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Habitat and water quality variables as predictors of community composition in an Indonesian coral reef: a multi-taxon study in the Spermonde Archipelago

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HIGHLIGHTS

- Taxa sampled: corals, sponges, foraminifera, bacteria, archaea
- Goal: relate variation in composition to habitat and water quality variables
- There were marked differences among taxa in the explanatory variables selected.
- Habitat variables generally explained more variation in composition.
- CDOM, Chlor-a and Rrs_645 were the most important satellite-derived variables.

GRAPHICAL ABSTRACT

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ABSTRACT

Assemblages of corals, sponges, foraminifera, sediment bacteria and sediment archaea were assessed at two depths in the Spermonde Archipelago. Our goal was to assess to what extent variation in composition could be explained by habitat and water quality variables. The habitat variables consisted of depth, substrate type and scleractinian coral cover while water quality variables were derived from ocean color satellite imagery, including the colored dissolved organic matter index (CDOM), chlorophyll-a (Chlor-a) and remote sensing reflectance at 645 nm (Rrs_645). Together, habitat and water quality variables explained from 31% (sediment bacteria) to 80% (forams) of the variation in composition. The variation in composition of corals, sponges, forams and sediment archaea was primarily related to habitat variables, while the variation in composition of sediment bacteria was primarily related to water quality variables. Habitat and water quality variables explained similar amounts of variation in the composition of corals and sediment bacteria. CDOM (sponges, sediment bacteria and sediment archaea), Chlor-a (corals and forams) and Rrs_645 (sponges and forams) proved significant predictors of

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variation in composition for the studied taxa. In addition to water quality variables, all taxa responded to a range of habitat variables including depth and the percentage cover of various benthic life forms including coral cover variables, rubble and sand. Sand cover was the most important habitat variable for corals, sponges, sediment bacteria and sediment archaea. Coral life forms including the cover of branching and tabular corals were important habitat variables for sponges and forams. These results show marked differences in how various taxa respond to variation in habitat and water quality in the Spermonde Archipelago. Moreover, our results indicate that variables estimated from ocean color satellite imagery proved to be better predictors of variation in marine community composition than commonly-used proxies such as the distance offshore or distance to the nearest river.

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1. Introduction

Coral reefs are among the most diverse and economically important marine ecosystems in the world (Hughes et al., 2010). They provide coastal protection, food, building materials and areas of recreation (Costanza et al., 2014; Burke et al., 2002). Additionally, they also function as marine hatcheries and refugia for a wide variety of marine organisms, many of which are commercially important (e.g., fish, shrimp, crabs, clams; Burke et al., 2002; Buddemeier et al., 2004; Mora et al., 2011; Hoeksema et al., 2012). Coral reefs are often located in areas of ongoing coastal development and subject to relatively high population growth rates (Bryant et al., 1998). This combination of factors threatens their existence and, as a result, the services they provide. Indeed, a majority of coral reefs are now considered vulnerable or have been seriously degraded (Burke et al., 2011). The latter includes the loss of reef structure, species, and shifts in community composition (Bellwood et al., 2004). For example, many fish species depend on the three dimensional structure provided by mature coral reefs (Pratchett et al., 2008). Losses of key structural components, such as branching *Acropora* species, can lead to the local extirpation of numerous dependent species (Pratchett et al., 2008). Some studies have shown that biodiversity loss can, in turn, adversely affect ecosystem functioning (Worm et al., 2006) while others have shown that, even the functional diversity of coral reefs with high species diversity is vulnerable to the loss of species (Mouillot et al., 2014). Hence, it is important to understand how individual taxa respond to changes in reef environmental conditions.

Pronounced on-to-offshore environmental gradients, including gradients in salinity, depth, nutrients, sedimentation and pollution (Fox and Bellwood, 2007; Cleary et al., 2005, 2008) determine community structure throughout the reef ecosystem. In addition to the above, community structure of coral reefs is also determined by storm damage, thermal stress, and overexploitation of grazers and predators, to mention just a few (Szmant, 2002). All of these stressors have distinct spatial components (Goatley and Bellwood, 2013).

Following the widespread ecological changes to Caribbean reefs and the realization that benthic community structure is to a great extent determined by the interplay between corals, algae, and herbivorous fishes, more scientific attention has been paid to these groups (e.g., Bellwood et al., 2004; Hughes et al., 2010; Berumen and Pratchett, 2006). The conservation of coral reefs also tends to rely on indicators from these taxa. Yet, there has been far less focus on other groups inhabiting the same reefs.

Bacteria and archaea, for instance, are abundant members of the vast marine microbial community and are important players in processes such as the geochemical cycling of carbon, nitrogen and sulfur, transformation and degradation of nutrients and organic matter derived from both surface ocean production and terrestrial runoff (Webster et al., 2004). For oligotrophic coral reefs, this cycling activity is of crucial importance in order to degrade organic matter and maintain high levels of primary production (Schöttner et al., 2011). According to Sneed et al. (2014) biofilm bacteria also play an important role in inducing the larval settlement of some corals. Coral reef carbonate sands due to their complex surface structure and highly porous matrix present a high abundance of prokaryotes (Wild et al., 2006). Coral reef sponges, in turn, have also been shown to harbor exceptional microbial densities, which can make up from 35 to 40% of sponge biomass (Hentschel et al., 2002, 2012).

In the present study, in addition to sponges and foraminifera studied in previous studies (Cleary et al., 2005; Becking et al., 2006; de Voogd et al., 2006) in the same study area (Spermonde Archipelago; Indonesia), we assessed the composition of bacterial and archaeal communities in sediment and sponges (of critical importance to the biogeochemical nutrient cycles in coral reef ecosystems) and the composition of scleractinian corals (important for maintaining the three-dimensional structure of coral reefs systems). These taxa were selected based on their ecological importance, distinct life-history strategies and on the taxonomic expertise of the research team.

The previous studies conducted in the Spermonde Archipelago (Cleary et al., 2005; Becking et al., 2006; de Voogd et al., 2006) related variation in composition of sea urchins, sponges, mushroom corals and larger foraminifera to offshore distance, depth, exposure, degree of human settlement, distance between sites and substrate type (remotely sensed). In summary, they showed that variation in community similarity of the studied taxa was primarily explained by environmental components with the exception of the sea urchins, for which the spatial component had a greater influence. Additionally, depth was the most important parameter for sponges, corals and foraminifera and human settlement was significantly associated with sponges and foraminifera community composition.

In the present study, our main goal was to investigate how beta diversity (change in species composition of assemblages between sites; Purvis and Hector, 2000) in the Spermonde coral reef system is related to habitat and water quality variables. Important environmental parameters such as coral reef habitat structure and remotely sensed data were used in this study to explain spatial variation in the composition of all taxa sampled. The remotely sensed data focused on four of the most important threats to coastal coral reefs: eutrophication (high nutrients; chlorophyll-a concentrations), bleaching (high-temperatures; sea surface temperature), sedimentation (high-sediments; remote sensing reflectance at 645 nm) and runoff (high-humic and fulvic substances; colored dissolved organic matter index). We compared to what degree habitat and water quality variables were able to explain variation in the composition of different taxa.

2. Material and methods

2.1. Study site

The Spermonde Archipelago (Fig. 1) is situated adjacent to the city of Makassar, capital of the Indonesian province of South Sulawesi and home to more than two million inhabitants (Renema, 2010). This archipelago consists of 160 cay-crowned reefs dispersed over a 40 km wide continental shelf (Moll, 1983; Renema and Troelstra, 2001; Cleary et al., 2005). It lies on a carbonate shelf, which increases in depth with distance from the coast, except for the outer rim consisting of a barrier reef (Renema and Troelstra, 2001; de Voogd et al., 2006; Hoeksema, 2012a). The westernmost islands lie on this rim beyond which the sea floor abruptly drops down to depths exceeding 800 m in the Makassar Strait (Moll, 1983). Its proximity to Makassar leaves these coral reefs exposed to many anthropogenic disturbances including river discharge

