

Relating species traits of foraminifera to environmental variables in the Spermonde Archipelago, Indonesia

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ABSTRACT: It is essential to understand how spatial differences in community composition are related to environmental variables in order to explain and predict patterns in biodiversity. We investigated spatial variation in the composition of foraminifera assemblages and assessed the degree to which this could be explained by environmental variables and/or the distance among sample sites. Together, environmental and spatial variables explained 33.5% of the spatial variation in assemblage structure, of which 25.7% was due to environmental variables alone, 2.8% due to spatial variables alone and 5.0% due to covariation of environmental and spatial variables. Associations between the distribution of foraminifera and environmental variables were significantly influenced by species traits. Dinoflagellate symbionts and an orbitoidal chamber arrangement were linked to exposed reefs and a hard substrate, whereas rhodophyte symbionts were linked to sheltered reefs and a sandy substrate. With respect to depth, a hyaline skeletal structure was most strongly associated with deep water, whereas dinoflagellate and rhodophyte symbionts, an orbitoidal chamber arrangement and an imperforate skeletal structure were most strongly associated with shallow water environments. The association with given environmental variables was less pronounced for other traits. Species with spines, for example, were usually restricted to hard-substrate environments, and species with a coin shape to shallow-water environments, but there were species that deviated strongly from this general trend. Results of this study highlight the importance of environment variables in structuring foraminifera assemblages, and further identify traits that appear to influence how species respond to these conditions.

KEY WORDS: Community composition · Coral reef · CCA · Indonesia · Ordination · RLQ · Sulawesi

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INTRODUCTION

A key goal of predictive ecology is to assess whether species will persist under changing environmental conditions. The occurrence of a species in a habitat patch will depend on the fit between its traits and the environmental conditions of the habitat patch in question, an ecological process. However, the presence of those traits is the product of evolutionary processes (Ribera et al. 2001). By sampling species and relating their presence to environmental variables, it should be possible to understand the environmental constraints

under which species persist and how biological traits can determine the locations of species within an ecosystem (Legendre et al. 1997). Importantly, previous studies have found that certain traits can predispose species to local extirpation under human-induced or other forms of disturbance (Henle et al. 2004). Identifying these traits and their association with environmental variables is essential for effective management and protection of marine taxa. Furthermore, ascertaining traits associated with disturbance sensitivity allows us to assign species to functional types, which will facilitate conservation by reducing the diversity of species

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to operational entities for prediction and modelling (Henle et al. 2004).

Previous studies have related variation in species traits to habitat use, including the use of disturbed environments. In Moorea, Legendre et al. (1997) studied fish assemblages across a range of habitats and related species traits to environmental variables, including offshore distance, depth and substrate type. The studied traits included feeding habits, ecological category (e.g. bottom dweller, pelagic species etc.), size class, egg type and activity rhythm. In general, results of Legendre et al.'s (1997) study confirmed predictions of habitat use based on species traits. Elsewhere (America and Europe), Lamouroux et al. (2002) showed that there was a strong effect of geomorphology and hydraulics on fish species-trait proportions. Traits of fish such as size and fecundity were, for example, related to variation in stream hydraulics, whereas shape and swimming factor were better related to geomorphology. Lamouroux et al. (2002) suggested that species that use e.g. pool-type habitats probably experience weaker selective pressures for being streamlined, small, benthic or strong swimmers owing to the lack of continuous high shear stresses.

In the present study, larger benthic foraminifera (LBF) assemblages were assessed across the Spermonde Archipelago, Indonesia, with the goal of explaining spatial variation in community composition with spatial variables (distance between sample sites) and environmental variables including depth, water transparency and habitat characteristics based on remotely sensed (live coral cover) and locally measured environmental variables. Foraminifera are widely used as environmental indicators and typically respond rapidly to environmental changes. In particular, reef building, zooxanthellate corals and foraminifera containing algal symbionts have similar environmental requirements. LBF are characteristic of warm, shallow surface waters, are restricted to the euphotic zone, and are relatively small and abundant, thereby facilitating the relatively inexpensive collection of large sample sizes with minimal impact on reef resources (Hohenegger 2004). Important environmental characteristics that were previously shown to influence the occurrence of LBF on and around reefs include depth, temperature, salinity, siltation and hydrodynamic energy (Hohenegger et al. 1999, Renema & Troelstra 2001). Many of these variables are interrelated and, apart from their magnitude, the (seasonal) variability is also important in structuring LBF communities (Renema & Troelstra 2001). Light intensity at the sea floor is controlled by water transparency and depth; transparency, however, is also affected by several environmental variables such as plankton densities, terrigenous influence, turbidity, substrate type

etc. (Renema & Troelstra 2001, Beavington-Penney & Racey 2004). Environmental factors, and possibly also interaction with other species, affects the distribution of LBF and results in left (shallow) or right (deep) skewness of the distribution of species (Hohenegger 2004).

LBF represent a polyphyletic group that contains a large amount of variation in shell structure and morphology. The occurrence of several types of symbionts further affects the distribution of species. There are 4 main types of endosymbionts recorded in larger foraminifera. Each of them is found in a limited set of taxa, which usually houses only 1 type of symbiont. The perforate nummulitids, amphisteginids and calcarinids and the imperforate alveolinids all house diatoms. Peneroplids house rhodophytic algae, most soritids have dinoflagellate symbionts, and *Parasorites* spp. and *Laevipeneroplis* spp. house chlorophytes. Since each symbiont type uses its own range of the light spectrum, the foraminiferal hosts are restricted in their depth distribution to depths at which that part of the light spectrum is available. Chlorophytes (using orange light) are usually restricted to the shallowest areas, whereas diatoms and dinoflagellates can live in the deepest settings.

