


RESEARCH ARTICLE

Macrozoobenthic community assemblage as key indicator for mangrove restoration success in North Sumatra and Aceh, Indonesia

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The recognition of the high value of mangrove forests and the wide array of ecosystem services they provide has motivated investment in worldwide restoration efforts. However, current metrics of functional restoration (other than seedling survival rates and plant community composition) are often not readily available for local community managers, highlighting an urgency to identify easy-to-measure indicators to assess the functionality of restored mangroves. The macrozoobenthic community could be such practical indicator, as macrozoobenthic communities are sensitive to changes in their environment, and can be easily surveyed within local managing programs. Focusing on three main mangrove management conditions (natural, planted, and naturally regenerated) in North Sumatra and the province of Aceh, Indonesia, we compared vegetation and macrozoobenthic community diversity indices and identified environmental variables that best describe the forest management conditions and their associated macrozoobenthic community assemblage. Results showed that community assemblage, rather than macrozoobenthic diversity index, was associated with management conditions. The highest dissimilarity in macrozoobenthic community assemblages occurred between planted versus natural mangroves, with nonsignificant dissimilarity between natural and naturally regenerated mangroves. The Lined Nerite gastropod (*Nerita balteata*) was identified as an indicator of natural mangroves, and the invasive Giant African snail (*Achatina fulica*) was abundant in mangrove plantations, but also in natural mangroves bordering harbors, oil palm plantations, and aquaculture ponds, suggesting associated anthropogenic pressures. This study showed that the macrozoobenthic community can be used as restoration indicator and could serve as a baseline to empower monitoring activities and community-based adaptive management practices to improve the outcomes of restoration efforts.

Key words: biodiversity, community assemblage, macrozoobenthos, mangrove restoration

Implications for Practice

- Mangroves undergoing restoration might host similar species richness and diversity indices as natural stands, but the community assemblage can differ if functional restoration has not been fully achieved.
- Macrozoobenthic community composition can vary across specific locations, thus site-specific baseline assessments (i.e. before degradation occurred or in natural forests neighboring the restoration sites) are needed to compare community assemblages between site conditions.
- Coastal communities that utilize the mangrove forest are familiar with the macrozoobenthos species. This familiarity will help in designing community-based monitoring programs to evaluate mangrove restoration success.
- Identifying indicator species to support rapid bioassessments can aid conservation diagnostics and management program design.

Introduction

Mangrove forests provide important habitat functions (e.g. nursing, feeding, and spawning) for marine biota such as fish, shrimp, crabs, and mollusks (Sukardjo 2004; Lugendo

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et al. 2007). Through high net primary productivity, mangroves contribute to maintaining a complex food web and thus support valuable ecosystem services, including fisheries (Able 2005; Aburto-Oropeza et al. 2008; Fitri et al. 2018). However, deforestation and conversion to other land uses such as aquaculture have resulted in an estimated loss of ~35% of their original cover worldwide (DasGupta & Shaw 2013; Richards & Friess 2016; Goldberg et al. 2020). Rapid mangrove loss rates have prompted the urgent implementation of conservation and restoration programs (Ellison 2008). Unfortunately current restoration efforts have high failure rates (Mukherjee et al. 2009; Kodikara et al. 2017) mainly because they only consider intensive planting of mangrove seedlings, often in monocultures and on low-lying tidal flats (Kusmana 2014; Kodikara et al. 2017). In many cases, this approach neglects the measure of ecosystem habitat functionality and adaptive management (Kodikara et al. 2017; Wodehouse & Rayment 2019).

Adaptive management involves monitoring indicators (biotic or abiotic factors that can inform on the progress of restoration activities), further facilitating the adequation of management (change or inclusion of new actions as a response to the results of monitoring practices) toward ecosystem recovery (Murray & Marmorek 2003; Zaldívar-Jiménez et al. 2010, 2017). Monitoring restoration progress facilitates the identification of successful and replicable practices and helps understand processes that contribute to the recovery of ecosystem functions (Ellison 2008). Suitable indicators usually include direct measurements of plant survival or forest structure (Wortley et al. 2013). However, monitoring of restoration success should also include associated ecosystem functions, since forest structure alone does not provide enough evidence that the recovered forest is providing similar functions and services as it did before disturbance (Ellison 2000; Mckee & Faulkner 2000; Bosire et al. 2008). Because monitoring functional indicators, such as nutrient cycling (Marquez et al. 2017) or nitrogen fixation (Vovides et al. 2011a, 2011b; Inoue et al. 2019), can be costly, there is a need for cost-efficient functional indicators. In this study, we explored the feasibility of using the mangrove-associated macrozoobenthic community assemblage as a practical indicator of mangrove restoration success.

The mangrove macrozoobenthic community consists of bottom-living invertebrates that depend partially or fully on mangrove habitats to complete their life cycle. This community plays a major role in ecosystem functioning and health (Ellison 2008; Cannicci et al. 2009; Wardiatno et al. 2015). Grazing arthropods and gastropods relieve pneumatophores, leaves, and stems from algal smothering (Ellison 2008). Crabs contribute to nutrient cycling through mechanical leaf breakdown and sediment bioturbation and aeration (Robertson 1992; Mohanty et al. 2019). Additionally, bivalves are effective biofilters that remove water pollutants and suspended sediments (Farooq & Siddiqui 2020; Al-Khayat et al. 2021). The macrozoobenthic community therefore contributes to ecosystem functioning and stability and has been positively correlated to mangrove flora species richness (Ellison 2008; Lee 2008).

The macrozoobenthic communities are susceptible to changes in habitat quality, the ability of the environment to

provide appropriate conditions for individual and population persistence (Hall et al. 1997). Although mangrove degradation has been correlated with loss of macrozoobenthic diversity (Farooq & Siddiqui 2020), degradation does not always translate into reduced richness or diversity. For instance, community assemblages can change from being dominated by benthic species characteristic of mature mangroves before disturbance to pioneer species after disturbance (Salmo et al. 2019), or from predominance of a single taxa within degraded mangroves (Macintosh et al. 2002; Salmo et al. 2017) to recolonization of species associated with restored mangroves (Zvonareva et al. 2015; Salmo et al. 2017). The abundance of the Belitong snail (*Terebralia sulcata*), for example, increases significantly in mangroves affected by wastewater (Meziane & Tsuchiya 2002), and the giant mangrove whelk (*T. palustris*) was absent from sewage-affected wetlands (Cannicci et al. 2009).

The recovery of the macrozoobenthic biota can also be associated to mangrove maturity stages. Salmo et al. (2017) found that epifaunal and infaunal gastropods, such as the Mud snail and the Polished nerite (*Pirenella cingulata* and *Nerita polita*, respectively), were associated with young and intermediate age plantations, whereas arboreal gastropods like the Belitong snail and the Flatspired nerite (*N. planosipra*) were more closely associated with mature mangrove plantations. Hence, monitoring the macrozoobenthic community assemblage might represent an effective approach to help assess the recovery of ecosystem functions (functional restoration) of mangroves (Cannicci et al. 2012; Leung & Cheung 2017). Most macrozoobenthos species are known in coastal communities by their local name due to their economic value (especially prawns and crustaceans, Aburto-Oropeza et al. 2008) and are relatively easy to identify using identification guides.

