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## ORIGINAL ARTICLE

# An analysis of sponge diversity and distribution at three taxonomic levels in the Thousand Islands/Jakarta Bay reef complex, West-Java, Indonesia

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## Keywords

Coral reef; disturbance; Indonesia; Java; sponges; taxonomic levels; Thousands Islands.

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## Abstract

Very few coral reefs are located close enough to large cities to study the influence of large urban populations on reef assemblages. An exception is the Thousand Islands reef complex to the north of Jakarta, the capital city of Indonesia, and one of the largest conurbations in the world. Here we present data from a detailed survey where sponge assemblages were assessed at 30 patch reefs associated with islands in three coastal zones along an in-to-offshore gradient. Sponge assemblages are described at three taxonomic levels of detail (species, genus and family level). We recorded a total of 118 sponge species, 64 genera and 36 families, *Aaptos suberitoides* (Brønsted, 1934), *Clathria (Thalysias) reinwardti* (Vosmaer, 1880), *Petrosia (Petrosia) nigricans* (Lindgren, 1897) and *Xestospongia testudinaria* (Lamarck, 1813) were the most common species overall. There was a pronounced difference in composition among zones with the most distinct difference between the inshore zone and the other two zones. The inshore environment was characterised by very high turbidity and low live coral cover; the dominant substrate consisted of algal turf and sand. Environmental conditions improved and sponge diversity increased further offshore, although most areas appeared to have been affected by some form of disturbance. Ordinations were also largely congruent, at species, generic and family levels of taxonomic resolution. This indicates that variation in composition at higher taxonomic levels is a good indicator of variation at lower taxonomic levels, at least when there is a pronounced environmental gradient.

## Problem

Urbanisation is expected to be a major determinant of species loss (McKinney 2002; Miller & Hobbs 2002). Relatively little is known about the impact of large human conurbations on coral reef ecosystems. The Pulau Seribu (Thousand Islands) and Jakarta Bay reef complex (hereafter known as PS) just to the north of Jakarta, the capital city of Indonesia, is exceptional in this respect. These reefs are well studied (Brown & Suharsono 1990; Tomashik *et al.* 1994; De Vantier *et al.* 1998; Cleary *et al.* 2006; Rachello-Dolmen & Cleary 2007) and one of the few

examples of still relatively intact reefs in the proximity of a major conurbation. At present, PS comprises around 105 island or cay-crowned reefs that are located in Jakarta Bay and extend to more than 80 km to the northwest of the bay. In recent years, a number of islands have disappeared due to severe environmental perturbation. All reefs are under various levels of pressure from a number of human activities including fishing, coral mining, dredging, anchor damage, oil spills, resort construction and the discharge of industrial and domestic effluent (Rees *et al.* 1999; Rachello-Dolmen & Cleary 2007). Sponge assemblages have not until present been assessed in PS. This is

due to the fact that they are one of the most difficult metazoan groups to identify, and are usually omitted from biodiversity assessments (Hooper *et al.* 2000). The difficulty of taxonomic identification previously hampered ecological studies of sponge assemblages (van Soest 1989; Hooper *et al.* 2000, 2002; de Voogd *et al.* 2006), but recent efforts have resolved many of the higher-order taxonomic problems and issues pertaining to species, generic and family synonyms (Hooper & van Soest 2002). Nevertheless, collection of data at species level is very time-consuming and requires a high degree of taxonomic expertise, especially in high diversity regions such as Indonesia. In addition, the intraspecific variation of some species can be so high that it is often very difficult to compare species assemblages across large geographic scales. Sponges are an important component of coral reefs, and together with soft and stony corals, form complex reef substrates and shelter a number of other invertebrate taxa (de Voogd *et al.* 2006). They compete intensively with other benthic taxa for available substrate and are therefore important components of reef dynamics (Van Veghel *et al.* 1996; Aerts & van Soest 1997; de Voogd *et al.* 2004). In addition to this, previous studies have demonstrated strong associations between sponge composition and environmental conditions, so that sponges could potentially be used as indicators in monitoring of marine habitats (Cleary & de Voogd 2007; de Voogd & Cleary 2007).

A number of studies have assessed to what degree taxonomic resolution (*e.g.* family level *versus* species level) influences our ability to detect structure in taxon composition (Williams & Gaston 1994; Balmford *et al.* 1996; Olgard *et al.* 1997; Stark *et al.* 2003; Anderson *et al.* 2005; Cleary *et al.* 2006). Hirst (2006) showed that family-level identifications were sufficient to differentiate faunal assemblages to a comparable resolution to species-level identifications on temperate rocky reef habitats in southern Australia. Olgard *et al.* (1997) showed that the level of congruence between species-level data sets and data sets aggregated at a higher taxonomic level was greater for macrofaunal communities disturbed by pollution than those inhabiting more pristine environments. Thus, the use of higher taxa, rather than species, may lead to greater efficiency, particularly for monitoring disturbed areas. When possible, species-level studies should be given preference, but given time constraints and when the goal is to monitor for disturbance, studies at higher taxonomic levels may be a practical compromise between time and financial constraints and level of survey detail.

Here we present data from a detailed survey of sponge assemblages on 30 patch reefs associated with islands in three zones along an in-to-offshore gradient in PS. Sponge assemblages are assessed at three taxonomic levels

of resolution (species, genus and family level) to determine whether higher level identifications (genus or family) mirror spatial variation in the composition assessed the species level.