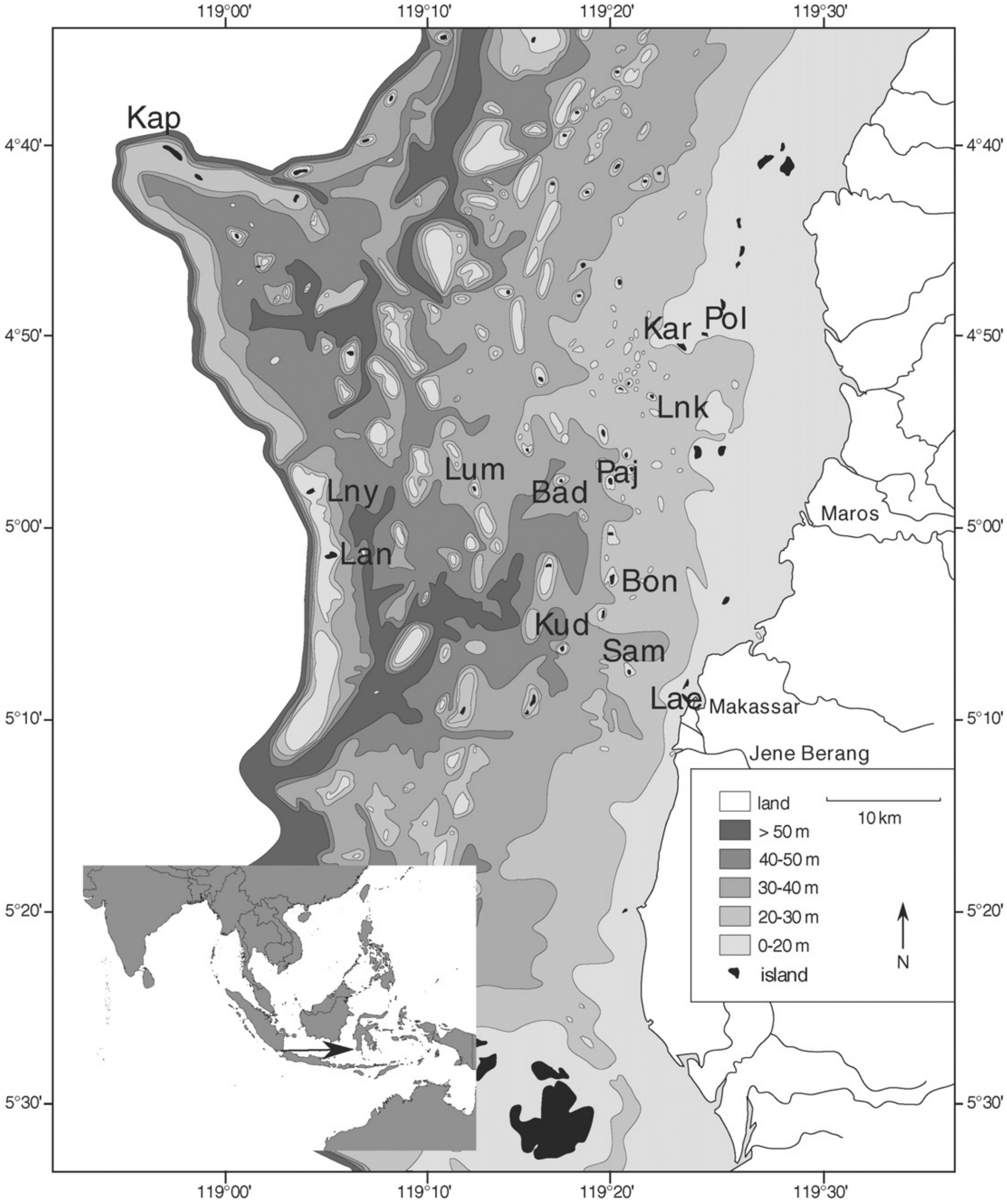

Fig. 1. Map of the study area (Spermonde Archipelago, Indonesia) showing the sampling sites.

(sedimentation, agricultural runoff, eutrophication), oil spills, destructive fisheries, tourism and coral mining (Hoeksema, 2004; de Voogd and Cleary, 2007).

Previous studies (Cleary et al., 2005; Becking et al., 2006; Cleary and Renema, 2007; Hoeksema, 2012a; Sawall et al., 2012) showed that the Spermonde is subject to strong on-to-offshore gradients in both biotic and abiotic factors (e.g., salinity, depth, oceanic currents, nutrification, pollution). Inshore reefs are also subject to more anthropogenic perturbations, e.g., river discharge, related to their proximity to the coast. The influence of these disturbances over the Spermonde Archipelago depends on factors such as distance from the coastline, shelf depth, and season. During the wet season (Northwest Monsoon from December to May), river discharge is stronger due to increased rainfall and the resultant plume of turbid water can reach a greater distance offshore. During the dry season (Southeast Monsoon in June–November) the easterlies are weakened by the high mountains of Sulawesi, thus strongly reducing their impact and reducing cross-shelf mixing when compared to the Northwest monsoon (de Klerk, 1983).

2.2. Data collection

Research for the present study was carried out from the 8th to the 25th of August, 2010. A total of fourteen sites were surveyed using SCUBA (Fig. 1). We sampled the northwest side of the reefs Lae Lae (Lae), Samalona (Sam), Kudingkareng Keke (Kud), Lumulumu (Lum), Bone Lola (Bon), Lankadea (Lnk), Pajenekang (Paj), Polewali (Pol), Karanrang (Kar) and Kapoposang (Kap) reefs, the west side of Langkai (Lan) and Lanyukan (Lny) reefs and the southwest side of Badi (Bad) reef. These reefs were chosen because they are distributed along an on-to-offshore gradient and are thus subjected to different environmental influences.

2.3. Corals

Scleractinian coral genera were visually identified during line-intercept transect surveys (English et al., 1997). Photos of unrecognized genera were taken for closer examination using Veron (2000). The line-intercept transect data was analyzed in order to calculate the percent cover of each coral genera and life form surveyed. In each site, we surveyed one transect (30 m long) at each of the two studied depths: at the top of the reef slope (3 m) and at the maximum depth of dense coral cover (12 m, with exception of the reefs Karanrang (11 m), Lae Lae (9 m) and Polewali (10 m) which did not reach deeper; for the sake of simplicity 12 m depth will be used throughout the text when referring to the deeper transects). In total, 25 transects were surveyed to characterize the Spermonde reef system.

2.4. Sponges

Sponge species and their abundance were recorded using 1 m^2 quadrats laid at each consecutive 1 m section along the 30 m transect line used for coral cover assessment. Smaller (cryptic, boring and thinly encrusting <4 cm) specimens were excluded from this study. Species were visually identified in the field, and fragments of unrecognized species were collected for closer examination. Voucher specimens have been preserved in 70% ethanol and housed in the sponge collection Naturalis Biodiversity Center.

2.5. Foraminifera

Foraminifera were collected every 3 m of depth in a transect starting at the reef base to the reef crest. However, for the purposes of this study, only samples at 3 ± 1 m and 12 ± 1 m were taken into consideration here. On the reef slope a sample of the reef substratum was collected down to a depth in the sediment/rubble where no LBF were observed anymore. Afterwards the samples were washed to remove the foraminifera from the larger and heavier parts of coral rubble, dried, and further processed in the laboratory. Foraminifera larger than 500 μm were subjected to further study. Only samples with more than approximately 200 individuals of LBF were identified at species level using a stereomicroscope and included in this study.

2.6. Microbes

In each site, sediment and sponge samples (when present) were collected. Sediment samples were taken using the mini-core method. Mini-cores, consisting of the top 5 cm of sediment, were collected using a plastic disposable syringe from which the end had been cut in order to facilitate sampling (Capone et al., 1992). Twenty-one fragments of *Stylissa massa* were collected including segments of surface and interior to sample, as much as possible, the whole prokaryotic community, stored in 96% EtOH (Cleary et al., 2013; Polónia et al., 2014) and kept at temperatures lower than 4 °C immediately after collection. Once in the laboratory, samples were stored at −20 °C until DNA extraction.

2.7. Habitat variables

In the present study, habitat variables consisted of 13 distinct forms of substrate and depth. Since the high habitat heterogeneity of reef systems is essentially created by the complex and diverse colonial structures of scleractinian corals, eight of the 13 distinct forms of substrate used to characterize the habitat heterogeneity of the Spermonde reef system were based on live coral and coral life form cover. Nevertheless, these coral-related variables were not used to predict variation in coral composition. The 13 distinct forms of substrate assessed included the cover of *Acropora* (Acrop), branching coral (CorBr), encrusting coral (CorEn), foliose coral (CorFo), massive coral (CorMa), submassive coral (CorSu), tabular coral (CorTa), mushroom coral (CorMu), dead coral (CorDd), crustose coralline algae (AlgCo), rock (Rock), rubble (Rubble) and sand (Sand). The percent cover of each of the previously mentioned life forms surveyed was assessed using the line-intercept transect method (Edinger and Risk, 2000). Sampling depth (Dep) was assessed with a Suunto D6i dive computer.

