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Diatoms from Indonesian mangroves and their suitability as sea-level indicators for tropical environments

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Abstract

We collected modern diatom samples from two mangrove environments of Sulawesi, Indonesia to provide a much needed dataset for the reconstruction of sea level from tropical environments. The diatom assemblages are dominated by mesohalobous species (e.g. *Amphora coffeaeformis*, *Amphora turgida*, *Achnanthes delicatula*, *Nitzschia sigma* and *Tryblionella balatonis*) and oligohalobous (e.g. *Amphora veneta*, *Diploneis ovalis* and *Progonoia didiomatia*) taxa. Both study sites show strong vertical zonations, which suggests that duration and frequency of intertidal exposure are important factors in controlling the relative abundance of diatoms. The assemblages can be generally divided into a mixed assemblage of mesohalobous, oligohalobous–halophilous and oligohalobous-indifferent diatoms that are found from the dense mangrove vegetation towards the landward edge of the transects, and mesohalobous diatom assemblages that are located within the fringing *Rhizophora* and tidal flat environments. We subsequently developed a diatom-based transfer function, which is a quantitative approach to sea-level reconstruction. The relationship between observed and diatom-predicted elevations suggests accurate and precise reconstructions are possible. The error estimate (±0.15 m) is comparable to diatom-based transfer functions from temperate marshes.

Keywords: Diatoms; Sea level; Transfer function; Mangroves; Indonesia

1. Introduction

Accurate knowledge of former sea levels from active and passive coastal margins is relevant to a wide variety of regional and global environmental studies. Although much contemporary sea-level research from passive margins has focused on datasets from temperate environments, it is widely recognized that tropical field sites provide the best possible estimate of the 'eustatic function' (e.g. Clark et al., 1978; Geyh and Kudrass, 1979; Tija, 1996; Nunn, 1998; Yokoyama et al., 2000; Peltier, 2002; Horton et al., 2005a), which provides information on the transfer of immense amounts of water between the ice sheets and the oceans (Lambeck et al., 2002). Such data are vital for many applications, ranging from calibrating models of earth rheology and ice sheet reconstructions (e.g. Clark et al., 2004; Peltier, 2004, Bassett et al., 2005; Milne et al., 2005; Tarasov and Peltier, 2005) to the development of coastal lowlands and human occupation (e.g. Kraft et al., 1977, 1980; Tooley and Jelgersma, 1992; Shennan and Andrews, 2000; Dickinson, 2001). Sea-level research from active coastal margins has provided estimates of time and frequency of Holocene earthquakes and tsunamis (e.g. Clague and

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Bobrowsky, 1994; Long and Shennan, 1994; Pinegina et al., 2003; Nanayama et al., 2003; Hamilton et al., 2005; Kelsey et al., 2005; Cisternas et al., 2005; Hawkes et al., 2005). Furthermore, sea-level research has validated models of Holocene paleoseismicity, which comprises coseismic land subsidence, rapid post-seismic land uplift, slow inter-seismic land uplift and slow preseismic land subsidence (e.g. Nelson et al., 1996; Shennan et al., 1996, 1998; Zong et al., 2003; Hamilton et al., 2005; Bourgeois, 2006; Shennan and Hamilton, 2006).

Much of the current diatom data regarding sea-level change is developed from the identification and analysis of stratigraphic boundaries between terrestrial freshwater sediments and littoral facies, and relies strongly on the simple classifications of taxa into freshwater, brackish or marine forms, and provides only qualitative estimates of ecological conditions (e.g. Vos and de Wolf, 1988, 1993; Juggins, 1992; Clague and Bobrowsky, 1994; Hemphill-Haley, 1995a,b,c; Zong and Tooley, 1996; Long et al., 1998; Cooper, 1999). Recent research in temperate environments, however, has provided empirical information regarding the inter-tidal distributions of diatoms and their relationship with sea level (e.g. Zong and Horton, 1998; Gehrels et al., 2001). These relationships have been quantified in a series of transfer functions (Birks, 1995; Juggins, 2006) that have been used to derive quantitative predictions of tidal-level and Holocene sea-level history from microfossil assemblages (e.g. Fritz et al., 1991; Zong and Horton, 1999; Sherrod, 1999; Gehrels et al., 2001, Zong et al., 2003; Sawai et al., 2004a,b; Hamilton and Shennan, 2005a,b; Hamilton et al., 2005; Horton et al., 2006). However, studies of diatoms and their relationship to relative sea level in coastal and estuarine environments from tropical or subtropical environments to support this conclusion are very sparse (e.g. Zong and Kamaludin, 2004), indeed, non-existent for Indonesia. Thus, this paper fills a major knowledge gap by documenting some characteristics of modern diatoms environments in the central Wakatobi Marine National Park, Sulawesi, Indonesia. Furthermore, we develop the first diatom-based transfer functions to aid sea-level interpretations made from Quaternary sediments of Indonesia and beyond (e.g. Tija et al., 1984; Gremmen, 1992; Ellison, 2005). In doing so, we test the applicability of the transfer function technique to tropical mangrove environments.

2. Study area

Extending over 13,900 km^2, the Wakatobi Marine National Park, Sulawesi, Indonesia, includes all coral reefs, islands, and communities within its boundaries and is centered around four principal islands (Wangi, Kaledupa, Tomea and Binongko), which form the Tukang Besi archipelago. The Wakatobi Marine National Park has a microtidal range of 0.98 m. The mean high high water (MHHW), mean low high water (MLHW), mean high low water (MHLW) and mean low low water (MLLW) are 1.92 m Indonesian Height Datum (IHD), 1.63 m IHD, 0.94 m IHD and 0.35 m IHD, respectively.

Like other regions in Indonesia, Sulawesi has a typical equatorial climate with a rainy and dry season. Starting in September, cool northwesterly winds pick up moisture while crossing the South China Sea and arrive in Sulawesi Sea in November. The wet season lasts from about November to March, but it is usually less pronounced than in many other parts of Southeast Asia. Mean temperatures at sea level are uniform, varying by only a few degrees throughout the year 78°–82 °F (25°–28 °C).

