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Daniel F.R. Cleary and Nicole J. de Voogd

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Environmental associations of sponges in the Spermonde Archipelago, Indonesia

Daniel F.R. Cleary^{*†‡} and Nicole J. de Voogd^{*†}

^{*}National Museum of Natural History Naturalis, PO Box 9517, 2300 RA Leiden, The Netherlands. [†]Institute for Biodiversity and Ecosystem Dynamics (Zoological Museum), University of Amsterdam, PO Box 94766, 1090 GT, Amsterdam, The Netherlands.

[‡]Corresponding author, e-mail: cleary@science.uva.nl

Relatively little is known about spatial turnover of marine benthic taxa in the diverse reef environments of Indonesia and how this is structured by environmental conditions. In the present study the community similarity of sponges was related to environmental and spatial variables. In total, 150 sponge species (N=15,842) were sampled within the Spermonde Archipelago in the Makassar Strait, off south-west Sulawesi. Ordination revealed that sponges are primarily structured by a complex interaction between depth, exposure and on-to-offshore variation in environmental variables. Together, environmental and spatial variables explained 56.9% of the variation in similarity of which 10.9% was due to environmental variables alone, 2.6% due to spatial variables alone and 43.4% due to covariation of environmental and spatial variables. The large amount of variation explained by the spatially structured environmental component is due to a strong on-to-offshore gradient in a number of environmental variables including temperature, velocity, salinity and suspended sediment load. Ordination was also used to identify associations between species and environmental variables.

INTRODUCTION

Identifying factors that determine spatial patterns of biological diversity is a fundamental topic in ecology (Williams et al., 2002). According to recent theories (Hubbell, 2001), communities may be largely a product of purely spatial processes related to the dispersal abilities of the taxa in question. The constituent species in a given patch will then be largely thrown together by chance, history or dispersal events. Recent studies in terrestrial and marine environments, however, have tended to show that environmental factors, as opposed to purely spatial factors, may be more important in structuring communities (Aguir et al., 2002; Ellingsen, 2002; Magalhaes et al., 2002; Tuomisto et al., 2003; Williams & Wisser, 2004; Cleary & Renema, 2007; Cleary et al., 2007).

The structure of coral reef taxa (octocorals, hexacorals, fish) in Mexico, Florida and Australia have, for example, previously been related to variation in a number of different abiotic environmental variables including depth, temperature, oxygen concentration, salinity and sedimentation (Lirman et al., 2003; Torruco et al., 2003; Syms & Jones, 2004). Coral reef habitats can also differ in their exposure to wave action and water currents (Done, 1982). Depth is an important composite environmental gradient that affects the composition of the benthic community. The main impact of depth is related to the reduction in light transparency. Transparency will invariably be lower in areas with high fluvial influx due to higher concentrations of particles and plankton (Renema & Troelstra, 2001). In addition to light transparency, both temperature and hydrodynamic energy decrease with depth.

Hydrodynamic energy can strongly influence community composition; organisms can be fragmented or unable to settle. Waves can also affect the substrate of coral reefs by, for example, creating open patches with coral rubble that can be used as substrate by some marine organisms. In addition to hydrodynamic energy, depth can influence habitat composition; live coral cover, for example, can be very dense between 12 and 24 m thereby limiting the available substrate for other organisms (Renema, 2002). In addition to abiotic processes, species play a critical role in the dynamics and functioning of ecosystems. In coral reef environments, corals play a major role in providing substrate to a myriad of other organisms but can also crowd out spatial competitors. Reef form and structure can therefore be seen as an interaction between abiotic environmental conditions, disturbance, and coral growth patterns. The type of reef can inhibit or facilitate habitat suitability for other taxa in synergy with the abiotic environment. Importantly, multiple processes can simultaneously influence communities. Separating the contribution of these environmental components to patterns of community similarity is necessary for understanding the mechanisms that structure communities (Spencer et al., 2002).

In the present study, sponges and environmental variables were sampled in a number of sites in the Spermonde Archipelago, Indonesia. Sponges are sedentary filter feeders. They are present in all aquatic habitats, but are mainly marine and occur in a wide range of depths and environments, from warm tropical coral reefs to the (Ant)-Arctic. Sponges efficiently filter large quantities of water for small food particles, but some sponges derive nutrients from symbiotic cyanobacteria. The Indo-Malayan region

contains the highest marine biodiversity in the world (Mora et al., 2003), although the published literature on sponge taxonomy remains incomplete in this region. As a result, only few studies have addressed sponge distribution, biodiversity and related subjects in Indonesia (de Voogd et al., 2004, 2006; Bell & Smith, 2004). The goal of the present study is to assess to what degree spatial variation in sponge similarity can be explained by variation in environmental variables and the distance between sample sites or a combination of the above, and to identify associations between species and environmental variables using ordination.