Test shape varies in response to environmental variables both within and among species. Test shape is a compromise between hydrodynamic energy resistance and light and metabolic requirements (Haynes 1965, Hallock et al. 1991). In shallow water, irradiation levels are high, and the light intensity reaching the symbiont must be reduced. This can either be achieved by moving the symbionts towards less irradiated places within the test (Leutenegger 1977, Hottinger 2005) or by thickening the test wall (Hallock et al. 1986). In contrast, in deep water, light intensity reaches very low levels and the host must find a way to concentrate the light on the symbionts. This is achieved by flattening the shell and by the production of interseptal piles. These interseptal piles increase the strength of the shell (allowing even further thinning) and serve as lenses to concentrate the available light on the symbionts (Hottinger 1997, 2000). These very thin shells are prone to breakage and can only live under very calm conditions, while more robust shells can occur in areas with higher hydrodynamic energy, where they should not break or be swept away or buried by sediment. Breakage is prevented by a more robust test. The development of a protoplasm sheath (e.g. *Heterostegina depressa*), pseudoplasm plugs at the end of spines (calcarinids) or changes in morphology of the apertural faces (amphisteginids) increase the potential to stick to the substrate surface (Hottinger 2000).

In the present study, variation in community composition was first related to environmental variables using canonical correspondence analysis (CCA), after

which the association between foraminifera traits including form/shape, symbiont type, chamber arrangement and skeletal structure and environmental variables was assessed using RLQ analysis (Dolédec et al. 1996, Ribera et al. 2001). With RLQ analysis, differences in habitat and environment can be directly related to species traits, instead of initially to taxonomic composition and then only indirectly to the functional traits of the species. This opens up the possibility for the use of species traits and RLQ scores in conservation management, in order to monitor and predict the effects of changes in land use (Ribera et al. 2001).

Our aims were to (1) identify the gradients of variation in community composition among sites in relation to environmental and spatial variables and (2) identify significant associations between biological traits and environmental variables.

MATERIALS AND METHODS

Study site. Sampling took place within the Spermonde Archipelago, southwest Sulawesi, Indonesia (Fig. 1). The Spermonde Archipelago, which developed during the Holocene sea level rise on top of Pleistocene topography (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. Reefs of the Spermonde are usually cay crowned (Umbgrove 1929, 1930, Renema 2002): the west side of these cays are exposed to oceanic swell and coral covered, the east side generally consists of carbonate sand with isolated coral patches. 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 (Edinger et al. 1998).

Data collections. Species datasets: LBF (size > 0.5 mm) and environmental data were sampled from July to October 1997. Sample stations were selected so that a wide range of microhabitats were covered along an in-to-offshore gradient (Fig. 1). At each station, samples were collected by SCUBA diving. During a dive, samples were taken every 2 to 3 m starting at 30 to 35 m depth (or shallower if the slope did not extend this far). In total, foraminifera were collected from 180 circular 1000 cm² plots.

The micro-substrate on which each sample was found was noted and fell within the following 5 categories from increasing soft to hard substrate: (1) sand;