In this study, we focused on mangrove forests in the North Sumatra and Aceh provinces, Indonesia, where mangrove clear cutting and conversion to aquaculture and oil palm plantations occurred between 1996 and 2008. These land uses have further undergone mangrove vegetation recovery either due to abandonment followed by natural regeneration of mangroves or due to mangrove planting efforts. This provided the possibility to compare two management conditions (i.e. planted and naturally regenerated) with mature natural mangroves, used as reference. In this study, we related site-specific environmental parameters, vegetation structure and species (Shannon index, H'), and taxonomic diversity (Δ^+) with the macrozoobenthic community assemblage and site “management” condition. We further investigated whether there are specific indicator species associated with mangrove management conditions (i.e. natural, planted, and naturally regenerated), which can be used for monitoring functional restoration success.

Methods

Study Area

The study was conducted in mangrove forests located in the provinces of Aceh and North Sumatra, Indonesia. The region is tropical, with an average precipitation of 150–200 mm/month

and a mean annual sea surface temperature ranging 26–30°C (MCGA 2018). Within these provinces, we selected five mangrove locations with one or more of the following management conditions: natural mangroves (without known history of change in land use), mangrove plantation (hereafter referred as “plantation”), and natural regeneration (hereafter referred as “regeneration”). Each location contained five sampling sites (Fig. 1) summarized in Table S1. The sampling sites located at Langsa, in the Aceh province, are in a large natural forest (sites Langsa 1–3), with some areas affected by clear cutting in 2000, which were later planted in 2015 (Site Langsa 4) with *Rhizophora* spp. (Rhizophoraceae) or left to regenerate (Site Langsa 5). The sampling sites at the location of Jarig Halus (sites Jarig Halus 1–5), in North Sumatra, included only natural mangroves, with no records of major disturbance other than the establishment of a fishing community of less than 3,000

inhabitants located northeast of the island. The mangroves at Percut Sei Tuan (sites Percut Sei Tuan 1–4) were converted into aquaculture ponds before the year 2000, which operated until being abandoned in 2007. In 2008, the abandoned ponds underwent mangrove planting programs (at sites Percut Sei Tuan 1–2) that were later extended in 2010 (to Percut Sei Tuan 3–4) using *R. mucronata* (Bakau), and *R. apiculata* (Bakau minyak or tall-stilted mangrove). Site Percut Sei Tuan 5 corresponded to a natural mangrove. The mangroves of Pulau Sembilan were lost to aquaculture ponds in 1996 and were later abandoned. Although the date of abandonment is unclear, Google Earth’s historical imagery showed signs of regeneration in 2002 in the area, and further, mangrove seedlings were planted in 2008 (Site Pulau Sembilan 1) and 2012 (Site Pulau Sembilan 2) with *R. mucronata*. Regeneration occurred at Pulau Sembilan sites 3 and 4, while Site Pulau Sembilan 5 corresponded to a natural

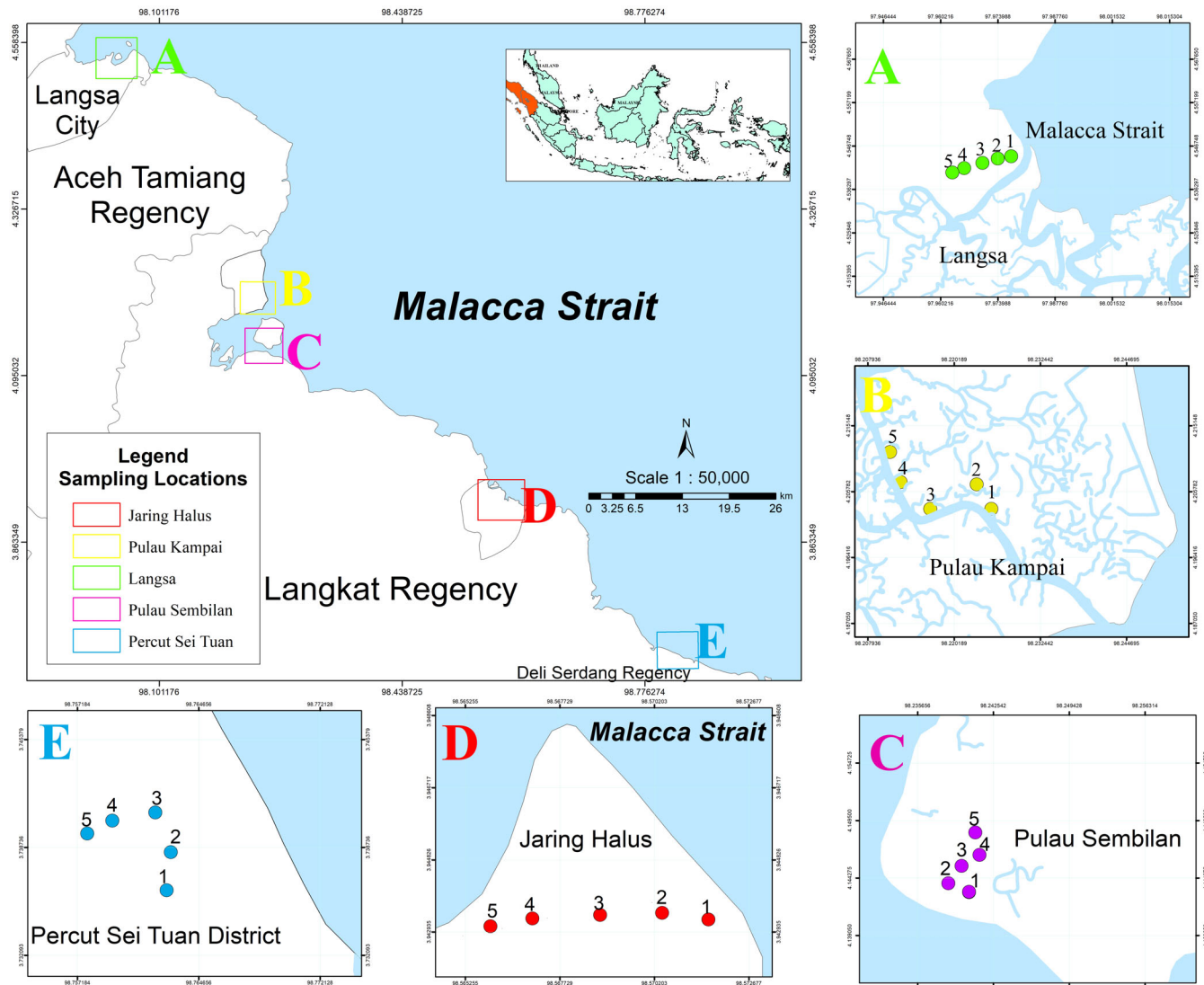


Figure 1. Map of study area showing the study sites (points) at locations (A) Langsa, Aceh Province, (B) Pulau Kampai, (C) Pulau Sembilan, (D) Jarig Halus, and (E) Percut Sei Tuan.

mangrove. At Pulau Sembilan, restoration efforts were expanded in 2012 by creating channel openings that improve hydrological connectivity between the abandoned ponds, the surrounding natural mangrove, and the main drainage channels that connect to the Teluk Ara Bay. The study sites in Pulau Kampai consist of abandoned aquaculture ponds and oil palm plantations. At Pulau Kampai 1, an aquaculture pond was abandoned, and natural regeneration has been reported since 2014, whereas at Pulau Kampai 2 planting of *Rhizophora* spp. took place between 2007 and 2008. Site Pulau Kampai 3 has naturally regenerated since 2012 after clear cutting, and while there are two sites with natural mangroves (i.e. Pulau Kampai 4–5), these are now being encroached by oil palm plantations and aquaculture pond conversion. Natural forest stands served as reference or benchmarks of the macrozoobenthic community assemblage to compare with the different management conditions. In total, there were 12 natural mangroves, 8 plantation, and 5 regeneration sites.