MATERIALS AND METHODS

Study site

All sampling took place within the Spermonde Archipelago, south-west Sulawesi, Indonesia. The Spermonde Archipelago, which developed during the Holocene sea level rise on top of Pleistocene topography (de Klerk, 1983; Renema, 2002), is suitable for studying coral reef biodiversity because it is a well documented carbonate coastal shelf, approximately 40 km across, with several vectorial environmental influences. On its western side the Spermonde is separated from open oceanic conditions by a discontinuous barrier reef. Vectorial influences are related to fluvial discharge and erosion products from rivers to the east and oceanic influences that stem from beyond the barrier reef to the west (Renema & Troelstra, 2001). Additional disturbances over the Spermonde reef system stem from storms during the monsoon season and from destructive fisheries (e.g. blast-fishing) (Edinger et al., 1998). Reefs of the Spermonde are usually cay crowned (Umbgrove, 1929, 1930; de Klerk, 1983; Renema, 2002); the exposed sides of these cays are strongly influenced by oceanic swell and are coral covered; the sheltered sides generally consist of carbonate sand with isolated coral patches. The geomorphology of the reefs is determined by the north-west monsoon, between November and April. The north-western sides of the reefs of Lae-Lae (05°08'S 119°23'E), Bone Baku (05°08'S 119°21'E), Samalona (05°07'S 119°20'E), Kudingareng Keke (05°06'S 119°17'E), Bone Lola (05°03'S 119°21'E), Barang Lompo (05°03'S 119°19'E), Langkai (05°01'S 119°05'E) and the south-eastern sides of the reefs Samalona (05°07'S 119°20'E) and Kudingareng Keke (05°06'S 119°17'E) were examined. A detailed description of the sample sites and study area is presented in de Voogd et al. (2006) and Cleary et al. (2005).

Data collection

Sponges and environmental data were sampled from January to November 1997; sponge data were supplemented with additional data collected in 2000. Plots were sampled at designated locations with respect to sheltered and exposed sites and at varying depths. Sponges were quantitatively sampled within 34 100 m² (100×1 m) rectangular plots. Smaller (cryptic, boring and thinly encrusting) specimens were excluded. Species were visually identified in the field, and fragments of unrecognized species were collected for closer examination. Sponges were sampled from reef flats and slopes (depth range: 3–15 m). All sponges sampled within the bounds of the sample plots, were identified to species

or morphospecies; 150 species were sampled, of which 79 were previously described species, 4 newly described species (Alvarez et al., 2002; de Voogd & van Soest, 2002; de Voogd, 2004) and the rest morphospecies. In total 15,842 sponge individuals were sampled. For a list of the most common sponges and their abundance see de Voogd et al. (2006). Voucher specimens from the surveys have been deposited at the Zoological Museum of the University of Amsterdam and at the National Museum of Natural History 'Naturalis', Leiden in The Netherlands.

Environmental variables (current velocity, salinity, temperature and suspended sediment load) were sampled at 37 sites within the study area in the open water column at 3 m depth during 25-h sample events in each location (de Rooij & Bruijnsvoort, unpublished data; Jimmink et al., unpublished data; see Cleary & Renema, 2007 for a detailed description of the sampling methodology). In the analyses both the mean value for each environmental variable as well as the standard deviation (fluctuation), recorded over the 25-h sampling event, are used. This dataset was utilized to predict values for each sample size using ArcGIS Geostatistical Analyst (ESRI, Redlands, CA, USA). The Geostatistical Analyst derives a surface using the values from the measured locations to predict values for each location in the area. The interpolation method used was kriging, which forms weights from surrounding measured values to predict values at unmeasured locations. The kriging weights were derived from a semivariogram based on the spatial structure of the data. This enabled us to construct a continuous surface or map of the phenomenon and thereby to predict values for locations in the study area based on the semivariogram and the spatial arrangement of proximate measured values.

The area of live coral formations surrounding the sample site was calculated with the use of a GIS image based on automatic and supervised classification processes applied to a SPOT-XS satellite image, K-J/Sat: 320-370/3, recorded on 30 August 1995. Verification, by field surveys, was completed in December 1995. Additional records and corrections were provided by a BCEOM (Le Bureau Central d'Etudes pour les Equipements d'Outre-Mer) consultant in August 1996. The data were collected as part of the Marine Resource & Education Project (MREP) and are presently managed by BAKOSURTANAL (Badan Koordinasi Survei dan Pemetaan Nasional), Indonesia. A 500×500 m area was assessed surrounding each sample site.