## Material and Methods

### Study area

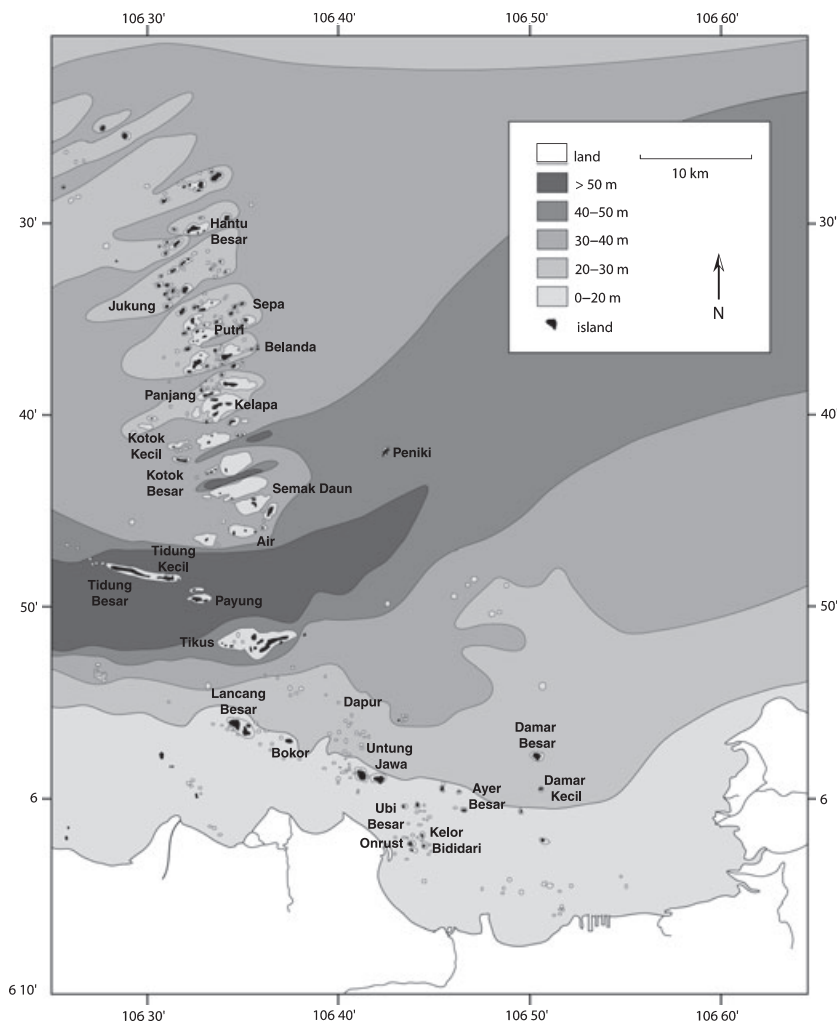
The research sites are located in the Pulau Seribu (Thousand Islands) and Jakarta Bay reef complex (northwestern coast of Java, Indonesia). The bay is bounded to the north by a 500-km<sup>2</sup> open embayment and the whole reef system extends >80 km to the northwest (Ongkosongo & Sukarno 1986; Fig. 1).

The Jakartan conurbation has at present >12 million inhabitants, and several rivers with a combined catchment area >2000 km<sup>2</sup>, which discharge storm water and sewage into the central sector of the bay, and two flanking delta systems with catchments totalling 6000 km<sup>2</sup>, which discharge peripherally (Rees *et al.* 1999). Annual precipitation averages 1700 mm·year<sup>-1</sup>, distributed in a 'wet' season from November to March, during the northwest monsoon, and a 'dry' season from May to September, during the southeast monsoon (Rees *et al.* 1999).

In the present study, we assess 30 reef sites associated with islands or shoals in three coastal zones, namely inshore, midshore and offshore. Inshore sites are located within 21 km from the port of Sunda Kelapa Jakarta (6°6'57" S, 106°48'28" E) (Fig. 1) and are dominated by sand and algal turf. The water quality is very poor, with high nutrient concentrations and accumulated rubbish. Severe contamination has been reported in the sediment and water of Jakarta Bay including heavy metals (Hg, Cd and Pb), pesticides (DDT and dieldrin) and pollution from oil spills (Hungspreugs 1988; Ongkosongo 1986 but see Williams *et al.* 2000 who suggest that the environment of Jakarta Bay was substantially cleaner in the mid 1990s than in previous decades). There is also a marked lack of primary sewerage treatment (Ongkosongo 1986). These reefs have also been seriously affected by dredging operations (De Vantier *et al.* 1998). Midshore sites are located 22–40 km from Jakarta and offshore sites more than 60 km from Jakarta. Shelf depth varies from shallow (a few meters) to a maximum of 20 m inshore, >50 m midshore, and up to 40 m offshore. For a more detailed description of the area, see Cleary *et al.* (2006) and Racheo-Dolmen & Cleary (2007).

### Data collection

Sampling took place using SCUBA diving on September 7–26, 2005 during a survey organised by the Research



**Fig. 1.** Map of the Jakarta Bay and the Thousand Islands (Pulau Seribu) reef complex. The sites sampled during this study are indicated.

Centre of Oceanography (PPO-LIPI) and the National Museum of Natural History, 'Naturalis', Leiden, the Netherlands. The northwestern sides of 30 patch reefs were visually surveyed during 1-h dives from deep (maximum 20 m) to shallow water (1 m). Smaller (cryptic, boring, and thinly encrusting <4 cm) sponge specimens were excluded from this study. Species were visually identified in the field, and fragments of all species were collected for closer examination and identification at species level. Voucher specimens were preserved in 70% ethyl alcohol and deposited in the sponge collection of "Naturalis" (RMNH Porifera).