2.8. Water quality variables

Morel and Prieur (1977) divided oceanic water into two different types concerning their color: case I and case II waters. Case I waters (also called “blue”) are those waters where the ocean color is mainly determined by the phytoplankton concentration since it is the component with major influence on the water optical properties. Despite the existence of other substances in this kind of waters, their proportion is very low and is directly related to the phytoplankton, co-varying with it (i.e., elements from decomposing phytoplankton debris). Conversely, in case II waters the phytoplankton co-exists in similar concentrations with many other substances that are not directly related to it and thus vary in an independent way (mainly organic and inorganic particles in suspension; CDOM; mineral particles and various suspended sediments) (IOCCG, 2000).

Spermonde coral reef waters are characterized as Case II. The contribution of all case II water constituents for the optical water leaving signal of Spermonde coral reef waters demands a careful analysis in order to infer the weight of each one of them in the final magnitude of the signal and thus avoid the overestimation of phytoplankton concentrations (Richardson and LeDrew, 2006).

In the present study, environmental variables including near-surface chlorophyll-a concentration (Chlor-a), sea surface temperature (SST), remote sensing reflectance at 645 nm (Rrs_645) and colored dissolved organic matter index (CDOM) were assessed for the study region using ocean color satellite imagery. Colored dissolved organic matter index was used as a tracer of riverine inputs (Fichot et al., 2013) and Rrs_645 as a proxy for total suspended sediments derived from land-based erosion (Miller and McKee, 2004; Chen et al., 2007). CDOM is largely composed of humic and fulvic substances resulting either from decaying plant material brought by land run-off in areas with high vegetation productivity or originating from mangroves and seagrasses (Carder et al., 1999 in Martin, 2004; Richardson and LeDrew, 2006). MODIS band 1 (645 nm) with 250-m pixel resolution has been shown to perform well in coastal turbid waters (Franz et al., 2006; Chen et al., 2007) and Miller and Mckee (2004) showed a significant and robust linear relationship ($r^2 = 0.89$) between Rrs_645 and total suspended matter concentration (TSM). In addition to being associated to a higher spatial resolution, this band also has a lower sensitivity, which avoids saturation problems in waters dominated by highly turbid sediment (Zhang et al., 2010). Similar results can be obtained from MODIS/Terra, however, according to some authors (Hu et al., 2004; Chen et al., 2007) MODIS/Aqua data are better calibrated and contain less noise. Here, we used MODIS/Aqua band 1 aggregated to 1 km resolution.

Atmospheric correction over coastal waters is still a subject of intense research. This is particularly due to the non-zero Rrs in the near-infrared and blue-absorbing aerosols. For quantitative estimations, several issues need to be resolved when using 250 m medium-resolution band, namely inadequate sensor calibration, highly problematic atmospheric correction, and bio-optical inversion procedures (Hu et al., 2004). For this reason, we used a used Rrs_645 as a qualitative proxy and not to estimate the amounts of TSM.

Turbid waters, can be highly reflective at the NIR bands producing considerable errors in the assessment of the derived products (Wang and Shi, 2007). In the present study, we employed a SWIR atmospheric correction for deriving chlorophyll (Chlor-a) (Wang et al., 2007) and Rrs_645 (Wang and Shi, 2005). The agreement between in situ chlorophyll values and MODIS in complex turbid waters is significantly improved when the SWIR algorithm is used (Franz et al., 2006). This satellite image treatment has been used in coastal waters with success in several studies (e.g., Chen et al., 2007; Zhang et al., 2010).

Aqua Moderate Resolution Imaging Spectro-radiometer (MODIS-Aqua) Level 1A LAC (1 km resolution) data were obtained from the NASA Goddard Space Flight Center through the Ocean Color web site (http://oceancolor.gsfc.nasa.gov/cgi/) and processed to Level 3 format using NASA's SeaWiFS Data Analysis System (SeaDAS version 7.0) software. Due to the satellite's incapacity to measure ambient temperature at depth, the temperature values used for the analyses at 12 m and 3 m depth were the same — i.e., the 'skin' sea temperature. Our results should thus be interpreted as how the skin surface temperature influences variation in taxon composition at 3 m and 12 m depth. However, the main goal of this study was to use the remote sensed variables as proxies of environmental patterns of variation and not to quantitatively estimate the parameters in Case II waters. Since the accuracy of satellite data (compared to in situ data) tends to be higher with long-term averaging (Patt et al., 2003), time series of monthly mean data were generated. Mean values were generated for the previously mentioned satellite-derived parameters for the years 2008, 2009 and 2010. In order to avoid months with high cloud cover, only the months of June, July and August were analyzed in this study.

In addition to the above satellite-derived variables, we also included the distance to land (Off), which was the shortest distance from the sample site to the coastline of Sulawesi, and the distance to the Jene Berang river (Jene), which was the shortest distance from the sample site to the mouth of the Jene Berang river. Both can be considered proxies of terrigenous pollution.

2.9. DNA extraction

We isolated PCR-ready genomic DNA from seawater, sediment and sponge samples using the FastDNA® SPIN Kit following the manufacturer's instructions. This is an extraction method frequently used for this purpose (Cleary et al., 2013). Briefly, we prepared sediment samples by centrifuging each one for 30 min at 4400 rpm at 4 °C and the sponge samples by cutting each fragment into small pieces. 500 mg of sediment and sponge were transferred to Lysing Matrix E tubes containing a mixture of ceramic and silica particles. The microbial cell lysis was performed in the FastPrep® Instrument (Q Biogene) for 80 s at the recommended speed. The extracted DNA was eluted into DNase/Pyrogen-Free Water to a final volume of 50 μl and stored at −20 °C until use.

2.10. PCR amplification

Archaeal and bacterial 16S rRNA gene fragments were amplified for DGGE using a nested PCR assay (two consecutive amplification reactions). For the archaeal 16S rRNA gene amplification, the first PCR amplification was performed using DNA with archaea-specific primers ARC344f-mod and Arch958R-mod (Pires et al., 2012). After a denaturation step at 94 °C during 5 min, 30 thermal cycles of 1 min at 94 °C, 1 min at 56 °C and 1 min at 72 °C were carried out followed by an extension step at 72 °C for 7 min (Pires et al., 2012). The second PCR amplification was carried out using a dilution (1:25) of the amplicons from the first PCR with DGGE archaea-specific primers 524F-10 and Arch958R-mod (GC) (Pires et al., 2012). After a denaturation step at 94 °C during 5 min, 35 thermal cycles of 1 min at 94 °C, 1 min at 50 °C and 1 min at 72 °C were carried out followed by an extension step at 72 °C for 7 min. For the bacterial 16S rRNA gene amplification, the first PCR amplification was performed from DNA using the F-27 and R-1494 primers (Gomes et al., 2008). After a denaturation step at 94 °C for 5 min, 25 thermal cycles of 45 s at 94 °C, 45 s at 56 °C and 1:30 min at 72 °C were carried out followed by an extension step at 72 °C for 10 min. The second PCR amplification was carried out using a dilution (1:25) of the amplicons of the first PCR with DGGE primers F984-GC and R-1378 (Gomes et al., 2008). After a denaturation step at 94 °C during 4 min, 25 thermal cycles of 1 min at 95 °C, 1 min at 53 °C and 1.30 min at 72 °C were carried out followed by an extension step at 72 °C for 7 min.

2.11. DGGE of 16S rRNA gene fragments

For DGGE analysis, we used the DCode Universal Mutation Detection System (Bio-Rad, Paris, France). A double gradient polyacrylamide gel (10–6% acrylamide) with a 50–58% denaturing gradient was loaded with PCR product (7 μl for *Stylissa massa* sponge samples and 4 μl for sediment samples) together with 5 μl of DGGE loading buffer. The run of loaded gels was carried out at constant temperature (58 °C) and voltage (160 V) during 16 h in a 1× Tris–acetate–EDTA buffer.

The DGGE gels were colored using the silver staining method (Heuer et al., 2001), scanned and analyzed with the BioNumerics Version 6.6 program (Applied Maths). The gel image was corrected for background noise (disk size = 10%) and densitometric curves were extracted using an averaging thickness of 15 pts. The densitometric profiles were filtered using an arithmetic averaging and a least square filtering cut-off below 1.00%. DNA bands were automatically selected with band search parameters set at: 1.0% minimum profiling and a shoulder sensitivity of 2%. Based on the densiometric curves, a binary numerical band matching matrix with the numerical intensities of the bands was created and exported.