Analyses

Community composition was assessed with unconstrained ordination, principal components analysis (PCA), and constrained ordination, redundancy analysis (RDA), using CANOCO for Windows 6.1 (ter Braak & Smilauer, 1998). Input for the PCA and RDA consisted of log₁₀ (X+1) species abundance data that were first 'transformed' within the program TRANSFORMATION (freely available at: <http://www.fas.umontreal.ca/biol/casgrain/en/labo/transformations.html>). Transformation consisted of modifying the species abundance data such that subsequent analyses, such as PCA and RDA, preserved the chosen distance among objects (plots). The species abundance data were transformed because of the inherent problems of the Euclidean-based

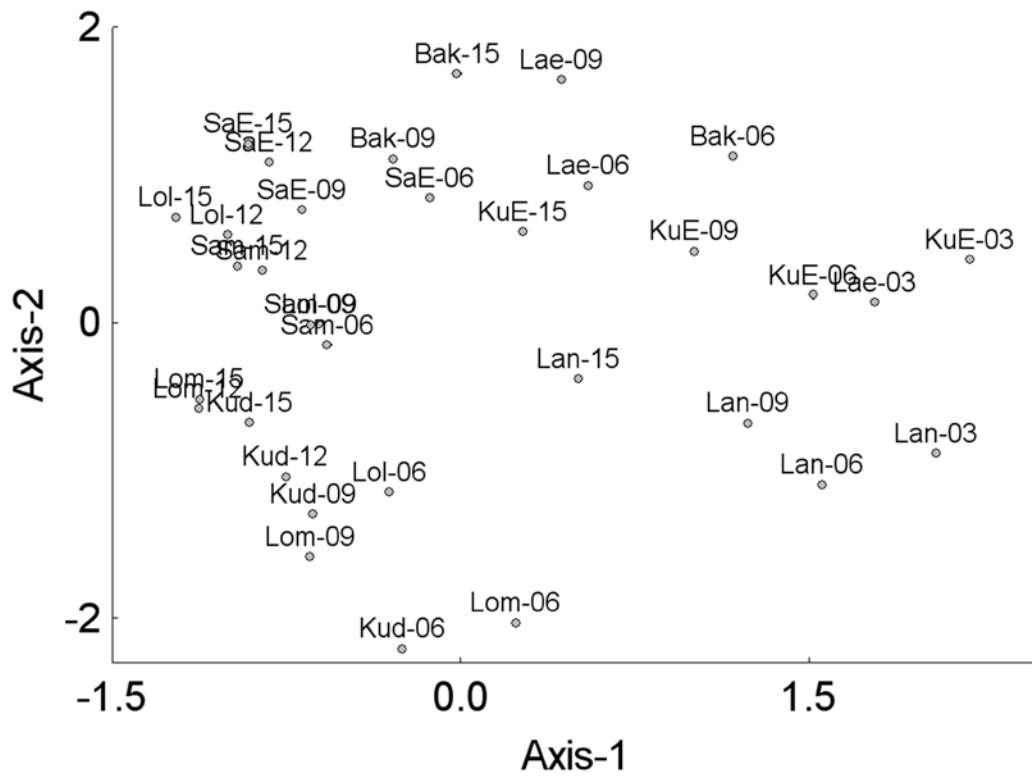


Figure 1. Principal components ordination showing site scores for the first and second axes. Codes represent: Bak, Bone Baku; Lae, Lae Lae; Lol, Bone Lola; Lom, Barang Lompo; Kud, Kudingareng Keke; KuE, Kudingareng Keke (sheltered site); Sam, Samalona; SaE, Samalona (sheltered site); Lan, Langkai. Numbers represent depth of plots.