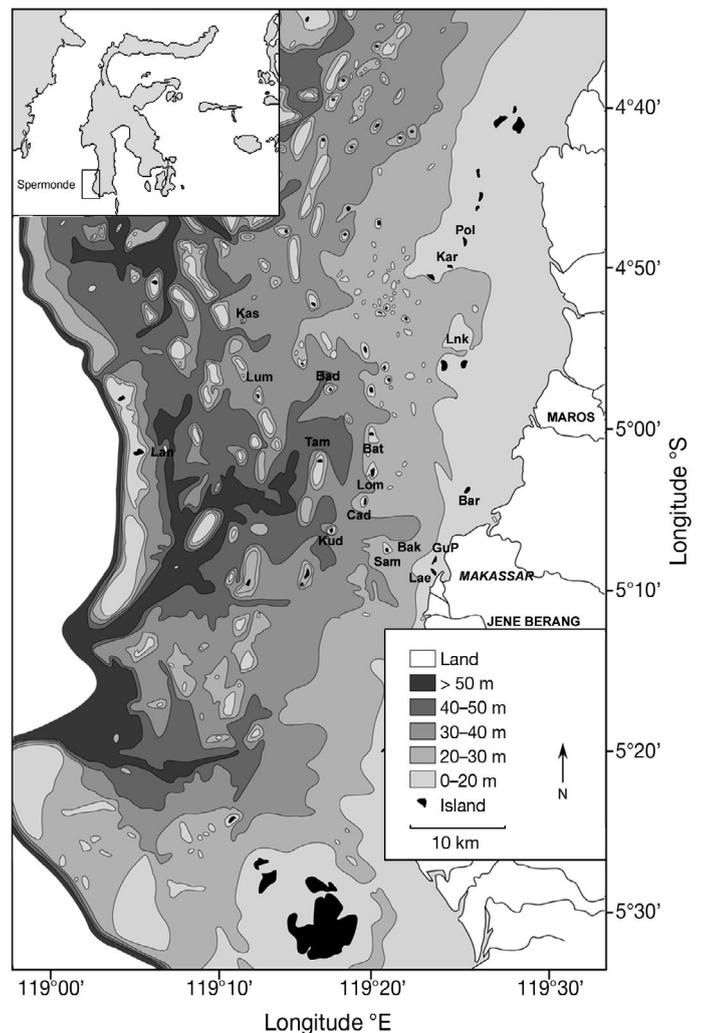


Fig. 1. Spermonde Archipelago, where various reefs were sampled. Isobaths are shown. Inset in upper left-hand corner shows location of the Spermonde Archipelago off the coast of Sulawesi, Indonesia. Reefs sampled include Badi (Bad; 2 sites), Bone Baku (Bak; 2 sites), Barang Barangan (Bar; 1 sites), Bone Batang (Bat; 2 sites), Barang Caddi (Cad; 1 sites), Gusung Panyoa (GuP; 2 sites), Karangan (Kar; 2 sites), Karang Krassi (Kas; 1 site), Kudingareng Keke (Kud; 3 sites), Lae Lae (Lae; 2 sites), Lankai (Lan; 2 sites), Lankadea (Lnk; 2 sites), Barang Lompo (Lom; 1 site), Lumulumu (Lum; 2 sites), Polewali (Pol; 2 sites), Samalona (Sam; 2 sites) and Bone Tambung (Tam; 2 sites)

(2) sand with seagrass; (3) sand with coral rubble; (4) coral rubble; (5) reef rock. Samples were sun-dried, after which the foraminifera were removed from their substrate. These were then sieved over a 0.5 mm sieve before sorting. The foraminifera that were alive when collected were separated from empty tests based on their symbiont colours. Voucher specimens were deposited at the National Museum of Natural History 'Naturalis', Leiden, The Netherlands.

Species traits: Traits were noted for each species based on (1) chamber arrangement (2) form, (3) symbiont and (4) skeletal material. The chamber arrangement was recorded as (1) trochospiral, (2) planispiral or (3) orbitoidal. The form was recorded as (1) coin-shaped, (2) lenticular or (3) spines. The symbionts were recorded as (1) chlorophytes (2) chloroplasts, (3) diatoms, (4) dinoflagellates or (5) rhodophytes. Skeletal structure was defined as (1) hyaline or (2) imperforate.

Environmental datasets: Locally assessed environmental variables (micro-substrate, water transparency) and the remotely sensed area of live coral formations were assessed for each site. Water transparency was measured multiple times at locations surrounding each sample site with a Secchi disk. The area of live coral formation (live coral cover > 60% of each pixel) was identified over a 500 × 500 m area surrounding each sample site with the use of a digital image based on automatic and supervised classification processes applied to a SPOT-XS satellite image (K-J/Sat: 320-370/3) recorded on August 30, 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 satellite data were collected as part of the Marine Resource & Education Project (MREP) and is presently managed by BAKOSURTANAL (Badan Koordinasi Survei dan Pemetaan Nasional), Indonesia.

In addition to above-mentioned 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 (G. Jimmink et al. unpubl., E. de Rooji & S. van Bruijnsvoort unpubl.). The current velocity was measured with a calibrated universal current meter (OTT Hydrometry), which consisted of a propeller placed at 3 m depth in the water column. Over 2 min, the number of revolutions made by the propeller was tallied. Velocity was subsequently calculated using the formula $v = 0.00118 + 0.00216n$, where v = current velocity (m s^{-1}) and n = number of turns per 2 min. Salinity and temperature were both measured with a Beckman portable salinometer (Beckman Instruments). The suspension load was assessed by collecting water samples with a horizontal water sampler from 3 m depth. At the Geological Laboratory, Hasanuddin University (Makassar, Indonesia), dry filters were weighed and placed in a filtering instrument, after which a known quantity of water was poured through a filter. Afterwards, filter and sediment were dried for 2 h in an oven at 105°C and weighed again. The difference in weight divided by the water volume is the suspended load concentration. All of these variables were assessed each hour in

a number of locations surrounding the sampling sites during 25 h measuring events. In the analyses, both the mean value for each environmental variable and the SD (fluctuation) recorded over the 25 h sampling event were used. A single location was sampled during each 25 h sample event. This dataset was utilized to predict values for each reef using ArcGIS Geostatistical Analyst (ESRI; www.esri.com). 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.

Analyses. Ordination: Direct gradient analysis using canonical correspondence analysis (CCA within CANOCO for Windows version 4; ter Braak & Smilauer 1998) was used to assess environmental gradients in the species data matrix. CCA arranges sites and species in a multidimensional space, whereby the axes are constrained to be linear combinations of environmental variables (Ohmann & Spies 1998). In CCA, the amount of variation in the species matrix 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. TV is the ratio of the dispersion of species scores to plot scores in the species-by-plot data matrix. Input for the CCA consisted of $\log_{10}(x + 1)$ transformed species abundance data; note that only species that were recorded at >5 sites were included. The environmental dataset used in the CCA consisted of the following variables: (1) depth; (2) maximum water transparency; (3) micro-substrate (sand, 1; sand with seagrass, 2; sand with coral rubble, 3; coral rubble, 4; reef rock, 5); (4) area of coral formations; (5) mean salinity; (6) mean suspended sediment load; (7) mean temperature; (8) mean current velocity; (9) SD salinity; (10) SD suspended sediment load; (11) SD temperature; and (12) SD current velocity. The importance of space in explaining variation in composition was assessed by supplementing the spatial universal transverse mercator (UTM) coordinates (easting 'x' and northing 'y') with all the terms of a bi-cubic trend surface, (i.e. x , y , x^2 , xy , y^2 , x^3 , x^2y , xy^2 and y^3 ; see Borcard et al. 1992).