2.12. Cloning

The DGGE of archaea from *Stylissa massa* only revealed a single band. We therefore decided to clone the PCR product. We added 0.25 μl of 10 mM dATP, and 0.5 unit of Taq polymerase to a composite of 5 archaeal *S. massa* PCR products. The resultant reaction was incubated at 70 °C for 20 min. These DNA fragments were purified with Gene clean II kit (MPbio) and subsequently cloned into the pGEM®-T Easy vector (Promega Corp., Madison, WI) according to the instructions provided by the supplier. The ligated plasmids were transformed into competent cells (*Escherichia coli* JM109; Promega) and plated on LB medium containing 5-bromo-4-chloro-3-indolyl-β-D-galactopyranoside (X-gal), isopropyl-β-D-thiogalactopyranoside (IPTG), and 100 μg/ml ampicillin. Plasmid DNA was isolated from white colonies, purified and sequenced in GATC Biotec (http://www.gatc-biotech.com). The obtained sequence data were compared with different sequences available in the GenBank database using blast-n search (http://www.ncbi.nlm.nih.gov/BLAST/).

2.13. Analyses

All environmental data [including satellite (water quality) and substrate (habitat) data] and species-by-transect abundance matrices were imported into R (R Core Team, 2013). We did not import the matrix of archaea from *S. massa* because there was only a single band. Sequence analysis using BLAST revealed that the dominant archaeal symbiont present in *S. massa* was very closely related (99%–100%) to an uncultured archaeon previously isolated from *Phakellia fusca* hosts in the South China Sea (Han et al., 2012). Taxon diversity was assessed with rarefied species richness (S) (Gotelli and Colwell, 2001) and Shannon's (H′) diversity index (Shannon and Weaver, 1949) using the diversity() and specnumber() functions of the Vegan package (Oksanen et al., 2009). All taxon data matrices were $\log_e(x+1)$ transformed and further 'transformed' using the decostand() function in the Vegan package (Oksanen et al., 2009) in R. Through this transformation, the species abundance data were adjusted so that subsequent ordination analyses preserved the chosen distance among sample sites. In the present case, the Hellinger distance was used, as recommended by Legendre and Gallagher (2001). For each taxon/group we then set up two models using redundancy analysis (RDA) with the Hellinger-transformed matrix as response variable and habitat and water quality variables as explanatory variables respectively. RDA arranges the data points in a multidimensional space where the axes represent gradients in species abundances, constrained by the explanatory variables (habitat and water quality variables) (Makarenkov and Legendre, 2002; Cleary et al., 2005). Here, the amount of variation in composition explained by the explanatory variables is the sum of all constrained eigenvalues divided by the total variation in the species data (Ohmann and Spies, 1998; Cleary et al., 2005). We used the ordistep() function in Vegan to select significant predictors of variation in composition using backward selection, maximum permutations set to 1000 and a selection criterion of $P = 0.05$. Reduced models were then run again in R using the rda() function with 1. habitat and water quality variables, 2. habitat variables with water quality variables partialled out and 3. water quality variables with habitat variables partialled out. Variance partitioning (Borcard and Legendre, 2002; Cleary et al., 2004) was then used to partition the variance explained 1. purely by habitat variables, 2. purely by water quality variables and 3. by habitat and water quality variables combined. The significance of the RDA ordination axes was tested with the anova() function in Vegan with the 'by' argument set to 'axis'. This function tests the joint effect of constraints in RDA using an ANOVA like permutation test. All figures were made using R.

3. Results

With the exception of sponge bacteria, which were only sampled at 3 m, all of the taxa were most diverse at 12 m depth (Table 1). Foraminifera were the least diverse and sediment bacteria the most diverse. At 3 m depth, species richness varied from 9 (Lum, Kud) to 24 (Lnk) for corals, 10 (Lae) to 26 (Kud) for sponges and 6 (Kud) to 15 (Lum, Pol, Sam) for forams. DNA band richness (DGGE) at 3 m depth varied from 46 (Lan) to 55 (Kar) for sediment bacteria, 29 (Bon, Kar, Kud, Pol) to 41 (Lnk) for sediment archaea and 33 (Bad, Pol) to 44 (Lum) for sponge bacteria. At 12 m depth, species richness varied from 7 (Lae) to 30 (Kud) for corals, 31 (Bad) to 60 (Bon) for sponges and 6 (Bad) to 38 (Kar) for forams. Band richness at 12 m varied from 47 (Lan, Pol) to 60 (Paj) for sediment bacteria and 28 (Lnk) to 41 (Paj, Lae) for sediment archaea.

Of the remotely sensed variables (Supplementary Table 1), CDOM was lowest at Kapoposang (2.295) and highest at Polewali (4.113). Chlor-a was lowest at Kudingkareng Keke (0.233 mg m^{-3}) and highest at Lae Lae (0.634 mg m^{-3}). SST and Rrs_645 were lowest at Langkai (29.3 °C; 0.000211 sr^{-1}) and highest at Lankadea (29.6 °C; 0.000921 sr^{1}).

At 3 m depth, live coral cover varied from 28.1% (Lny) to 82.6% (Bad); dead coral cover from 3.9% (Kud) to 34.5% (Lae); rubble cover from 0.0 (Kap) to 49.1% (Kud) and sand cover from 0.0 (Bad; Kar; Kud; Lnk; Lum; Pol) to 28.6% (Kap). At 12 m depth, live coral cover varied from 4.5 (Lae) to 71.5% (Lum); dead coral cover from 13.2 (Sam) to 37.5% (Pol); rubble cover from 0.0 (Pol) to 40.4% (Sam) and sand cover from 0.0 (Bad: Kud; Lum; Paj; Sam) to 28.2% (Lae) (Table 2).

The habitat component alone determined from 13% (sediment bacteria) to 50% (forams) of variation in composition. The water quality component alone explained from 7% (forams) to 21% (sediment archaea) of variation in composition. The combined effects of both of these two sets of predictors (after removing the habitat and water quality only components) explained from 5% (corals) to 23% (forams) of variation in composition. The percentage of unexplained variation in composition varied from 20% (forams) to 69% (sediment bacteria) (Table 3). In summary, the variation in composition of sponges (45%), forams, corals (20%) and sediment archaea (30%) was primarily explained by habitat predictors while the variation in composition of sediment bacteria was primarily explained by water quality predictors (12.9%). Habitat (20%, 12.7%) and water quality (18.5%, 12.9%) sets of predictors explained similar amounts of variation in the composition of corals and sediment bacteria. None of the habitat or water quality variables were significant predictors of variation in sponge bacterial composition.

Variation in coral composition was primarily related to the habitat variables sand and dead coral. Significant water quality predictors of coral composition included Chlor-a and distance to land and to Jene Berang River (Table 4). Coral genera mainly found in sites with high sand cover (Kap 3 m; Lae 9 m) included *Porites* and *Favia* while genera mainly found in sites with low sand cover (e.g., Bad 12 m) included *Montipora* and *Fungia* (Fig. 2a and b; Supplementary Table 2). Corals of the genera *Echinopora* and *Pectinia* were mainly found in sites with high Chlor-a concentrations (e.g., Sam; Kar) while the genera

Table 1
Shannon's (H′) diversity index and rarefied species richness (S) for corals, sponges, forams, sediment bacteria, sediment archaea and sponge bacteria from the sampled reefs at both depths (3 and 12 m).