We selected two field sites from the island of Kaledupa that had different physiographic conditions and mangrove species distributions (Fig. 1A). The first site, Ambeua, had a northeastern aspect and the mangroves were protected by a reef flat located 50 m offshore (Fig. 1B). The study area had a small tidal flat due to the presence of a channel separating the mangrove from the reef flat. There was a small jetty but this had no influence on tidal inundation. The mangroves of Ambeua, and along much of the north coast of Kaledupa, were 100 m wide with vegetation up to 8 m in height. The mangroves do not have any freshwater input and showed a strong mangrove plant zonation parallel to the shoreline with a fringing *Rhizophora* zone that transgressed into a mixed *Rhizophora*/*Sonneratia* zone and then an *Avicennia* mangrove zone (Engelhart et al., in press). The landward edge of the mangrove environment terminated on an exposed coral terrace. Silt was the dominant sediment substrate within the *Avicennia* mangrove zone with a relative abundance greater than 40% in all samples. The silt substrate was replaced by coarser grains sizes within the mixed *Rhizophora*/*Sonneratia* zone. The relative abundance of sand was greater than 40% for the remainder of the intertidal zone. The clay fraction was relatively low across the intertidal zone; its relative abundance did not exceed 19%. Organic content was greater than 12% in all samples from the intertidal zone with higher values within the mixed *Rhizophora*/*Sonneratia* mangrove zone where the maximum values exceeded 54%.

The second site, Mantigola was located on the southwestern side of Kaledupa (Fig. 1C). The mangroves were protected by a reef flat 200 m from the shoreline and a large tidal flat. Similar to Ambeua, there

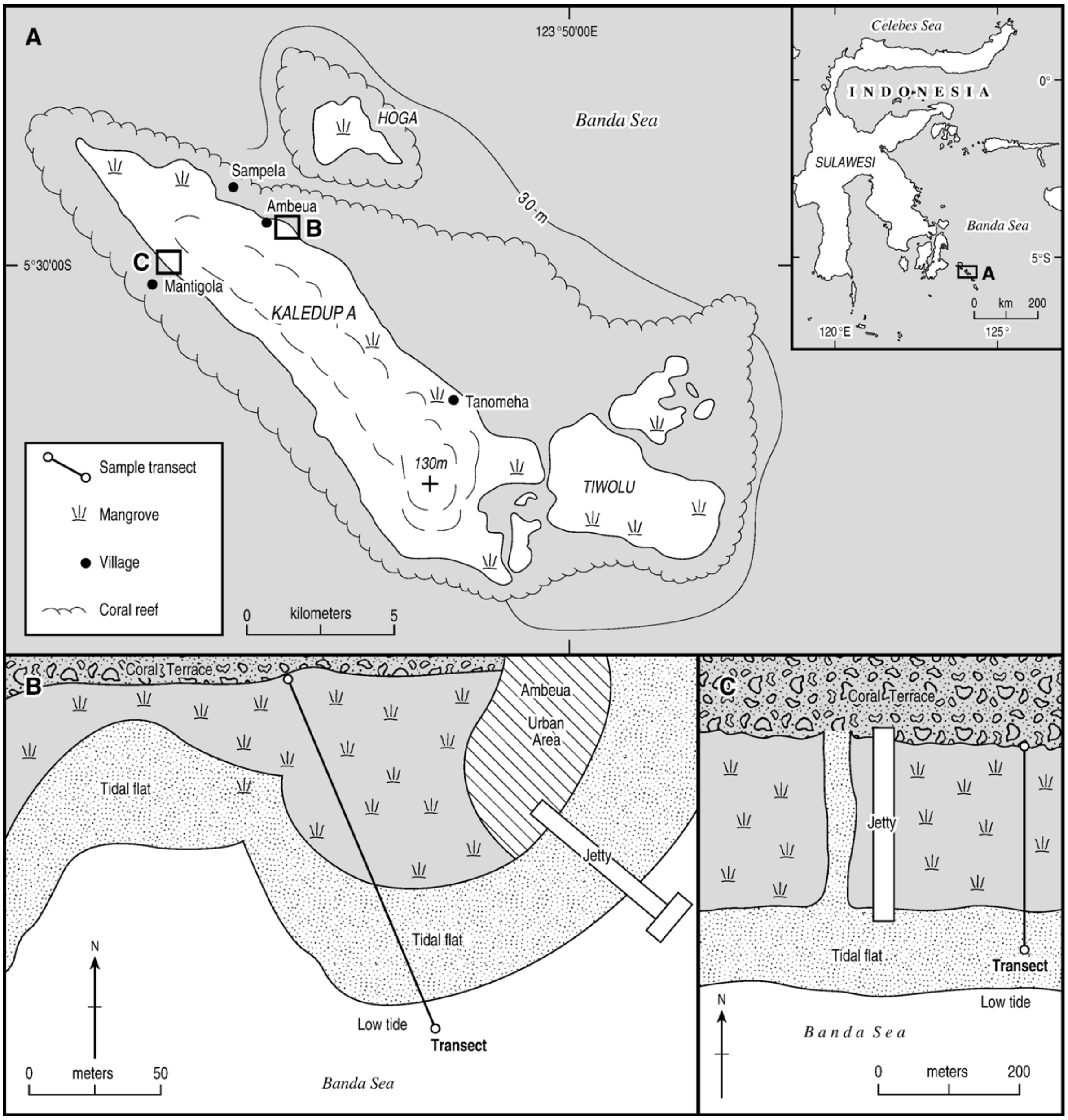

Fig. 1. Location map of study area showing (A) Kaledupa Island, Wakatobi Marine National Park, (B) Ambeua study site and (C) Mantigola study site.

was a small jetty but again this had no influence on tidal inundation. The mangroves also show zonations parallel to the shoreline, although the species composition differ (Engelhart et al., in press). The fringing mangrove was exclusively *Rhizophora*, which transgressed into a dense mangrove composed of *Rhizophora* and *Bruguiera* species, which accounted for over half of the transect. *Bruguiera* species declined with distance from the seaward edge of the mangrove. The *Rhizophora* and *Bruguiera* mangrove was followed by a mixed zone of *Rhizophora, Avicennia* and *Ceriops*. Towards the landward section of the transect *Ceriops* and *Avicennia* became increasingly prevalent. The landward zone was also characterized by the presence of *Nypa* palms, isolated *Xylocarpus* and *Acanthus* species. The vegetation attained maximum heights of 10 m. The site had some freshwater influence from a 3 m wide channel. The substrate of the *Rhizophora* and *Bruguiera*, and the mixed zone of *Rhizophora*, *Avicennia* and *Ceriops* mangrove environments was predominantly silt with relative abundances greater than 33%. The fringing *Rhizophora* mangrove marked a transition to a sand substrate. The relative abundance of sand was greater than 58% for the remainder of the intertidal zone. The abundance of clay remained low throughout the intertidal zone. The organic content was greater than 22% throughout the mangrove environment. The values decreased to 12% within the tidal flat.

