

THE DEVELOPMENT OF A MODERN FORAMINIFERAL DATA SET FOR SEA-LEVEL RECONSTRUCTIONS, WAKATOBI MARINE NATIONAL PARK, SOUTHEAST SULAWESI, INDONESIA

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ABSTRACT

We collected modern foraminiferal samples to characterize the foraminiferal environments and investigate the role that temporal and spatial variability may play in controlling the nature and significance of foraminiferal assemblages of the mangroves of Kaledupa, Wakatobi Marine National Park, Southeast Sulawesi, Indonesia. The study of foraminiferal live and dead assemblages indicates that dead assemblages are least prone to vary in time and space, and furthermore, they accurately represent the subsurface assemblages that are the focus of paleoenvironmental reconstructions.

Further analyses of the dead assemblages indicate a vertical zonation of foraminifera within the intertidal zone. Zone D-Ia is dominated by agglutinated foraminifera *Arenoparrella mexicana*, *Miliammina fusca*, *M. obliqua* and *Trochammina inflata*. Zone D-Ib has mixed agglutinated/calcareous assemblages with species such as *T. inflata* and *Ammonia tepida*. Zone D-II is dominated by numerous calcareous species including *A. tepida*, *Discorbinella bertheloti*, *Elphidium advenum* and *Quinqueloculina* spp. Zone D-Ia is found to be the most accurate sea-level indicator and its assemblages are omnipresent world-wide. Zones D-Ib and D-II are subject to both spatial and temporal variations which must be included in any sea-level reconstructions.

INTRODUCTION

The recent transition of the earth climate system from a glacial to interglacial state produced a dramatic global sea-level response. Regions distant from the major glaciation centers, known as far-field sites, are typically characterized by relative sea-level (RSL) rise of ~120 m since the last glacial maximum (LGM) due, largely, to the influx of glacial meltwater to the oceans. In contrast, RSL dropped by many hundreds of meters in regions once covered by the major ice sheets (near- and intermediate-field sites) as a consequence of the isostatic 'rebound' of the solid Earth (Lambeck and others, 2002; Peltier and others, 2002; Shennan and others, 2002). Field observations of RSLs from far field locations provide essential constraints to geophysical models because model predictions depend upon three mechanisms: ocean siphoning caused mainly by gravitational effects due to the collapse of peripheral forebulges (Mitrovica

and Peltier, 1991); continental levering associated with local ocean loading; and global ice melt since the LGM (magnitude and source).

Although much contemporary research to test such theoretically derived models has focused on data sets from near- and intermediate-field sites (e.g., Shennan and others, 2000; Shennan and Horton, 2002), it is widely recognized that far-field sites provide the best possible estimate of the 'eustatic function' (Clark and others, 1978; Fleming and others, 1998; Yokoyama and others, 2001; Peltier, 2002). Consequently, model-derived reconstructions are increasingly recognizing the importance of these areas to constrain and test their geophysical earth models. With notable exceptions (e.g., Fairbanks, 1989, 1990; Bard and others, 1996; Chappell and others, 1998; Nunn and Peltier, 2001; Yokoyama and others, 2001), few studies have examined the sea-level histories from far-field areas. Furthermore, much of the data is derived from cored corals, which 'are not the clear indicators of past sea-levels that they are sometimes suggested to be' (Hopley, 1986). Problems encountered focus on the large elevational range exhibited by some coral species and the delayed response of a reef system to the sea-level change. Consequently, this study of Wakatobi Marine National Park, Southeast Sulawesi, Indonesia, which is a far-field site, begins to address the need to acquire accurate sea-level indicators (e.g., foraminifera).

Many researchers have used foraminiferal distributions across the intertidal zone of temperate saltmarshes as sea-level indicators (e.g., Scott and Medioli, 1978, 1980a; Patterson, 1990; Gehrels, 1994; de Rijk, 1995; Horton, 1999; Horton and others, 1999a b; Gehrels and others, 2001). The intertidal distributions can be divided into two parts: an agglutinated assemblage that is restricted to the vegetated marsh; and a calcareous assemblage that dominates the mudflats and sandflats of the intertidal zone. The agglutinated assemblage is commonly employed as a sea-level indicator in the reconstruction of former sea levels. Saltmarsh foraminiferal zonation is a significantly more accurate indicator of sea level than undifferentiated marsh deposits since well-defined zones subdividing the marsh increase the vertical resolution of the deposits (Scott and Medioli, 1978). Furthermore, Scott and others (2001) state that vertical zonations are observed in marshes throughout the world, and suggest that marsh foraminifera are ubiquitous worldwide. However, studies of microfossils and their relationship to RSL in coastal and estuarine environments from tropical or subtropical environments to support this conclusion are sparse, indeed, non-existent for Indonesia. Thus, this paper seeks to document, for the first time, some characteristics of modern foraminiferal environments in the central Wak-

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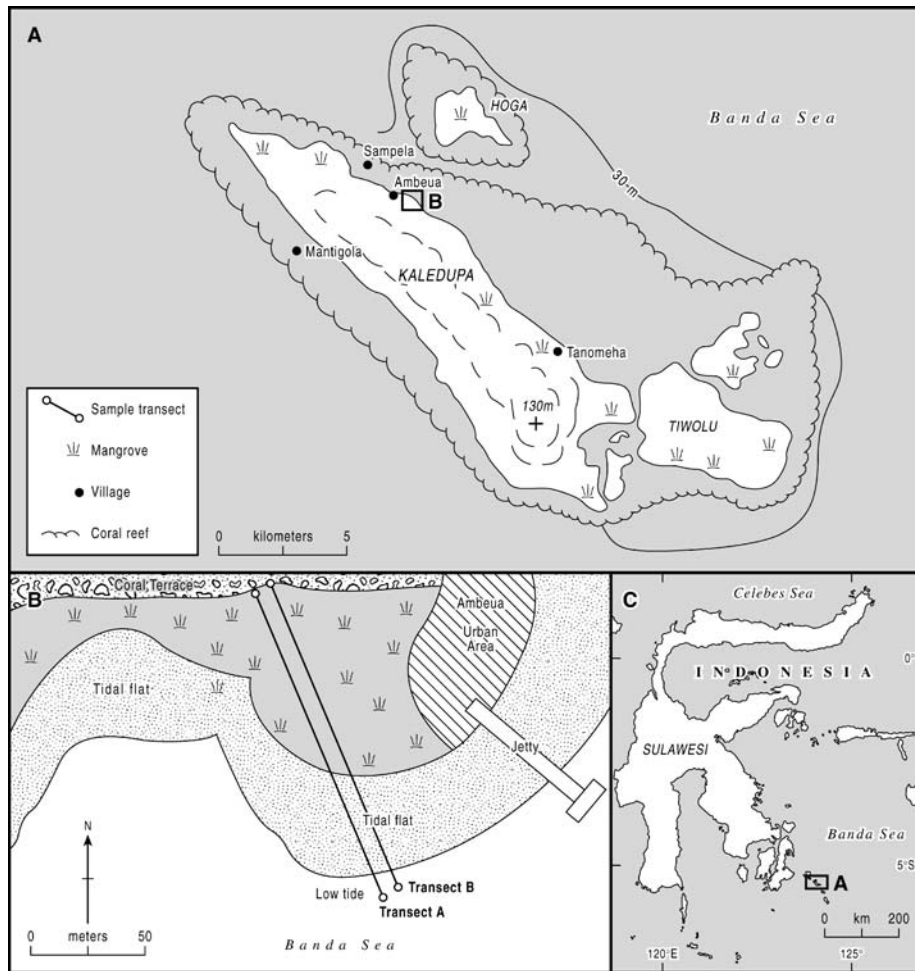


FIGURE 1. Location map of study area. (A) Kaledupa, Wakatobi Marine National Park, (B) Transects A and B on a tidal mangrove creek and (C) Sulawesi, Indonesia.

atobi Marine National Park province for use in paleoenvironmental interpretations made from Quaternary sediments of Indonesia.