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. In 'Results', the conditional

effects of environmental and spatial variables on composition (λ_A) are presented in addition to p-values from the Monte Carlo test. The conditional effects (λ_A) 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. Variance partitioning was subsequently used to partition the spatial variation in composition into variation only explained by spatial variables, variation only explained by environmental variables and variation explained by covariation of environmental and spatial variables. A quantitative variance partitioning technique, described in detail by Borcard et al. (1992), was used on results of separate partial CCAs.

As a complement to the species ordination analysis above, we assessed univariate variation in the abundance of a subset of species with depth using CurveExpert 1.3 (available at <http://curveexpert.webhop.biz>), which uses the Levenberg-Marquardt method to solve non-linear regressions and automatically selects the best fitting functions. In the present study, Gaussian

$$(y = ae^{-\frac{(x-b)^2}{2c^2}}), \text{ logistic } (y = \frac{a}{1+b^{-cx}}) \text{ and rational } (y = \frac{a+bx}{1+cx+dx^2})$$

were only used from offshore reefs owing to the limited depth range in inshore reefs.

Association of species traits with environmental variables: Species traits were directly linked to environmental variables with a 3-table ordination method known as RLQ analysis (Dolédéc et al. 1996, Ribera et al. 2001). RLQ analysis is an extension of coinertia analysis; 'R' is a table of p environmental variables at m locations, 'L' a contingency table representing the abundance of k species at m locations and 'Q' a table of k species with n biological traits. When using RLQ analysis, both traits and environmental conditions affected by disturbance, as well as their interrelationships, can be assessed (Dolédéc et al. 1996, Ribera et al. 2001).

Three separate ordinations of the R (environmental variable), L (species composition), and Q (species trait) tables were performed prior to the coinertia analysis (see Fig. 2). First, the species abundance table containing the $\log_{10}(x+1)$ abundance of each species occurring at each site was analysed by correspondence analysis (CA), an eigenanalysis approach that provides a joint scaling of sites and species scores. Only species observed at 5 sites or more were included in the analyses owing to the sen-

sitivity of correspondence analysis to 'rare' species (Lesica & Cooper 1998). We also excluded *Celanthus craticulatum*, '*Parasorites*' sp. 2 and *Alveolinella quoyii* because they were the only species (>5 ind.) to have chloroplast symbionts, chlorophyte symbionts or a fusiform chamber arrangement respectively. The sites and species scores (or coordinates) were used to link the R and Q tables, because sites are shared by the R and L tables and species are shared by the Q and L tables (Ribera et al. 2001). Next, the relationship between sites and environmental attributes (i.e. R table) was analysed. For the quantitative set of variables, principal components analysis (PCA) was applied using weights obtained from the CA of species, thereby linking the R to the L table. The final step in this initial procedure was the analysis of the Q table of categorical species traits, with row weights obtained from the correspondence analysis of species, using multiple correspondence analysis (Tenenhaus & Young 1985). After these 3 steps, a single inertia analysis was performed on the cross-matrix of R, L and Q. The significance of the relationship between the environmental attributes (R) and species traits (Q) was assessed with a Monte Carlo permutation test (Dolédéc et al. 1996). All analyses were carried out using the ADE4 software package (<http://pbil.univ-lyon1.fr/ADE-4>) within R (www.r-project.org).

RESULTS

Ordination

In the CCA, the total inertia (sum of all unconstrained eigenvalues) in the dataset was 1.867 and the sum of all constrained (canonical) eigenvalues 0.625 (Figs. 2 & 3). The environmental and spatial variables thereby explained 33.5% of the variation in the dataset, of which 2.8% was due to the purely spatial component, 5.0% due to the spatially structured environmental component and 25.7% due to the purely environmental component. The eigenvalues of the first 4 axes were 0.303 (variation explained [VE] = 16.2%), 0.162 (VE = 8.7%), 0.065 (VE = 3.5%) and 0.035 (VE = 1.9%) for the 1st, 2nd, 3rd and 4th axes respectively. The species-environment correlations of the first 4 axes were moderate to high (range: 0.589 to 0.910), indicating a reasonably strong association between the species matrix and the environmental matrix. A Monte Carlo test revealed that the first axis, and all 4 axes taken together, explained a highly significant amount of variation in community structure (both tests, $p < 0.001$).

Significant environmental variables selected with a Monte Carlo forward selection procedure included depth ($\lambda_A = 0.25$, $p < 0.001$), micro-substrate ($\lambda_A = 0.15$,

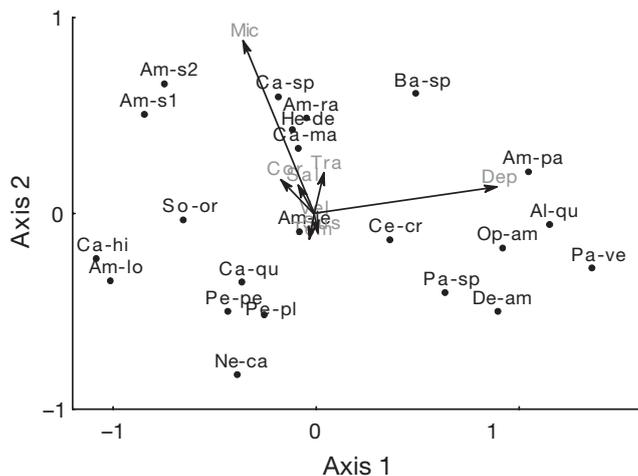


Fig. 2. Ordination based on CCA: 1st and 2nd axes. Biplots show species and environmental variables. Selected species indicated by 4-letter abbreviations (see Table 1 for full names). Arrows represent environmental factors: The orthogonal projection of a species-point onto an environmental arrow represents the approximate center of the species distribution along a particular environmental gradient. Dep, depth; Mic, micro-substrate; Tra, water transparency; Cor, area of coral formation; Vel, mean velocity; Tem, SD of temperature; Sal, mean salinity; Sus: SD of suspended sediment load.