Forest Structure

At each sampling site, three 10 × 10-m plots were established to collect basic forest stand attributes. All trees within plots were identified at species level as described by Kitamura et al. (1997). Tree height (m) was measured using a clinometer (Suunto Tandem 360PC/360R DG Clino/Compass, Finland), and measuring tape. Tree stem basal diameter was measured using a diametric tape (Yamayo Million Diameter Tape 10 m, Japan). These data were then used to calculate different forest structure parameters such as tree density (trees/ha), basal area, relative dominance, relative frequency, and importance value index (IVI) following standard methods described by Cintrón and Schaeffer-Novelli (1984).

Macrozoobenthic Epifauna

Macrozoobenthos samples were collected five times at 2-week intervals within three 1 × 1-m subplots randomly chosen within the 10 × 10-m plots. Sample collection was performed manually during low tide, using a portable shovel (13 × 7 cm). Between 15 February and 15 April 2018, samples were collected fortnightly at 0–10, 10–20, and 20–30 cm depths to assess vertical structure of macrozoobenthos (Mimier, Godzich & Zbikowski 2017). The sediment samples were then carefully washed using fresh water and a 1.0 × 1.0-mm sieve to separate macrozoobenthos from the sediments. Samples were then placed inside individual labeled bags containing a 4% alcohol solution as a preservative. Samples were subsequently identified using a dichotomous key (Schrijvers et al. 1995). After identification, the samples were rinsed with distilled water and placed inside plastic bags containing 70% alcohol for preservation. The validity of the scientific names was further confirmed consulting the World Register of Marine Species database (<http://www.marinespecies.org>, accessed on 12 June 2020), and revised names were updated.

Environmental Parameters

The following environmental parameters were randomly recorded in triplicate for five periods at 2-week intervals

(15 February–15 April 2018) in each study site: salinity (ppt), pH, humidity, dissolved oxygen (DO), current velocity, and water temperature (°C, hereafter referred as WT) at the water surface, and air temperature (°C) in the shade (hereafter referred as AT). Measurements of WT and AT were taken during the morning using a portable thermometer. DO was measured in water using a DO meter (Lutron DO-5510). pH was measured in water using a pH meter (EcoTestr pH 2, Eutech), calibrated with a standard buffer solution. Humidity (*H*) at each site was measured using a humidity meter (HTC-2, Outest), and current velocity (*C*) was measured manually using a stopwatch. Salinity in each site water was measured using a hand-refractometer (Atago Master S28 M).

Data Analyses

For each sampling site, we calculated the Shannon–Wiener diversity index (H' ; cf Krebs 1998) and the taxonomic index (Δ^+ ; cf Clarke & Warwick 1998, 2001) for both vegetation and macrozoobenthic communities. We compared differences in H' and Δ^+ between management conditions and locations through two-way Wilcoxon tests. Environmental parameters were compared between locations by means of one-way analysis of variance (ANOVA). A principal component analysis (PCA) was used to assess the main environmental parameters describing sampling locations. Two canonical correspondence analyses (CCA) were used to identify the main environmental parameters associated with the vegetation and macrozoobenthos community compositions.

Nonmetric multidimensional scaling (NMDS) tests were implemented to evaluate the differences in macrozoobenthic- and forest-community compositions between management conditions and locations and to identify key species that might potentially serve as indicators of successful restoration or ecosystem degradation. To emphasize the similarities in the composition of species' identities between samples, the NMDS tests were implemented using the Bray–Curtis dissimilarity method (Anderson & Walsh 2013; Anderson & Santana-Garcon 2015). A two-dimensional configuration was used for the vegetation community and a three-dimensional configuration for the macrozoobenthic communities, based on returned stress value. Stress values less than 2 indicate a low disagreement between the configuration and the predicted values from the regression between the configuration and the observed distances.

The NMDS analysis of the macrozoobenthic community was complemented with a cluster analysis using the Ward method, using Bray–Curtis ranked distances to group sampling sites (Clarke 1993; Anderson & Walsh 2013). Further, location community assemblages were compared in a pair-wise step-by-step process via analysis of similarity (ANOSIM).

Further, potential indicator species retrieved from the NMDS tests were corroborated with improved indicator species analysis, as described by De Cáceres et al. (2010). Since this method can be used to characterize qualitative environmental preferences regarding habitat and management conditions, we were able to detect indicator species associated with combinations of management condition and on combinations of specific

sampling locations. This was done through two permutation tests (with 9,999 permutations, each). The first was performed for single site-group, where the observed test statistic was compared to a distribution obtained by randomly reordering the data (see De Cáceres & Legendre, 2009 for details on mathematical computations). The second permutation test considered combinations of location-groups and incorporated the process of selecting location-group combinations into the distribution of the null hypothesis (see De Cáceres et al. 2010 for detailed mathematical computations). We implemented the permutations for locations (i.e. Langsa, Jaring Halus, etc.) and management condition with a group-equalized index, which assigned equal weights to all site-groups, assuming that the ecological variability of each group-site combination was proportional to the number of site-groups it contained (De Cáceres et al. 2010).

All statistical analyses were conducted using R, version 4.0.3 (R Core Team 2020). Specific used packages were: *mangroveStructure* (Araújo & Shideler 2019) to compute forest structure parameters; *vegan* (Oksanen et al. 2019) for PCA, CCA, NMDS, and ANOSIM; and *indicspecies* (De Cáceres et al. 2010) to detect site-group and site-group combinations for indicator species. To plot all figures, we used package *ggplot2* (Wickham 2016) in combination with *ggpubr* (Kassmbara 2020).

Results

Forest Structure

At the five geographic locations, forests were mixed stands where *Avicennia marina* (Gray mangrove) and *Rhizophora apiculata* (Bakau minyak) were either the dominant (e.g. *R. apiculata* at Pulau Kampai) or codominant species (e.g. *A. marina* and *R. apiculata* represent >60% of the mangrove vegetation at Jaring Halus). Total stand density ranged between 100 and 380 trees/ha, with the highest stand density obtained at a natural forest (Jaring Halus) and the lowest corresponding to the site undergoing restoration from abandoned aquaculture ponds (Percut Sei Tuan). Consistently, the tallest trees were located at the natural forest of Jaring Halus (mean stem heights >7.9 m, Table S2), while the shortest were located at Pulau Kampai (mean heights <4.9 m, Table S2).