			Corals		Sponges		Forams		Sediment bacteria		Sediment archaea		Sponge bacteria	
Reef code	Reef name	Depth	H'	S	H'	S	H'	S	H'	S	H'	S	H'	S
Bad	Badi	3	1.518	13	–	–	–	–	3.505	51	2.627	35	2.877	33
Bad	Badi	12	1.597	18	3.028	31	0.798	6	–	–	–	–	–	–
Bon	Bone Lola	3	1.804	18	2.452	20	–	–	3.545	53	2.959	29	2.913	38
Bon	Bone Lola	12	2.827	23	3.267	60	1.550	12	3.496	55	3.101	40	–	–
Kap	Kapoposang	3	1.707	13	1.385	11	–	–	3.557	52	2.900	32	2.977	38
Kar	Karanrang	3	2.315	23	2.135	21	1.247	12	3.514	55	2.908	29	3.019	34
Kar	Karanrang	12	2.843	29	3.408	44	2.414	38	3.569	54	3.097	33	–	–
Kud	Kudingkareng Keke	3	1.597	9	2.753	26	0.738	6	3.528	50	2.847	29	2.936	39
Kud	Kudingkareng Keke	12	2.794	30	3.511	57	1.538	12	3.551	55	3.037	35	–	–
Lae	Lae Lae	3	2.121	15	1.855	10	1.465	12	3.636	53	2.822	30	3.178	43
Lae	Lae Lae	12	1.791	7	3.197	38	0.964	14	3.492	50	3.217	41	–	–
Lan	Langkai	3	1.773	12	–	–	–	–	3.352	46	2.849	33	2.898	37
Lan	Langkai	12	2.395	16	3.135	43	1.784	25	3.435	47	3.077	34	–	–
Lnk	Lankadea	3	2.659	24	–	–	–	–	3.391	48	3.120	41	3.035	38
Lnk	Lankadea	12	2.830	25	–	–	2.171	27	3.546	52	2.777	28	–	–
Lny	Lanyukang	3	1.983	11	–	–	–	–	–	–	–	–	–	–
Lny	Lanyukang	12	2.405	18	–	–	–	–	–	–	–	–	–	–
Lum	Lumulumu	3	1.448	9	–	–	1.523	15	–	–	–	–	3.176	44
Lum	Lumulumu	12	2.350	24	3.066	35	1.934	18	3.514	53	3.168	39	–	–
Paj	Pajenekang	3	2.535	20	–	–	0.738	8	3.405	49	2.847	33	3.098	41
Paj	Pajenekang	12	2.266	27	–	–	1.530	16	3.702	60	3.391	41	–	–
Pol	Polewali	3	2.133	17	2.357	24	1.458	15	3.478	52	2.773	29	2.884	33
Pol	Polewali	12	2.440	20	3.375	47	–	–	3.370	47	3.080	35	–	–
Sam	Samalona	3	1.526	10	2.699	17	1.015	15	3.576	54	3.027	36	3.107	41
Sam	Samalona	12	2.671	22	2.891	37	1.486	16	–	–	–	–	–	–

Table 2
Percentage cover of the distinct forms of substrate assessed in the sampled reefs at both depths (3 and 12 m). Acrop: *Acropora*, CorBr: branching coral, CorEn: encrusting coral, CorFo: foliose coral, CorMa: massive coral; CorMu: mushroom coral; CorSu: submassive coral; CorTa: tabular coral; CorDd: dead coral; AlgCo: crustose coralline algae; Rubble: rubble; Rock: rock; and Sand: sand. For reef names see Table 1.

Reef code	Depth	Acrop	CorBr	CorEn	CorFo	CorMa	CorMu	CorSu	CorTa	CorDd	AlgCo	Rubble	Rock	Sand
Bad	3	9.6	59.6	0.3	3.7	1.2	4.3	0.3	3.7	14.8	0.0	1.9	0.0	0.0
Bad	12	2.3	2.3	0.8	26.0	1.4	19.2	0.3	5.1	25.4	1.3	10.5	0.0	0.0
Bon	3	0.0	1.9	5.6	3.2	8.6	20.7	0.6	0.0	19.6	0.0	29.6	0.0	5.2
Bon	12	0.0	1.4	5.3	3.9	2.2	5.0	1.0	1.2	26.4	0.0	25.3	0.0	17.9
Kap	3	0.0	0.8	6.9	0.0	25.7	0.0	1.8	0.0	16.2	0.0	0.0	17.4	28.6
Kar	3	2.5	41.0	4.9	4.4	13.9	8.5	2.0	2.4	15.2	1.0	3.4	0.0	0.0
Kar	12	0.2	21.9	2.3	20.3	10.7	7.6	0.9	3.8	20.0	0.1	1.5	0.0	5.4
Kud	3	2.9	23.1	1.5	11.7	5.1	2.3	0.3	0.0	3.9	0.0	49.1	0.0	0.0
Kud	12	3.5	4.4	8.1	14.9	7.3	7.1	0.9	3.1	29.9	0.6	14.2	0.0	0.0
Lae	3	2.9	9.3	7.7	0.0	10.9	0.0	0.0	0.0	34.5	0.1	2.9	1.7	19.4
Lae	12	0.0	0.0	0.9	0.3	2.8	0.5	0.0	0.0	21.8	0.0	27.1	0.0	28.2
Lan	3	4.3	8.7	3.0	0.5	0.5	13.1	0.1	0.0	30.3	0.0	16.8	0.0	12.6
Lan	12	6.3	1.3	2.5	0.5	6.6	0.7	0.7	0.0	13.8	0.0	39.6	0.0	22.8
Lnk	3	9.0	3.4	4.1	21.8	25.7	7.8	8.4	2.3	13.7	0.0	1.2	0.0	0.0
Lnk	12	0.0	0.7	1.6	8.8	11.8	11.7	0.8	3.4	17.5	0.2	28.0	0.0	4.4
Lny	3	1.9	6.4	2.0	0.0	16.0	0.0	1.8	0.0	17.2	0.0	31.5	0.0	21.5
Lny	12	4.0	2.9	5.5	0.0	10.5	0.8	0.0	0.0	19.3	0.0	35.4	0.0	12.9
Lum	3	8.2	25.9	0.3	9.5	1.7	3.0	0.1	5.7	19.8	0.3	19.6	0.0	0.0
Lum	12	13.3	11.7	11.1	19.9	4.9	4.9	1.1	4.5	26.7	0.0	1.6	0.0	0.0
Paj	3	2.1	6.2	12.1	0.4	10.4	0.0	2.7	0.0	11.6	0.9	45.6	6.4	0.2
Paj	12	0.2	0.7	9.0	10.0	0.7	16.4	0.0	5.7	31.0	0.5	21.6	0.0	0.0
Pol	3	0.0	48.9	1.0	6.4	11.5	6.7	1.9	0.0	7.1	0.7	8.9	0.0	0.0
Pol	12	0.0	13.4	1.8	4.8	4.2	4.8	0.5	7.8	37.5	0.0	0.0	0.0	14.8
Sam	3	52.5	3.5	0.5	0.0	7.3	1.9	1.2	0.0	21.8	0.0	7.5	0.0	0.9
Sam	12	0.0	1.3	9.9	6.4	1.0	7.1	0.0	2.7	13.2	4.5	40.4	0.0	0.0

Seriatopora and *Acropora* were mainly found in sites with low Chlor-a concentrations.

Sponge composition was primarily related to habitat variables including sand, depth and the cover of branching, *Acropora*, mushroom and foliose corals (Table 4). CDOM and Rrs_645 were significant water quality predictors of sponge composition. Most sponge species seemed to prefer deeper water (12 m), e.g., *Clathria reinwardti* and *Haliclona* sp. *ufo*. *Neopetrosia chaliniformis* and *Stelletta clavosa*, in contrast, were mainly found in shallow water (Fig. 2c and d; Supplementary Table 2). Most sponge species were also mainly found in sites with higher coral cover, the exception being *S. clavosa*. *Niphates* sp. (sticky), *Chondrosia*_aff. *chucalla* and *Mycale sulcata* were mainly found in sites with high *Acropora* cover (Sam 3 m) while *Amphimedon paraviridis*, in contrast, was mainly found in sites with low *Acropora* cover (Pol). Sponge species mainly found in sites with high CDOM values (Pol) included *Lamellodysidea herbacea* and *Clathria cervicornis*.

Foram composition was primarily related to the cover of tabular, submassive and dead coral and crustose coralline algae (Table 4). Significant water quality environmental predictors of foram composition included Chlor-a and Rrs_645. The foram species *Calcarina spengleri* was mainly found in sites with high crustose coralline algae cover (Paj 12 m; Bad 12 m; Kar 3 m) (Fig. 2e and f; Supplementary Table 2). *Calcarina mayori,* in contrast, was most abundant in sites with high Chlor-a values (Lae; Pol).

Table 3
Variance partitioning for corals, sponges, forams, sediment bacteria and sediment archaea explained by 1. purely habitat variables (Habitat only), 2. purely water quality variables (Water Quality only) and 3. habitat and water quality variables combined (Combined).

	Total explained	Habitat only	Water Quality only	Combined	Unexplained
Corals	0.437	0.204	0.185	0.048	0.563
Sponges	0.648	0.449	0.082	0.118	0.352
Forams	0.798	0.496	0.070	0.232	0.202
Sediment bacteria	0.312	0.127	0.129	0.055	0.688
Sediment archaea	0.659	0.298	0.210	0.151	0.341

Significant habitat predictors of sediment bacteria composition included sand and *Acropora* cover while significant water quality predictors included CDOM and distance to land (Table 4; Fig. 3a; Supplementary Table 2). Significant habitat predictors of sediment archaea composition included sand, rubble, branching coral and *Acropora* cover while significant water quality predictors included CDOM, distance to land, and to the Jene Berang river and SST (Table 4; Fig. 3b; Supplementary Table 2).