#### Data analyses

Total species richness and species richness for each zone separately were assessed using the program ESTIMATES! (Colwell 2000). In the results we present sample-based rarefaction estimates of cumulative species richness in addition to estimates of species richness obtained using

the Chao2 non-parametric richness estimator (see Colwell & Coddington 1994). The Chao2 estimator gave the least biased estimate of true species richness for small numbers of samples in a comparative study of eight species-richness estimators (Colwell & Coddington 1994) and has been previously used to assess marine benthic diversity (Ellingsen 2002).

Variation in sponge community composition among zones was tested for significance using ANOSIM (non-parametric analysis of similarities; Clarke & Gorley 2001) based on the Sørensen similarity matrix within the package PRIMER v6 (Primer-E Ltd, Plymouth, UK). The results of the ANOSIM analyses are presented in addition to multidimensional scaling (MDS) ordinations based on the same similarity matrix. Analyses were performed separately at three different taxonomic levels using species, genera and families. Multidimensional scaling is frequently used in ecological studies and the results have been found to be robust under a wide range of conditions; it has no stringent model assumptions, such

as correspondence analysis, which assumes a unimodal response, and any similarity measure can be used for ordination (Warwick *et al.* 1990; Beck *et al.* 2002; Cleary 2003; Cleary & Genner 2004; Cleary & Mooers 2004).

In addition to the MDS, we performed principal components analyses using the package CANOCO (ter Braak & Smilauer 1998). Input for these analyses consisted of  $\log_{10}(x + 1)$  species abundance data transformed using the programme TRANSFORMATION (<http://www.bio.umontreal.ca/casgrain/en/labo/transformations.html>). The species data were transformed because of the inherent problems of the Euclidean-based distance metric (in standard Principal Components Analysis, PCA) for community data (see Legendre & Gallagher 2001). In the present case, the Chord distance was used, which gave good results in comparison to various distance metrics (Legendre & Gallagher 2001).

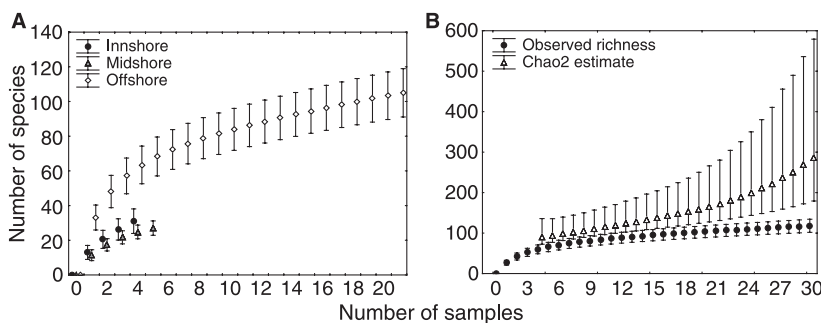
## Results

We recorded a total of 118 sponge species, 64 genera and 36 families, in PS (Fig. 2). The number of sponge species found in each of the 30 surveyed sites varied between 8 and 42. Cumulative sample species richness was similar in the inshore and midshore zones and, surprisingly, even somewhat higher inshore. The highest sample species richness was, however, recorded in the offshore zone (Fig. 2). Note, however, that this is also at least partially due to the higher cover and therefore number of individual sponge colonies in the offshore zone when compared to the other two zones. Because only presence/absence data were collected we were not able to rarefy and thereby eliminate the effect of abundance on species richness. The highest number of species was found at offshore sites (see Fig. 1): Panjang (42 spp.), Hantu Besar (41 spp.), Tidung Kecil (39 spp.) and Jukung (38 spp.), whereas the lowest number of species was recorded at the inshore sites, including Damar Kecil (6 spp.), Ubi Besar (8 spp.), Ayer Besar (8 spp.) and Damar Besar (12 spp.).