Environmental Parameters

The ANOVA tests showed that environmental parameters did not vary significantly throughout the sampled season (February 2018–April 2018, data not shown), but there were significant differences between locations for all environmental variables (Table 1). Salinity ($F_{[4]} = 946$, $p = 0.0001$) had similar values only for Pulau Kampai ($34.6 \pm 0.11\text{‰}$, values are means \pm SE) and Pulau Sembilan ($34.3 \pm 0.15\text{‰}$), the lowest salinity was recorded at Jaring Halus (18.40 ± 0.33) and highest at Langsa ($36.90 \pm 0.28\text{‰}$). WT ($F_{[4]} = 59.15$, $p < 0.0001$) ranged from 28.14 ± 0.2 (Jaring Halus) to $31.89 \pm 0.26^\circ\text{C}$ (Langsa); DO ($F_{[4]} = 1,403$, $p < 0.0001$), pH ($p < 0.0001$, $F_{[4]} = 82.8$, $df = 4$), and current velocity ($p < 0.0001$, $F_{[4]} = 100$) had their lowest values at Percut Sei Tuan

(3.60 ± 0.08 mg/L, pH = 5.2 ± 0.08 and current velocity at 0.07 ± 0.001 m/s), and highest values at Jaring Halus (7.72 ± 0.01 mg/L of O₂), Jaring Halus and Pulau Kampai (pH = 6.8 ± 0.05), and Langsa (current velocity = 0.12 m/s). All locations differed significantly in relative humidity ($F_{[4]} = 199$, $p < 0.0001$) ranging from 84.30 ± 0.33 to $93.50 \pm 0.31\%$, with the lowest recorded at Percut Sei Tuan and the highest at Pulau Kampai (Table 1).

Macrozoobenthic and Vegetation Diversity

A total of 656 invertebrate individuals composed of 21 species were recorded. Gastropods were the most abundant invertebrates, with 17 species from 7 families representing 74% compared to 4 species of 2 crustacean families representing 26% of the collection. Species are listed in Table S3 (including their common names in different languages) along with their common habitats. Overall, a total of eight mangrove species were recorded, including two species of *Sonneratia* (Lythraceae), three *Avicennia* species, and three *Rhizophora* species (Table S4). The diversity of the macrozoobenthic and vegetation communities showed higher variation between locations than between management conditions (Table S5). Wilcoxon tests performed on both the Shannon index (H') and taxonomic diversity (Δ^+) showed no statistical differences between management conditions for the macrozoobenthic community (p -values >0.05 for all comparisons, Fig. S1A & S1B) and only significantly higher H' diversity in vegetation for planted mangroves as compared to natural stands (Fig. S1C). However, pair-wise comparisons carried out on locations showed that macrozoobenthic H' was significantly higher at Jaring Halus (natural mangrove) than at any other location ($p < 0.01$, 0.03, 0.03, and <0.01 compared to Langsa, Percut Sei Tuan, Pulau Kampai, and Pulau Sembilan, respectively; see Fig. S2A). H' was also higher at Pulau Kampai when compared to Pulau Sembilan ($p = 0.01$), but there were no statistical differences between Langsa, Percut Sei Tuan, and Pulau Kampai ($p > 0.05$ for all comparisons, Fig. S2A). In contrast, the macrozoobenthic Δ^+ was lowest for Pulau Kampai, with significant differences when compared to Langsa ($p = 0.02$) and Pulau Sembilan ($p < 0.01$, Fig. S2B). For the vegetation community, H' remained below 1.7, showing the highest values at Pulau Sembilan, with statistically significant differences when compared to Pulau Kampai ($p = 0.03$), Percut Sei Tuan ($p = 0.03$), Langsa ($p = 0.01$), and Jaring Halus ($p = 0.03$) (Fig. S2C). The vegetation's Δ^+ was higher at Pulau Sembilan only when compared to Langsa ($p < 0.01$) and Percut Sei Tuan ($p < 0.01$), while it had high variability within the locations Jaring Halus, Pulau Kampai, and Percut Sei Tuan (Fig. S2D).

Relationship Between Environmental Conditions and Macrozoobenthic Community

The PCA showed a clear separation of study sites (Fig. S3) based on environmental parameters, where principal components PC1 and PC2 explained 73.6% of the variations. Current velocity, pH, WT, and salinity (eigenvalues = 0.50, 0.47,

Table 1. Environmental variables summary. Values are means (\pm SE), and different superscript alphabetical letters denote statistical differences between locations as per two-way ANOVAs with $p < 0.05$ and post hoc multiple comparisons Tukey test (at 95% confidence intervals).

	Salinity (ppt)	pH	Water Temperature ($^{\circ}$ C)	Dissolved Oxygen (mg/L)	Current Velocity (m/s)	Humidity (%)
Jaring Halus	18.4 (0.33) ^d	6.8 (0.05) ^a	29.26 (0.26) ^c	7.72 (0.01) ^a	0.10 (0.001) ^b	87.2 (0.31) ^b
Langsa	36.90 (0.28) ^a	6.62(0.04) ^a	31.88 (0.26) ^a	4.07 (0.11) ^c	0.13 (0.002) ^a	88.4 (0.53) ^b
Percut Sei Tuan	24.8 (0.18) ^c	5.2 (0.08) ^c	28.14 (0.20) ^d	3.6 (0.08) ^d	0.07 (0.001) ^d	84.30 (0.33) ^c
Pulau Kampai	34.6 (0.11) ^b	6.8 (0.05) ^a	28.12 (0.14) ^d	6.50 (0.03) ^b	0.08 (0.002) ^c	93.5 (0.31) ^a
Pulau Sembilan	34.30 (0.15) ^b	6.04 (0.08) ^b	30.12 (0.33) ^b	6.54 (0.02) ^b	0.09 (0.002) ^b	92.4 (0.14) ^a

0.45, and 0.38, respectively) were the environmental variables with most influence on PCA1, while DO (eigenvalue = 0.65), WT (eigenvalue = -0.43), humidity (eigenvalue = 0.39), and pH (eigenvalue = 0.33) were the variables most important for PC2 (Fig. S3). A strong separation of the sampling sites of the location Percut Sei Tuan was associated to environmental parameters. Percut Sei Tuan had the lowest values of current velocity, pH, and DO. The sites found at Langsa were characterized by the highest salinity and WT values compared to Jaring Halus, Pulau Sembilan, and Pulau Kampai (Table 1; Fig. S3).

The CCAs associated the vegetation and macrozoobenthos community compositions with environmental parameters and management conditions (Fig. S4). The CCA model for the vegetation community (Fig. S4A) explained 43% of the variation ($r^2 = 0.43$), with 24% of the variability explained by CCA1 and 8% by CCA2. The main environmental variables associated with the vegetation community were DO (eigenvalue = 0.63) and pH (eigenvalue = 0.42) for CCA1, and humidity (eigenvalue = -0.48), salinity (eigenvalue = -0.45), and pH (eigenvalue = 0.42) for CCA2. The mangrove species from the genus *Avicennia* were most abundant at sites with higher salinity and lower oxygen concentrations (Fig. S4A), whereas *Rhizophora* spp. were associated with sites that had lower salinity, high oxygen concentrations, and higher pH values (Fig. S4A). Different management conditions were characterized by environmental conditions and species abundances of mangrove species. Natural mangrove sites grouped with higher DO and pH, where the *R. stylosa* (Spotted mangrove), the Tall-stilted mangrove (*R. apiculata*), and *S. alba* (Apple mangrove) had higher abundances. Overall, *Avicennia alba* (Api api putih) was more abundant in mangrove plantations sites characterized by low pH, DO, and higher salinity. While no clear environmental parameters could be associated to regenerated mangroves, they had overall higher abundances of *A. lanata* (Sia sia) and *S. alba* (Fig. S4).