3. Methodology

We collected samples of surface sediment from 16 and 15 stations along transects from Ambeua and Mantigola, respectively in July 2004 (Fig. 1 B, C). Both transects crossed the intertidal zone from an exposed former coral terrace through a mangrove swamp and onto an unvegetated tidal flat. All stations were leveled to a temporary benchmark and the height above local sea-level was determined by staff and autolevel and time of the observation recorded. These raw elevations were reduced to IHD by reference to tidal records for the region from the Proudman Oceanographic Institute, UK. Repeated measurements suggested the elevation of the Temporary Bench Mark (TBM) relative to IHD was accurate to ±20 cm.

At each station, one sample of approximately 10 cm^3 volume (10 cm^2 surface sample by 1 cm thick) was taken for diatom analysis. A critical issue for coastal paleoenvironmental reconstructions using diatom data is the autochthonous/allochthonous problem because daily tides can easily transport diatom valves and frustules (Simonsen, 1969; Denys, 1999; Vos and de Wolf, 1993; Hemphill-Haley, 1995a; Nelson et al., 1996; Sawai, 2001; Sawai et al., 2002). Thus, following standard procedures, we mixed the 1 cm thick modern surface sediment samples (e.g. Zong, 1997; Zong et al., 2003; Hamilton and Shennan, 2005a). In these intermittently high energy environments, the surface diatom assemblage at any sampling point is likely to be a mixture of locally produced taxa and transported taxa. Such a mixture of allochthonous and autochthonous diatom valves would also occur in sediments that accumulated in the past (Zong, 1997; Sawai, 2001). Therefore, we did not attempt to separate the allochthonous component from the diatom assemblages.

We prepared all diatom samples for investigation using light microscopy following standard methodology (e.g. Zong and Horton, 1998, 1999). Briefly, the samples were digested in 70–100 ml of 20% H_2O_2 by heating gently in a water bath for up to 24 h, or until all organic matter was removed from the sample. Two and five drops of digested sample were pipetted on to two cover slips with 10 drops of distilled water and dried on a warm hotplate. Cover slips of differing concentration were then inverted and placed onto a glass slide, using Zrax, a high refractive index medium mountant. We counted a minimum of 300 diatoms at a magnification of 1000 times using the keys of Hartley (1996), van der Werff and Huls (1958–1966) and Patrick and Reimer (1966/1975) with reference to the tropical publications that provide illustrations (e.g. Mann, 1925; Hustedt, 1938; Hagelstein, 1938; Navarro, 1982; Foged, 1984; Vyverman, 1991) held at the Patrick Center for Environmental Research, Academy of Natural Sciences. The classification of salinity was based on Vos and de Wolf (1993). Polyhalobous species thrive in fully marine conditions, with a salt concentration exceeding 30 practical salinity units (psu). Mesohalobous diatoms thrive in salt concentrations of between 0.2–30 psu. Oligohalobous diatoms generally occur in salt concentrations less than 0.2 psu. Vos and de Wolf (1993) further divided this category into oligohalobous–halophilous, which have an optimum in weakly brackish waters, and oligohalobous-indifferent, which show a preference for fresh water, but are tolerant of slightly brackish conditions. Halophobous diatoms are highly intolerant of salt and are found exclusively in fresh water. The classification of life form is based on Denys (1991/1992). Euplanktonic diatom species only live in the planktonic habitat, that is, metabolize and reproduce in the water column. Tychoplanktonic diatoms occur in the plankton, but are derived primarily from other habitats. Epontic diatom species are sessile and normally live firmly attached to substrata. For example, epiphytic live attached to plants and episammic species live attached to sand grains. Benthic diatoms live within the sediment, but are not attached to it.

3.1. Statistical analyses

We used unconstrained cluster analysis based on unweighted Euclidean distance and detrended correspondence analysis (DCA) to detect, describe and classify the vertical distribution of diatoms at Ambeua and Mantigola. Cluster analysis is effective in classifying the samples according to their diatom assemblage into more-or-less homogeneous cluster zones (Grimm, 2004), but DCA gives further information about the pattern of variation within and between groups (ter Braak and Smilauer, 1997–2003). Similar samples are located together and dissimilar samples apart. Birks

(1986, 1992) stressed the complementary relationship between cluster analysis and DCA.

We have developed a diatom-based transfer function, using a unimodal-based technique known as weighted averaging partial least squares (WA-PLS; Juggins, 2004). The WA-PLS transfer function produces results for five components. The choice of component depends upon the root-mean square of the error of prediction (RMSEP), the squared correlation (r^2) of observed versus predicted values and the principle of parsimony, that is, choosing the lowest component that gives an acceptable model. We calculated RMSEP and r^2 as 'apparent' measures, which use the whole training set to generate the transfer function and assess the predictive ability, and also 'jack-knifed' measures, which assess the overall predictive abilities of the dataset (Birks, 1995).

For all statistical analyses we removed all species that contributed less than 5% in all samples (Patterson and Fishbein, 1989; Fatela and Taborda, 2002). We did not transform or standardize the percentage data.

4. Modern diatom assemblages

We have identified 95 diatom species from 31 samples from the mangrove environments of Ambeua and Mantigola with 46 species common at both sites (Appendix A and B). The diatom assemblages were dominated mesohalobous, oligohalobous–halophilous and oligohalobous-indifferent diatoms with additional influences of polyhalobous and halophobous taxa.