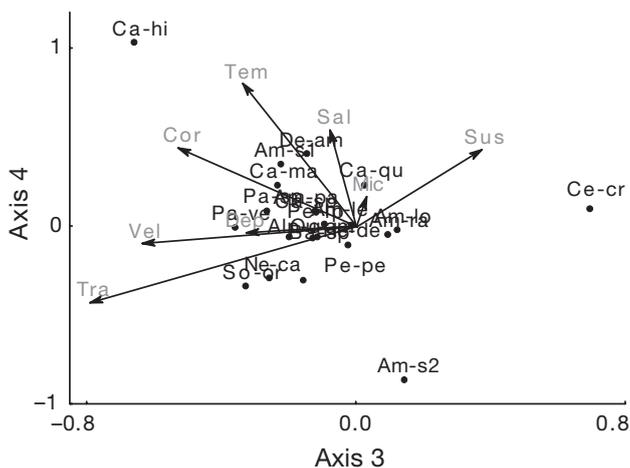


Fig. 3. Ordination based on CCA: 3rd and 4th axes. Abbreviations as in Fig. 2

$p < 0.001$), water transparency ($\lambda_A = 0.06$, $p < 0.001$), area of coral formations ($\lambda_A = 0.03$, $p < 0.001$), SD of temperature ($\lambda_A = 0.03$, $p < 0.001$), mean velocity ($\lambda_A = 0.03$, $p < 0.001$), mean salinity ($\lambda_A = 0.02$, $p < 0.001$) and the SD in suspended sediment load ($\lambda_A = 0.02$, $p < 0.001$). Significant spatial factors included x^3 ($\lambda_A = 0.04$, $p < 0.001$), x ($\lambda_A = 0.03$, $p < 0.001$) and xy ($\lambda_A = 0.04$, $p < 0.001$). Ordinations of the CCA constrained using environmental variables only are presented in Fig. 2, 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 shallow water (low Axis 1 values, i.e. Fig. 2 x-axis) (Table 1) included *Calcarina hispida*, *Amphistegina lobifera* and *Amphisorus* spp., whereas species strongly associated with deeper water (high Axis 1 values, i.e. Fig. 2 x-axis) included *Dendritina ambigua*, *Amphistegina papillosa*, *Palaeonummulites venosus*, *Alveolinella quoyii* and *Operculina ammonoides*. Species strongly associated with a hard micro-substrate (high Axis 2 values, i.e. Fig. 2 y-axis) included *Amphisorus* spp., *Amphistegina radiata*, *Calcarina spengleri* and *Baculogypsinoides spinosus*, while species associated with a sandy micro-substrate (low Axis 2 values, i.e. Fig. 2 y-axis) included *Dendritina ambigua*, *Peneroplis* spp. and *Neorotalia calcar*. Species moderately associated with increasing water transparency and the area of coral formation (low Axis 3 values, i.e. Fig. 3 x-axis) included *Sorites orbiculus*, *Palaeonummulites venosus* and *Calcarina hispida*. The only species with a pronounced inshore distribution was *Celanthus craticulatum*.

The importance of depth in structuring foraminifera assemblages in midshelf reefs is illustrated in Fig. 4. Correlations between observed and fitted values using various functions varied from 0.896 to 0.999 (Table 2). In Fig. 4, *Amphistegina lobifera* and *Amphisorus* sp. 1 prefer shallow water (<10 m depth); *Calcarina spengleri* and *Heterostegina depressa* prefer intermediate depths and reach maxima between 10 and 20 m; *Operculina ammonoides*, *Baculogypsinoides spinosus*, *Amphistegina papillosa* and *Celanthus craticulatum* prefer deeper water (>20 m). Note that in inshore reefs, *C. craticulatum* prefers shallower depths (10 to 20 m).

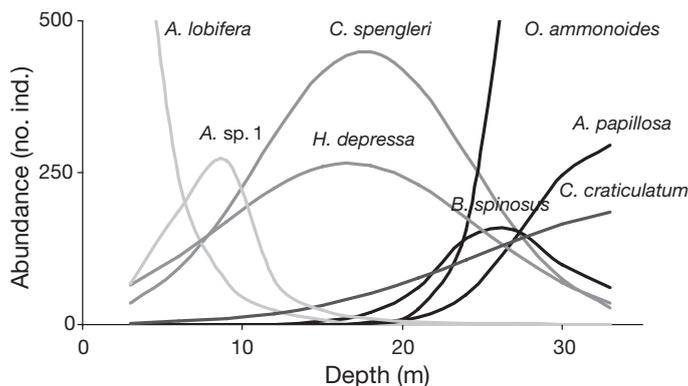


Fig. 4. Relationship between abundance and depth for a subset of the most-abundant foraminifera species sampled during this study: *Calcarina spengleri*, *Baculogypsinoides spinosus*, *Amphistegina lobifera*, *Amphistegina papillosa*, *Operculina ammonoides*, *Heterostegina depressa*, *Celanthus craticulatum* and *Amphisorus* sp.1 (cf. *A. saurosenensis*) Lines represent fits to observed data from plots in mid-shelf reefs

