypnea cervicornis*	X		8	*Gelidiella acerosa*	X	
4	*Amphiroa fragilissima*	X		9	*Gracilaria coronopifolia*	X	X
5	*Padina australis*	X	X				

The nMDS ordination of sea-urchins (Figure 2A) and macroalgae (Figure 2B) show similar distinct patterns, with dense and sparse seagrass beds tending to cluster separately from one another. This indicates that the sea-urchin and macroalgal assemblages in the dense and sparse seagrass sites were distinct and dissimilar in composition. This result is supported by the pairwise comparison test (one-way ANOSIM) which showed a significant difference between the two seagrass sites (dense and sparse seagrass beds) for sea-urchin community composition ($R=0.2$, $p<0.01$) and macroalgal community composition ($R=0.4$, $p<0.01$).

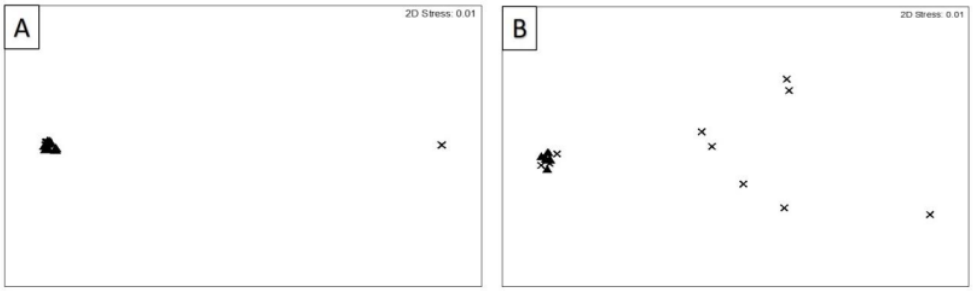

Figure 2. nMDS ordination plots of sea-urchin (A) and macroalgal (B) communities. Natural (dense) seagrass beds = ▲; Restored (sparse) seagrass beds = x.

The similarity (SIMPER) analysis indicated that the mean dissimilarity of sea-urchin species composition between dense and sparse seagrass beds was 70.57%. The species which contributed most to the dissimilarity were *Diadema setosum* (49.53%) and *Mespilia globulus* (23.27%) (Figure 3).

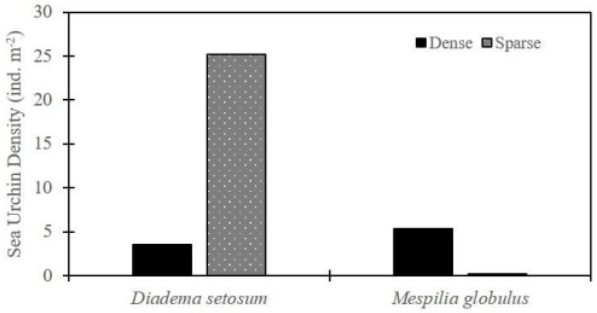

Figure 3. Mean density of species contributing most to differences in sea urchin community structure between natural and restored seagrass beds.

The SIMPER analysis of macroalgal communities showed a high dissimilarity (94.27% on average) in species composition between the natural and restored seagrass beds, with all species making a significant contribution. The species making the greatest contribution (more than 10%) to the difference in community composition were *Amphiroa fragilissima*, *Dictyota ciliata*, *Boodlea composita*, and *Gracilaria coronopifolia* (Figure 4).

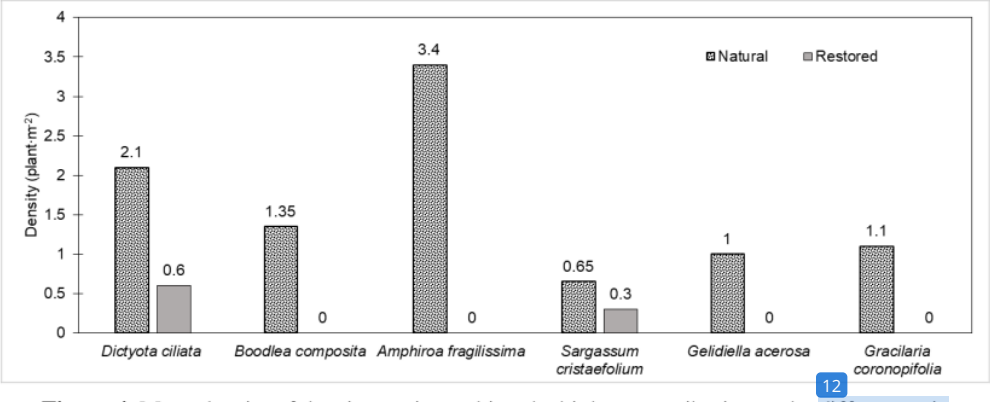

Figure 4. Mean density of the six species making the highest contribution to the differences in macroalgal community structure between natural and restored seagrass beds.

Macroalgal density significantly increased with the increase in seagrass density (R^2 = 0.64, p<0.0001) (Figure 5). However, there was no significant relationship between seagrass and sea-urchin densities or between the densities of macroalgae and sea-urchins (p>0.05).