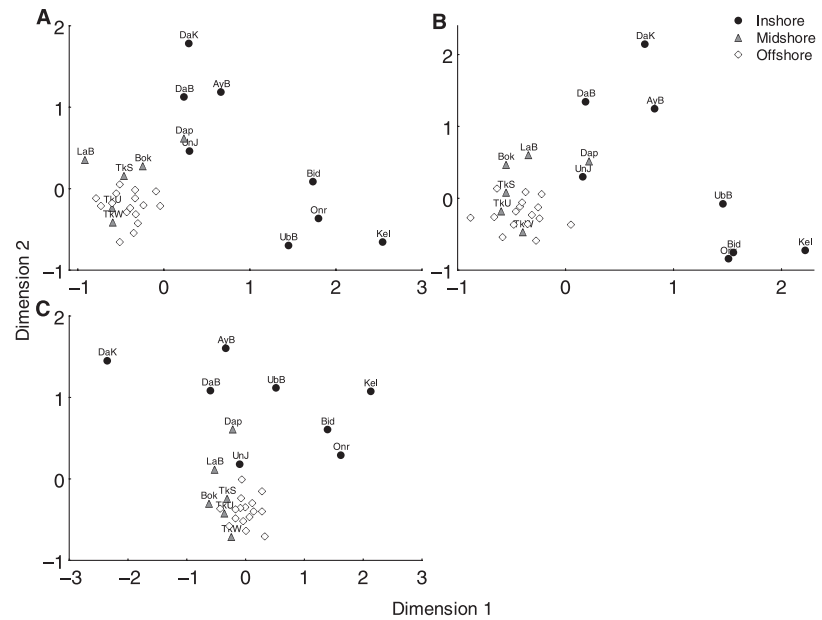
Only seven species were common, *i.e.* co-occurred in >20 different sites (66% level of sites); these were *Aptos suberitoides* (Brønsted, 1934) (Hadromerida Suberitidae), *Amphimedon cf. paraviridis* (Fromont, 1993) (Haplosclerida Niphatidae), *Cinachyrella australiensis* (Carter, 1886) (Hadromerida Tetillidae), *Clathria (Thalysias) reinwardti* (Vosmaer, 1880) (Poecilosclerida Microcionidae), *Lamellodysidea herbacea* (Keller, 1889) (Dictyoceratida Dysideidae), *Petrosia (Petrosia) nigricans* (Lindgren, 1897) and *Xestospongia testudinaria* (Lamarck, 1813) (both Haplosclerida, Petrosiidae). The most common genera were *Aptos*, *Amphimedon*, *Axinyssa*, *Callyspongia*, *Cinachyrella*, *Clathria*, *Dysidea*, *Lamellodysidea*, *Petrosia*, *Stylissa* and *Xestospongia*; and finally, the most common families were Ancorinidae, Callyspongiidae, Chalinidae, Dictyonellidae, Dysideidae, Halichondriidae, Microcionidae, Niphatidae, Petrosiidae, Suberitidae, Tetillidae and Thorectidae.

There were a total of 43 unique species (only found in a single sample site), which belonged to 14 unique genera and five unique families. The most speciose families were the Chalinidae (containing two genera and 12 species) and the Petrosiidae (containing four genera and 12 species). More than a third of the observed 36 families contained a single species: Acarnidae, Clathrinidae, Coelosphaeridae, Crambeidae, Darwinellidae, Hemiasterellidae, Placospongiidae, Plakinidae, Pseudoceratinidae, Raspailidae, Rhabderemiidae, Spongiidae, Suberitidae and Theonellidae. Because of the large number of unique species, the Chao2 richness estimator resulted in an estimated 286 species (95% CI: 179–579 species) with no evidence of an asymptote. This is a very strong indication that actual non-encrusting sponge species richness is much higher than the 118 species recorded during this study, even excluding thinly encrusting, cryptic and boring species (Fig. 2).

The multidimensional scaling (stress = 0.13 for species, genera and families) and ANOSIM revealed a similar pattern of spatial variation in composition (Fig. 3). As expected, the greatest difference was between in- and offshore sites (species:  $R_{ANOSIM} = 0.850$ ,  $P < 0.001$ ;



**Fig. 2.** (A) Observed sample-based species richness in the inshore, midshore and offshore zones and (B) observed sample-based species richness and estimated species richness based on the Chao2 non-parametric richness estimator across the whole sample area.



**Fig. 3.** Multidimensional scaling ordinations based on (A) species-level data, (B) genus-level data and (C) family-level data. Sample sites from different zones are indicated by symbols.

genera:  $R_{ANOSIM} = 0.826$ ,  $P < 0.001$ ; families:  $R_{ANOSIM} = 0.780$ ,  $P < 0.001$ ). Midshore sites generally overlapped with offshore sites with the exception of Dapur, which more closely resembled inshore sites (inshore and midshore: species:  $R_{ANOSIM} = 0.435$ ,  $P = 0.006$ ; genera:  $R_{ANOSIM} = 0.381$ ,  $P = 0.011$ ; families:  $R_{ANOSIM} = 0.308$ ,  $P = 0.013$ ; Midshore and offshore: species:  $R_{ANOSIM} = 0.348$ ,  $P = 0.011$ ; genera:  $R_{ANOSIM} = 0.342$ ,  $P = 0.011$ ; families:  $R_{ANOSIM} = 0.401$ ,  $P = 0.004$ ).