Table 1. Species encountered during surveys of the Spermonde Archipelago. n, total abundance; Code, species abbreviation used in Figs. 2 & 3; Dinoflag, Dinoflagellates; Chloropl, chloroplasts; Chloroph, chlorophytes; Rhodoph, rhodophytes; Imper, imperforate. Axis values refer to species scores for the first 4 axes obtained from CCA

Species	n	Code	Chamber arrangement	Form	Symbiont	Skeletal structure	Axis 1	Axis 2	Axis 3	Axis 4
<i>Alveolinella quoyii</i>	233	Al-qu	Fusiform	Spindle	Diatoms	Imper	1.166	-0.058	-0.197	-0.079
<i>Amphisorus</i> sp. 1	1945	Am-s1	Orbitoidal	Coin	Dinoflag	Imper	-0.831	0.505	-0.222	0.328
<i>Amphisorus</i> sp. 2	478	Am-s2	Orbitoidal	Coin	Dinoflag	Imper	-0.731	0.661	0.144	-0.882
<i>Amphistegina lessonii</i>	24485	Am-le	Planispiral	Lenticular	Diatoms	Hyaline	-0.067	-0.094	-0.014	-0.009
<i>Amphistegina lobifera</i>	7005	Am-lo	Planispiral	Lenticular	Diatoms	Hyaline	-0.997	-0.348	0.125	-0.040
<i>Amphistegina papillosa</i>	1524	Am-pa	Planispiral	Lenticular	Diatoms	Hyaline	1.060	0.212	-0.116	0.061
<i>Amphistegina radiata</i>	7583	Am-ra	Planispiral	Lenticular	Diatoms	Hyaline	-0.031	0.483	0.096	-0.066
<i>Baculogypsinoides spinosus</i>	766	Ba-sp	Trochospiral	Spines	Diatoms	Hyaline	0.509	0.608	-0.128	-0.084
<i>Calcarina hispida</i>	111	Ca-hi	Trochospiral	Spines	Diatoms	Hyaline	-1.066	-0.232	-0.657	1.013
<i>Calcarina mayori</i>	807	Ca-ma	Trochospiral	Spines	Diatoms	Hyaline	-0.071	0.332	-0.233	0.212
<i>Calcarina quoyii</i>	4209	Ca-qu	Trochospiral	Spines	Diatoms	Hyaline	-0.348	-0.354	0.026	0.215
<i>Calcarina spengleri</i>	3367	Ca-sp	Trochospiral	Spines	Diatoms	Hyaline	-0.169	0.594	-0.120	0.065
<i>Celanthus craticulatum</i>	5009	Ce-cr	Trochospiral	Lenticular	Chloropl	Hyaline	0.381	-0.135	0.696	0.080
<i>Dendritina ambigua</i>	414	De-am	Planispiral	Lenticular	Rhodoph	Imper	0.911	-0.504	-0.145	0.389
<i>Heterostegina depressa</i>	3803	He-de	Planispiral	Lenticular	Diatoms	Hyaline	-0.102	0.428	-0.024	-0.122
<i>Laevipeneroplis malayensis</i>	15			Coin	Chloroph	Imper				
<i>Neorotalia calcar</i>	2502	Ne-ca	Trochospiral	Spines	Diatoms	Hyaline	-0.371	-0.827	-0.258	-0.311
<i>Operculina ammonoides</i>	9032	Op-am	Planispiral	Coin	Diatoms	Hyaline	0.935	-0.177	-0.115	-0.080
<i>Operculina complanata</i>	6		Planispiral	Coin	Diatoms	Hyaline				
<i>Palaeonummulites venosus</i>	644	Pa-ve	Planispiral	Lenticular	Diatoms	Hyaline	1.378	-0.283	-0.359	-0.025
'Parasorites' sp. 2	461	Pa-sp	Orbitoidal	Coin	Chloroph	Imper	0.653	-0.407	-0.263	0.070
<i>Peneroplis pertusus</i>	95	Pe-pe	Planispiral	Coin	Rhodoph	Imper	-0.420	-0.506	-0.156	-0.319
<i>Peneroplis planatus</i>	1903	Pe-pl	Planispiral	Coin	Rhodoph	Imper	-0.238	-0.523	-0.094	-0.003
<i>Sorites orbiculus</i>	78	So-or	Orbitoidal	Coin	Dinoflag	Imper	-0.639	-0.035	-0.328	-0.357

Association of species traits with environmental variables

RLQ analysis revealed a highly significant (Monte Carlo test; $p < 0.001$) relationship between environmental variables and species traits. We only consider the first 2 RLQ axes, which together explained 92.1% of variance in the analysis. Because the RLQ analysis represents the partial ordination of the environmental characteristics, the species abundances and the species traits, the proportion of variance attributed to each

Table 2. Relationship between abundance and depth for a subset of the most common species. Correlations indicate fits to observed transect data with various functions

Species	Function	Correlation
<i>Calcarina spengleri</i>	Gaussian	0.973
<i>Baculogypsinoides spinosus</i>	Rational	0.971
<i>Amphistegina lobifera</i>	Rational	0.999
<i>Amphistegina papillosa</i>	Logistic	0.997
<i>Operculina ammonoides</i>	Logistic	0.922
<i>Heterostegina depressa</i>	Gaussian	0.896
<i>Celanthus craticulatum</i>	Gaussian	0.981
<i>Amphisorus</i> sp. 1	Rational	0.998

matrix was compared with that resulting from their separate analyses. The first (eigenvalue = 0.050; VE = 69.8%; covariance = 0.223; correlation = 0.247) and second (eigenvalue = 0.016; VE = 22.3%; covariance = 0.126; correlation = 0.116) axes of the RLQ analysis accounted for 56.8% (4.07/7.18) and 76.1% (0.982/1.291) of the variance of the first 2 axes of the separate analyses of environmental variables and traits.