4.1. Ambeua

We identified 73 diatom species from the 16 sample stations. The assemblages were dominated by mesohalobous species (e.g. *Achnanthes delicatula*, *Amphora coffeaeformis*, *Amphora turgida*, *Nitzschia sigma* and *Tryblionella balatonis*) with the presence of both polyhalobous (e.g. *Diploneis smithii*) and oligohalobous (e.g. *Amphora veneta*) taxa (Fig. 2). *D. smithii* had its peak abundance (36%, 20 m along the transect) within the *Avicennia* mangrove zone, at the landward edge of the transect, together with relatively high abundances of *A. delicatula*, *T. balatonis* and *A. veneta*. *D. smithii* was also present at the landward portion of the *Rhizophora*/*Sonneratia* mangrove floral zone. *N. sigma* dominated the *Rhizophora*/*Sonneratia* mangrove with a maximum abundance of 39% 176 m along the transect. In addition oligohalobous–halophilous species *A. veneta* (14%), *Navicula cincta* (12%) and *Navicula cryptocephala* (11%) had high relative abundances within this mangrove zone (140 m, 114 m and 114 m along the transect, respectively). The fringing *Rhizophora* mangrove zone was dominated by the mesohalobous species *A. coffeaeformis*, *A. delicatula* and *A. turgida*. The former two species had their highest relative abundances within this zone (19% and 21%, respectfully). The same three mesohalobous species, plus *N. sigma*, dominated the tidal flat zone of the transect with the maximum relative abundance of *A. turgida* (13%) at the seaward edge of the transect.

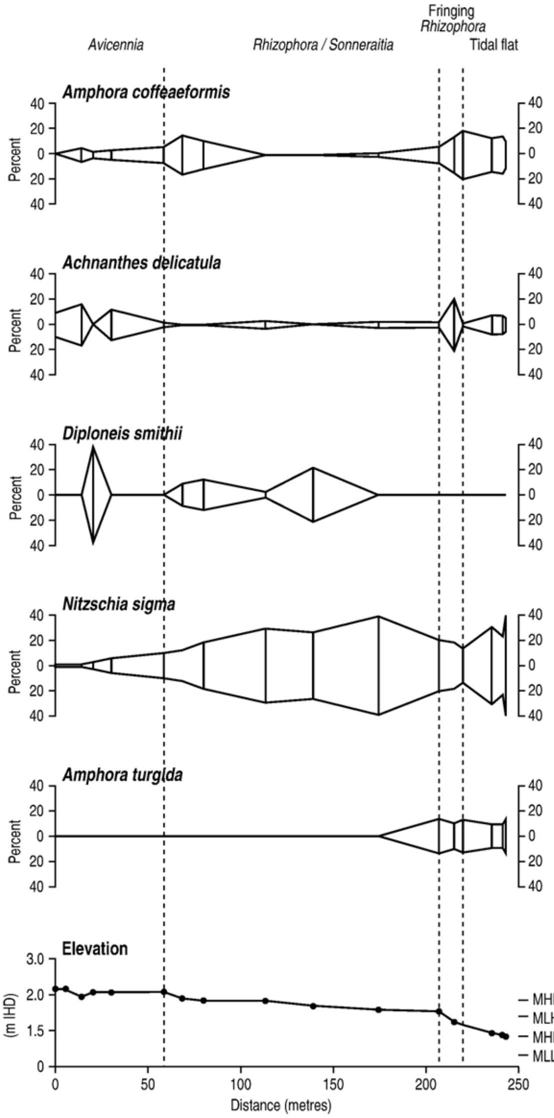

Fig. 2. Diatom abundance (%) of five diatom species from Ambeua. The elevation, tidal levels (mean high high water (MHHW), mean low high water (MLHW), mean high low water (MHLW) and mean low low water (MLLW) and mangrove zonation are indicated.

4.2. Mantigola

We identified 62 diatom species from 15 sample stations. The assemblages were dominated by mesohalobous (*A. delicatula*, *A. turgida* and *N. sigma*) and oligohalobous–halophilous (*Progonoia didiomatia* and *Diploneis ovalis*) species (Fig. 3). At the landward portion of the transect, within the *Rhizophora*, *Avicennia* and *Ceriops* mangrove zone, *A. delicatula* and *D. ovalis* species dominated, together with the oligohalobous-indifferent taxa *Cocconeis disculus* var *diminuta*. The maximum relative abundance of *A. delicatula* (38%), *D. ovalis* (21%) and *C. disculus* var *diminuta* (14%) occurred 0 m, 0 m and 30 m along the transect, respectively. The abundance of these three species decreased within the *Rhizophora* and *Bruguiera* mangrove zone. This mangrove zone was dominated by *A. turgida*, *N. sigma* and *P. didiomatia.* The latter two species had their maximum relative abundances (19% and 11%, respectfully) 190 m along the transect within the *Rhizophora* and *Bruguiera* mangroves. *A. turgida* continued to dominate the fringing *Rhizophora* and tidal flat zones of the transect, with a maximum relative abundance at the seaward end of the transect (36%, 450 m along the transect). High relative abundances of the polyhalobous species *Achnanthes modica* (11%) were also found within the tidal flat.

5. The vertical distribution of mangrove diatoms

From the results of cluster and DCA analyses the transects of Ambeua (Fig. 4) and Mantigola (Fig. 5) were divided into three diatom zones at each site, with each zone covering a distinctive elevation range. At both sites, a mixed assemblage of mesohalobous, oligohalobous–halophilous and oligohalobous-indifferent diatoms was found from the dense mangrove vegetation towards the landward edge of the transects. A predominantly mesohalobous diatom assemblage was recorded within the fringing *Rhizophora* and tidal flat environments. Indeed there was a very strong correlation between the mangrove floral zones and the diatom assemblage zones (Fig. 6).