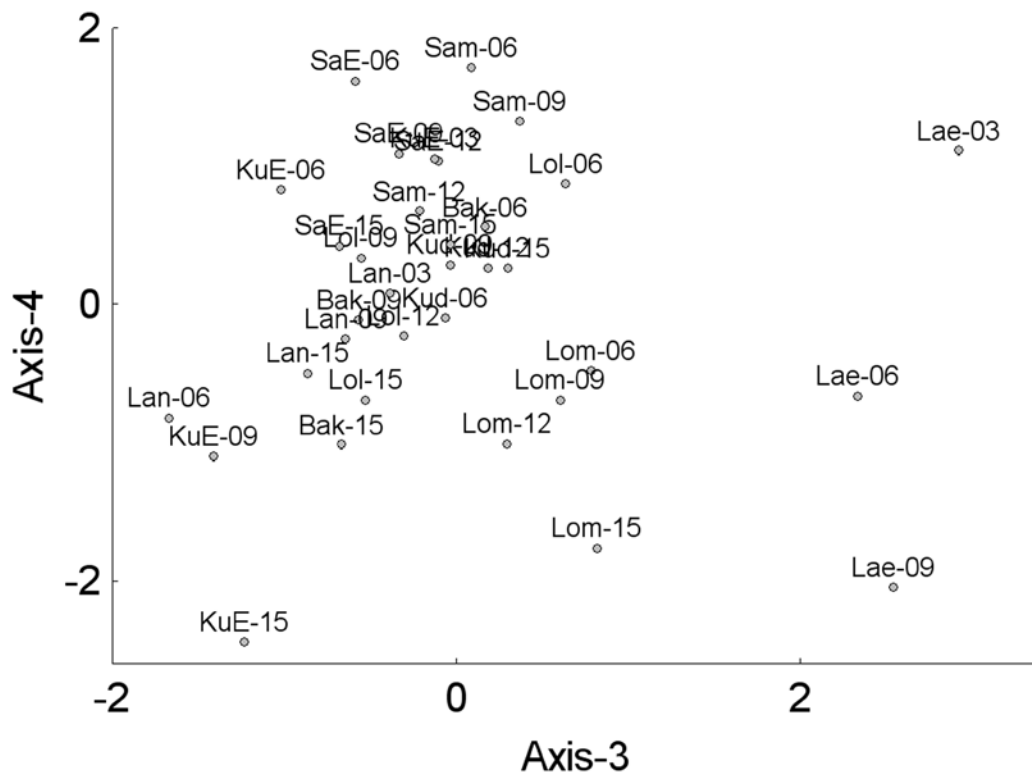


Figure 2. Principal components ordination showing site scores for the third and fourth axes. For codes see Figure 1.

distance metric (in standard PCA) and the Chi-square metric (in correspondence analysis, CA) for community data (see Legendre & Gallagher, 2001). In the present case, the Hellinger (Rao, 1995) distance was used, which

gave very good results in a comparison of various distance metrics (Legendre & Gallagher, 2001). Constrained gradient analysis using RDA (within CANOCO for Windows v. 4; ter Braak 1986; ter Braak & Smilauer, 1998) was used to