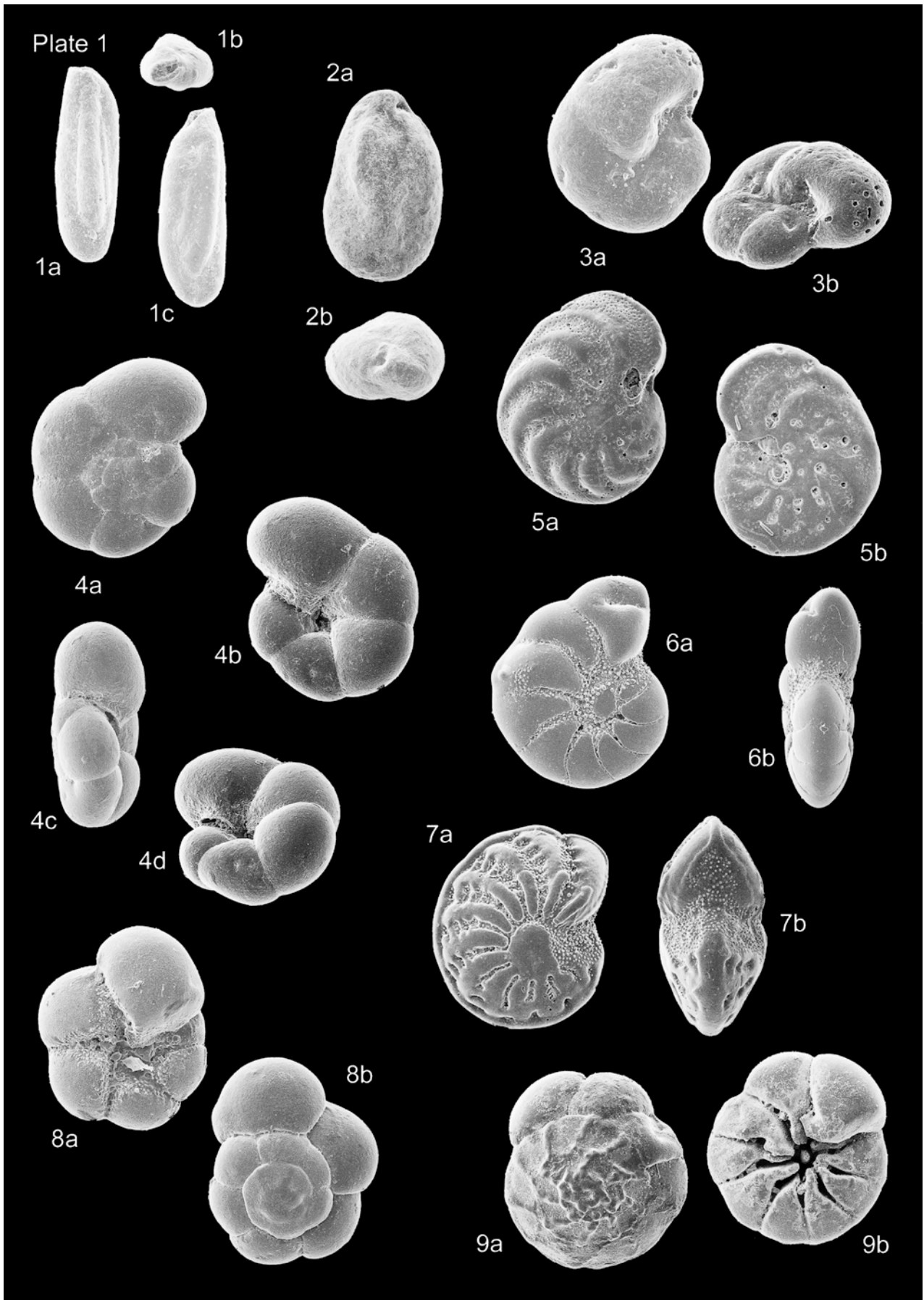
This paper also discusses which assemblage constituents (live, dead and/or total) are best applied for foraminiferal-based sea-level reconstructions studies in tropical locations and investigates the role that temporal and spatial variability may play in controlling the nature and significance of foraminiferal assemblages. Many researchers state that total assemblages most accurately represent general environmental conditions because they integrate seasonal and temporal fluctuations (e.g., Scott and others, 2001). However, Murray (1991, 2000) suggests that the use of total assemblages disregards changes that will affect live assem-

blages after their death. Furthermore, depositional changes are sample dependent because the greater the vertical depth of a sample, the more important the dead contribution. Horton (1999) indicates that the dead assemblages from temperate marshes are the most appropriate for paleoenvironmental studies because these assemblages are less susceptible to seasonal variations and closely resemble subsurface assemblages. Horton (1999) and Horton and Edwards (2003) concluded that if the live assemblages are variable and not transferred into subsurface environments, their combination with the dead assemblage to produce a total assemblage simply degrades the utility of the latter. Thus, in this paper we have only investigated the live and dead assemblages.

PLATE 1

1. *Miliammina fusca* (Brady). a. side view, $\times 136$. b. oblique apertural view, $\times 176$. c. side view, $\times 176$.
2. *Miliammina obliqua* (Heron-Allen and Earland). a. side view, $\times 200$. b. apertural view, $\times 200$.
3. *Arenoparrella mexicana* (Anderson). a. side view, $\times 200$. b. oblique apertural view, $\times 200$.
4. *Trochammina inflata* (Montagu). a. side view, $\times 176$. b. side view, $\times 176$. c. edge view, $\times 176$. d. oblique apertural view, $\times 176$.
5. *Discorbinella bertheloti* (d'Orbigny). a. spiral view, $\times 200$. b. apertural view, $\times 200$.
6. *Haynesina depressula* (Walker and Jacob). a. side view, $\times 200$. b. edge view, $\times 200$.
7. *Elphidium advenum* (Cushman). a. side view, $\times 200$. b. edge view, $\times 200$.
8. *Ammonia tepida* (Cushman). a. spiral view, $\times 200$. b. apertural view, $\times 200$.
9. *Ammonia takanabensis* (Ishizaki). a. spiral view, $\times 200$. b. apertural view, $\times 200$.

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STUDY AREA

Extending over 13,900 km², the Wakatobi Marine National Park includes all coral reefs, islands, and communities within its boundaries and is centered around the main islands in the Wakatobi archipelago (Fig. 1). The area is considered 'a geological and biological anomaly' (Daws and Fujita, 1999) and is located at a zone of transition between the two distinct faunas associated with the Asian and Australian continents. Wallace (1869) postulated that the islands of Sulawesi had been isolated far longer than the surrounding islands, giving evolution a much greater opportunity to shape a unique fauna.

The field site is located on a tidal mangrove creek system on the northern coast of the island of Kaledupa (Fig. 1B). At the mouth of the creek, and along much of the coast of Kaledupa, is a 150 m-wide fringing mangrove swamp, with vegetation up to 7 m in height. The mangroves of Kaledupa exhibit a pronounced zonation of species similar to many other mangrove swamps (e.g., Chapman, 1944; Macnae, 1968; Snedaker, 1982) with a fringing *Rhizophora* zone, transgressing into a mixed *Rhizophora/Sonneratia* zone and then an *Avicennia* mangrove zone (Barnes, written communication, 2002). The landward edge of the mangrove environment terminates on an exposed coral terrace. Tides in the area are semi-diurnal and microtidal, with mean spring tidal ranges of 1.6 m. On the flood tide, water enters the mangroves and saltflats via a network of small channels.

METHODOLOGY

Samples of surface sediment were collected from 20 stations along two 160 m transects (A and B). Both transects cross the intertidal zone from an exposed former coral terrace through a mangrove swamp and onto an unvegetated intertidal mudflat. All stations were leveled to sea level using a level and staff at regular spatial and temporal intervals throughout the study, and the tidal curve from Boeton Island was used to calculate elevations with respect to Indonesian Height Datum (IHD). At each station, one sample of approximately 10 cm³ volume (10 cm² surface sample by 1 cm thick) was taken for foraminiferal analysis.

To investigate the role that temporal and spatial variability may play in controlling the nature and significance of foraminiferal assemblages, samples were taken twice during a two-month period (Transects A1 and A2) and once from an additional adjacent transect (Transect B). Foraminiferal sample preparation followed Scott and others (2001). The species were identified with reference to a number of publications, namely Collins (1958), Albani (1968), Albani and Yassini (1993), Brönnimann and Whittaker (1993), Yassini and Jones (1995), Hayward and others (1999a) and Revets (2000), and by study of reference collections in the Natural History Museum, London (Plate 1). Samples were stored in buffered ethanol with protein stain Rose Bengal to identify organisms living at the time of collection, and thus allow the analyses of live and dead assemblages (Walton, 1952; Scott and Medioli, 1980b; Murray, 1991; Murray and Bowsler, 2000).