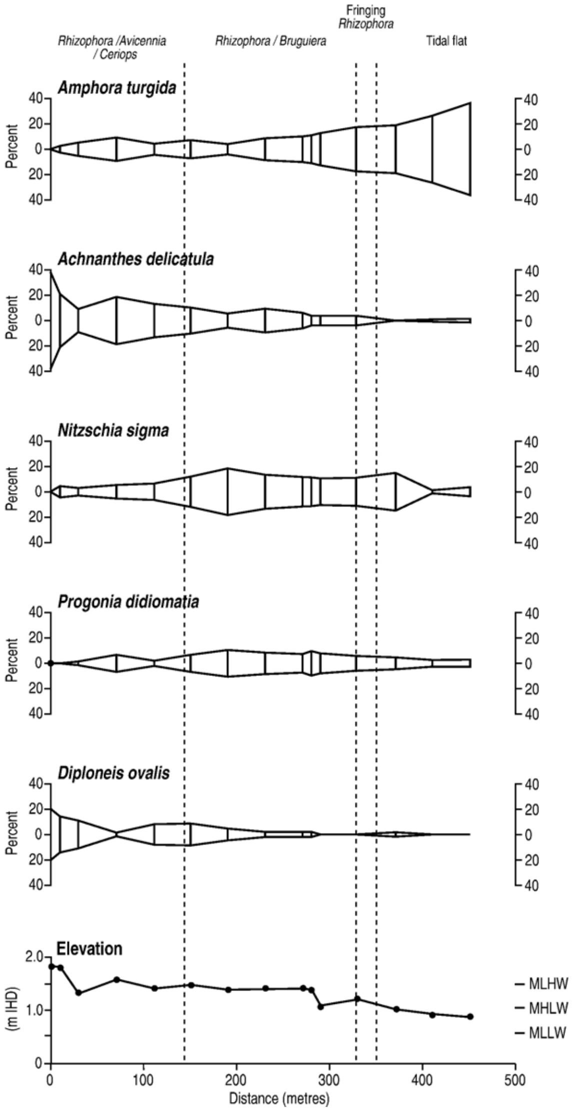

Fig. 3. Diatom abundance (%) of five diatom species from Mantigola. The elevation, tidal levels (mean low high water (MLHW) and mean high low water (MHLW) and mean low low water (MLLW) and mangrove zonation are indicated.

Zone AM-I was found at the landward edge of the Ambeua transect within the *Avicennia* mangrove zone and spans from 2.21 m to 1.87 m IHD. This zone had a mixed assemblage of mesohalobous (e.g. *A. delicatula*, *Gyrosigma scalproides* var *eximi* and *T. balatonis*), oligohalobous–halophilous (e.g. *A. veneta* and *N. cryptocephala*) and oligohalobous-indifferent (*Cymbella silesiaca*) species. *A. delicatula*, a brackish episammic species (Vos and de Wolf, 1993), occurred throughout the intertidal zones of Ambeua and Mantigola. Similarly, Hudtedt (1938) discovered the species to be common in the brackish environments of Java, Bali and Sumatra. *A. delicatula* dominated the mangrove environments of Malaysia (Zong and Kamaludin, 2004). Hudstedt (1938) and Zong and Kamaludin (2004) also found *G. scalproides* var *eximia* and *N. cryptocephala* within their studies of the mangroves of Southeast Asia. Furthermore, Foged (1984) and Vyverman (1991) found *G. scalproides* var *eximia* and *N. cryptocephala* more frequently in the freshwater environments of Cuba and the coastal lowlands of

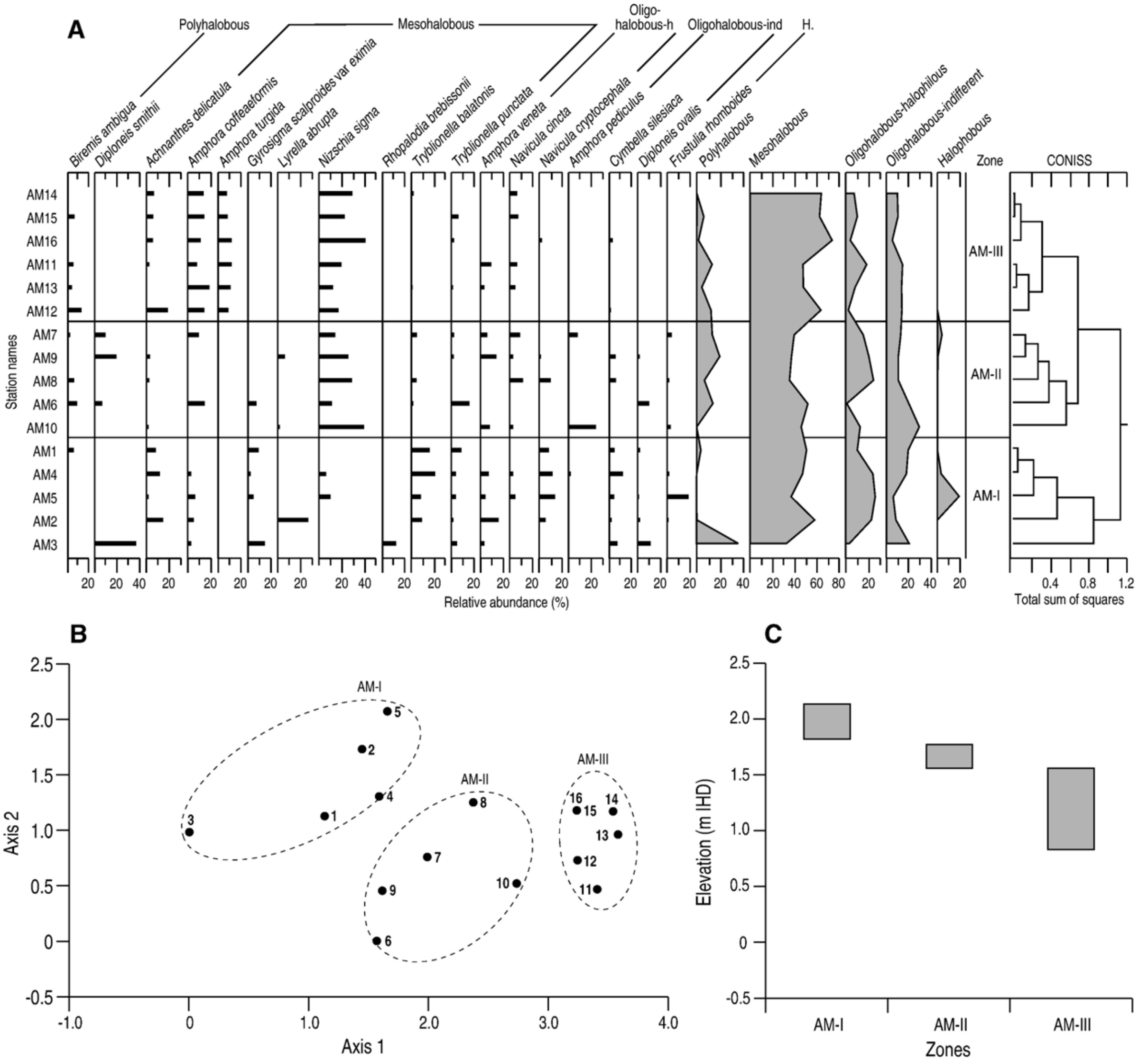

Fig. 4. (A) Unconstrained Incremental Sums of Squares cluster analysis (CONISS) based on unweighted Euclidean distances showing the diatom assemblages versus order of samples on dendrogram, (B) detrended correspondence analysis and (C) vertical zonation of the diatom assemblages of Ambeua. Only diatom species with relative abundances greater than 10% are shown.