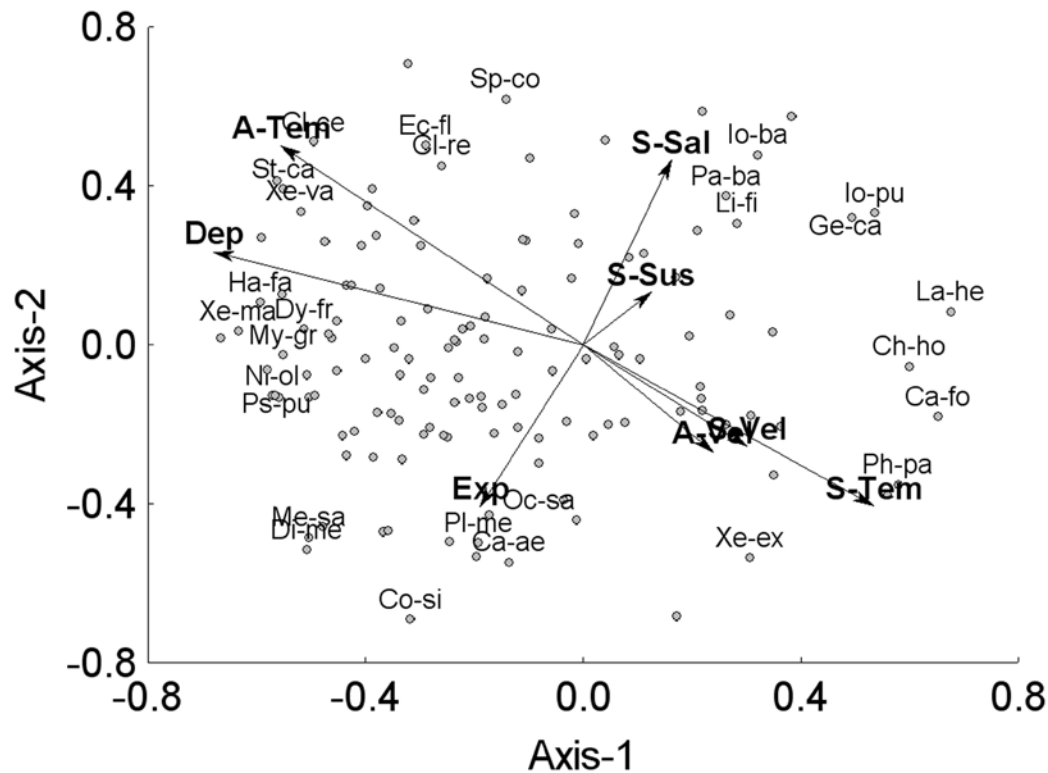


Figure 3. Redundancy analysis ordination showing species scores for the first and second axes. Species codes represent: Ca-ae, *Callyspongia aerizusa*; Ca-fo, *Carterospongia foliascens*; Ch-ho, *Chalinula hooperi*; Cl-ce, *Clathria cervicornis*; Cl-re, *Clathria reinwardti*; Co-si, *Coelocarteria singaporensis*; Di-me, *Diacarnus megaspinorhabdosa*; Dy-fr, *Dysidea frondosa*; Ec-me, *Echinodictyum mesenterium*; Ge-ca, *Gelliodes callista*; Ha-fa, *Haliclona fascigera*; Io-ba, *Iotrochota baculifera*; Io-pu, *Iotrochota purpurea*; La-he, *Lanellodysidea herbacea*; Li-fi, *Lissodendoryx fibrosa*; Me-sa, *Melophylus sarassinorum*; My-gr, *Myrmekeioderma granulata*; Ni-ol, *Niphates olemda*; Oc-sa, *Oceanapia sagittaria*; Pa-ba, *Paratettilla bacca*; Ph-pa, *Phyllospongia papyracea*; Pl-me, *Placospongia melobesioides*; Ps-ar, *Pseudoceratina verrucosa*; Sp-co, *Sphaciospongia congenera*; St-ca, *Stylissa carteri*; Xe-ex, *Neopetrosia exigua*; Xe-ma, *Xestospongia mammillata*; Xe-va, *Xestospongia vansoesti*. Environmental codes (block) represent: Dep, depth; Exp, exposure; A-Tem, average temperature; S-Sus, standard deviation in suspended sediment load; S-Sal, standard deviation in salinity; A-Vel, average velocity; S-Tem, standard deviation in temperature.

assess environmental gradients in the species data matrix. Redundancy analysis arranges sites and species in a multidimensional space whereby the axes are constrained to be linear combinations of environmental variables (Ohmann & Spies, 1998). In RDA, the amount of species variation explained by the explanatory variables, or the total variation explained (TVE) is the sum of all constrained eigenvalues divided by the total variation (TV) in the species data.

The environmental dataset used in the RDA consisted of the following variables: (1) depth; (2) maximum water transparency; (3) exposure (sheltered: 0, exposed: 1); (4) area of coral formations; (5) mean salinity; (6) mean suspended sediment load; (7) mean temperature; (8) mean current velocity; (9) standard deviation (SD) in salinity; (10) SD in suspended sediment load (11) SD in temperature; (12) SD in current velocity.

The importance of space in explaining variation in composition was assessed by supplementing the spatial UTM coordinates (easting 'x' and northing 'y') with all the terms for a bicubic trend line (Borcard et al., 1992) of form:

$$\hat{z} = b_1x + b_2y + b_3x^2 + b_4xy + b_5y^2 + b_6x^3 + b_7x^2y + b_8xy^2 + b_9y^3$$

Within CANOCO a forward selection procedure using a Monte Carlo permutation test (999 permutations) and the

full model option (ter Braak & Smilauer, 1998) was used to test environmental and spatial variables for significance (ter Braak & Verdonschot, 1995). In the results, the conditional effects of environmental and spatial variables on composition (λ_N) are presented in addition to *P* values from the Monte Carlo test. The conditional effects (λ_N) represent the additional fit or increase in eigenvalue with each consecutively selected environmental variable. Only variables with $P < 0.001$ were included in the final model. The significance of the association between the species and environmental datasets was also assessed using Monte Carlo simulations (999 permutations) of constrained ordination scores against environmental variables.

A quantitative variance partitioning technique described in Borcard et al. (1992) and Økland (2003) was used on results of separate partial RDAs. This enabled the variation in community composition explained by spatial variables alone, environmental variables alone, and spatial and environmental variables combined to be quantified. Briefly, the procedure was as follows: first, the community similarity matrix was constrained using the total set of environmental (X_e) and distance (X_s) variables to obtain the variance explained by all = V_T ($V_T = X_s \cup X_e$). Next, the community similarity matrix was constrained using environmental variables only with spatial variables as covariates to obtain