The RLQ analysis showed that differences between exposed sites with a hard substrate and sheltered sites with a sandy substrate (Fig. 5) accounted for most of the variation (69.8%) in species traits (Fig. 6), in as far as this could be related to the available set of environmental predictors. Traits including dinoflagellate symbionts and an orbitoidal chamber arrangement were linked to environmental conditions found in exposed, hard-substrate sites. In contrast, rhodophyte symbionts were linked to sheltered, soft-substrate sites. The second RLQ axis accounted for an additional 22.3% of variation. A hyaline skeletal structure was the trait most strongly linked to deep-water environments, whereas dinoflagellate and rhodophyte symbionts, an orbitoidal chamber arrangement and an imperforate skeletal structure were linked to shallow-water environments.

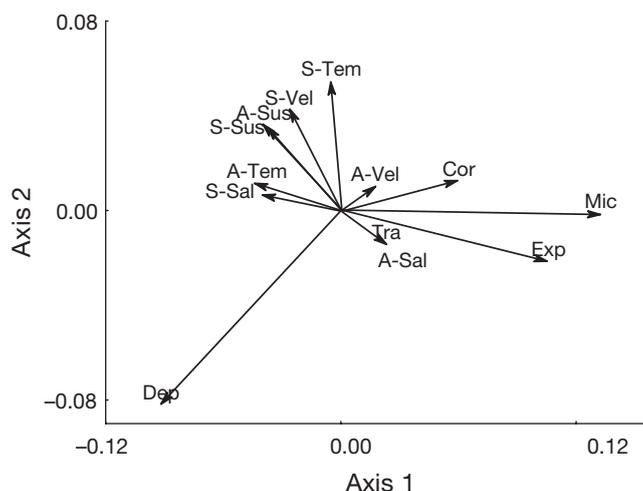


Fig. 5. RLQ scores of environmental variables. Dep, depth; Mic, micro-substrate; Cor, area of coral formation; Tra, transparency; Exp, exposure; A-Vel, average velocity; A-Tem, average temperature; A-Sus, average suspension load; A-Sal, average salinity; S-Vel, SD in velocity; S-Tem, SD in temperature; S-Sus, SD in suspension load; S-Sal, SD in salinity

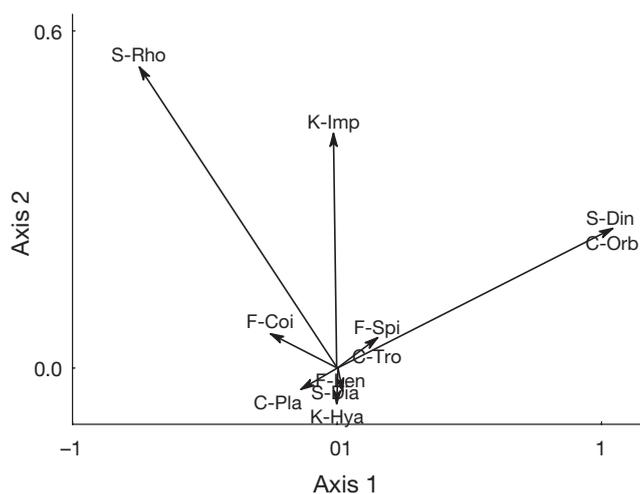


Fig. 6. RLQ scores of species traits. C-Orb, orbitoidal chamber arrangement; C-Pla, planispiral chamber arrangement; C-Tro, trochospiral chamber arrangement; F-Coi, coin form; F-Len, lenticular form; F-Spi, spiny form; S-Dia, diatom symbionts; S-Din, dinoflagellate symbionts; S-Rho, rhodophyte symbionts; K-Hya, hyaline skeletal structure; K-Imp, imperforate skeletal structure

DISCUSSION

Under the prevalent conditions of this study, without obvious habitat discontinuities that could act as dispersal barriers, foraminifera significantly responded to spatial variance in environmental conditions. Environmental and spatial variables, together explained 33.5% of the

variation in community composition. However, although there was a significant spatial component, space alone only explained 2.8% of the total variation. The modest amount of variation explained by spatial versus environmental variables is an indication that dispersal limitation only plays a minor role in structuring foraminifera assemblages within the study area. Various studies have attributed spatial variation in community structure predominantly to deterministic (environmental) processes (Cleary et al. 2004, Williams & Wisner 2004, Cleary & Genner 2006, Cleary et al. 2006, de Voogd et al. 2006). However, most of the variation in composition remained unexplained, as was also the case in the above-mentioned studies, which is logical when dealing with diverse assemblages and where the presence of e.g. rare species cannot be related to environmental gradients. Unexplained variation in community similarity may also be due to the effects of unmeasured environmental variables, such as the abundance of food, predators, or parasites. However, it is also probably linked to the influence of stochastic events on local survivorship or recruitment (Newberry et al. 1996, Nekola & White 1999). In foraminifera, the major environmental constraints were depth, micro-substrate and water transparency, the latter of which was a function of in-to-offshore processes. In the Spermonde, there is a cross-shelf vectorial gradient of decreasing land-based influence and increasing shelf depth and photic zone (Edinger et al. 1998, Renema 2002). Fluvial input from various river systems is the most dominant environmental factor; however, 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 northwest monsoon, and this time of year is also associated with increased fluvial discharge and the inflow of terrigenous sand and silt.