For the macrozoobenthos community, the first two CCAs of the model explained 37.1% of the variance: 25.1% by CCA1 and 12% by CCA2 ($r^2 = 0.69$). The environmental parameters that mainly defined CCA1 were WT (eigenvalue = 0.77), current velocity (eigenvalue = 0.72), and salinity (eigenvalue = 0.31), while humidity (eigenvalue = 0.47), vegetation's Shannon diversity (eigenvalue = 0.42), and current velocity (eigenvalue = -0.38) had the highest weights in CCA2. Higher aggregation of sampling sites as a function of the location was observed for the macrozoobenthic community than for the vegetation (Fig. S4) and a more distinctive community assemblages at Pulau Sembilan was related

to a higher salinity H' , salinity, and atmospheric humidity while that of Langsa was related to WT and current velocity. The species *Nerita balteata* (Lined nerite) and *N. planospira* (Flatspired nerite) were more abundant in sites with higher current velocity and WT, opposite to *Volegalea cochlidium* (Spiral melongena) and *Achatina fulica* (Giant African snail), which were most abundant at planted and regenerated sites at Pulau Kampai and Percut Sei Tuan (i.e. at restoration sites from aquaculture ponds, see Fig. S4B). Whereas *Murex tribulus* (Caltrop murex), *Telescopium telescopium* (Mud whelk), and *Pirenella cingulata* had higher abundances at sites with lower salinity and atmospheric humidity (Fig. S4B).

Site-Grouping in Relation to Community Assemblage

The NMDS stress value, using a two-dimensional configuration for the vegetation community (stress value = 0.14), can adequately identify dissimilarities between the community assemblages. Two vegetation community associations were recognized, with a considerable overlap of the groups defined by site management condition. Figure S5A shows a closer association in community assemblage between natural and regenerated forests. The species *A. alba* was the major contributor to NMDS1 and defined the grouping of vegetation communities at Percut Sei Tuan (score = 0.93, $r^2 = 0.60$, $p < 0.01$), followed by *R. stylosa* (score = -0.90, $r^2 = 0.67$, $p = 0.01$) and *R. apiculata* (score = -0.83, $r^2 = 0.56$, $p < 0.01$). NMDS2 was mainly weighted by *A. marina* (score = -0.85, $r^2 = 0.79$, $p = 0.01$) and *S. alba* (score = -0.98, $r^2 = 0.42$, $p < 0.001$).

The NDMS analyses better represented the macrozoobenthic community in a three-dimensional arrangement, with a stress value = 0.13 (Fig. 2A & 2B). The first axis (NMDS1) was mainly explained by the abundance of the arboreal snail *A. fulica* (score = 0.97, $r^2 = 0.73$, $p = 0.001$) and epifaunal and infaunal macrozoobenthos *V. cochlidium* (score = 0.96, $r^2 = 0.001$), *Turkeyana hirtipes* (Blue land crab, score = -0.83, $r^2 = 0.38$, $p < 0.02$), and *Cardisoma carnifex* (Brown crab, score = -0.81, $r^2 = 0.48$, $p < 0.01$). The arboreal snails *N. planospira* and *N. balteata* had a balanced weight between NDMS1 (score = -0.86, $r^2 = 0.51$, $p < 0.001$ and score = -0.66, $r^2 = 0.77$, $p = 0.01$ for *N. planospira* and *N. balteata*, respectively) and NDMS2 (Fig. 2A, score = -0.86, $r^2 = 0.54$, $p < 0.001$ and score = -0.66, $r^2 = 0.63$, $p = 0.01$ for *N. planospira* and *N. balteata*, respectively), while the highest weights on NDMS2 were mainly associated to the snail *T. telescopium* (score = 0.96, $r^2 = 0.58$, $p = 0.001$) and *Thalamita crenata* crab (Crenate swimming crab, score = 0.80, $r^2 = 0.38$,