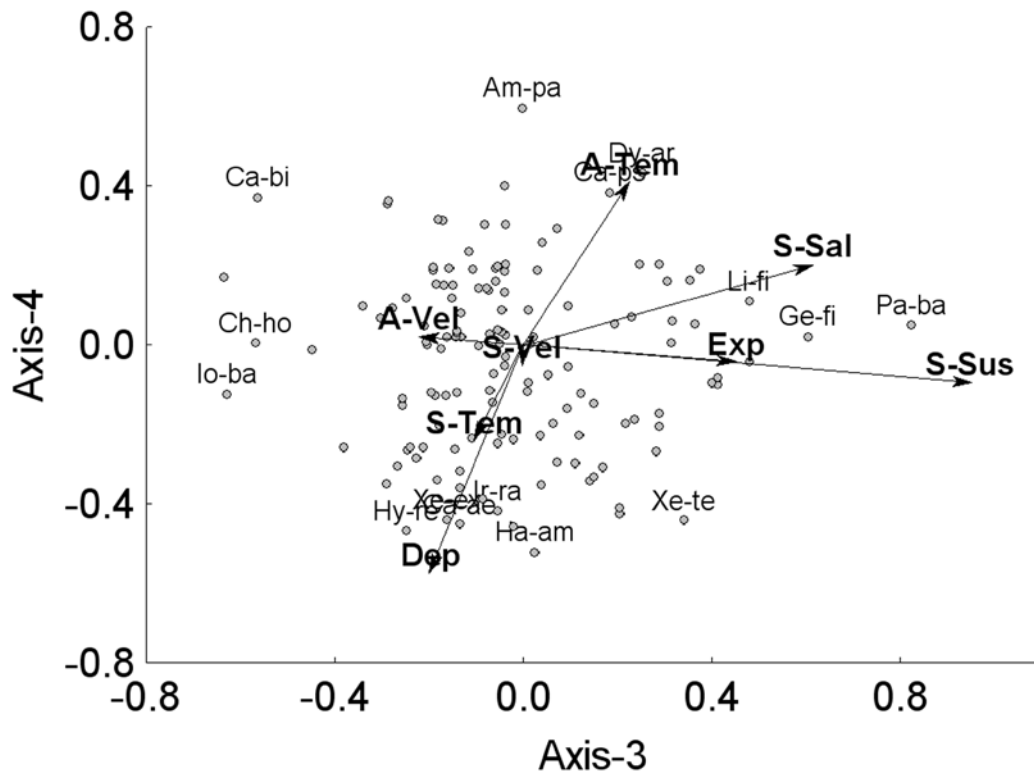


Figure 4. Redundancy analysis ordination showing site scores for the third and fourth axes. Codes represent: Am-pa, *Amphimedon paraviridis*; Ca-ae, *Calyspongia aerizusa*; Ca-bi, *Calyspongia biru*; Ca-ps, *Calyspongia* aff. *pseudofibrosa*; Ch-ho, *Chalinula hooperi*; Dy-ar, *Dysidea arenaria*; Ge-fi, *Gelliodes fibulata*; Ha-am, *Haliclona amboinensis*; Hy-re, *Hyrtios reticulata*; Io-ba, *Iotrochota baculifera*; Ir-ra, *Ircinia ramosa*; Li-fi, *Lissodendoryx fibrosa*; Pa-ba, *Paratetilla bacca*; Xe-ex, *Neopetrosia exigua*; Xe-te, *Xestospongia testudinaria*.

$V_{PE}(V_{pe} = X_e | X_s)$, and the community similarity matrix was constrained using distance variables only with environmental variables as covariates to obtain $V_{PS}(V_{ps} = X_s | X_e)$. It was then possible to calculate the spatially structured environmental fraction $V_{SSE}(V_{sse} = X_s \cap X_e = X_s \cup X_e - X_s | X_e - X_s | X_s)$ and the unexplained variation $V_{UN} = I - V_T$.

RESULTS

The first axis of the PCA (%VE: 16.5%) on sponge data represented a synthetic gradient structured by a combination of depth and offshore distance (Figure 1). Shallow and offshore plots tended to have high PC1 values while deeper and inshore plots usually had low PC1 values. The second axis of the PCA (%VE: 11.7%) on sponge data separated sheltered (indicated by 'E') and inshore (e.g. 'Lae' and 'Bak') plots from offshore (e.g. 'Lan' and 'Kud') plots. The third axis (Figure 2) of the PCA (%VE: 8.4%) separated the most inshore plots (Lae Lae) from all other plots. Finally, the fourth axis of the PCA (%VE: 11.7%) separated deeper and more offshore plots (e.g. 'Lan', 'Lom' and 'KuE') from shallower and more inshore (e.g. 'Sam' and 'SaE') plots.