4. Discussion

Gordon et al. (2012) reported a warmer Indonesian Throughflow during the southeast monsoon (boreal summer) in the years preceding our sampling. These years were used for the satellite data analysis (2008–2009). The Indonesian Throughflow consists of a water mass fed essentially by waters from the North Pacific Thermocline, which flows through the Makassar Strait. This warmer water mass reaches the northern reefs of the Spermonde Archipelago leading to higher SST values in these reefs. River discharge from the Jene Berang (that passes through the south of Makassar) and the Maros river (north of the city) strongly influence water transparency of the closest reefs (5 km offshore) through the input of terrigenous sand, silt and land-based sources of pollution (Cleary et al., 2005). Due to the proximity to Makassar city, major river discharge reaches inshore reefs such as Lae Lae more during the wet season than during the dry season. The high concentrations of organic nutrients (POC), Chlor-a and turbidity (eutrophication; Sawall et al., 2011) and clay/silt content in these reefs (Erftemeijer, 1993) result in the lowest diversity of stony corals registered in the Spermonde archipelago (Hoeksema, 1990). Between 5 and 12.5 km offshore the influence of the Jene Berang River is not strong; however, during the wet season the river plume can reach this zone causing poor water transparency (Renema and Troelstra, 2001). While the discharge of the Maros river is mainly derived from a carbonate rich drainage area, the discharge of the Jene Berang river, besides being larger and containing volcanically derived erosion products, also includes land-based agricultural and urban run-off as well as effluents from the Makassar sewer system (Renema and Troelstra, 2001). Additionally, the rivers located further north (e.g., Pangkajene River) cross essentially rural areas. Increasing agricultural land use and

Table 4
Results of stepwise model building for constrained ordination (Habitat: habitat predictors; Water quality: water quality predictors) for corals, sponges, forams, sediment bacteria and sediment archaea. Expl. var. cod.: explanatory variable code; Expl. var.: explanatory variable; AIC: Aikake's information criterion; N. perm: number of permutations.

Response variable	Expl. var. cod.	Expl. var.	AIC	F	N. perm	P
Corals — habitat	Dep	Depth	−21.4190	1.7095	399	0.0625
	CorDd	Dead coral	−21.2030	1.9072	199	0.0350
	Sand	Sand	−18.9120	4.1091	99	0.0100
Corals — water quality	Jene	Distance to the Jene Berang River	−20.4990	1.9688	99	0.0300
	Chlor-a	Chlorophyll-a	−19.8330	2.5908	99	0.0200
	Off	Distance to Land	−20.3750	2.0834	99	0.0100
Sponges — habitat	CorEn	Encrusting coral	−5.9758	1.6393	999	0.0840
	CorFo	Foliose coral	−5.6332	1.8480	199	0.0450
	CorMu	Mushroom coral	−5.5018	1.9292	199	0.0400
	Acrop	Acropora	−5.3120	2.0477	99	0.0300
	CorBr	Branching coral	−5.6466	1.8397	99	0.0200
	Dep	Depth	−5.0916	2.1870	99	0.0200
	Sand	Sand	−5.1598	2.1437	99	0.0100
Sponges — water quality	Rrs_645	Remote sensing reflectance (645 nm)	−4.6292	1.7543	99	0.0300
	CDOM	Colored dissolved organic matter	−4.7099	1.6800	99	0.0200
Forams — habitat	CorMu	Mushroom coral	−23.1950	1.8776	999	0.0880
	Rubble	Rubble	−23.0530	1.9657	299	0.0567
	CorEn	Encrusting coral	−23.1280	1.9195	199	0.0500
	AlgCo	Crustose coralline algae	−20.8580	3.4314	99	0.0200
	CorDd	Dead coral	−21.6840	2.8561	99	0.0100
	CorSu	Submassive coral	−19.2970	4.6027	99	0.0100
	CorTa	Tabular coral	−17.6600	5.9601	99	0.0100
Forams — water quality	Rrs_645	Remote sensing reflectance (645 nm)	−18.8600	2.3408	299	0.0400
	Chlor-a	Chlorophyll-a	−16.7490	4.5044	99	0.0300
Sediment bacteria — habitat	Acrop	Acropora	−18.5560	1.4817	299	0.0433
	Sand	Sand	−17.3570	2.6240	99	0.0100
Sediment bacteria — water quality	Off	Distance to land	−18.5200	1.5651	199	0.0250
	CDOM	Colored dissolved organic matter	−18.2610	1.8074	199	0.0250
Sediment archaea — habitat	CorDd	Dead coral	−17.7510	1.5662	999	0.0980
	Dep	Depth	−17.7000	1.6035	999	0.0910
	Acrop	Acropora	−17.3440	1.8653	99	0.0200
	CorBr	Branching coral	−17.2270	1.9525	99	0.0200
	Rubble	Rubble	−17.1740	1.9921	99	0.0100
	Sand	Sand	−15.8470	3.0205	99	0.0100
Sediment archaea — water quality	SST	Sea surface temperature	−18.8500	1.7646	99	0.0200
	Jene	Distance to the Jene Berang River	−18.2300	2.2931	99	0.0200
	Off	Distance to land	−17.5310	2.9080	99	0.0100
	CDOM	Colored dissolved organic matter	−16.9440	3.4415	99	0.0100

deforestation has led to high rates of soil erosion and sedimentation which, through river transportation, reach the marine environment and the coastal coral reefs.

Several studies have reported a strong spatial gradient in the Spermonde Archipelago (e.g., Moll, 1983; Hoeksema, 1990; Renema and Troelstra, 2001; Cleary et al., 2005; Sawall et al., 2011; Ambo-Rappe, 2014). Turbidity, Chlor-a and particulate organic carbon (POC) in seawater and zinc, copper and lead in sediment (Ambo-Rappe, 2014) were higher near-shore while the C/N ratio (Sawall et al., 2011) and phosphate in seawater and cadmium in sediment (Ambo-Rappe, 2014) were higher in offshore reefs (Kapoposang).

The diversity indices varied considerably between depths. Interestingly, at 3 m depth, reefs close to Makassar city (Sam, Lae, Kud and Bon) had high diversities of sponges, sediment bacteria, sediment archaea and sponge bacteria. In contrast, the northeastern reefs (Lum, Paj, Kar and Pol) had high diversities of corals and forams. At 12 m depth, the diversity of sponge and sediment bacteria and archaea was high at Kudingkareng Keke and in northern reefs such as Pajenekang and Karanrang. For corals and forams, Karanrang and Lankadea had higher diversity followed by Bone Lola and Kudingkareng Keke for corals and Lumulumu and Langkai for forams. This reinforces the notion that a number of these taxa are sensitive to high concentrations of certain water quality variables (particulate and dissolved nutrients, chlorophyll and suspended solids; Fabricius et al., 2005) associated with coastal areas adjacent to large cities such as Makassar. These conditions appear to have a more adverse effect on photosymbiont-hosting organisms such as corals and forams (although not all of the foraminifera collected in the present study are symbiont-bearing) than bacteria, archaea and sponges (opportunistic feeders; de Goeij et al., 2008) that rely on dissolved organic matter assimilation to fulfill an important part of their energetic needs (de Goeij et al., 2008; Shank et al., 2010). Persistent exposure to land-based perturbations has also led to the high sand, rubble and dead coral cover in inshore reefs (Lae Lae, Samalona and Polewali). These results also suggest that the influence exerted by land-based pollution on water quality over the diverse taxa is distinct at different depths in the Spermonde Archipelago. Interestingly, while at 3 m depth Kudingkareng Keke and Bone Lola were among the reefs with the highest diversity of sponges and prokaryotes, at 12 m depth these reefs were among the reefs with the highest diversities of corals; conversely at 3 m depth Pajenekang and Karanrang were among the reefs with the highest diversities of corals while at 12 m depth these reefs were among the reefs with highest diversities of sponges and prokaryotes.