Variation in depth has been previously identified as a significant variable in the diversity and distribution of various taxa including Mexican hexacorals (Torruco et al. 2003), Indopacific scleractinian corals (Baird et al. 2003), Tanzanian corals and fishes (Garpe & Ohman 2003) and Indonesian sponges (de Voogd et al. 2006). Depth is a composite environmental variable that influences assemblages by reducing light transparency, which in turn is influenced by nutrient availability and fluvial influx. A high fluvial influx will invariably reduce transparency, due to higher concentrations of inorganic and organic particles coupled with increased planktonic abundance (Renema 2002). Temperature and hydrodynamic energy also decline with depth. In the Spermonde, the hydrodynamic energy also varies depending on the exposure to oceanic swell. In areas with elevated rates of hydrodynamic energy, organisms can be swept away, fragmented, or are not able to successfully settle. Waves can affect substrate/habitat composition by

breaking down coral colonies and creating open patches with coral rubble that can be used as a substrate for marine organisms.

Although cross-shelf variation in foraminifera assemblages was less pronounced than in other taxa in the Spermonde (Cleary et al. 2005), it proved a significant determinant of foraminifera composition as reflected by the importance of water transparency, and the area of coral formations, which both increased from inshore to offshore (Cleary et al. 2005). The only abundant species on inshore reefs was *Celanthus craticulatum*, in line with the findings of Renema & Troelstra (2001). The species is, however, also abundant in reef-base assemblages. In midshelf reefs, the species had a pronounced preference for deeper environments and was virtually absent from shallow-water environments. The chloroplast husbandry (instead of symbiosis) of *C. craticulatum* is probably directly related to environmental variables by conferring greater resistance to increased and (seasonally) variable nutrient availability (Renema & Troelstra, 2001). The deepest part of the photic zone and the coastal area are most subject to seasonal changes in light intensity and nutrient levels.

We found a significant association between environmental variables and species traits, which appeared to be particularly driven by variation in symbiont type. Diatom-bearing species occur abundantly on coral rubble in shallow environments as well as on sandy substrate in deep environments (e.g. *Operculina ammonoides* and *Amphistegina papillosa*), and were the symbionts with the strongest association with deep water. Most shallow-living foraminifera such as *Lavipeneroplis malayensis* or the dinoflagellate-bearing *Amphisorus* sp. 1 and *Sorites orbiculus* occurred amongst rubble at the exposed sides of reefs. However, species with rhodophytes such as *Peneroplis pertusus* and *Peneroplis planatus* were mainly found on sandy substrate at relatively modest depths and were absent from deeper environments. These species were particularly abundant in sheltered reef environments where sand often accumulates. In other areas, such as Berau and Wakatobi, Indonesia, rhodophyte-bearing species are particularly abundant in very shallow reef flat conditions (W. Renema pers. obs.).

Other traits, such as form and skeletal structure, showed considerable variation in habitat. Coin-shaped species, for example, were generally found in shallow-water environments. Coin-shaped foraminifera that house diatoms usually have imperforate tests in which the calcite crystals are randomly orientated (Anderson & Bé 1978). This reduces the transparency of the test and, in order for the symbionts to receive enough light, higher light intensities are necessary than would be required by more transparent and perforate hyaline tests. In shallow-water environments, the coin-shaped foraminifera can regulate the exposure to light by moving the symbionts

in their test. However, this light-regulation system only functions when they are attached to a dark, light-adsorbing substrate, i.e. coral rubble covered by coralline algae. Exceptions to this trend included *Parasorites* sp., which — despite having an imperforate test — preferred deeper environments, and *Operculina ammonoides*, which was coin-shaped but had a hyaline test and a pronounced preference for deep-water environments. Species with spiny tests were in general restricted to highly structured coral rubble habitats, which are in turn restricted to the exposed reef slope, and thus usually occur at shallower depths than do species associated with the sandy reef base. Again, a notable exception was *Neorotalia calcar*, which showed a strong preference for sandy substrate environments.

Lenticular species occurred predominantly on the reef slope and reef base but over a large depth range, with species such as *Amphistegina lobifera* preferring shallow-water and species such as *Amphistegina papillosa* deep-water environments. *Amphistegina* spp. and *Heterostegina depressa* are able to attach to rubble, and thus can survive intermediate exposure to hydrodynamic energy. However, upper-slope and reef-flat (i.e. shallow) environments are exposed to levels of hydrodynamic energy that are too high; therefore, these species are usually swept away. Poorly attaching species such as *Operculina* spp. and *Palaeonummulites venosus* that lay about on the sediment surface were generally restricted to deeper-water environments.

In summary, this study demonstrated that foraminifera assemblages in the Spermonde Archipelago are strongly associated with spatial variance in the environment, implying that deterministic ecological processes are important in structuring observed spatial variation in assemblage structure. In turn, species traits — particularly symbiont type — influence how species respond to this environmental variation.

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