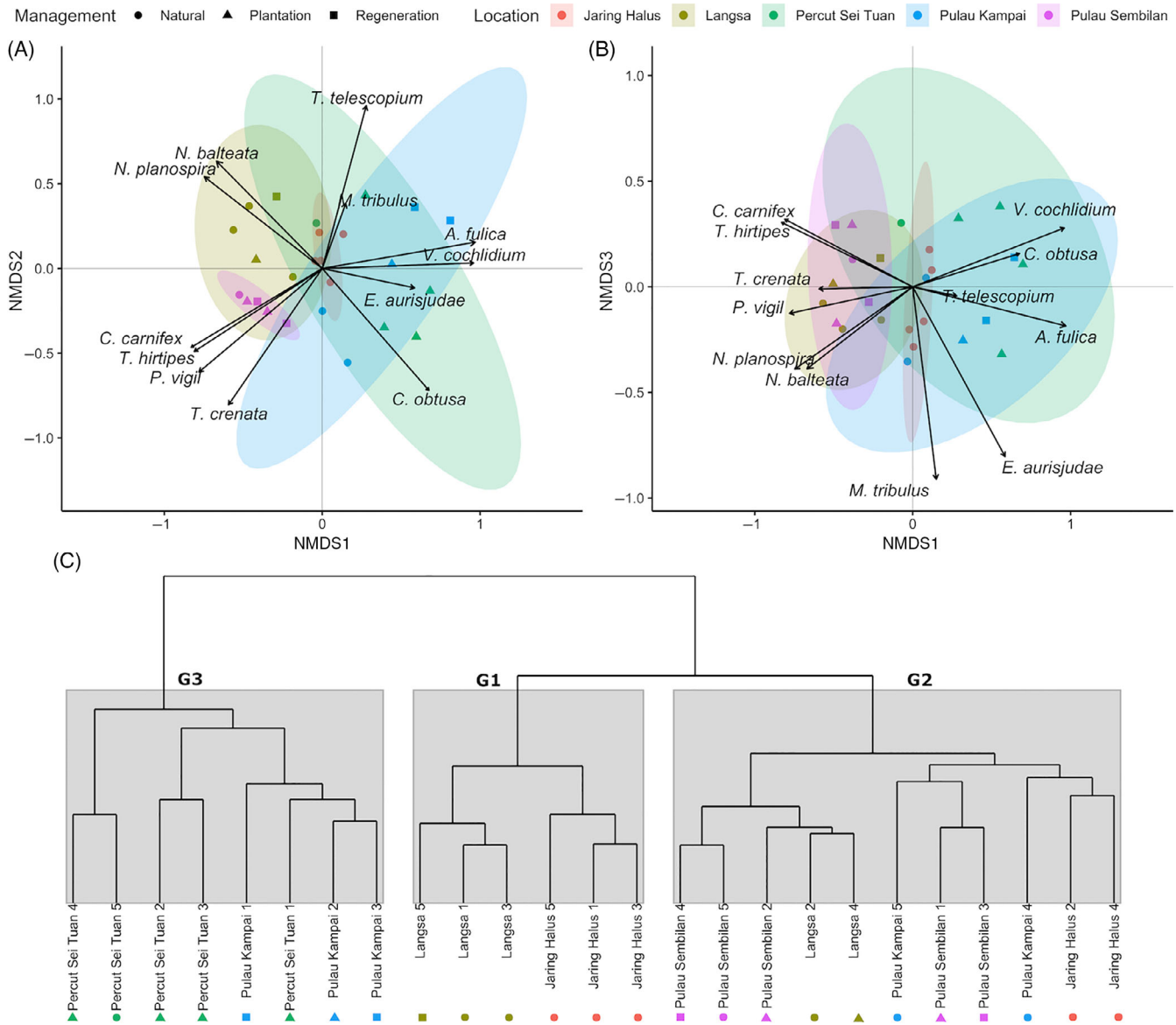


Figure 2. Nonmetric multidimensional scaling of the macrozoobenthic community optimally represents the community in three dimensions. (A) Presents NMDS1 and NMDS2 and (B) NMDS1 against NMDS3. Shapes represent the forest management condition: Circles = natural stands, triangles = planted mangroves, and square = natural regeneration of mangroves. Colors are associated with locations; shaded ellipses delimit 95% confidence intervals. Arrows denote the contribution of species to community dissimilarity; the size of the arrow is scaled to the r^2 calculated for each species. (C) Cluster analysis of locations based on the dissimilarity of the macrozoobenthic community composition with shaded rectangles delimit three groups of sampling sites sharing higher similarities in their macrozoobenthic community assemblage, group G1 composed almost entirely by natural mangroves stands, and group G3 represented predominantly by planted mangroves, whereas G2 aggregates mostly natural and regenerated mangroves.

$p < 0.02$). NMDS3 was mainly represented by epifaunal snails *M. tribulus* (score = -0.91 , $r^2 = 0.63$, $p = 0.001$) and *Ellobium aurisjudae* (Judas ear cassidula, score = -0.80 , $r^2 = 0.59$, $p < 0.001$, Fig. 2B).

The macrozoobenthic community was strongly associated to location. Those locations dominated by natural mangroves (Jaring Halus, Langsa) and Pulau Sembilan (Fig. 2A & 2B) showed shorter distances between sites from the same location and narrower confidence interval ellipses (Fig. S5B). However, the cluster analysis revealed three main groups based on the

similarity of their community assemblages where groups were dominated by management conditions (Fig. 2C). The first group (G1 in Fig. 2C) was mainly represented by natural mangroves from Jaring Halus and Langsa, the second group (G2 in Fig. 2C) was dominated by natural stands and contains all Pulau Sembilan sites, whereas G3 was dominated by sites with plantations and regeneration from Percut Sei Tuan and Pulau Kampai.

The ANOSIM pair-wise community assemblage showed that natural stands differed significantly from mangrove plantations ($r = 0.26$, significance = 0.03), and significant but weak

Table 2. Identified indicator species for different mangrove management conditions. The coefficient of determination indicates the probability of the association between the species and management condition found for this study, while references point to other studies that have also identified the species as indicators.

Species	Component	Indicator of	Coefficient of Determination	Study
Gastropod				
<i>Nerita balteata</i>	Arboreal	Mature planted mangroves	$r^2 = 0.86, p < 0.001$	Salmo et al. (2017)
		Jaring Halus Langsa (natural)		This study
		Natural mangroves		This study
<i>Telescopium telescopium</i>	Epifauna	Jaring Halus and Pulau Kampai	$r^2 = 0.77, p = 0.047$	This study
		Jaring Halus and Pulau Kampai	$r^2 = 0.78, p = 0.046$	This study
<i>Ellobium aurisjudae</i>	Epifauna	Jaring Halus and Pulau Kampai	$r^2 = 0.78, p = 0.046$	This study
<i>Acahina fulica</i>	Arboreal	Disturbance	$r^2 = 0.83, p = 0.01$	Nurinsiyah and Hausdorf (2019)
		Jaring Halus and Pulau Kampai		This study
<i>Volegalea cochliidiom</i>		Percut Sei Tuan and Pulau Kamapi	$r^2 = 0.89, p = 0.01$	This study
Decapod				
<i>Cardisoma carnifex</i>	Epifauna, infauna	Jaring Halus and Pulau Sembilan	$r^2 = 0.91, p = 0.001$	This study
<i>Podophthalmus vigil</i>	Epifauna and infauna	Jaring Halus and Pulau Sembilan	$r^2 = 0.87, p < 0.001$	This study

differences when compared to regeneration stands ($r = 0.26$, significance = 0.05, Table S6), whereas community assemblages in plantations did not vary significantly from

regeneration sites (significance = 0.60). When comparing communities by management and location, different locations did not differ significantly for plantation and regeneration