Papua New Guinea, respectively. *N. cryptocephala* was also identified by Lange-Bertalot (2002) from Madagascar. Mann (1925) and Foged (1984) identified *A. veneta* in habitats of the Philippines and Cuba.

Zones AM-II and MA-I had similar elevation ranges. The former zone occurred within the *Rhizophora*/*Sonneratia* mangrove environment of Ambeua with elevations ranging from 1.83 m to 1.54 m IHD. The latter zone was at the landward portion of the Mantigola transect within *Rhizophora*/*Avicennia*/*Ceriops* mangrove vegetation from 1.84 m to 1.45 m IHD. Zone AM-II had many similar species to its landward counterpart. It was dominated by mesohalobous, oligohalobous–halophilous and oligohalobous-indifferent species, with notable additions of *D. smithii*, *N. cincta* and *N. sigma*. *D. smithii,* a polyhalobous species, was found in low abundances in the mangrove environments of Florida (Navarro, 1982) and Malaysia (Zong and Kamaludin, 2004). Furthermore, it was identified by Navarro (1989) and Foged (1984) in coral reef and mangrove environments of Puerto Rico and Cuba, respectively. *N. cincta* is described as a marine/brackish species (Vos and de Wolf, 1993) and adapted to dry subaerial habitats (Denys, 1991/1992).

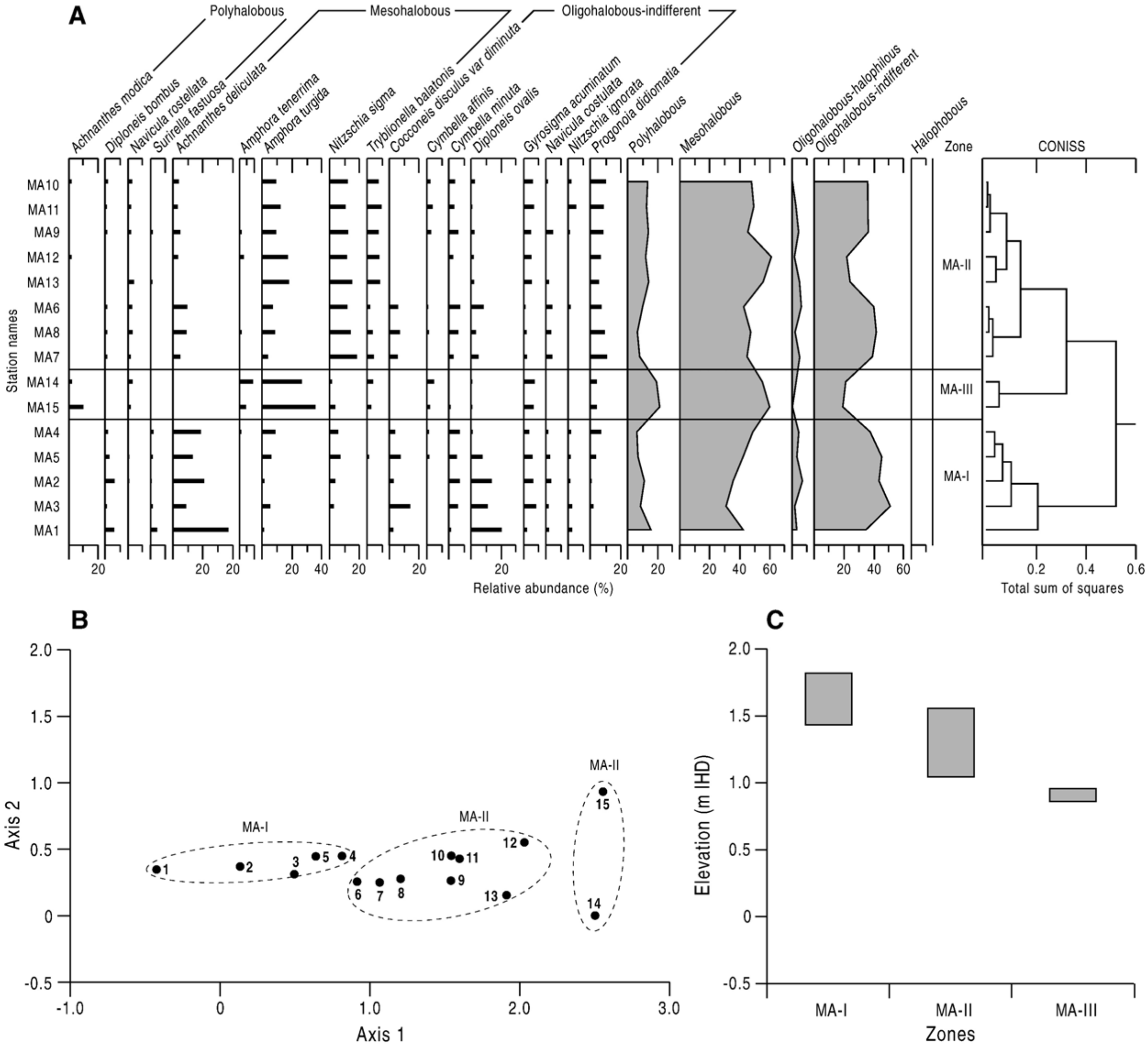

Fig. 5. (A) Unconstrained Incremental Sums of Squares cluster analysis (CONISS) based on unweighted Euclidean distances showing the diatom assemblages versus order of samples on dendrogram, (B) detrended correspondence analysis and (C) vertical zonation of the diatom assemblages of Mantigola. Only diatom species with relative abundances greater than 10% are shown. Constrained.