We used two multivariate methods to detect, describe and classify patterns within the live and dead foraminiferal data set: unconstrained cluster analysis and detrended correspon-

dence analysis (DCA). Unconstrained cluster analysis based on the unweighted Euclidean distance, using no transformation or standardization of the percentage data, was used to classify modern samples into more-or-less homogeneous faunal zones (clusters). Detrended correspondence analysis, an ordination technique, was used to represent samples as points in a multidimensional space. Similar samples are located together and dissimilar samples apart. Thus, cluster analysis is effective in classifying the samples according to their foraminiferal assemblage, but DCA gives further information about the pattern of variation within and between groups. This is important, as the precise boundaries between clusters can be arbitrary. Thus, we selected reliable faunal zones when the samples within each cluster were mutually exclusive in ordination space. The elevation of each station within the reliable clusters determined the vertical zonation of each intertidal environment.

We employed Student's T-Test to determine whether two samples from A1 and A2, and A1 and B are likely to have come from the same two underlying populations. We use a two-tailed distribution.

RESULTS

Forty species of foraminifera were identified from the study of surface samples from the mangroves of Kaledupa. The maximum number of species per 10 cm³ sample was 23, with maximum and minimum foraminiferal total (live plus dead) abundance of 632 and 134 individuals per sample, respectively. The live and dead assemblages are dominated by three agglutinated species, *Arenoparrella mexicana*, *Miliammina fusca*, and *Trochammina inflata*, and four calcareous species, *Ammonia tepida*, *Discorbinella bertheloti*, *Elphidium advenum* and *Quinqueloculina* spp. Tables of the relative percentages of live and dead foraminifera for transects A1, A2 and B are JFR Data Repository item JFR DR200502 at website <http://cushforams.niu.edu>.

LIVE ASSEMBLAGES

The live assemblage of Transect A1 is dominated by calcareous species, which represent over 75% of the total count. Calcareous taxa such as *A. tepida*, *E. advenum*, *D. bertheloti*, and *Q.* spp. dominate the unvegetated mudflat and fringing *Rhizophora* mangrove section of the transect (0–60 m along the transect). Maximum percentages of *E. advenum* (15%), *A. tepida* (30%) and *D. bertheloti* (13%) occur 0 m, 18 m and 40 m along the transect, respectively (Fig. 2). In addition, the *Rhizophora* floral zone has a relatively high foraminiferal abundance, with an average count of 253 live specimens per 10 cm³. The *Rhizophora/Sonneratia* floral zone (60–90 m along the transect) is also dominated by calcareous species with the maximum percentage of *Haynesina depressula* occurring within this zone (12%). However, there is an increasing agglutinate presence, in particular *T. inflata*, which reaches 22% 90 m along the transect. The majority of calcareous species are replaced by agglutinated species within the *Avicennia* mangrove zone (90–160 m along the transect). However, maximum percentages of *Q.* spp. (71%) occur 120 m along the transect. The maximum percentage of the dominant agglutinated taxa

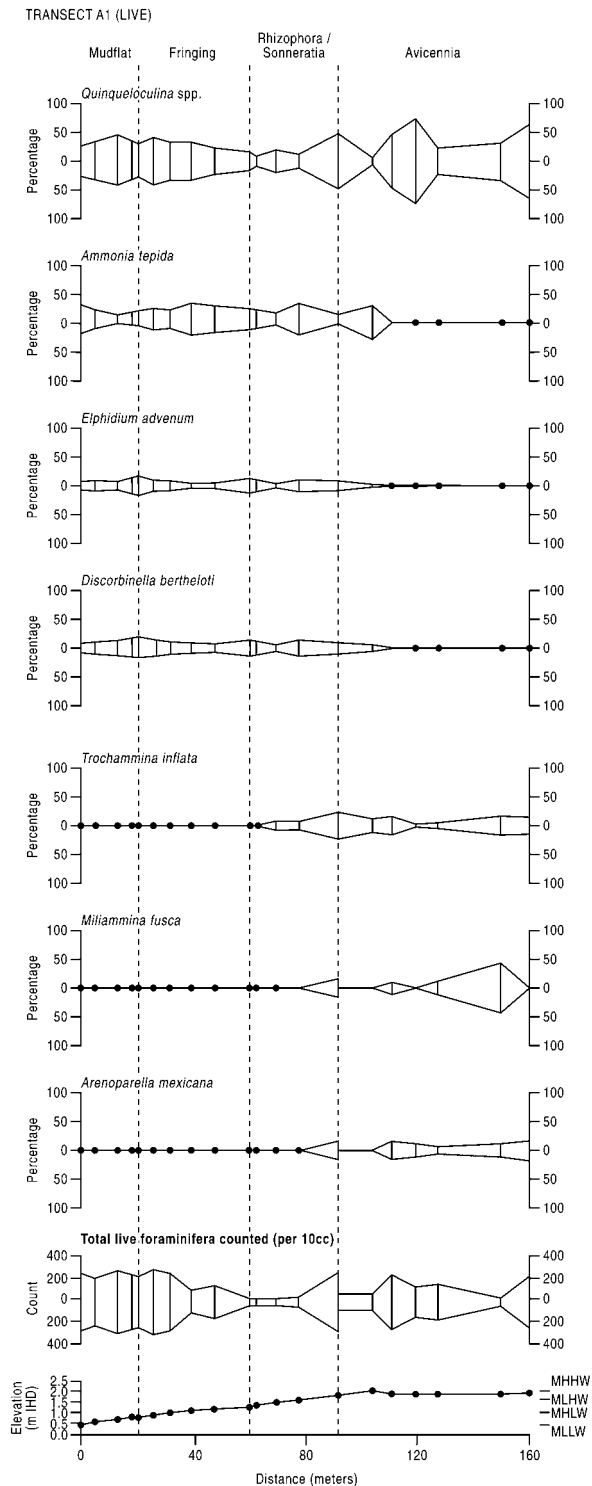


FIGURE 2. Live foraminiferal abundance (%) of seven foraminiferal species and foraminiferal populations of the mangroves of Kale-dupa Transect A1. The elevation, tidal levels (mean high high water (MHHW), mean low high water (MLHW) and mean high low water (MHLW) and mean low low water (MLLW) and floral zonation are indicated.

T. inflata, *M. fusca*, and *A. mexicana* occur within this *Avicennia* zone (24%, 41% and 16%, respectively).

The total number of live foraminifera from the twenty stations of the Transect A1 is 3648 compared to 4102 specimens for the temporal Transect A2 (taken 2 months later). There are also differences in the dominant live foraminiferal species (Fig. 3). The relative contribution of *Q. spp.* between 5 and 32 m along the transect is greater than 30% at each sampling station of Transect A1 compared to less than 19% for Transect A2. Furthermore, 90 m along the transect the relative contributions of *Q. spp.* are 44% on A1 to 15% on A2, whereas 105 m along the transect A1 is 8% and A2 is 30%. Indeed, T-tests suggest that the relative abundances of *Q. spp.* between transects A1 and A2 are statistically significantly different and did not come from the same underlying population (Table 1). Other notable differences include lower percentages of *T. inflata* between 128 m and 150 m along the transect for A1 (<16%) compared to Transect A2 (>26%), and appreciably lower percentages of *A. mexicana* at the landward edge of the transect (5% on A1 to 56% on A2).

The total number of live foraminifera also increases from the original transect (A1) to spatial Transect B (4057 specimens) taken adjacent to A1. The difference in contribution of *Q. spp.* between transects is amplified 90 m along the transect (44% on A1 to 6% on B), whereas 105 m along the transect A1 is 8% and B is 44% (Fig. 4). Other notable dissimilarities include the increase in relative abundance of *M. fusca* 150 m along the transect (13% on A1 to 44% on B) and a corresponding decrease in *A. mexicana* (41% on A1 to 19% on B). Statistical analyses (T-tests) support the inference that these three species show significantly different assemblages between transects A1 and B (Table 1).

DEAD ASSEMBLAGES

There is an increase in the relative abundance of agglutinated foraminifera in the dead assemblage, with agglutinated species contributing over 35% to the total dead assemblage of Transect A1. However, the unvegetated mudflat and fringing mangrove floral zones are dominated by calcareous foraminifera such as *A. tepida*, *E. advenum*, *D. bertheloti*, *H. depressula* and *Q. spp.*, with the two most dominant species reaching their maximum abundance within this zone (*A. tepida*—30% and *Q. spp.* 37%). The unvegetated mudflat and fringing mangrove have the highest foraminiferal counts within the intertidal zone with an average count of 216 dead species per 10 cm³ (Fig. 5).