Substrate complexity can influence community composition (Nakamura and Sano, 2005; Cleary et al., 2008). Here, habitat variables (e.g., sand, rubble and coral cover variables) tended to be more important explanatory variables than water quality, the exception being sediment bacteria. This contrasts somewhat with Cleary et al. (2006) who reported proxies of water quality as the primary explanatory variables of coral assemblages. In the present study, despite being higher (20.04%), the percentage of variation in composition explained by habitat predictors was similar to that explained by water quality predictors (18.5%). These discrepancies between studies can be related to the differences in the habitat and water quality environmental variables assessed; in Cleary et al. (2006), habitat variables consisted of parameters related to variation in human habitation and land use, while

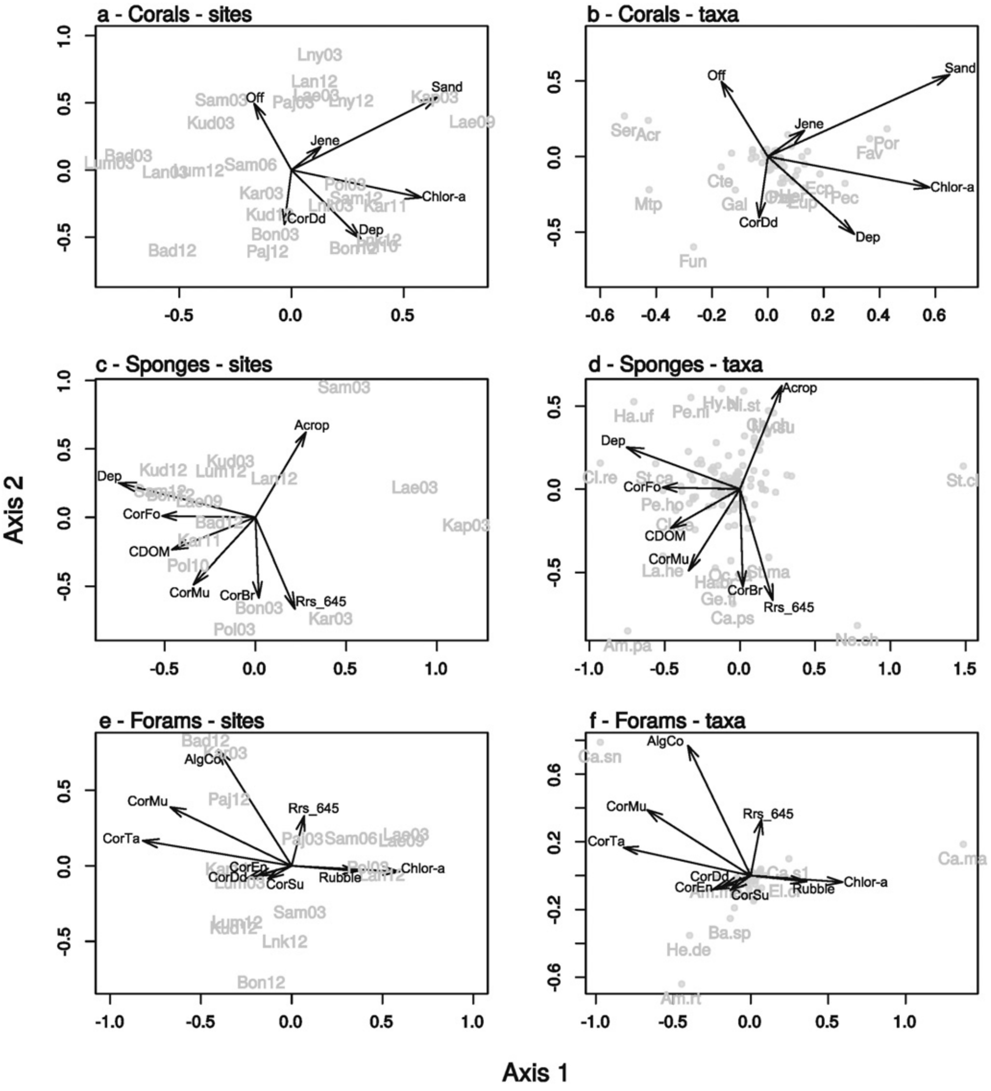

Fig. 2. Ordination of corals (a and b), sponges (c and d) and foraminifera (e and f) based on Redundancy Analysis (RDA) shows species and environmental variables on the first and second axes. Arrows represent environmental variables, and their direction and length indicates their contribution to variation along those axes. For codes of sample sites and significant environmental variables see Tables 1 and 4 respectively. Selected coral genera are indicated by three-letter codes: **ACR**: *Acropora*; **CTE**: *Ctenactis*; **ECP**: *Echinopora*; **EUP**: *Euphyllllia*; **FAV**: *Favia*; **FUN**: *Fungia*; **GAL**: *Galaxea*; **HER**: *Herpolitha*; **MTP**: *Montipora*; **OXY**: *Oxypora*; **PAC**: *Pachyseris*; **PEC**: *Pectinia*; **POR**: *Porites*; **SER**: *Seriatopora*. Selected sponge species are indicated by four-letter codes: **Am.pa**: *Amphimedon paraviridis*; **Ca.ps**: *Callyspongia pseudofibrosa*; **Ch.ch**: *Chondrosia* aff *chucalla*; **Cl.ce**: *Clathria cervicornis*; **Cl.re**: *Clathria reinwardti*; **Ge.fi**: *Gelliodes fibulata*; **Ha.br**: *Haliclona sp.* (brown); **Ha.uf**: *Haliclona sp.* (ufo); **Hy.bl**: *Hyrtios sp.* (black); **Ja.sp**: *Jaspis splendens*; **La.he**: *Lamellodysidea herbacea*; **My.su**: *Mycale sulcata*; **Ne.ch**: *Neopetrosia chaliniformis*; **Ni.st**: *Niphates sp.* (sticky); **Oc.sa**: *Oceanapia sagittaria*; **Pe.ho**: *Petrosia hoeksemai*; **Pe.ni**: *Petrosia nigricans*; **St.ca**: *Stylissa carteri*; **St.cl**: *Stelletta clavosa;* **St.ma**: *Stylissa massa.* Selected foram species are indicated by four-letter codes: **Am.me**: *Amphisorus median*; **Am.rt**: *Anomalinella rostrata*; **Ba.sp**: *Baculogypsinoides spinosus;* **Ca.ma**: *Calcarina mayori*; **Ca.sn**: *Calcarina_spengleri*; **Ca.s1**: *Calcarina sp.*; **El.cr**: *Elphidium craticulatum*; **He.de**: *Heterostegina depressa;* **Op.am:** *Operculina_ammonoides*.

water quality environmental variables were related to the proximity to Jakarta. Similar to the present study, variation in the local richness of reef-building corals was shown to be determined by both local and regional variables with regional variables explaining approximately equal amounts of variation to that of each of the local variables (depth and habitat; Cornell and Karlson, 1996). Cleary et al. (2005) and Hoeksema (2012a,b) in turn, reported depth and offshore distance as significant predictors of variation in mushroom coral composition in the present research areas. Distance offshore reflects the strong on-to-offshore environmental gradient in the Spermonde Archipelago; where inshore reefs are subjected to stronger land-based perturbations when compared to offshore reefs. Depth was reported as the most important explanatory variable for sponges, corals and foraminifera, followed by distance offshore (Cleary et al., 2005, 2006). In the present study, depth was a significant predictor of variation in sponge composition. Of the 144 sponge species sampled during this study, 78 were observed in 3 m transects whereas 126 were observed in 12 m depth transects. The abundance of sponge individuals was also greater at 12 m depth (n = 961) versus 3 m depth (n = 356). Sponge assemblages at 3 m depth were thus sparser and less diverse. Coral composition in the study area is well-known to be depth-related (Moll, 1983; Hoeksema, 2012a), but in the present study scleractinians were only recorded at genus level, which may explain why there was not such a clear difference between 3 and 12 m depth.

Water quality variables also vary with depth. As depth increases, light penetration and temperature are reduced (Cleary et al., 2005; Lesser, 2006), and the influence of variables such as dissolved organic matter, suspended sediment and nutrient availability are altered. These conditions can influence community composition directly in addition to having an indirect effect on habitat composition (Cleary et al., 2005). Reefs in turbid waters can experience a reduction in light penetration of about 70% in the first 2 m depth (Browne et al., 2010).