Foged (1984) found the species in the freshwater environments of Cuba and Hudtedt (1938) inferred that the species was common in Java, Bali and Sumatra. *N. sigma* is commonly found in coastal areas and estuaries (Vyverman, 1991). For examples, the species has been found in varying abundances in the brackish and marine environments of Puerto Rico, Java, Bali and Sumatra, Florida, Cuba, Papua New Guinea and Malaysia (Hagelstein, 1938; Hustedt, 1938; Navarro, 1982; Foged, 1984; Vyverman, 1991; Zong and Kamaludin, 2004). Zone MA-I was dominated by the mesohalobous species *A. delicatula* and the oligohalobous–halophilous species *D. ovalis*. Vyverman (1991) noted the occurrence of *D. ovalis* in slightly brackish water from Papua New Guinea, but suggested its distribution in tropical regions needs to be further investigated because of the unclear taxonomic relationship with *Diploneis subovalis*. For example, Hudtedt (1938) found *D. subovalis* to be a cosmopolitan species in Java, Bali and Sumatra, but did not identify *D. ovalis.* Conversely, *D. ovalis* was present in zones AM-II and MA-I but we did not find *D. subovalis* in either Ambeua or Mantigola mangroves (Figs. 4 and 5).

Diatom zones AM-III, MA-II and MA-III were found at the seaward portion of both transects, and had many similar species (e.g. *A. delicatula*, *A. turgida* and

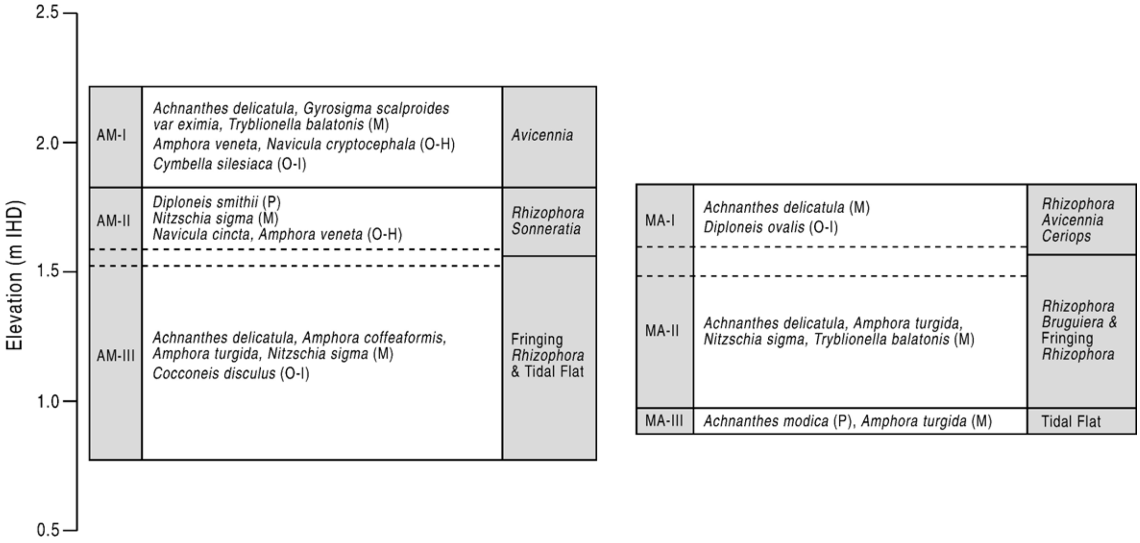

Fig. 6. Vertical zonation of the diatom assemblages of Ambeua and Mantigola. Mangrove zonations are shown. Dashed lines show overlapping boundaries.

N. sigma) and strong correlations with the mangrove floral zones. Zone AM-III was comprised of the fringing *Rhizophora* and tidal marsh habitats and was dominated by the mesohalobous species *A. delicatula*, *A. coffeaeformis*, *A. turgida* and *N. sigma*. The elevations of Zone AM-III spanned from 1.56 m IHD to the seaward edge of the transect (0.78 m IHD). *A. coffeaeformis* and *A. turgida* are aquatic, epontic and benthic species. Navarro (1982) found small numbers of *A. coffeaeformis* in the sub-tidal environments of Florida. In contrast, Vyverman (1991) and Zong and Kamaludin (2004) found very high abundances of this species in brackish water environments of Papua New Guinea and Malaysia, respectively. *A. turgida* has been found in tropical environments of the Philippines, Puerto Rico and Cuba (Mann, 1925; Hagelstein, 1938; Foged, 1984).

Zone MA-II occurred within the *Rhizophora*/*Bruguiera* and fringing *Rhizophora* mangrove environments. It was dominated by mesohalobous species and had an elevation range of 0.52 m (1.57 m to 1.05 m IHD). Zone MA-II was characterized by having the highest relative abundances of the mesohalobous species *A. turgida* and the marine/brackish species *N. sigma* and *T. balatonis* (Vos and de Wolf, 1993). Zone MA-III was characterized by the highest percentage of polyhalobous species (e.g. *A. modica*) and was found within the tidal flat environment. The elevation of this zone ranged from 0.97 m IHD to the seaward edge of the transect (0.88 m IHD).

The results indicate that the mangrove environment of Wakatobi Marine National Park, and by inference others of similar type, appears ideally suited for correlations between diatom relative abundances and elevation with the duration and frequency of intertidal exposure as the most important factors. Organic content, grain size and canopy cover may further influence the distribution and abundance of species. However, these variables vary along the elevational gradient of the intertidal zone and, thus, are dependent upon the frequency of tidal flooding.

6. Development of a transfer function

We have developed a diatom-based transfer function using a combined dataset of Ambeua and Mantigola that consists of 95 species and 31 samples. We have chosen component three of the WA-PLS transfer function because it performs significantly better than components one and two when jack-knifed errors are considered: prediction errors (RMSEP) were lower and squared correlations (r^2) were higher (Table 1). Using component three, the relationship between observed and diatom-predicted elevation was very strong (Fig. 7), which illustrated the robust performance of the WA-PLS transfer functions ($r^2_{\text{jack}} = 0.86$). Indeed, these results indicated that precise reconstructions of former sea levels are possible. The transfer function provided an error estimate for sample-specific former sea-level reconstructions ($\text{RMSEP}_{\text{jack}} = 0.15$ m), which is comparable to diatom-based transfer functions from temperate marshes. Zong and Horton (1999) recorded the diatom assemblages from six UK coastal sites. The resulting

Table 1
Apparent and jack-knifed errors of estimation and prediction for the diatom-based transfer function

Component	Apparent RMSE (m)	Prediction RMSEP (m)	Apparent (r^2)	Prediction (r^2)
1	0.16	0.21	0.84	0.73
2	0.11	0.17	0.92	0.83
3	0.08	0.15	0.96	0.86
4	0.06	0.16	0.97	0.85
5	0.04	0.16	0.99	0.83

transfer function had a precision of c. ±0.25 m, although this value is dependant on local tidal range. Similarly, Gehrels et al. (2001) produced a diatom-based transfer function from three sites in the UK with a precision of ±0.22 m. The transfer function developed using diatom assemblages from five saltmarshes of northern Japan had an error estimate of ±0.29 m (Sawai et al., 2004a,b). Hamilton and Shennan (2005a) collected diatoms data from modern intertidal and supratidal environments of Alaska to produce a transfer function with sample-specific errors between 0.08 m and 0.35 m. Horton et al. (2006) collected modern diatom samples from three saltmarshes of the Outer Banks, North Carolina, USA, which had different salinity regimes due to their varying distances from a major barrier island inlet. The transfer function had a precision of ±0.08 m.

