

## Monitoring the recolonization of the Mt Pinatubo 1991 ash layer by benthic foraminifera

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### Abstract

Benthic foraminifera from the South China Sea were studied to assess mass mortality and to monitor the composition and recovery of the benthic communities following the 1991 Mt Pinatubo ashfall. Surface distribution data from monitoring stations in the eastern South China Sea that were occupied during four cruises between spring 1994 and summer 1998 display the following trends in recolonization patterns: (1) Suspension feeding epifaunal benthic foraminifera (i.e. *Cibicides wuellerstorfi*, *Saccorhiza ramosa*) and large xenophyophores (i.e. *Syringammina (?) fragilissima*) were absent in spring 1994 and only rare individuals were observed in June 1996, but in larger numbers in December 1996 and in summer 1998. Then, they were important recolonizers of the ash layer. (2) Diversity and population densities have changed significantly since 1994. Following an abundance maximum in winter 1996, the numbers of living individuals in summer 1998 decreased again and the deep sea benthic foraminiferal community started to return to a normal ecological structuring. However, infaunal foraminifera were still strongly dominated by several species of the genus *Reophax*. We interpret the changing abundance and diversity pattern during the recolonization process in two ways: (1) the markedly increasing activity of burrowing macrofauna observed since 1998 opened new ecological niches for infaunal benthic foraminifera but also intensified predator pressure; (2) competitive interactions within the recolonizing fauna began to play a major role. Opportunistic pioneer species, characterized by rapid reproduction rates and the capability to colonize disturbed environments, were outcompeted by non-opportunistic species. © 2001 Elsevier Science B.V. All rights reserved.

**Keywords:** benthic foraminifera; recolonization; succession; recovery; South China Sea

### 1. Introduction

The 1991, June 15th eruption of Mt Pinatubo was by some estimates one of the greatest volcanic event of the 20th century, forming a cloud that extended from the Philippines to Sumatra. Within three days, a sediment trap system moored in the South China

Sea, 586 km west of Mt Pinatubo, recorded an ash accumulation of 9 kg/m<sup>2</sup>. Numerical simulations of the ashfall resulted in tephra settling rates through the water column of more than 1670 m/day (Wiesner et al., 1995). The resulting ash layer covers about 30% of the deep South China Sea (more than 4 × 10<sup>5</sup> km<sup>2</sup>) in a westward elongated lobe that reflects the prevailing wind direction at the time of the eruption (Wiesner et al., 1995; Wiesner and Wang, 1996; Wiesner et al., unpublished data, 2001). Close to the volcano, parts of

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the sea floor were blanketed by as much as 8–9 cm of volcanic material (Wiesner et al. unpublished data, 2001). When the RV *Sonne* visited the area in 1994, the benthic communities were in the initial stage of recovery after being buried and decimated by the ashfall (Hess and Kuhnt, 1996). This ashfall event in the South China Sea provides a unique opportunity to examine disequilibrium processes in marine benthic communities and to assess the rates of recovery of deep marine ecosystems after a catastrophic event.

Important information can be obtained from recent recolonization studies about benthic community dynamics in the deep sea. Detailed recent observations can help one to understand and interpret fossil analogues. Benthic foraminifera represent an ideal group for such studies because they are abundant in the deep sea and well preserved in the geological record. However, only few investigations are available on recent recolonization processes.

Most studies focused on benthic foraminifera in shallow water environments (Finger and Lipps, 1981; Ellison and Peck, 1983; Schafer, 1983; Buzas et al., 1989; Alve, 1995) or investigated the colonization of sterilized substrate at the deep sea floor (Kaminski et al., 1988; Kitazato, 1995). Kaminski et al. (1988) studied foraminiferal recolonization succession in the Panama Basin by mooring defaunated sediment trays in the deep sea. After nine months, the abyssal faunal recovery was still in an early stage (less than 10% recovery). Kitazato (1995) studied in situ the recolonization of different substrates by benthic foraminifera to get information about their substrate preferences. His results showed only small differences between assemblages colonizing defaunated mud and artificial sediment (glass beads). Due to the lower porosity of the artificial substrate, the colonizing species concentrated on the upper thin and newly deposited sediment layer while in the defaunated mud specimens were able to dig deeper into the sediment. The recolonizing assemblages generally showed similar composition and were comparable to those of surrounding undisturbed areas, although the number of species and individuals remained very low, even after two years. Therefore, the crucial time window for monitoring recovery is on the scale of years. Kaminski (1985) investigated the effects of deep sea bottom disturbances by benthic storms on benthic foraminiferal assemblages along the continen-

tal rise off Nova Scotia in comparison to undisturbed assemblages from neighbouring areas. The results indicated a first recolonization by opportunistic species such as *Reophax bilocularis* or *Reophax* aff. *dentaliniformis*, also found in the recolonization fauna of the Mt Pinatubo ash layer (Hess and Kuhnt, 1996).