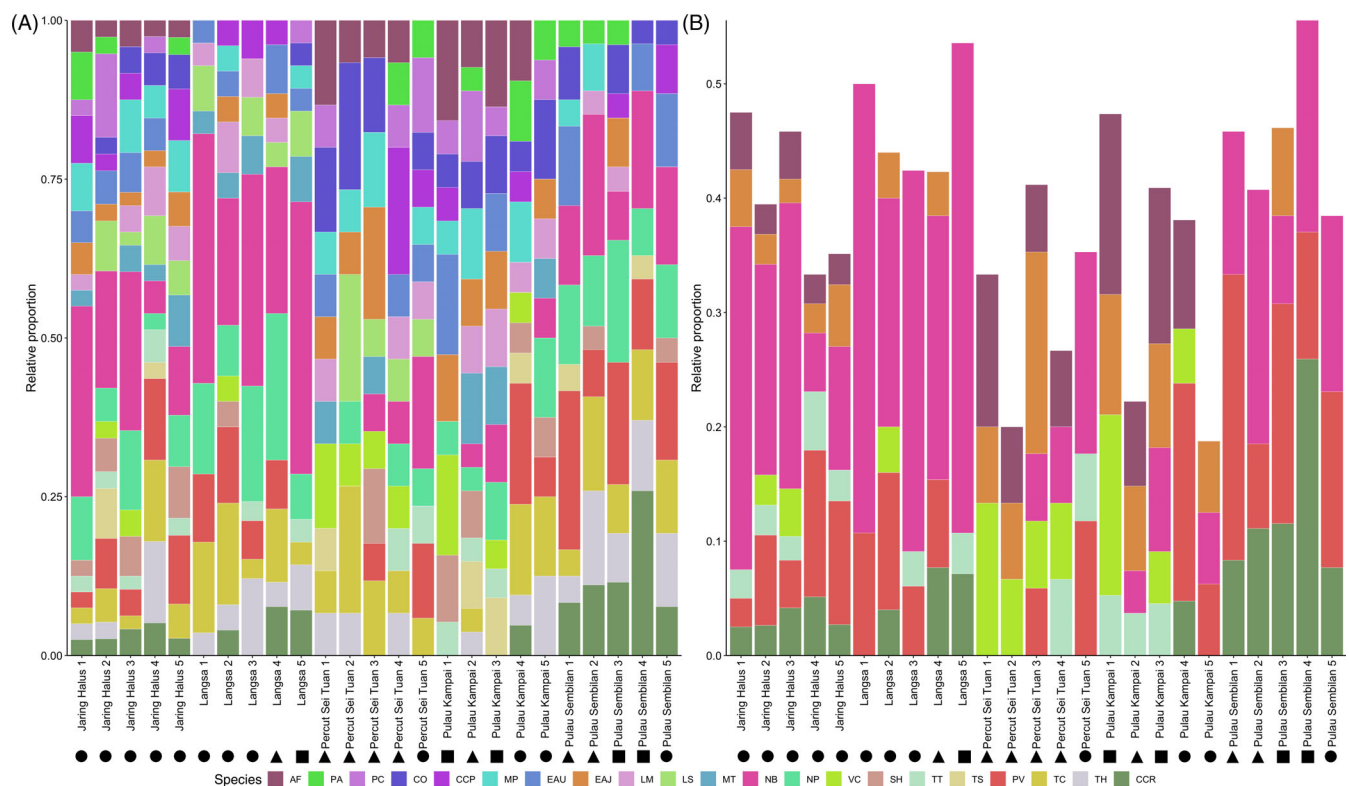


Figure 3. Relative abundances of all species found at each study location (A), and relative abundances of indicator species only (B), separated by location. Symbols denote management condition (circles represent natural forests, squares are naturally regenerated mangroves, and triangles represent mangrove plantations). Species keys are: AF = *Acahina fulica*, PA = *Pirinella alata*, PC = *P. cingulata*, CO = *Cerithidea obtusa*, CCP = *Chicoreus capucinus*, MP = *Monoplex pilearis*, EAU = *Ellobium aurismidae*, EAJ = *E. aurisjudae*, LM = *Littoraria melanostoma*, LS = *L. scabra*, MT = *Murex tribulus*, NB = *Nerita balteata*, NP = *N. planospira*, VC = *Volegalea cochliidiom*, SH = *Stramonita haemastoma*, TT = *Telescopium telescopium*, TS = *Terebralia sulcata*, PV = *Podophthalmus vigil*, TC = *Thalamita crenata*, TH = *Turkeyana hirtipes*, and CCR = *Cardisoma carnifex*.

managements (see Table S6). Although Jaring Halus and Langsa had different environmental parameters, their macrozoobenthic community assemblages did not differ significantly (Table S6). Both locations, however, had weak significant differences when compared to the natural mangrove sites of Pulau Kampai (significance = 0.05 for both comparisons, Table S6).

Macrozoobenthic Indicator Species

The gastropod *N. balteata* was the only species clearly associated with natural mangroves (stat = 0.53, $p = 0.04$), where it was most abundant. This gastropod was also a good indicator species for the natural mangroves of Jaring Halus and Langsa (stat = 0.87, $p < 0.0001$, Table 2). No indicator species were identified exclusively for either plantation or regeneration sites. However, indicator species were identified for combinations of locations (Table 2). Locations Jaring Halus and Pulau Kampai were characterized by high abundances of the gastropods *T. telescopium* (stat = 0.88, $p < 0.01$) and *A. fulica* (stat = 0.88, $p < 0.01$), whereas decapods *C. carnifex* and *P. vigil* were well represented at Jaring Halus and Pulau Sembilan (stat = 0.91, $p < 0.0001$ and stat = 87, $p < 0.001$, respectively) and the decapod *V. cochlidium* was associated to Percut Sei Tuan and Pulau Kampai (stat = 0.81, $p = 0.02$). The differences in the macrozoobenthos community assemblage can be seen in Figure 3A, with notably high relative abundances of *N. balteata* in natural mangroves and more distinctive community assemblages for Pulau Kampai, and Percut Sei Tuan (Fig. 3A). This is more evident when looking only at the relative abundances of the identified indicator species (Fig. 3B), which account for between 40 and 60% of the total community abundances at Jaring Halus, Langsa, and Pulau Sembilan but represent less than 40% of the community composition in Percut Sei Tuan and Pulau Kampai.

Discussion

The first world record of mangrove restoration efforts dates back to the 1950s in China (Ellison 2000). Despite 70 years of local and regional investments on mangrove ecosystem recovery across tropical coastlines, current success rates of around 20% prove dramatically low (Ellison 2000; Kodikara et al. 2017; Ellison et al. 2020). Although there is now a wide recognition of the importance of local hydrology and plant community biology for restoration programs (Ellison 2000; Bosire et al. 2008; Balke et al. 2013; Ellison et al. 2020), other identified elements contributing to low functional restoration success are: (1) the lack of community involvement and (2) a failure to monitor, report, and transfer the acquired knowledge (Kodikara et al. 2017). The local guardians with substantial knowledge of the mangrove system can support effective monitoring. However, involvement of local communities requires to identify indicators that are easy to monitor and relate to restoration practices.

In this study, we showed that the macrozoobenthic community assemblage, rather than diversity indices, can serve as an indicator of functional mangrove restoration success, when compared to local reference conditions. The community assemblages found at natural sites had higher similarities with

regeneration sites than with planted mangroves. However, the community was also closely linked to the study locations, which could be partly associated to site-specific environmental attributes (i.e. sediment composition, salinity, pH, temperature, etc.) that influence both the vegetation and the macrozoobenthic community assemblage (Bae et al. 2018). For instance, in this study, the vegetation community was associated to site salinity, pH, and tidal current velocities. There were, however, potential confounding effects (i.e. seasonal variations and changes in management condition that were not monitored during this study) that impede us from accurately assessing the environmental factors that are modulating the restoration trajectories (Nuttle et al. 2017). The genus *Avicennia*, for example, has a wide range of salinity tolerance, up to hypersaline conditions (Vovides et al. 2011). *Avicennia marina* and *A. alba* accounted for 60% of the relative dominance at Percut Sei Tuan, although the abandoned aquaculture ponds at this location were planted using *Rhizophora apiculata*, *R. mucronata*, and *R. stylosa*. The low salinities measured at this site were inconsistent with the salinity tolerance of the genus and may not reflect peak salinities outside the monitoring period. Furthermore, the abundance of *Avicennia* spp. could also be associated to its pioneer nature, suggesting early successional stages are naturally occurring at Percut Sei Tuan (Balke et al. 2011, 2013).

Environmental conditions at mangrove restoration sites can rapidly change, as evidenced by Pulau Sembilan, which was first managed through planting between 2008 and 2012, but then additionally underwent hydrological connectivity restoration. This mainly concerned Pulau Sembilan sites 1 and 2 (connecting to Teluk Ara Bay) and areas northeast of Site Pulau Sembilan 4, connecting with a major tidal channel that further reaches the Teluk Ara Bay. Hydrological connectivity allows greater water exchange within all restoration sites (Zaldívar-Jiménez et al. 2010; Pérez-Ceballos et al. 2017; Echeverría-Ávila et al. 2019); however, the lack of high-frequency monitoring after channels was opened, reduced the ability to link habitat to hydrological changes. Generally, in contrast to Percut Sei Tuan, Pulau Sembilan had significantly higher DO and pH, suggesting the plantation sites of Percut Sei Tuan and Pulau Kampai remained hydrologically impaired. Percut Sei Tuan had the longest restoration effort history within this study (starting in 2007, Yagasu, personal communication, 2018), but had less than half the stand density recorded for Pulau Sembilan (100 and 230 trees/ha for Percut Sei Tuan and Pulau Sembilan, respectively). Despite the limitations of this study, low pH and DO at Percut Sei Tuan are probable evidence of hydrologically impaired conditions (Vovides et al. 2011; Echeverría-Ávila et al. 2019). These environmental attributes, alongside with the early pioneer vegetation recorded at Percut Sei Tuan, point to low restoration success due to a continued hydrological impairment.