The transfer function technique has the potential to produce reliable, high-resolution sea-level reconstructions from tropical environments because of the strong environmental gradient within their intertidal zones, which has been documented by several studies of the zonation of mangrove vascular plant and pollen (e.g. Grindrod, 1985, 1988, Ellison, 1989, 2005; Kamaludin, 1993; Engelhart et al., in press), and foraminifera (e.g. Debenay et al., 1998, 2000; Wang and Chappell, 2001; Horton et al., 2003, 2005b; Woodroffe et al., 2005). However, by far the most widely used sea-level indicators in tropical locations are coral. There are many different types of coral, but only a few species are found in narrow elevation ranges (e.g., *Acropora* and *Porites* species). Corals in growth position are constrained by water depth, being only able to survive up to mean low water spring tides. Unfortunately the lower depth limits of *Acropora* and *Porites* growth are poorly constrained, leaving coral-based sea-level indicators with a large error range (c. ±5 m) (Fairbanks, 1989; Toscano and MacIntyre, 2003). In contrast, microatolls are a particular type of intertidal coral that live near low water and have an error range as low as 3 cm (e.g. Smithers and Woodroffe, 2000). They are seen as the most precise, geologically persistent and useful diagnostic sea-level indicator on coral reefs systems. Other widely used sea-level indicators in tropical environments include geomorphological features, such as paleoshoreline notches, paleoreef flats and beach deposits (e.g. Tija, 1996; Dickinson, 2001). These indicators have large error terms associated with any reconstructions. Fixed biological indicators are also used as precise sea-level indicators. These include rock clinging oyster beds and fossil calcareous tubeworm species preserved in sediments (e.g. Baker and Haworth, 2000).

The development of diatom-based transfer functions has given modern researcher the potential to produce reliable, high-resolution sea-level reconstructions (e.g. Fritz et al., 1991; Zong and Horton, 1999; Sherrod, 1999; Gehrels et al., 2001, Zong et al., 2003; Sawai et al., 2004a,b; Hamilton and Shennan, 2005a,b; Hamilton et al., 2005; Horton et al., 2006). However, the transfer function technique has a number of limitations (Horton et al., 2003; Horton and Edwards, 2006). Huntley (1993) stated that transfer functions may give misleading results because they unrealistically force the influence of all environmental factors onto a

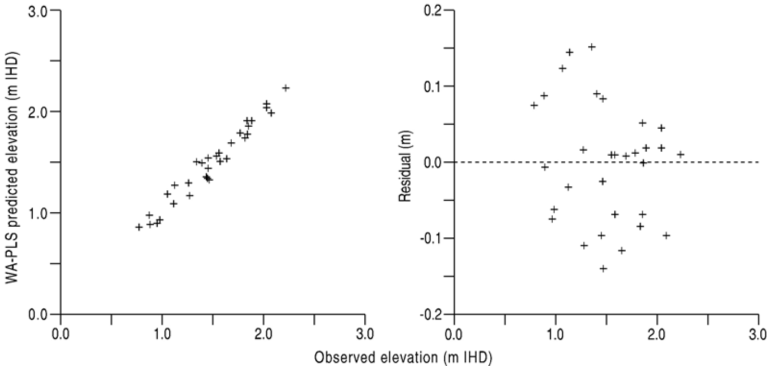

Fig. 7. (a) Scatter plots and (b) residuals showing the relationship of the regression of the of observed elevations versus diatom-predicted elevations using weighted averaging partial least squares (WA-PLS) from Ambeua and Mantigola mangroves.

single parameter. In addition, it is assumed that the relationship between the diatoms and the environment has not changed significantly over the time span represented by the fossil assemblage (Birks, 1995). Further, Jennings and Nelson (1992) and Horton and Murray (2006) demonstrated that spatial and temporal variability in microfossil distributions may reduce the precision of sea-level reconstructions using transfer functions. The microfossil assemblages may also be reworked through storm, and possible tsunami, activity (Horton et al., 2003). However, we have observed three diatom zones at Ambeua and Mantigola with an absence of broken valves, which suggests that the intertidal diatoms are not transported very far.

The next step to realize the potential of diatom-based sea-level reconstructions is to sample a broader range of the mangrove environments, with different hydrologies and mangrove species composition (Thom, 1967; Chapman, 1976; Bunt, 1982; Whitten et al., 1987; Clark and Guppy, 1988; Grindrod, 1988; Bunt and Bunt, 1999). In addition, the employment of transfer functions using multiple indicators, such as foraminifera, pollen and/or testate amoebae may improve the accuracy and precision (Gehrels et al., 2001; Patterson et al., 2005). A firm understanding of diatoms and their relationship to the environment must remain central to the development and application of these transfer functions (Horton and Edwards, 2006).

7. Conclusions

We have identified 95 diatom species from 31 samples from the mangrove environments of Ambeua and Mantigola. The study sites showed a strong vertical zonation. The diatom assemblages were divided into a mixed assemblage of mesohalobous, oligohalobous–halophilous and oligohalobous-indifferent diatoms that were found the dense mangrove vegetation towards the landward edge of the transects, and mesohalobous diatom assemblages that were located within the fringing *Rhizophora* and tidal flat environments.

We developed a diatom based transfer function to reconstruct former sea-levels. The relationship between observed and diatom-predicted elevations suggested accurate and precise reconstructions of former sea levels are possible. The error estimate is comparable to diatom-based transfer functions from temperate marshes.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.marmicro.2006.11.005.

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