The *Rhizophora/Sonneratia* mangrove zone shows an increasing contribution of agglutinated species, most notably *T. inflata*. However, *A. tepida* contributes at least 16% at each station and the zone still possesses the maximum abundances of numerous calcareous species, including *A. takanabensis* and *H. depressula* (28% and 14%, respectively). Nevertheless, the tendency of the increasing contribution of agglutinated species continues within the *Avicennia* mangrove zone, which is dominated by agglutinated species such as *T. inflata*, *M. fusca*, *M. obliqua* and *A. mexicana*; agglutinated species make up at least 65% of the assemblage landwards of 105 m.

The foraminiferal dead assemblage count is relatively sta-

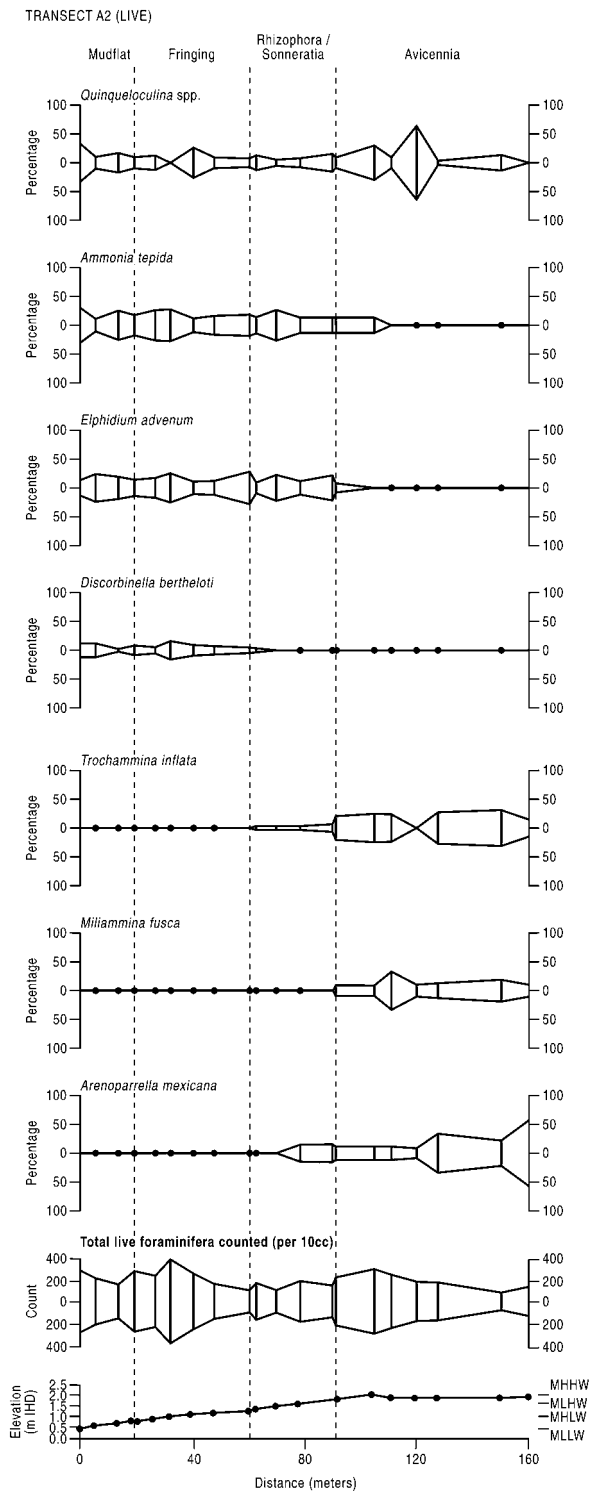


FIGURE 3. Live foraminiferal abundance (%) of seven foraminiferal species and foraminiferal populations of the mangroves of Kaledupa Transect A2. The elevation, tidal levels (mean high high water (MHHW), mean low high water (MLHW) and mean high low water (MHLW) and mean low low water (MLLW) and floral zonation are indicated.

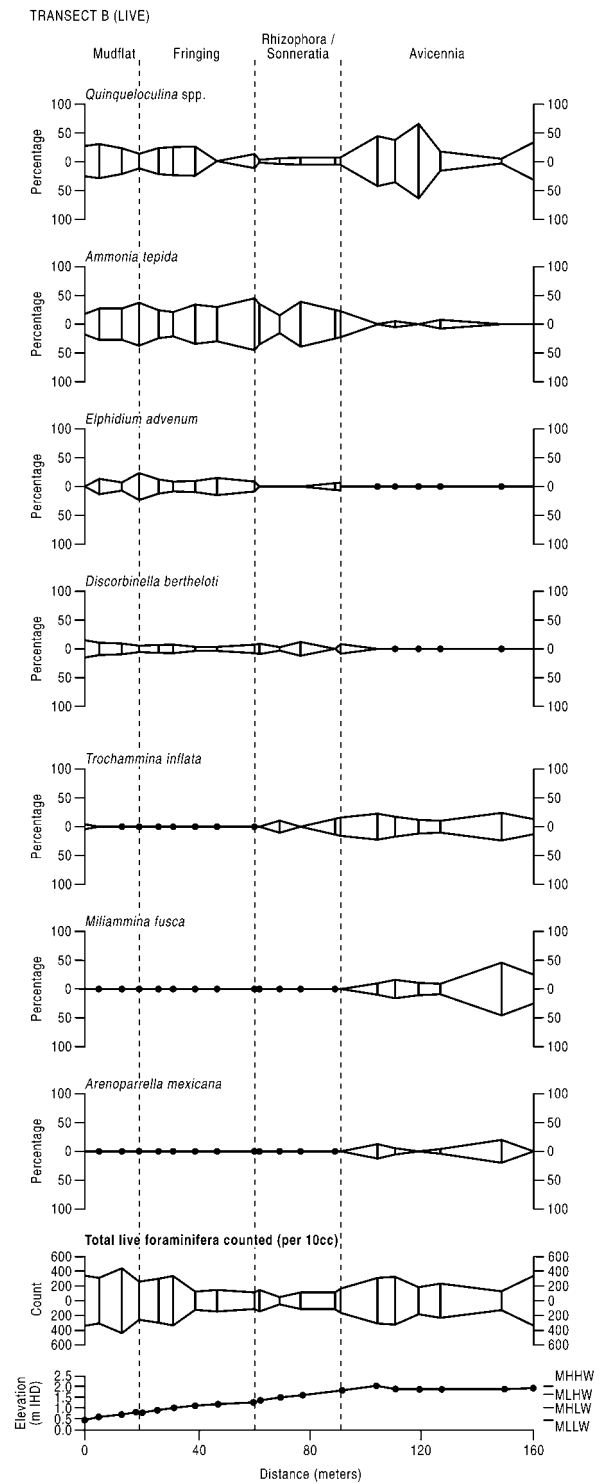


FIGURE 4. Live foraminiferal abundance (%) of seven foraminiferal species and foraminiferal populations of the mangroves of Kaledupa Transect B. The elevation, tidal levels (mean high high water (MHHW), mean low high water (MLHW) and mean high low water (MHLW) and mean low low water (MLLW) and floral zonation are indicated.

TABLE 1. T-Test to determine whether two samples (from transects A1 and A2, A1 and B) are likely to have come from the same two underlying populations and thus assess temporal and spatial influences. Values in bold exceed the $p < 0.05$ significance value (2.09) and indicate rejection of the null hypothesis that the A1 and A2, and A1 and B are equal.

Species	Temporal (A1 and A2)		Spatial (A1 and B)	
	Live	Dead	Live	Dead
<i>Quinqueloculina</i> spp.	2.94	1.82	5.51	0.54
<i>Ammonia tepida</i>	0.92	0.20	1.66	2.00
<i>Elphidium advenum</i>	3.10	0.09	2.08	0.54
<i>Discorbinella bertheloti</i>	0.84	1.15	1.19	0.79
<i>Trochammina inflata</i>	0.82	0.64	0.39	0.62
<i>Miliammina fusca</i>	1.02	0.28	2.38	0.55
<i>Arenoparrella mexicana</i>	1.97	0.22	2.20	0.93

ble among the original (A1), temporal (A2) (Fig. 6) and spatial (B) (Fig. 7) transects. The total number of dead foraminifera is also relatively constant; 3712 on A1, 3708 on A2 and 3955 specimens on B. Statistical analyses do not show any significant differences although there are noteworthy differences at individual stations (Table 1). For example, the relative contribution of *A. mexicana* fluctuates from 12% on A1 to 32% on A2, and 48% on A1 to 12% on A2 at 120 m and 150 m along the transect, respectively.