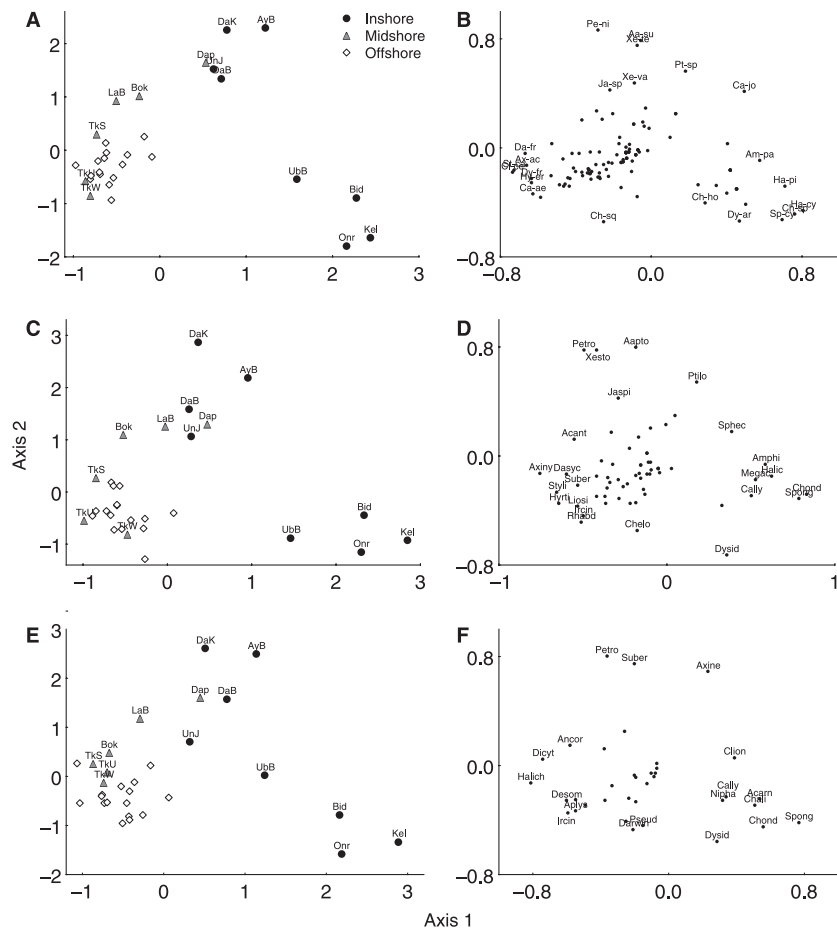
The results of the ordination based on the first two axes of the PCA (variation explained: species, 27.4%; genera, 31.3%; families, 33.7%) were very similar to those of the MDS. Furthermore, both PCA and MDS revealed only minor differences in composition among offshore sites but showed pronounced differences among inshore sites (Fig. 4). The inshore sites in turn showed two distinct groups, an inner bay group consisting of the sites Bididari, Onrust, Kelor and Ubi Besar, and sites just outside the bay consisting of Ayer Besar, Untung Jawa, Damar Besar and Damar Kecil. Species associated with inner bay sites included *Haliclona (Gellius) cymaeformis* (Esper, 1794), *Chondrilla cf. australiensis* (Carter, 1873) and *Spongia ceylonensis* (Dendy, 1905); those associated with outer bay sites and Dapur include *Aaptos suberitoides*, *Petrosia nigricans*, *Xestospongia testudinaria* and *Xestospongia vansoesti* (Bakus & Nishiyama, 2000). Species associated with mid- and offshore sites included *Callyspongia aerizusa* (Desqueyroux-Fáunderz, 1984), *Clathria (Thalysias) cervicornis* (Thiele, 1903), *Dasychalina fragilis* (Ridley & Dendy, 1886) and *Stylissa carteri* (Dendy, 1889). Genera associated with inner bay sites included *Dysidea*, *Spongia*, *Chondrilla*; those associated with outer

bay sites and Dapur included *Aaptos*, *Jaspis*, *Petrosia* and *Xestospongia*. Genera associated with mid- and offshore sites included *Axinyssa*, *Stylissa* and *Hyrtios*. Finally, families associated with inner bay sites included Spongiidae, Chondrillidae and Acarnidae; those associated with outer bay sites and Dapur included Petrosiidae, Suberitidae and Axinellidae. Families associated with mid- and offshore sites included Ancorinidae, Dictyonellidae and Halichondriidae.

Further associations between species, genera and families with sites are presented in Fig. 5, which shows ordination based on the third and fourth PCA axes (variation explained: species, 13.3%; genera, 13.9%; families, 16.4%). Gradients in composition include variation from Lancang Besar with the species *Haliclona sp.* and *Xestospongia mammillata* (Pulitzer-Finali, 1982) to a cluster of offshore sites (Sepa Besar, Putri, Kotok Kecil and Belanda) associated with the species *Rhabdastrella globostellata* (Carter, 1879), *Pseudoceratina purpurea* (Keller, 1889) and *Suberea sp.*

## Discussion

The highest number of species was found at offshore sites furthest from Jakarta, whereas considerably fewer species were recorded at inshore sites, particularly within the inner bay. The reef zones varied in geomorphology, oceanographic conditions and distance from the city of Jakarta; thus inshore sites tended to be very shallow, and seldom exceeded 10 m in depth. It has been shown that the diversity of coral reef-associated sponges increases with increasing depth (Fromont *et al.* 2006; de Voogd *et al.* 2006) but, importantly, the environment in the