The community assemblage dissimilarities found between management conditions evidence the advantages of implementing ecological restoration strategies (i.e. hydrological restoration) that can facilitate or accelerate natural regeneration. For instance, the communities in planted mangroves deviated significantly from natural forests. However, allowing natural regeneration to occur without any intervention could result in prolonged

functional recovery times or not occur at all, depending on the nature, intensity, and duration of the disturbance (Ellison et al. 2020). Here, both vegetation and macrozoobenthos community assemblages formed three distinct groups associated to management. The vegetation NMDS showed high dissimilarities between natural and planted mangroves, where the differences in vegetation and environmental attributes might in turn influence the macrozoobenthic community assemblage, as was found to occur in riparian streams (Nuttle et al. 2017). Based on the macrozoobenthos community dissimilarities, three distinct groups were identified. Group G1 was characterized mainly by natural mangrove stands of Langsa and Jaring Halus, G2 by natural and regeneration sites, and G3 by sites with planted mangroves.

The observed grouping pattern, along with the indicator species found in our study, is consistent with studies describing arboreal invertebrates dominating the macrozoobenthos of natural and mature planted mangroves (Macintosh et al. 2002; Salmo et al. 2017, 2019), whereas epifaunal gastropods are most abundant in intermediate age plantations (Salmo et al. 2017). In the natural mangroves of Jaring Halus and Langsa, the arboreal mollusk *Nerita balteata* had the highest abundances, and its lowest or absence at the planted mangroves of Percut Sei Tuan and Pulau Kampai. *N. balteata* has been particularly associated with *Rhizophora* spp. trees (Jahid & Singh 2018), which could explain the higher relative abundance of this species in Langsa natural stands and at restored Pulau Sembilan, where the *Rhizophora* genus dominates the vegetation composition.

Consistent with the findings of Salmo et al. (2017), in this study, macrozoobenthos epifauna and species composition were closely associated to substrate environmental characteristics. The indicator species identified in this study characteristic for planted mangroves had epifaunal or infauna habits (linked to young plantations on Salmo et al. 2017), whereas arboreal gastropods were characteristic of natural mangroves (associated to mature mangrove plantations by Salmo et al. 2017). Infauna and epifauna organisms were also associated to local environmental attributes, for example, the decapods with *Cardisoma carnifex* and *Podophthalmus vigil* were more abundant at locations with higher DO, whereas other invertebrates with arboreal habits such as Neritids (Neritidae) were less important in characterizing communities relative to sediment environmental attributes, but were strongly associated to natural and regenerated mangroves.

Although it remains uncertain which environmental elements most contribute to the association between mangrove stages (i.e. maturity or restoration progress) and the relative abundances of infauna, epifaunal, and arboreal macrozoobenthos, it is possible that arboreal gastropods find better feeding grounds and refuge from predators in mature and natural mangroves. Whereas epifaunal mollusks benefit from softer sediments in mangrove swamps that have a lower vegetation density, and thus lower compaction due to root biomass (Salmo et al. 2017). Additionally, epifaunal invertebrates could also be more sensitive to water chemistry, for instance, *Telescopium telescopium* had its lowest abundance or was absent from sites with high salinity and WT_s, while the terrestrial crab *C. carnifex* had higher relative abundances at locations with higher DO.

The grapsid *C. carnifex* was associated to location rather than management condition, with its highest abundance at Jaring Halus (natural mangrove) and Pulau Sembilan (mostly sites restored through plantations and regeneration). Grapsids have been previously associated to mature mangroves (Lee 1998; Macintosh et al. 2002). Interestingly, *C. carnifex* has a complex life cycle, tightly linked to mangrove trees at higher elevations, close to which they dig their borrows. The adults are equipped with lungs that allow them to breathe in dry terrestrial areas of the forest. Young crabs, however, are born with branchias and depend on the moist sheltered borrows of their adult conspecifics, where they remain hidden until their adulthood, when their aerial respiratory system becomes sufficiently developed (Vannini et al. 2003). The presence of *C. carnifex* in natural and regenerated mangroves could be associated to higher vegetation H' and DO concentrations. Whereas its absence from planted locations (particularly from Percut Sei Tuan and Pulau Kampai) is most likely due to low pH and oxygen concentrations related to an impaired hydrology in the case of Percut Sei Tuan (Vovides et al. 2011; Pérez-Ceballos et al. 2017). In Pulau Kampai, the absence of *C. carnifex* could probably be associated to longer and more frequent inundations, which would be less suitable for *C. carnifex* adults to reproduce. In contrast, *V. cochlidium*, a decapod best adapted for swimming, had its highest abundances in plantation sites on aquaculture ponds with low vegetation cover and likely higher inundation durations (i.e. Percut Sei Tuan).

In contrast, the presence of the Giant African Snail (*Acauthina fulica*), an invasive species considered an indicator of anthropogenic disturbance (Nurinsiyah & Hausdorf 2019), in the natural forest of Jaring Halus, additionally suggests some anthropogenic disturbance is taking place in this location that was not accounted for within this study. Although our analyses do not highlight *A. fulica* as an indicator species, this could be related to the fact that *A. fulica* is present in all mangrove management conditions described for this study (natural, planted, and regeneration sites). The abundance of *A. fulica* at Percut Sei Tuan and Pulau Kampai is consistent with the fact that oil palm plantations, aquaculture ponds, and human establishments border these locations. For example, Jaring Halus, although considered a natural mangrove, neighbors a densely populated fishing community, while Percut Sei Tuan is surrounded by oil palm plantations, aquaculture ponds and is located close to Belawan harbor (the busiest harbor outside Java in Indonesia) and Medan (North Sumatra's capital city). Although the ecological consequences of *A. fulica*'s presence in mangrove ecosystems remain unknown, it has been suggested that this species represents more a threat for plant species of agricultural importance than it does to natural forests (Nurinsiyah & Hausdorf 2019). Still, studies are needed to better understand the implications of the giant African snail for mangrove ecosystem integrity.

Overall, this study showed that the community assemblage has the potential to be an indicator for mangrove functional restoration success. It showed that natural mangrove regeneration favors the recovery of "natural" macrozoobenthic functional groups over plantations. Consistent with findings by Salmo et al. (2017), especially arboreal invertebrates can be indicators

of successful functional restoration. Facilitating natural mangrove regeneration through ecological and hydrological restoration may take longer than direct planting, but will create the suitable flooding regimes and “natural” species assemblages needed to facilitate functional recovery of the macrozoobenthic communities. A key to better understand functional restoration trajectories lays in documenting the macrozoobenthic community under different mangrove conditions (including bare mudflats) and throughout the restoration programs. Further, combining nature-based solution (i.e. elevation or hydrological restoration) with planting or dispersal of local pioneer species could help accelerate natural functional recovery of ecosystems.

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Multiple comparisons between mangrove management types.

Figure S2. Multiple comparisons via Wilcoxon test for macrozoobenthic (A–B) and Vegetation (C–D) communities.

Figure S3. A current principal component analysis shows sites group by location (73.6% of deviance explained by the first two components).

Figure S4. CCA analyses of biotic communities.

Figure S5. Non-metric multidimensional scaling of vegetation (A) and macrozoobenthic communities (B) grouped by forest management condition.

Table S1. Site description summary based on Google Earth time-line images and ground check on the field.

Table S2. Forest structure attributes at the five study locations.

Table S3. List of macrozoobenthos species found in this study, their habitat and common names.

Table S4. Mangrove species found in this study, scientific and common names.

Table S5. Location diversity attributes for the forest and macrozoobenthos communities.

Table S6. Pair-wise comparison of the macrozoobenthos communities via ANOSIM (analysis of similarity) between management types and study locations.

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