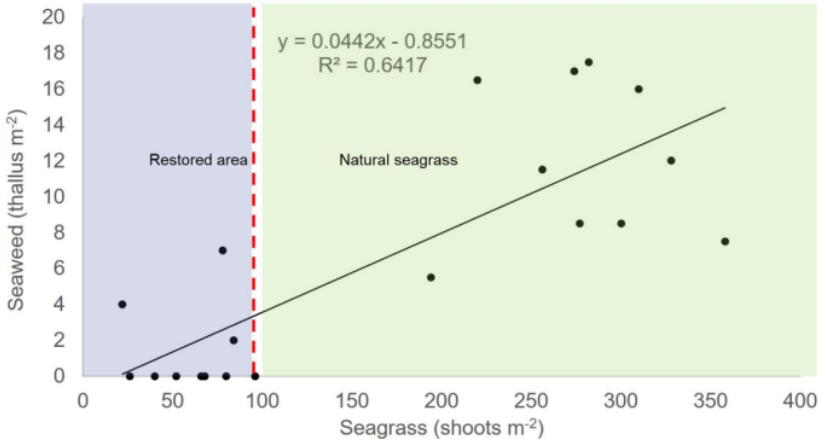

Figure 5. Correlation between the densities of seagrass and macroalgae in restored (sparse) and natural (dense) seagrass beds around Barrang Lompo Island.

4. Discussion

One of the ecosystem functions of seagrasses is the trapping of sediment by seagrass roots to stabilise the substrate [53,54]. Therefore, it is to be expected that substrate will be more effectively stabilized

when seagrass density is higher. According to [55], the diversity and abundance of benthic marine algae in seagrass beds are influenced by the substrate, and are generally higher in more stable substrates. It should be noted that, although this study did not collect data in unrestored close to the observation area, these areas clearly did not benefit from any level of substrate stabilisation by seagrasses. These areas had a barren appearance and did not support macroalgae with holdfasts, although algal fronds (thallus), especially *Sargassum* sp., could sometimes be seen either floating in the water column or laying on the substrate in these areas. It is therefore possible that the higher macroalgal density and diversity observed in the natural seagrass site in this study may be related to more effective substrate stabilisation in these denser seagrass beds compared to the sparser seagrass cover in the restored site.

Sea urchins, in particular the genus *Diadema*, are widely considered as ecologically important herbivores in tropical coastal ecosystems, especially coral reefs [41,56]. In this study the linier regression analysis did not show a significant correlation between sea-urchin density and the density of either macroalgae or seagrasses, despite the greater abundance of urchins in the sparser restored seagrass area and the greater abundance of macroalgae in the denser natural seagrass beds. It is interesting to note that these findings are similar to the results of research in Singapore [57], which also found no significant correlation between urchin and macroalgal density, and Fiji, where urchins density did not correlate significantly with either seagrass or macroalgal density [58]. However, the results contrast with a study in Karimunjawa National Park, Jepara in western Indonesia [59] where seagrass and sea urchin density were strongly and negatively correlated. One reason for the lack of observed correlation could be the limited temporal and spatial scale of this study, indicating that more detailed studies might provide more detailed and definitive answers regarding the interactions between sea urchins and marine plants at this site. However, these conflicting results could indicate that sea-urchins may not always play a major role in regulating macroalgal density and/or seagrass density in seagrass beds. In particular, the sea-urchins present in the research site may not form a major component of the guild of herbivores in the seagrass ecosystems around Barrang Lompo Island, despite the widespread perception of sea urchins as keystone herbivores influencing marine plant populations, especially macroalgae [47,56,60].

Despite the lack of a statistically significant correlation with sea urchin density at the aggregated species level, the macroalgae present in the restored seagrass beds were more abundant in the natural seagrass beds, hinting at a possible causal relationship. Diadematid urchins are mobile, and can move between nearby habitats for grazing, to seek shelter and as part of their generally impermanent aggregating behaviour [61,62]. Statistically significant preference between adjacent habitats was observed in the Banggai Islands east of Sulawesi, with reef flat habitat (with sparse seagrass and scattered corals) was preferred to dense seagrass beds or coral reefs [42]. Grazing on macroalgae might be easier in the sparser restored seagrass due to the more open structure; this could account for both the lower abundance of these macroalgal taxa and the higher abundance of urchins, especially *Diadema setosum*, in the restored seagrass compared to the natural seagrass beds. The tendency to aggregate [61] might also cause *D. setosum* to favour relatively seagrass beds offering more spaces for aggregation while still providing some shelter from adverse weather and predation, both of which can pose a risk to populations of this sea urchin [40,63]. While *Diadema* appears to prefer a more open canopy structure, the other sea urchin species may well prefer the additional shelter and higher potential for avoiding detection in the denser natural seagrass beds, with some species possibly feeding (directly or as detritus) on the greater variety of macroalgae.