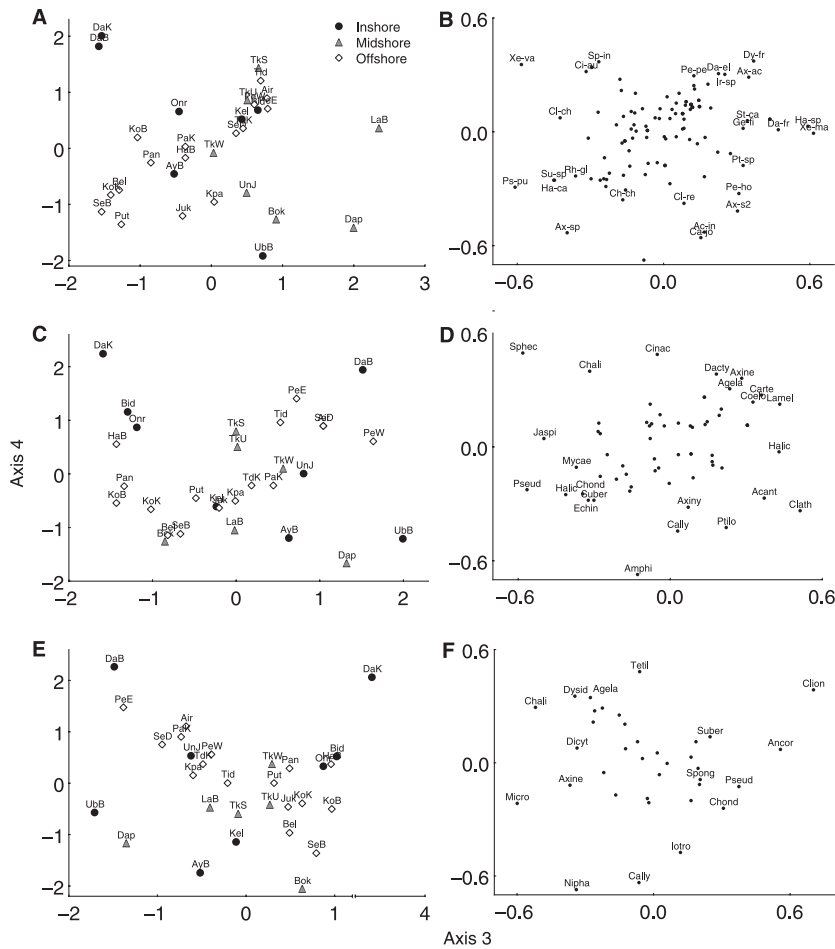


**Fig. 4.** Species-level ordination based on Principal Components Analysis (PCA) showing the first and second axes. (A) Sample site scores, sites from different zones are indicated by symbols. (B) Species scores, selected species are indicated by four-letter codes: Aa-su: *Aaptos suberitoides*, Am-pa: *Amphimedon* cf. *paravidis*, Ax-ac: *Axinyssa* aff. *aculeata*, Ca-ae: *Callyspongia aerizusa*, Ca-jo: *Callyspongia joubini*, Ch-ho: *Chalinula hooperi*, Ch-sp: *Chondrilla* aff. *australiensis*, Ch-sp: *Chelonaplysilla* aff. *violacea*, Cl-ce: *Clathria* (*Thalysias*) *cervicornis*, Da-fr: *Dasychalina fragilis*, Dy-ar: *Dysidea arenaria*, Dy-fr: *Dysidea frondosa*, Ha-cy: *Haliclona* (*Gellius*) *cymaeiformis*, Ha-pi: *Haliclona* (*Halichocona*) sp. 'Pink', Hy-er: *Hyrtios erectus*, Ja-sp: *Jaspis splendens*, Pe-ni: *Petrosia nigricans*, Pt-sp: *Ptilocaulis* sp., Sp-ce: *Spongia ceylonensis*, St-ca: *Stylissa carteri*, Xe-te: *Xestospongia testudinaria*, Xe-va: *Xestospongia vansoesti*. (C) Genus-level ordination based on Principal Components Analysis (PCA) showing the first and second axes. Sample site scores. (D) Genus scores, selected genera are indicated by five-letter codes: Aapto: *Aaptos*, Acant: *Acanthella*, Amphi: *Amphimedon*, Axiny: *Axinyssa*, Cally: *Callyspongia*, Chelo: *Chelonaplysilla*, Chond: *Chondrilla*, Dasyc: *Dasychalina*, Dysid: *Dysidea*, Halic: *Haliclona*, Hyrti: *Hyrtios*, Ircin: *Ircinia*, Jaspi: *Jaspis*, Liosi: *Liosina*, Megac: *Megaciella*, Petro: *Petrosia*, Ptilo: *Ptilocaulis*, Rhabd: *Rhabdastrella*, Sphec: *Spheciospongia*, Spong: *Spongia*, Styli: *Stylissa*, Suber: *Suberea*, Xesto: *Xestospongia*. (E) Family-level ordination based on Principal Components Analysis (PCA) showing the first and second axes. Sample site scores, sites from different clusters are indicated by symbols. (F) Family scores, selected families are indicated by five-letter codes: Acarn: Acarnidae, Ancor: Ancorinidae, Aplys: Aplysiniellidae, Axine: Axinellidae, Cally: Callyspongiidae, Chali: Chaliniidae, Chond: Chondrillidae, Clion: Clionidae, Darwin: Darwinellidae, Desom: Desmoxyidae, Dicty: Dictyonellidae, Dysid: Dysideidae, Halich: Halichondriidae, Ircin: Irciniidae, Nipha: Niphatidae, Petro: Petrosiidae, Pseud: Pseudoceratinidae, Spong: Spongiidae, Suber: Suberitidae.

inshore zone was characterised by high turbidity and very low cover of live corals, with the dominant substrate composed of silt and sand (Rachello-Dolmen & Cleary 2007). Environmental conditions improved offshore, although most areas showed evidence of human-induced disturbance, with sponge diversity increasing as the environmental conditions improve. A recent study from this area has indicated that disturbances can differentially affect the marine environment, which in turn interacts

with coral species traits to determine local species composition (Rachello-Dolmen & Cleary 2007). Also, a multi-taxon study has shown that inshore coral assemblages tended to consist largely of stress-tolerant corals (e.g. massive corals such as *Porites* spp.) and contain locally high densities of potentially destructive species such as the sea urchin *Diadema setosum* (Cleary *et al.* in press).