DISCUSSION

There is much debate about which foraminiferal assemblage constituents (live, dead and/or total) to use for sea-level reconstructions (Buzas, 1968; Scott and Medioli, 1980b; Scott and Leckie, 1990; de Rijk, 1995; Murray, 2000; Scott and others, 2001). These studies have, however, concentrated on foraminiferal species from temperate intertidal areas. This new study assesses the applicability of live and dead assemblages from tropical environments. Analyses of the spatial and temporal variations of the dominant species show that the dead assemblages are less susceptible to temporal and spatial variations compared to live counterparts. We investigated this further by examining the differences in the vertical zonation of the live and dead assemblage. Figures 8 and 9 both show the combined foraminiferal data (original A1, temporal A2 and spatial B transects) of the live and dead assemblages separated into three reliable zones by cluster analysis and DCA. The live assemblages do not show any vertical zonations due to the heterogeneity of living assemblages in space and time, in particular Zone L-Ib, which covers the full elevational range of the transects. Similar spatial and temporal variations have been documented by many studies (Buzas, 1968; Schafer, 1968; Jones and Ross, 1979; Schafer and Mudie, 1980; Alve and Murray, 1999, 2001; Murray and Alve, 2000; Swallow, 2000; Buzas and others, 2002; Hippensteel and others, 2002; Horton and Edwards, 2003). Schafer and Mudie (1980) discovered an order of magnitude difference in average foraminiferal number between pairs of sites. Alve and Murray (2001) demonstrated significant temporal variability over a 27-month period with the number of species found at any single sampling event varying between 5 and 22. Such temporal and spatial patterns of live assemblages re-

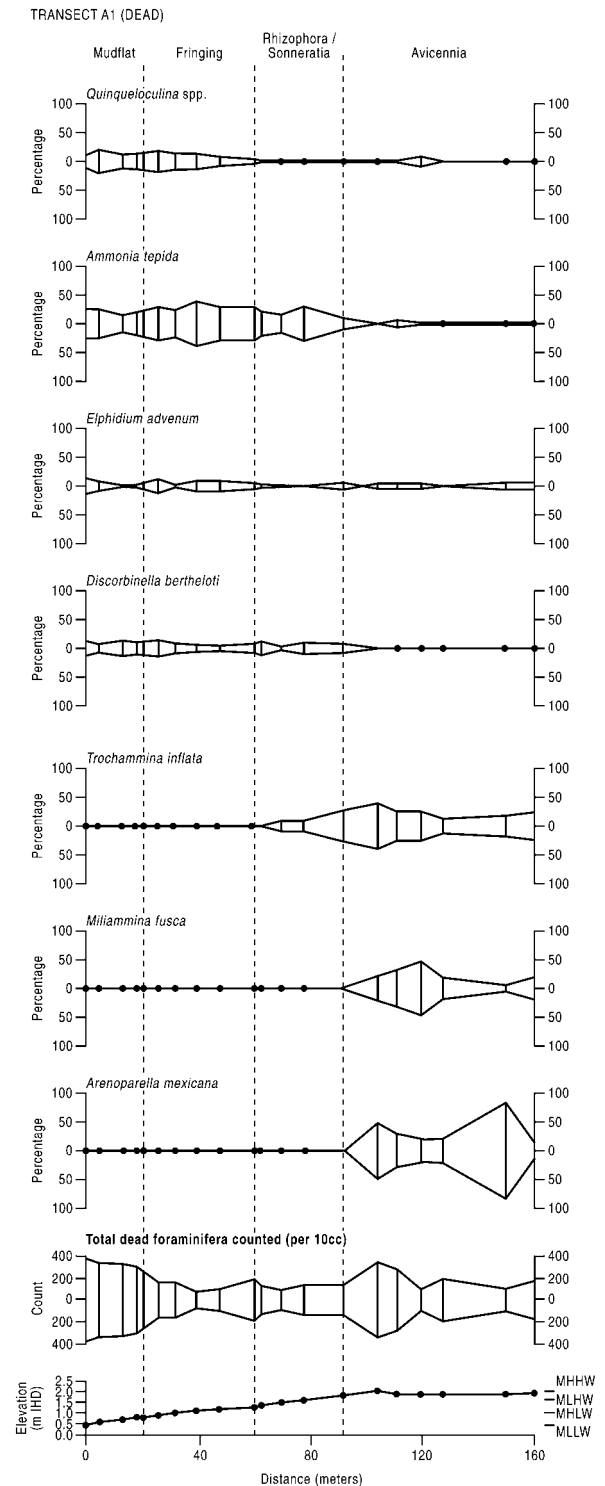


FIGURE 5. Dead foraminiferal abundance (%) of seven foraminiferal species and foraminiferal populations of the mangroves of Kale-dupa Transect A1. The elevation, tidal levels (mean high high water (MHHW), mean low high water (MLHW) and mean high low water (MHLW) and mean low low water (MLLW) and floral zonation are indicated.

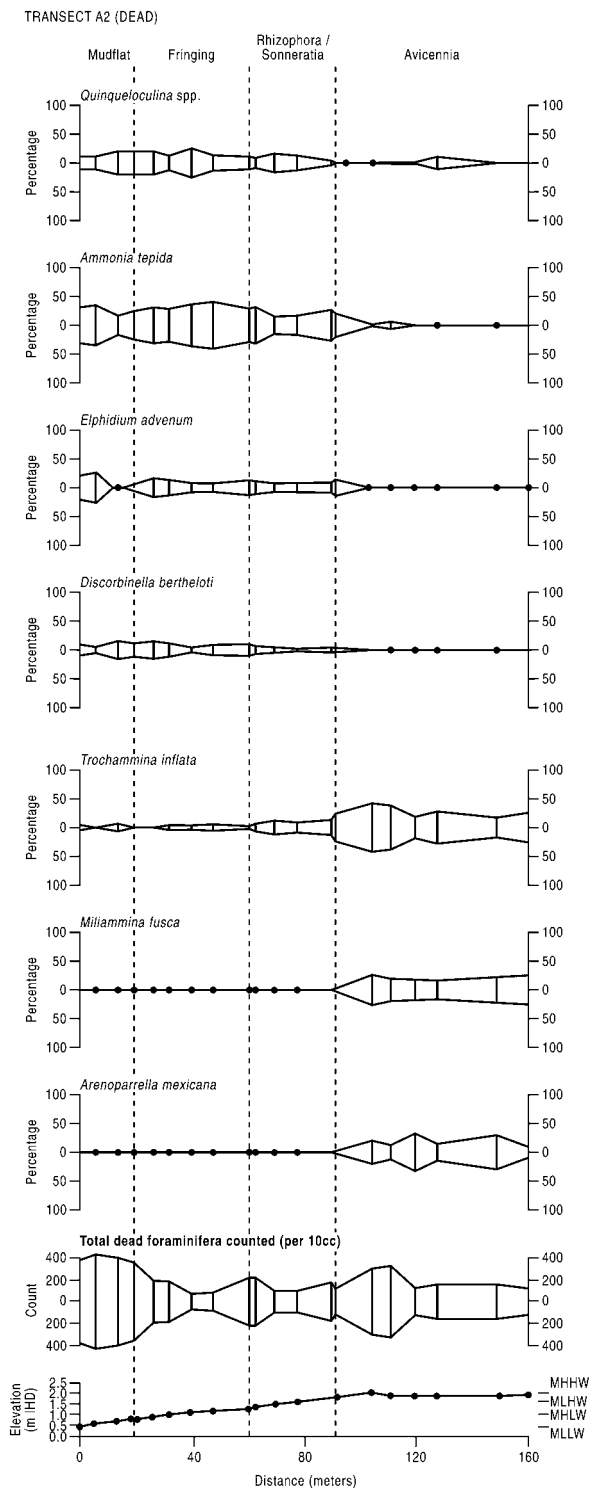


FIGURE 6. Dead foraminiferal abundance (%) of seven foraminiferal species and foraminiferal populations of the mangroves of Kaledupa Transect A2. The elevation, tidal levels (mean high high water (MHHW), mean low high water (MLHW) and mean high low water (MHLW) and mean low low water (MLLW) and floral zonation are indicated.