In the RDA, the sum of all constrained (canonical) eigenvalues was 0.569 thus explaining 56.9% of the variation in the dataset (Figures 3 & 4). Of this 2.6% was due to the purely spatial component, 43.4% due to the spatially structured environmental component (covariation of space and environment) and 10.9% due to the purely environmental component. Using only the environmental

predictors, the eigenvalues of the first four axes were 0.152, 0.109, 0.078 and 0.059 for the first, second, third and fourth axes respectively (Monte Carlo test of trace, $P < 0.001$). The species–environment correlations of the first four axes were high (range: 0.922 to 0.978) indicating a strong association between the species matrix and the environmental matrix.

Significant ($P < 0.001$) environmental variables selected with the Monte Carlo forward selection procedure included depth ($\lambda_A = 0.10$), mean temperature ($\lambda_A = 0.09$), standard deviation in suspended sediment load ($\lambda_A = 0.08$), standard deviation in salinity ($\lambda_A = 0.06$), exposure ($\lambda_A = 0.05$), standard deviation in velocity ($\lambda_A = 0.07$), mean velocity ($\lambda_A = 0.05$) and the standard deviation in temperature ($\lambda_A = 0.04$). Significant ($P < 0.05$) spatial factors included x^2 ($\lambda_A = 0.09$), xy ($\lambda_A = 0.08$), x^3 ($\lambda_A = 0.05$), x^2y ($\lambda_A = 0.07$), xy^2 ($\lambda_A = 0.06$), y ($\lambda_A = 0.04$) and y^3 ($\lambda_A = 0.06$).

Ordinations of the RDA constrained using environmental variables only are presented in Figures 3 and 4 whereby arrows represent significant environmental variables superimposed onto the ordination; the length of the arrow indicates the correlation between the environmental variable and the ordination axis. Species strongly associated with deeper water include *Xestospongia mammillata*, *Haliclona fascigera* and *Niphates olemda*, whereas species associated with shallow water include *Chalinula hooperi*, *Carteriospongia foliascens* and *Lamellodysidea herbacea*. Species associated with sheltered sites include *Clathria mixta* and *Iotrochota baculifera* whereas *Placospongia melobesioides* and *Oceanapia sagittaria* preferred exposed sites. *Neopetrosia exigua* was widespread

but more abundant in offshore environments whereas *Coelocarteria singaporensis* was restricted to exposed midshore reefs (Kudingareng Keke and Barang Lompo). Species found in turbid inshore environments included *Paratetilla bacca*, *Gelliodes fibulata* and *Lissodendoryx fibrosa* whereas those restricted to more pristine offshore reefs included *Iotrochota baculifera*, *Chalinula hooperi* and *Calyspongia biru*.

DISCUSSION

We found pronounced differences in sponge assemblages among sample sites. Gradients in species composition varied in relation to a number of environmental variables including depth, exposure to wave energy and environmental variables that varied along an on-to-offshore gradient including temperature, water velocity and suspended sediment load. Previous studies have found that local distribution patterns of benthic marine taxa are highly influenced by local environmental factors, such as reef geomorphology, depth, water turbidity and nutrients (Wilkinson & Cheshire, 1989; Alvarez et al., 1990; Cheshire & Wilkinson, 1991; Barnes, 1999; Bell & Barnes, 2000; Hooper et al., 2002; Becking et al., 2006; Cleary & Renema, 2007; de Voogd & Cleary, 2007) in addition to competition with other reef organisms (VanVeghel et al., 1996; Aerts & van Soest, 1997).

Some sponge species were restricted to the highly sedimented inshore reefs of Lae Lae and Bone Baku including the massive *Lissodendoryx fibrosa* and the globular *Paratetilla bacca*. *Lissodendoryx fibrosa* is often covered by a fine sheet of sediments, and species belonging to this genus are known to have a wide ecological amplitude (van Soest, 2002). *Paratetilla bacca* has a globular morphology and sponges belonging to the same family (Tetillidae) have pronounced preferences for habitats with a high sediment load. Sponges, in general, inhabit hard-bottom communities, and only a few sponges have adapted to soft bottom and often highly sedimented habitats, including burrowing in the substrate, and protrusion of spicules (Ilan & Abelson, 1995).

Species found predominantly in deeper plots included the tube forming *Niphates olemda*, the globular *Melophlus sarassinorum*, the creeping ramose *Pseudoceratina verrucosa*, the massive *Xestospongia mammillata* and the globular *Diacarnus megaspinorhabdosa*; the latter two were completely absent from inshore reefs. When present, *N. olemda* is often very common and has a very broad geographical range; it is also frequently found on vertical walls (N.J. de Voogd, personal observation). Other sponges that were found in more offshore environments included *Neopetrosia exigua* and *Coelocarteria singaporensis*. These species are known to occur in pristine densely coral covered reefs in Palau (de Laubenfels, 1954) and curiously enough in the muddy intertidal regions of Darwin (Bergquist & Tizard, 1967).