Interestingly, we also found low levels of species richness in the midshore zone, despite the relatively benign



**Fig. 5.** Species-level ordination based on Principal Components Analysis (PCA) showing the third and fourth axes. (A) Sample site scores, sites from different zones are indicated by symbols. (B) Species scores, selected species are indicated by four-letter codes: Ac-in: *Acanthostrongylophora ingens*, Ax-ac: *Axinyssa* aff. *aculeata*, Ax-s2: *Axinyssa* sp. 'ch', Ax-sp: *Axinyssa* sp. 'or', Ca-jo: *Callyspongia joubini*, Ch-ch: *Chondrosia chucalla*, Ci-au: *Cinachyrella australiensis*, Cl-ch: *Clathria (Clathria)* cf. *chelifera*, Cl-re: *Clathria (Thalysias) reinwardti*, Da-el: *Dactylospongia elegans*, Da-fr: *Dasychalina fragilis*, Dy-fr: *Dysidea frondosa*, Ge-fi: *Gelliodes fibulata*, Ha-ca: *Halichondria cartilaginea*, Ha-sp: *Haliclona* sp. 'uf', Ir-sp: *Ircinia* sp. 'br', Pe-ho: *Petrosia hoeksemai*, Pe-pe: *Petrosia (Petrosia)* aff. *pellasarca*, Ps-pu: *Pseudoceratina purpurea*, Pt-sp: *Ptilocaulis* sp., Rh-gl: *Rhabdastrella globostellata*, Sp-in: *Sphēciospongia inconstans*, St-ca: *Stylissa carteri*, Su-sp: *Suberea* sp. 'pi', Xe-ma: *Xestospongia mammillata*, Xe-va: *Xestospongia vansoesti*. (C) Genus-level ordination based on Principal Components Analysis (PCA) showing the third and fourth axes. Sample site scores, sites from different clusters are indicated by symbols. (D) Genus scores, selected genera are indicated by five-letter codes: Acant: *Acanthostrongylophora*, Agela: *Agelas*, Amphi: *Amphimedon*, Axine: *Axinella*, Axiny: *Axinyssa*, Cally: *Callyspongia*, Carte: *Carteriospongia*, Chali: *Chalinula*, Chond: *Chondrosia*, Cinac: *Cinachyrella*, Clath: *Clathria*, Coelo: *Coelocarteria*, Dacty: *Dactylospongia*, Echin: *Echinodictyum*, Halic: *Haliclona*, Jaspi: *Jaspis*, Lamel: *Lamellodysidea*, Mycae: *Mycale*, Pseud: *Pseudoceratina*, Ptilo: *Ptilocaulis*, Sphec: *Sphēciospongia*, Suber: *Suberea*. (E) Family-level ordination based on Principal Components Analysis (PCA) showing the third and fourth axes. Sample site scores, sites from different clusters are indicated by symbols. (F) Family scores, selected families are indicated by five-letter codes: Agela: Agelasidae, Ancor: Ancorinidae, Axine: Axinellidae, Cally: Callyspongiidae, Chali: Chalinidae, Chond: Chondrillidae, Clion: Clionidae, Dicty: Dictyonellidae, Dysid: Dysideidae, lotro: lotrochotidae, Micro: Microcionidae, Nipha: Niphataidae, Pseud: Pseudoceratinidae, Spong: Spongiidae, Suber: Suberitidae, Tetil: Tetillidae.

environmental conditions, when compared to the inshore zone. This contrasts strongly with results from other taxa (corals, echinoderms and fishes) sampled across the same study area (Cleary *et al.* in press). For all other taxa, species richness was higher in the midshore zone than in the in- and offshore zones. The midshore zone has the greatest range in depth and highest mean cover of live corals.

The composition of the sponge assemblages in the midshore zone, however, was closer to the off- than the inshore zone. It would appear that sponges have benefited from disturbances in the offshore zone that have removed live corals but have not yet caused severe degradation, as is the case in the inshore zone. This result also shows the importance of multi-taxon surveys for reef monitoring



and assessment and suggests that the cover, composition and diversity of taxa, such as corals, have important effects on the diversity of other taxa, such as sponges.

During this study, only a few species could be considered common, *i.e.* co-occurring at >66% of all sites. These included the species *Cinachyrella australiensis*, *Lamellodysidea herbacea* and *Xestospongia testudinaria*. These species are known to have a wide Indo-Pacific, tropical occurrence and very broad ecological distribution, and have been recorded in pristine as well as severely disturbed habitats (McDonald *et al.* 2002; Bell & Smith 2004; Fromont *et al.* 2006). Conversely, various sponge species that are common elsewhere in Indonesia, such as *Haliclona (Reniera) fascigera* (Hentschel, 1912), *Niphates olemda* (de Laubenfels, 1954) and *Ianthella basta* (Pallas, 1766) were absent in PS (van Soest 1989; de Voogd *et al.* 2006). Also a high percentage (48%) of species were recorded from only a single site (these are known as uniques as opposed to singletons, which means that only a single individual was recorded; Colwell 2000), and only 6% were found at two stations (duplicates). This result concurs with earlier studies from northwestern Australia, where a similar percentage of uniques was found (Fromont *et al.* 2006), and eastern Australia, where 32% of the species were uniques (Hooper & Kennedy 2002). One of these species, the phototrophic species *Carterospongia foliascens*, was only observed at Tidung Besar in the offshore zone. Phototrophic species mainly rely on the translocation of nutrients from their symbiotic cyanobacteria, and are believed to be favoured in oligotrophic waters. Thus their absence from many of the studied sites may be an indication of adverse environmental conditions. Carballo *et al.* (1996) suggested that the presence of particular species in either pristine or environmentally perturbed habitats permits us to deduce their importance as biological indicators. Of course, this is more difficult at higher taxonomic levels, such as genus or family level. However, the uniques are most likely the result of incomplete sampling, and it is therefore expected that the real biodiversity lies much higher than the observed 118 species found using our sampling method. The inclusion of encrusting and cryptic species would further dramatically increase the number of sponge species.