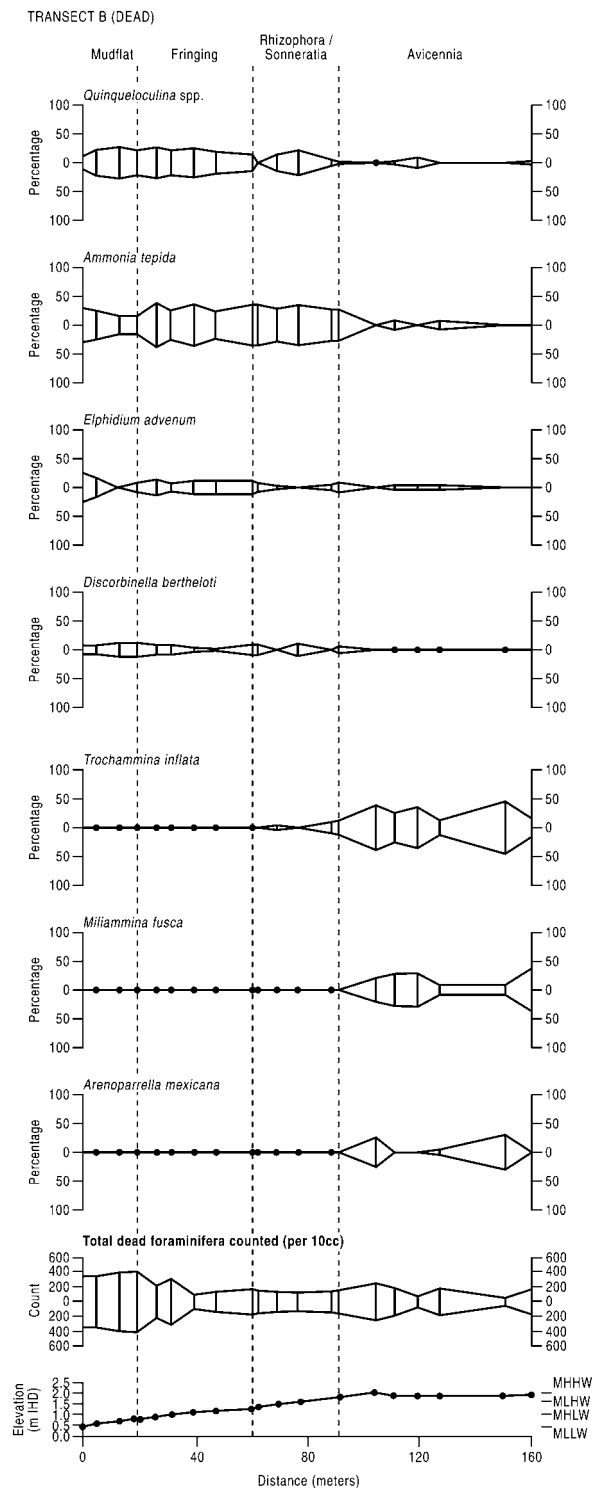


FIGURE 7. Dead foraminiferal abundance (%) of seven foraminiferal species and foraminiferal populations of the mangroves of Kaledupa Transect B. The elevation, tidal levels (mean high high water (MHHW), mean low high water (MLHW) and mean high low water (MHLW) and mean low low water (MLLW) and floral zonation are indicated.

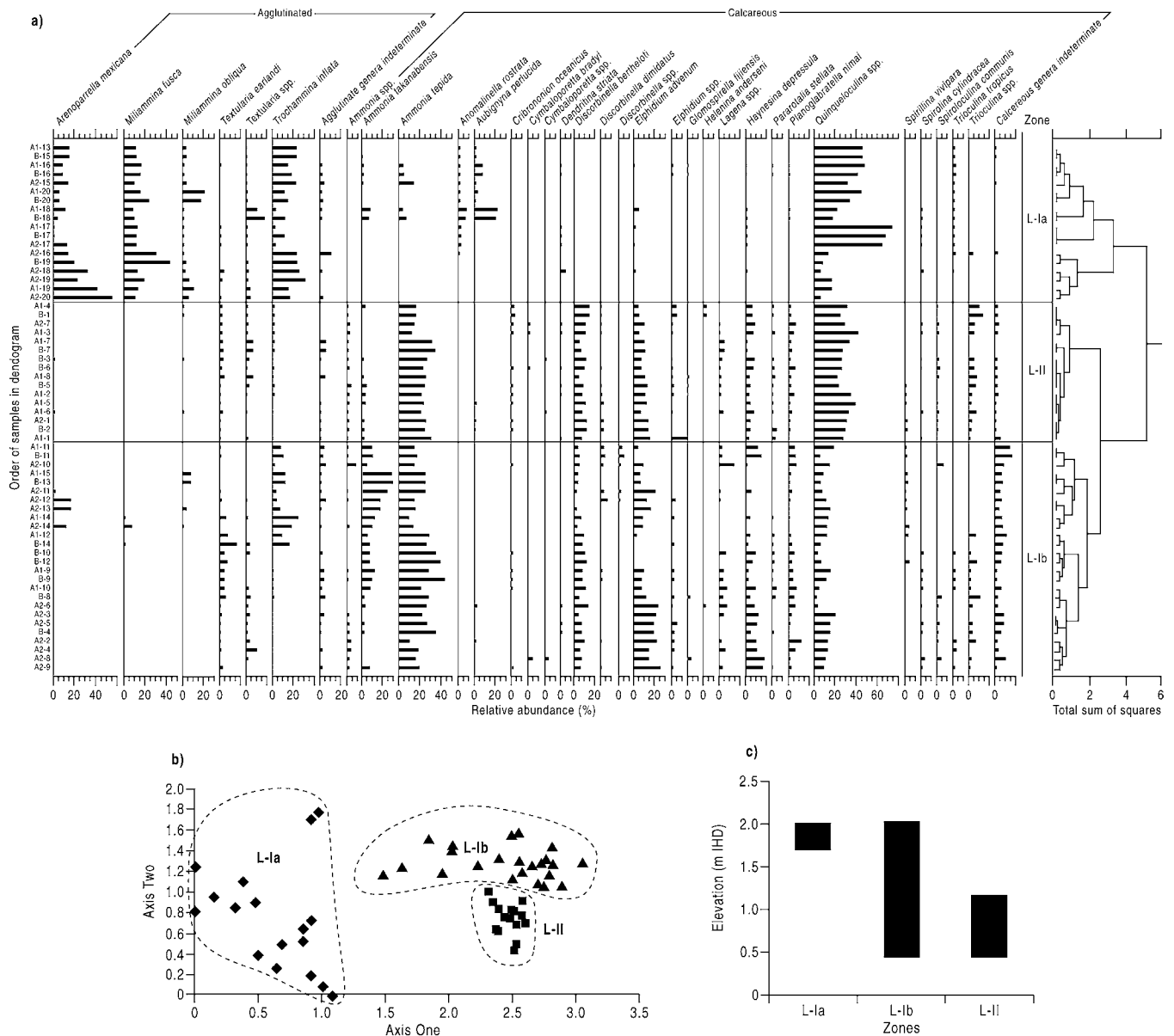


FIGURE 8. (a) Unconstrained cluster analysis based on unweighted Euclidean distances showing the live foraminiferal assemblages versus order of samples on dendrogram, (b) detrended correspondence analysis and (c) vertical zonation of the mangroves of Kaledupa transects A1, A2 and B. Only samples with counts greater than 40 individuals and species which reach 2% of the total sum are included.

flect the impact of factors such as seasonality, predation, reproduction, mode, sources and distribution pattern of food particles and species interactions (Buzas, 1968; Schafer, 1968; Scott and others, 2001).

In contrast to the live assemblages, the dead assemblages present a more homogeneous spatial and temporal distribution as a probable consequence of post-mortem lateral and vertical mixing of empty tests by biological and physical agents (Scott and others, 2001). The dead assemblages assimilate all temporal variation and spatial patchiness into an 'average signal' that tends to reduce the inter-sample variance. For example, the combined dead assemblages are classified into three reliable zones that show a strong vertical zonation (Fig. 9), which indicates that the distribution of

dead foraminifera are a direct function of elevation, with the duration and frequency of intertidal exposure as the most important environmental factors.