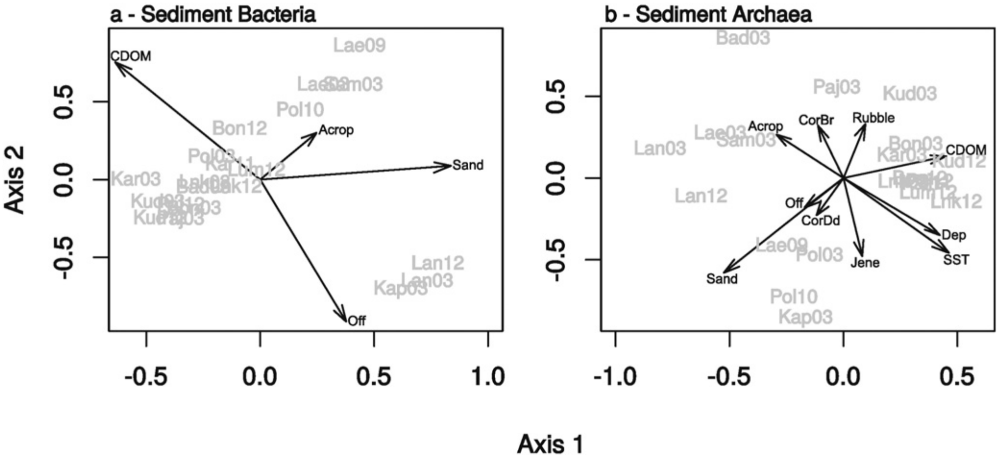

Fig. 3. Ordination of Sediment bacteria (a) and Sediment archaea (b) based on Redundancy Analysis (RDA) shows species and environmental variables on the first and second axes. Arrows represent environmental variables, and their direction and length indicates their contribution to variation along those axes. For codes of sample sites and significant environmental variables see Tables 1 and 4 respectively.

Conversely, in reefs with low levels of turbidity similar reductions in light availability are only attained at 10 m depth (Browne et al., 2010). This suggests that complex interactions among environmental parameters can affect variation in the composition of several taxa.

The relationship between coral composition and sand cover reflects the dominant coral groups in habitats with high coral versus high sand cover. In high coral cover environments, branching corals, particularly *Acropora* spp., tend to dominate. In habitats with high sand cover, massive and encrusting corals belonging, e.g., to the genus *Porites* tend to be the dominant corals (Done et al., 2007; Zhao et al., 2014; Cleary et al., 2008, 2014). Habitats with a high sand cover are sometimes the result of previous environmental perturbations, such as coral mining, dredging or land-based pollution (Brown and Dunne, 1988; Rogers, 1990; Cleary et al., 2006; Rachello-Dolmen and Cleary, 2007; Dharani et al., 2010). *Acropora* species have, for example, been shown to be particularly sensitive to pollution (Bellwood and Hughes, 2001; Torres and Morelock, 2002). In the Pulau Seribu reef system, inshore reefs that have been adversely impacted by their proximity to the city of Jakarta had very high sand cover (63%) compared to reefs (22%) further offshore (Rachello-Dolmen and Cleary, 2007; Cleary et al., 2008, 2014). *Acropora* species have largely disappeared from these inshore reefs (Cleary et al., 2014). In the present study, however, Kapoposang had the highest sand cover value at 3 m depth. Kapoposang is the furthest offshore reef that was studied and thus this high level of sand cover cannot be explained by land-based perturbations. The sand that is present on Kapoposang reefs is carbonate sand that is locally produced. The reef zone close to the steep wall (~5 m depth) is exposed to the currents of the Makassar Strait. However, the slope of the reef crest is very gentle and 3 m depth (sample depth) is hundreds of meters away from the top of the steep wall and therefore less exposed to wave breaking. Additionally, this high level of sand cover can also be the result of destructive fishing practices frequently associated with the Spermonde Archipelago (Nurdin and Grydehøj, 2014).

Differences in coral reef substrate were previously reported to alter the microbial community (Wild et al., 2006). Here, sand cover was the most important habitat predictor for sediment bacteria and sediment archaea together with *Acropora* for sediment bacteria and rubble, and branching coral and *Acropora* cover for sediment archaea. The abundance of prokaryotes in carbonate reef sands, for example, was reported to be one order of magnitude higher than in silicate sands of a similar grain size spectrum (Wild et al., 2006). The complex surface structure and highly porous matrix of the carbonate reef sands enhances the surface area available for prokaryotes to penetrate (Wild et al., 2006; Schöttner et al., 2011). This is consistent with our results showing sand cover as the most important explanatory variable of variation in the composition of prokaryote communities. The higher availability of land-based organic matter inshore and near rivers may diminish the substrate importance in structuring bacteria composition and enforce the water quality environmental variables such as distance to land and CDOM. For archaea, adapted to chronic energetic stress (Valentine, 2007), the proximity to sources of land based organic matter may be less important.

CDOM, Chlor-a and Rrs_645 were the most important water quality variables in terms of variation explained in the composition of the taxa studied here. CDOM was the most significant predictor of variation in the composition of sponges, sediment bacteria and sediment archaea, while Chlor-a was an important water quality predictor for corals and forams. Rrs_645 was a significant predictor of variation in the composition of sponges and forams.

As an important absorber of short wavelengths in the visible light region, dissolved organic matter has been reported to protect marine organisms from ultraviolet (UV) radiation and shorter wavelengths of PAR (Shank et al., 2010; Ayoub et al., 2012). High CDOM concentrations normally occur in reefs adjacent to intact shorelines, i.e., close to high densities of mangroves, seagrasses and/or inputs from terrestrial vegetation through runoff. Some studies have shown higher attenuation of UV radiation in inshore reefs resulting in a lowered susceptibility of inshore reef organisms to photic stress when compared to their offshore counterparts (Ayoub et al., 2009, 2012). The photo breakdown of CDOM, during a series of photochemical reactions, results in low molecular weight byproducts which are liable to be assimilated by microbial communities enhancing their activity (Daniel et al., 2006; Shank et al., 2010). Curiously, in contrast to sediment-dwelling bacteria and archaea, no variation in sponge bacterial composition was explained by CDOM or any other variable. The relatively isolated, stable and nutrient-rich environment (namely a constant supply of ammonia, a metabolic waste product excreted by sponges; Hentschel et al., 2012) provided by sponge hosts appears to protect bacteria from environmental fluctuations. Additionally, sponges as filter feeders can also be affected by variation in CDOM composition and concentrations since they rely on dissolved organic matter assimilation to fulfill part of their carbon needs (Yahel et al., 2003; de Goeij et al., 2008). Our results support studies that have shown dissolved organic matter to be important in structuring coastal communities (e.g., Ayoub et al., 2009; Baña et al., 2014). Organic matter fluxes have also been reported to be enhanced by high chlorophyll-a concentrations and to be an important food source for benthic foraminifera and corals (Renema and Troelstra, 2001; Eberwein and Mackensen, 2006; Houlbreque and Ferrier-Pagès, 2009).

Here, Chlor-a was an important predictor of variation in foram and coral composition. In reefs with high light availability photosymbiont-hosting organisms putatively rely more on their symbionts to acquire energy than in turbid reefs where they tend to rely more heavily on heterotrophy. In addition to this, heterotrophy (dissolved organic matter) is also used to acquire nutrients that cannot be supplied by symbiotic algae (Tremblay et al., 2014; Houlbreque and Ferrier-Pagès, 2009). The importance of Chlor-a as a significant predictor of variation in the composition of photosymbiont hosting taxa (corals and forams) as opposed to other taxa (sponges, sediment bacteria and archaea) suggests marked differences among taxa in their response to water quality environmental gradients.

Variation in Rrs_645 explained significant amounts of variation in the composition of foraminifera and sponges. Suspended sediments are key determinants of turbidity and consequentially of the amount of light available for photosynthetic organisms. Although not all symbiont-bearing, foraminifera are very sensitive to variations in the depth of the photic zone. In response to turbid waters, foraminifera may alter their depths of occurrence (Renema and Troelstra, 2001). Sponge diversity and richness have been shown to be higher in sites of moderate and high sedimentation (e.g., Bell and Barnes, 2000). This high diversity can be explained by a higher resistance of these organisms to increased sedimentation when compared to corals and algae (Zea, 1994). Corals are susceptible to smothering by sediments and can die if this disturbance persists for a few days, depending on the sediment load (Erftemeijer et al., 2012). Sponges take advantage of the available space for colonization and spread rapidly.

5. Conclusions

In the present study, both habitat and water quality variables explained significant amounts of variation in the composition of a range of coral reef taxa. The proportion explained by these sets of variables and the variables themselves, however, differed among different taxa. The variation in composition of corals, sponges, forams and sediment archaea was primarily related to habitat variables, while the variation in composition of sediment bacteria was primarily related to water quality variables. For corals and sediment bacteria, habitat and water quality variables explained similar amounts of variation in composition. The importance of the satellite derived environmental variables including CDOM, Chlor-a and Rrs_645 in explaining variation in the composition of eukaryote and prokaryote taxa supports remote sensing as an important tool for predicting both water quality and the composition and diversity of coral reef taxa. The variables distance offshore and distance to the nearest river, often used as proxies for water quality including the impact of riverine pollution and urbanization, proved poorer predictors of variation in composition than satellite-derived variables.

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.scitotenv.2015.07.102.

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