Few true endemics were found; so far only *Agelas linnei* (de Voogd *et al.* 2008) appears to be restricted to the studied area. At present, many Indo-Pacific coral reefs remain unexplored, and thus many apparent endemics are likely to be discovered eventually in other Indonesian reefs. For instance, the apparent endemic and new sponge *Gelliodes* sp. was found at several sites in PS, but was most recently also discovered in the coral reefs of Singapore (Lim *et al.* 2008; de Voogd & Cleary *in press*). Hooper & Kennedy (2002) partially ascribed

the 'apparent endemics' to difficulties in sponge taxonomy. Sponge faunas from different geographic regions are difficult to compare when different authors have described them. Nevertheless, van Soest (1989) remarked that different geographic regions within the Indo-West Pacific all have in the complement of their common species some endemic species, making these regions very dissimilar.

The most speciose families were the Chalinidae (containing two genera and 12 species) and the Petrosiidae (containing four genera and 12 species). These families both belong to the Haplosclerida and this order is thought to be the most diverse of all sponge orders (van Soest & Hooper 2002). For instance, the genus *Haliclona* currently contains 574 species, but many more are thought to exist. Interestingly, 13 of the observed 36 families contained only a single species, but these were often present at numerous sites, *e.g.* *Chelonaplysilla* aff. *violacea* (Lendenfeld, 1883) (Darwinellidae), *Pseudoceratina purpurea* (Pseudoceratinidae), *Echinodictyum mesenterinum* (Lamarck, 1814) (Raspailiidae) and *Aaptos suberitoides* (Suberitidae).

In the present study we found a pronounced difference in composition among zones with the most distinct assemblages in the inshore zone. The sponge families Chondrillidae, Spongiidae, Dysideidae, Chalinidae, Niphatidae and Callyspongiidae characterised the inshore sites, although these were also present in the mid- and offshore zones. Species found in the most perturbed inner bay inshore sites include *Haliclona cymaeformis*, *Chondrilla* aff. *australiensis* and *Spongia ceylonensis*.

*Haliclona cymaeformis* lives in symbiotic association with the rhodophyte alga *Ceratodictyon spongiosum* (Zanardini, 1878), and this species prefers intertidal habitats. It has been suggested that the sponge can survive air exposure (the sponge stops filtering when partially emerged during low tide) because of the symbiosis with the algae, and that the latter also provides protection against UV radiation (Steindler *et al.* 2002; Azzini *et al.* 2007). This would enable this species to survive in extreme or highly perturbed habitats. Bath sponges (*e.g.* *Spongia* spp.) are also known to thrive in shallow water habitats, and thus the species and genera that characterise the inner bay reefs are probably a combination of species that prefer shallow habitats and/or are able to cope with severe environmental perturbation. No baseline studies of the sponges at these sites are known that would allow us to compare pre- and post-disturbance faunistic changes, to test this hypothesis.

It is also noteworthy to mention that the number of species varies substantially per family, from a few species (*e.g.* 10 species for Placospongiidae) to numerous species (*e.g.* >100 for Raspailiidae). This is of particular

importance when assessing community structure at supra-specific taxonomic level.

Importantly, our results revealed that species-, genera- and family-level data yielded similar results with respect to spatial compositional variation, confirming similar findings from other biomes and taxa (e.g. corals, butterflies; Warwick *et al.* 1990; Cleary 2004; Cleary *et al.* 2006). In a study of small-scale variation of kelp-holdfast assemblages, Anderson *et al.* (2005) also concluded that family-level identifications are sufficient to distinguish natural spatial patterns of variability. They proposed that the processes which determine the presence or absence of particular species, genera and families are principally governed by large spatial scales, such as oceanographic dispersal and transport strategies, biogeography, history, climate and latitudinal gradients in environmental variables. Although this study only consisted of presence/absence data, other studies have shown similar trends using species-, genera- or family-level data with quantitative data (Vanderklift *et al.* 1996; Olsgard *et al.* 1997; Stark *et al.* 2003; Anderson *et al.* 2005; Cleary *et al.* 2006).

On a final note, it must be observed that sponge identifications at any level require subsequent close laboratory examination, which is usually impossible or unreliable in the field, unless there is a prior good knowledge of the particular regional fauna at the outset of the study. High intraspecific variability of most sponge species is also a major problem when relying on field-based sponge identifications using morphological characters, with the essential requirement to confirm all putative species with histological examination of voucher specimens to differentiate between environmental plasticity and genetic differences between all morphospecies. Encouragingly, sponge identification at family and genus levels has now been made more accessible to non-specialists through the Systema Porifera (Hooper & Soest 2002). Finally, our results support previous studies in marine environments elsewhere in Indonesia and confirm the importance of on-to-offshore gradients in structuring marine assemblages, particularly in relation to coastal cities (Cleary *et al.* 2005; Cleary & Renema 2007). More studies are, however, necessary to understand and predict the effects that growing urban environments will have on coastal marine habitat, including comprehensive baseline studies of similar marine habitats in areas not presently under anthropogenic pressure, and still relatively pristine. .

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