Agglutinated species *A. mexicana*, *M. fusca*, *M. obliqua* and *T. inflata* dominate Zone D-Ia, which is found at the landward edge of the mangrove study site with an elevational range of 2.02–1.02 m IHD (range 0.20 m). Similar faunal assemblages have been observed at the landward margins of both tropical mangroves and temperate salt-marshes. Brönnimann and others (1992) and Brönnimann and Whittaker (1993) found assemblages of *A. mexicana* in mangrove sediments of the Fiji and Malay archipelagos, respectively. Assemblages dominated by *T. inflata* have been identified by Haslett (2001) and Horton and others (2003)

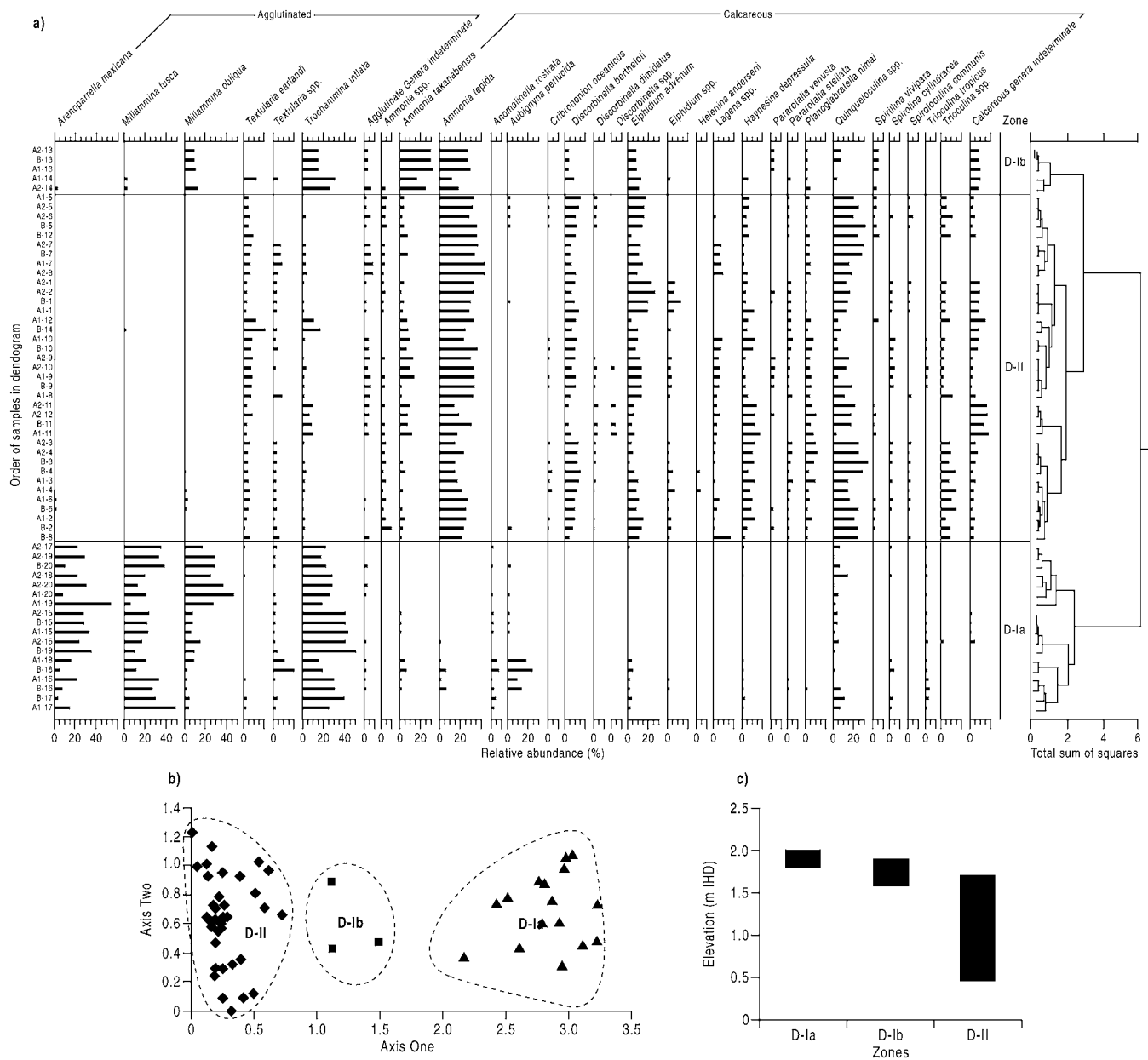


FIGURE 9. (a) Unconstrained cluster analysis based on unweighted Euclidean distances showing the dead foraminiferal assemblages versus order of samples on dendrogram, (b) detrended correspondence analysis and (c) vertical zonation of the mangroves of Kaledupa transects A1, A2 and B. Only samples with counts greater than 40 individuals and species which reach 2% of the total sum are included.

at the landward limit of mangrove distributory channels from the Great Barrier Reef coastline, Australia. Many studies have identified high abundances of *M. fusca* in the mangroves of Fiji, southwest Australia, Brazil, New Zealand, northern Australia and the Great Barrier Reef coastline (Brönnimann and others, 1992; Brönnimann and Whittaker, 1993; Yassini and Jones, 1995; Debenay and others, 1998, 2000; Hayward and others, 1999a, b; Wang and Chappell, 2001; Horton and others, 2003). Studies of temperate salt-marshes have commonly identified a high marsh zone dominated by *T. inflata* and a low marsh zone dominated by *M. fusca* (Scott and Medioli, 1978, 1980a; Gehrels, 1994; Horton, 1999; Horton and others, 1999a; Spencer, 2000; Hip-

pensteel and others, 2000; Horton and Edwards, 2003, 2005 in press).

Faunal Zone D-Ib has a mixed agglutinated/calcareous assemblage composed of *Ammonia* species, with lower frequencies of *T. inflata* and *M. obliqua*. The zone ranges from 1.90–1.60 m IHD (range 0.30 m). Other tropical and temperate studies have observed mixed agglutinated/calcareous assemblage zones but with an increase in the relative abundance of the former (Scott and Medioli, 1978, 1980a; Gehrels, 1994; Yassini and Jones, 1995; Debenay and others, 1998, 2000; Hayward and others, 1999a, b; Wang and Chappell, 2001; Horton and Edwards, 2003; Horton and others, 2003).

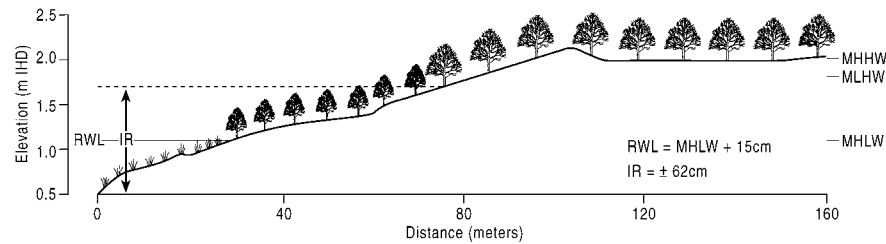


FIGURE 10. The indicative meaning of the mangroves of Kaledupa illustrating the indicative range (IR) and reference water level (RWL) for Zone D-II. Mean high high water (MHHW), mean low high water (MLHW) and mean high low water (MHLW) are shown.

Zone D-II is found at the seaward edge of the transects and is dominated by numerous calcareous species such as *A. tepida*, *D. bertheloti*, *E. advenum* and *Q. spp.*, with a relatively large elevation range of 1.71–0.47 m IHD (range 1.24 m). Other calcareous faunal zones with relatively high abundances of *A. tepida* are common in many tropical or subtropical locations (Hayward and others, 1996; Debenay and others, 2000; Wang and Chappell, 2001; Horton and others, 2003), although there are many species that are site specific. For example, studies of tidal flat environments of the Great Barrier Reef coastline by McIntyre (1997) and Horton and others (2003) have identified a foraminiferal faunal zone dominated by cosmopolitan *Ammonia* species, in addition to *Miliolinella spp.*, the endemic *E. discoidale multiloculum* and extinct *Pararotalia venusta*. The presence of *P. venusta* indicates some reworking of material within the intertidal zone of this study site. Analyses of temperate saltmarshes show differences from the Kaledupan transect. Studies of British saltmarshes display tidal flat assemblages dominated by *Haynesina germanica* and other *Elphidium* species (Horton, 1999; Edwards and Horton, 2000; Murray and Alve, 2000; Gehrels and others, 2001; Horton and Edwards, 2003, 2005 in press).