Environmental and spatial variables together explained 56.9% of the variation in sponge similarity and this was predominantly related to environmental parameters (pure and spatially structured), indicating that the more similar the environment, the more similar the sponge assemblages present. This identifies a strong deterministic interaction between the environment and community present within a site. These results agree with previous studies in marine and terrestrial environments that have attributed spatial

variation in community structure to predominantly deterministic (environmental) processes (Aguilar et al., 2002; Ellingsen, 2002; Magalhaes et al., 2002; Tuomisto et al., 2003; Williams & Wisser, 2004; Cleary et al., 2004, 2005, 2006; Cleary & Genner, 2006).

Results of the present analysis using canonical ordination are also in line with the findings of de Voogd et al. (2006), with respect to the variance explained by environmental and spatial variables, in which a matrix regression technique was used. Legendre et al. (2005) suggested that the variation in composition is preferably partitioned using canonical ordination as opposed to the matrix regression technique used in de Voogd et al. (2006).

The importance of spatially structured environmental variables indicates that species and environment have similar spatial structure (Borcard et al., 1992). In the study area there was clear evidence of such a spatial–environmental gradient related to fluvial input from rivers such as the Jene Berang from the east and south and oceanic influences from the west. Fluvial input from various river systems is the most dominant environmental factor although this is mediated by annual variation related to the monsoon and the geomorphology of the Spermonde shelf (Renema, 2002). Stronger winds generally occur during the north-west monsoon and this time of year is also associated with increased fluvial discharge and the inflow of terrigenous sand and silt. During the south-east monsoon, there is an increase in upwelling along the outer shelf rim lowering water temperatures and dissolved oxygen and increasing salinity and nitrate–nitrogen content (Ilahude, 1978). Upwelling, during the south-east monsoon (Ilahude, 1978), and wave action, during the north-west monsoon (van der Stok, 1922), primarily affect the outer rim of the shelf.

During the north-west monsoon, silt and clay may be deposited a considerable distance offshore due to increased fluvial inflow causing low salinity and nutrient enrichment (Sobur, 1985; Erfemeier, 1993; Renema & Troelstra, 2001). The reefs in the immediate vicinity of Makassar (e.g. Lae Lae) are directly under fluvial influence of the Jene Berang river and a sediment-loaded plume (de Klerk, 1983; Edinger et al., 1998; Renema, 2002). This plume can at times reach offshore reefs, such as the sheltered side of Kudingareng Keke, although most of the sediment load has then been lost with characteristic surface fronts of foam and detritus (Hockstra, 1989). The effect of the river plume decreases as the distance increases from shore (Edinger et al., 1998; Renema & Troelstra, 2001) so that the various reefs not only differ in exposure to land-based pollution, but also in geomorphology and maximum depth. In the study area, observed values of mean water velocity and salinity and the variation in velocity and temperature increased from in-to-offshore due to the reduction in the influence of the Jene Berang and increasing oceanic influences. On the contrary, the mean sediment load and the variation in salinity and sediment load declined from in-to-offshore. Numerous studies have shown that temperature, salinity and sedimentation can be important in structuring communities (Arnold & Ormerod, 1997; Marshall & Elliott, 1998; Josefson & Hansen, 2004). In Florida, for example, temperature, salinity and sedimentation limited coral abundance,

diversity and distribution within Biscayne Bay. In the bay, sedimentation rates were very high, often burying corals. Temperatures also exhibited high fluctuations, known to cause severe coral stress and mortality. The inshore environment of the bay, furthermore, experienced low mean salinity and high salinity fluctuation due to freshwater inputs (Lirman et al., 2003).

In addition to influencing the species composition of reefs, the fluvial influx appears to have had an impact on the habitat structure of these reefs. Inshore reefs such as Lae Lae, for example, usually consist of cay-crowned reefs with relatively low live coral cover and are predominantly composed of hard rock substrata (e.g. dead coral) and soft sediment. As the distance from shore increases, the reefs change to live coral dominated reefs crowned by islets and submarine shoals with relatively few emerging cays. Coral cover can be very high on exposed offshore reefs, particularly in the proximity of the reef barrier.

In summary, results of the present study indicate that sponge assemblages within the Spermonde are structured by environmental variables. Understanding the nature of these environmental constraints is essential for the protection and sustainable exploitation of sponges and other marine taxa. In order to conserve biodiversity by designing and placing conservation refugia in appropriate locations, it is crucial to understand the spatial patterns of species and how assemblages change in space (Plotkin & Muller-Landau, 2002; Tuomisto et al., 2003). Species with pronounced environmental preferences may also be expected to be particularly susceptible to environmental degradation and may be locally extirpated if their environment is greatly altered.

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