Other ecological factors which could explain the observed lack of statistically significant correlation between seaweed or seagrass density and sea urchin abundance include sea urchin dietary preference and the intensity of sea urchin grazing pressure. Herbivorous sea urchins might affect the abundance of certain species and/or the size of grazed plants rather than or more than the overall density of seaweed plants (thalli) or seagrasses. The sea-urchin *Mespilia globulus* was considerably more abundant at the natural seagrass site, comprising 43% of the sea urchins observed. In contrast, few individuals were present at the restored site, comprising under 1% of the urchin community at this

site. There is evidence that this sea urchin is predominantly detrivorous [52]. It is therefore likely that the difference in *M. globulus* density may be related to the greater amount of detritus from seagrass litter produced and retained in the denser natural seagrass beds compared to the sparser seagrass vegetation at the restoration site.

The diadematid urchins can be considered as potentially omnivorous rather than true herbivores, with a wide range of reported feeding behaviours including detrivory [61] and in come cases even carnivory [40]. However, a study in Fiji [46] found a significant correlation between the distribution and abundance of *Diadema savignyi* and *D. setosum* and that of their preferred macroalgal/seagrass food. In terms of herbivory, there is evidence from several studies that *Diadema setosum* in particular can have marked dietary preferences although these can vary between populations, and tend to prefer seaweeds (macroalgae) to seagrasses [46–48]. The seagrass species present in the natural and restored seagrass beds were similar; combined with their reported preference for macroalgae, it seems likely that grazing by *D. setosum* had minimal if any impact on seagrass community composition at the research sites. Conversely, all macroalgal genera found in the restored as well as the natural seagrass beds are known to be consumed by *D. setosum*, at least in some regions. Three of these genera are reported as preferred *D. setosum* foods: *Gracilaria* [48,64], *Padina* [46,47,64] and *Dictyota* [64]. Although *Gracilaria* density was less than 0.01 plants.m^{-2}, an order of magnitude lower than *Dictyota* (0.6 plants.m^{-2}) and *Padina* (0.4 plants.m^{-2}), in at least one study it was the most preferred food [48]. Occasional offerings of *Sargassum* sp. were consumed with apparent relish by *D. setosum* from Barrang Lompo held in captivity [48], although "sustained avoidance" of *Sargassum* has been reported from Fiji [46] and Zanzibar [64], and the congeneric urchin *D. savignyi* was shown to be capable of reducing the density of *Sargassum* on reefs in Mo'orea, French Polynesia [65] and in cage experiments in Japan [60]. These contrasting reports indicate possible regional differences in *Diadema* grazing preferences and/or the *Sargassum* species present. Meanwhile, of the macroalgal genera observed only in the natural seagrass beds, three are reported as being avoided by *Diadema setosum* (*Amphiroa* [46], *Boodlea* and *Hypnea* [64]). Finally, *Gelidiella* does not appear to be explicitly mentioned as consumed by *D. setosum* in studies on diadematid urchin grazing or dietary habits, although data in [66] suggest this may be the case. Overall, the sea urchin population seems unlikely to be a major factor affecting the presence of these macroalgal species, while seagrass density (see Figure 4) does appear to be an important factor. In addition to the aforementioned role in substrate stabilisation, the differences in canopy structure likely result in greater protection from wave action [67] in the denser natural seagrass beds and thus more effectively promote the establishment and growth of macroalgae.

A potential confounding factor in this study is the level of human activity which is considerably higher in the restored seagrass area than in the natural seagrass area. This difference in anthropogenic impacts could affect all three components studied. In addition to the impacts on the seagrass community from boat access, mooring and human trampling [30,31], these activities could also impede the settlement, retention and growth of macroalgae through physical damage. With respect to sea urchin communities, the collector urchins (genus *Tripneustes*) are especially vulnerable, as when concealed they could be trampled on, and if seen they would likely be collected. Exploitation of *Tripneustes* is high and increasing across the Spermonde Archipelago [68], and they have long been a favoured gleaning commodity for the Barrang Lompo community. Harvesting could be a reason for the relatively low density of collector urchins in the dense seagrass beds and (possibly aggravated by the lesser availability of material for camouflage) could account for the absence of *Tripneustes* in the restored seagrass bed patches sampled, although it is worth noting that *Tripneustes* were observed in that area on other occasions during a similar time period (A. M. Moore, pers. com., 2017-2018). At the time of the study, other sea urchins were rarely collected and consumed, although *D. setosum* began to be consumed around or shortly after this study, apparently under the influence of migrant seacucumber fishermen who began to work based in Barrang Lompo a few years ago (A. M. Moore, pers. com., 2017-2018). By 2021, *D. setosum* had become the most commonly consumed sea urchin on Barrang Lompo [69], a factor which might affect future ecosystem dynamics.

5. Conclusion

This study shows the potential of restored seagrass beds with low density to support sea-urchin and seaweed communities. It also highlights the importance of maintaining dense seagrass beds to support marine biodiversity, including sea-urchins and macroalgae. Monitoring is recommended to provide more insights into the processes affecting restoration success and observe the dynamic changes within the restored seagrass area.

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