IMPLICATIONS FOR SEA-LEVEL STUDIES

The understanding of former sea levels based on the identification and interpretation of foraminiferal assemblages requires that their indicative meaning is known, i.e., the vertical relationship of the local environment in which the assemblage accumulated to a reference tide level (van de Plasche, 1986; Shennan, 1986; Horton and others, 1999b, 2000). The indicative meaning is commonly expressed in terms of an indicative range and a reference tidal level, the former being a vertical range within which the assemblage can occur, and the latter a tidal level to which the assemblage is assigned, e.g., mean high high water (MHHW) (Fig. 10).

Estimates of the indicative meaning of faunal zones from the mangroves of Kaledupa (Table 2) are developed from the premise that zones found vertically adjacent, without a hiatus, must have formed in environments that existed side by side in space (Walther's Law). Therefore, the transition from faunal Zone D-Ib to Zone D-II has an indicative range equal to the range of the transition from one zone to the other, not that of the individual zone. For example, the indicative range of Zone D-II is ± 0.62 m, whereas the range of Zone D-Ib directly above Zone D-II is only ± 0.06 m. The ranges cover the elevational limits of the boundary when observed during the 2 sampling months.

Despite the conclusion that dead assemblages are less variant than live assemblages in most spatial and temporal fluctuations, it is important to identify any variations in the vertical zonation that must be included in any sea-level reconstruction to avoid errors in accuracy and precision (Horton and Edwards, 2003). Multivariate analyses of each individual transect (A1, A2 and B) show that the elevational range of the Zone D-Ia remains virtually constant; however, spatial and temporal variations in the dead assemblages are observed for faunal zones D-Ib and D-II (Fig. 11). The elevation of the boundary between zones D-Ib and D-II fluctuates from 1.86 m IHD at A1 to 1.42 m IHD at B, suggesting that some of the variability in the live assemblages is being transmitted to the dead assemblages.

In addition to spatial and temporal variations, it is also important for sea-level reconstructions to assess the influence of post-depositional processes on the assemblage constituents. Thus, subsurface dead assemblages, the focus of paleoenvironmental reconstructions, were collected from the mudflat, fringing *Rhizophora*, mixed *Rhizophora/Sonneratia* and *Avicennia* environments to determine which modern assemblage constituents are most appropriate for paleoenvironmental reconstruction. Subsurface samples were collected at a depth of 12 cm; 97% of live specimens occurred above this depth. Scatter plots (Fig. 12) show a clear posi-

TABLE 2. Indicative range and reference tide level for faunal zones of the mangroves of Kaledupa.

	Indicative Range	Reference Water Level	Reference Water Level (m IHD)
Zone D-Ia	± 10 cm	MHHW	1.92 m
Zone D-I directly above Zone D-Ib	± 4 cm	MHHW - 6 cm	1.86 m
Zone D-Ib	± 15 cm	[MHHW + MLHW]/2 - 3 cm	1.75 cm
Zone D-Ib directly above Zone D-II	± 6 cm	MLHW - 6 cm	1.66 cm
Zone D-II	± 62 cm	MHLW + 15 cm	1.09 cm

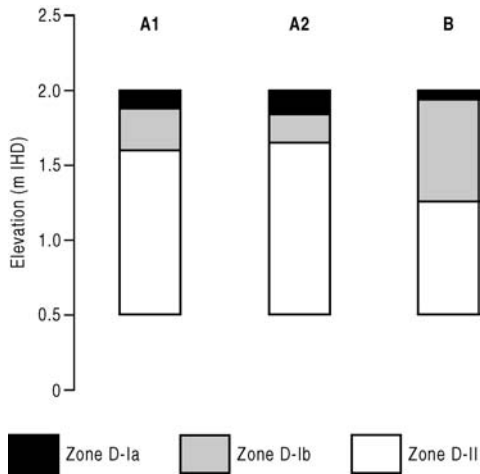


FIGURE 11. Vertical zonation of the Transects A1, A2 and B of the mangroves of Kaledupa determined by unconstrained cluster analysis based on unweighted Euclidean distance and detrended correspondence analysis of relative abundances of dead individuals. Only samples with counts greater than 40 individuals and species which reach 2% of the total sum are included.

tive linear correlation between the subsurface and surface dead assemblages ($r^2 = 0.90$) from Transect A1. The dead assemblages fluctuate little between the subsurface and surface because calcareous species such as *Q.* spp. are relatively minor contributors to surface dead assemblages in mangrove environments. In contrast, the live assemblages ($r^2 = 0.29$) show little relationship to subsurface dead assemblages. The live assemblages of the surface samples incorporate live calcareous species, which can represent over 85% of the assemblage from mangrove floral zones. However, post-depositional changes result in calcareous species being removed and the subsurface assemblages become more dominated by agglutinated species. Calcareous tests can be rapidly destroyed after death through dissolution in acidic pore waters (Green and others, 1993).

CONCLUSIONS

The study of foraminiferal dead assemblages of the mangroves of Kaledupa indicates that the assemblage accurately represents the subsurface assemblages which are the focus of paleoenvironmental reconstructions, and furthermore that they do not show as many spatial and temporal fluctuations as do the live assemblages. Statistical analyses of the dead assemblages support numerous studies from temperate or tropical regions that indicate a vertical zonation of foraminifera within the intertidal zone: Agglutinated foraminifera such as *A. mexicana*, *T. inflata*, and *M. fusca* dominate Zone D-Ia; Zone D-Ib contains a mixed agglutinated/calcareous assemblages with species such as *T. inflata* and *A. tepida*; and Zone D-II is dominated by numerous calcareous species. Zone D-Ia is found to be the most accurate sea-level indicator and its assemblages are omnipresent worldwide. Zone D-Ib and D-II are subject to both spatial and temporal variations, which must be incorporated into any sea-level reconstructions.

Tables of the relative percentages of live and dead foraminifera for transects A1, A2 and B are JFR Data Reposi-

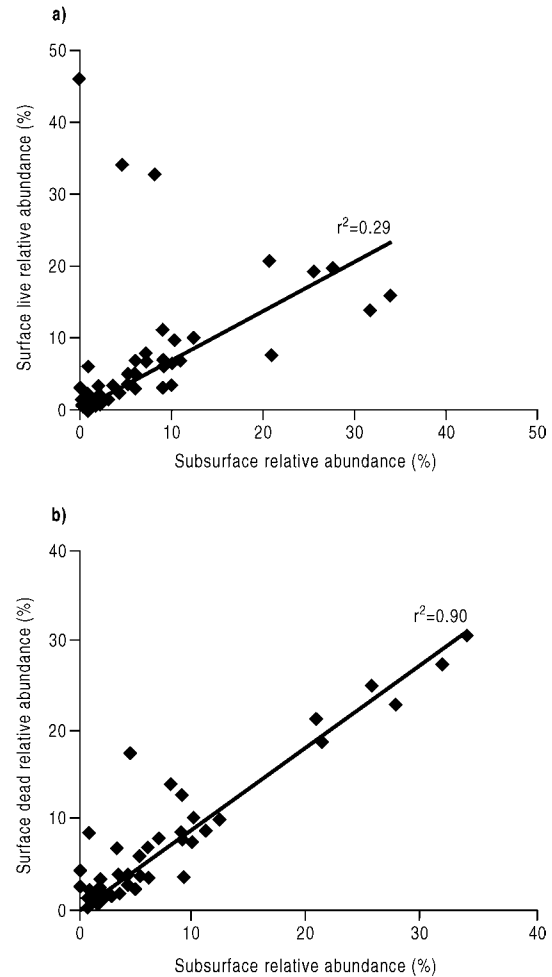


FIGURE 12. Scatter plots and r^2 showing the relationship between (a) live and (b) dead surface and subsurface foraminiferal assemblages (%) from the mangroves of Kaledupa.

tory item JFR DR200502 (<http://cushforams.niu.edu/JFRdata.htm>). A data repository of all foraminiferal (percentage and raw counts) and environmental data can be found on the following website: <http://www.sas.upenn.edu/~bphorton>

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