The comparability of small-scale experiments with the vast deep sea area disturbed by the Mt Pinatubo ashfall in the South China Sea is limited. The environmental factors, which play no role in small-scale recolonization experiments contribute significantly to the recolonization process of the Mt Pinatubo ash: (1) additional sediment gravity transport occurred after the main deposition of the Mt Pinatubo ash, such as redeposition of ash by turbidity currents, river-transported lahar deposits, and tropical storm deposits; (2) pronounced monsoon-driven seasonality in nutrient recycling and phytodetritus flux to the deep sea; (3) the graded volcanic ash layer with extremely small pore space represents a very unique composition and texture of the new habitat; (4) the huge size of the area covered by the ash and the long distance for recolonizing species to reach the centre of the ash lobe from marginal areas, where survival was possible; (5) the virtual lacking predation by macrobenthic animals in the early stages of the recolonization process. To understand the complex interplay of these processes using living foraminiferal counts would require sampling intervals at least on a seasonal scale. In our series of monitoring cruises, we could collect seasonal data only in 1996. However, an estimate of seasonal vs. long-term changes is obtained from our comparison of dead and living fauna from each cruise.

The reestablishment of the benthic foraminiferal community on the Mt Pinatubo ash layer has now been monitored for the first seven years of the recolonization process. The Mt Pinatubo ash lobe thus provides a unique natural laboratory for understanding recolonization processes of disturbed areas on scales of several hundred kilometres.

## 2. Oceanography and sediments of the deep South China Sea

The tropical South China Sea is a large marginal basin of the West Pacific. Its north-west and south-west are characterized by broad shelf areas (southern

China, Vietnam and Sunda shelf) including large river deltas with enormous particle input (e.g. Mekong). Water depths of up to 5016 m are observed in the Manila Trench. The nearly 2500 m deep Bashi Strait between Taiwan and Luzon connects the South China Sea with the open western Pacific and allows exchange between Pacific intermediate and deep water with South China Sea water masses. Consequently, the deep water characteristics of the South China Sea are similar to those of Pacific water masses (Wyrтки, 1961; Shaw, 1991; Shaw and Chao, 1994; Su and Wang, 1994; Chao et al., 1996).

The hydrography of the South China Sea is strongly affected by monsoonal changes (Huang et al., 1994). During the south-west monsoon (May to September), the wind regime produces surface water currents flowing to the north-east. This system reverses to south-westward surface currents during the stronger north-east monsoonal period from October to April (Wang and Wang, 1990; Shaw, 1991; Shaw and Chao, 1994; Chao et al., 1996; Wiesner et al., 1996). The reversal and strength of the surface water current system influences the depth of the mixed layer and causes seasonally changing upwelling areas, during the south-west monsoon off South Vietnam and during the north-east monsoon off Northwest Luzon. The nutrient concentrations and the biological productivity of the surface waters increase during upwelling periods leading to higher flux rates to the ocean floor; thus, the primary production and the carbon flux in the South China Sea are strongly coupled to semi-annual monsoonal changes.

The sediments of the deeper areas in the South China Sea are fairly uniform, mainly brownish–grayish pelagic or hemipelagic mud. The calcite lysocline in the South China Sea is at approximately 3200 m water depth while the calcite compensation depth (CCD) is at 3800 m (Miao and Thunell, 1993). In water depths above the calcite lysocline, the sediments contain medium to high concentrations of carbonate (foraminifera ooze). Carbonate content is generally increasing to the south where carbonate platforms are located (e.g. Dangerous Grounds).

Volcanic ash layers are commonly found in all regions of the South China Sea and are particularly abundant in the eastern part of the basin along the coastline of Luzon (Philippines) (Sarnthein et al., 1994; Bühring and Sarnthein, 2000; Wang et al.,

2000). The most recent ash layer originates from the 1991 Mt Pinatubo eruption (Luzon, Philippines) and was deposited as a huge elongate lobe west off Luzon (Wiesner and Wang, 1996; Wiesner et al., 1995, 1996, unpubl.data, 2001) (Fig. 1). Highest values for the ash thickness were recorded off Luzon in water depth between 2000 and 2500 m. There, the ash consists of a relatively coarse-grained basal layer containing mainly pumice and phenocrysts ('Salt and Pepper'). This part is overlaid by a fine-grained ash enriched in glass shards. The whole sequence is normally graded (Wiesner et al., 1995). In the proximal part of the ash lobe a thin grayish–greenish layer was observed directly beneath the thick ash layer. This layer represents the upper part of the underlying, now buried undisturbed sediment consisting of dark brown clay with high contents of biogenic carbonate, which became anoxic. The previous sediment surface was sealed by the ash, which prevented downward oxygen diffusion, so the pore water oxygen was completely utilized by the buried meiofauna, microfauna and microbes (Haeckel et al., unpubl. data, 2001).

A laminated ash/mud sediment (turbidite) was observed on top of the primary ash layer at some of the stations (marked with an asterisk in the station list Table 1; Wiesner, 1997; Wiesner et al., 1998). Such deposits were also found at one of the main monitoring stations (site 2 in Table 1). In 1994, during RV *Sonne* cruise 95, already a thin muddy layer was visible on top of the primary ash deposit (Sarnthein et al., 1994). The thickness of this layer increased during the following years (from approximately 10 mm in 1994 to 25–30 mm in 1998). The reworked material may be related to lahar or river transported pyroclastic material from the shoreline of Luzon.

### 3. Material and methods

The present investigation is based on 42 short cores (box cores and multicores) from 30 sites, which were recovered during four cruises in the central and eastern part of the South China Sea (Sarnthein et al., 1994; Wiesner, 1997; Wiesner et al., 1998). The water depths at the sample sites range from 2327 to 4320 m.

Samples were collected to examine the extension of the ash lobe of the 1991 Mt Pinatubo eruption in the South China Sea, which has an approximate E–W

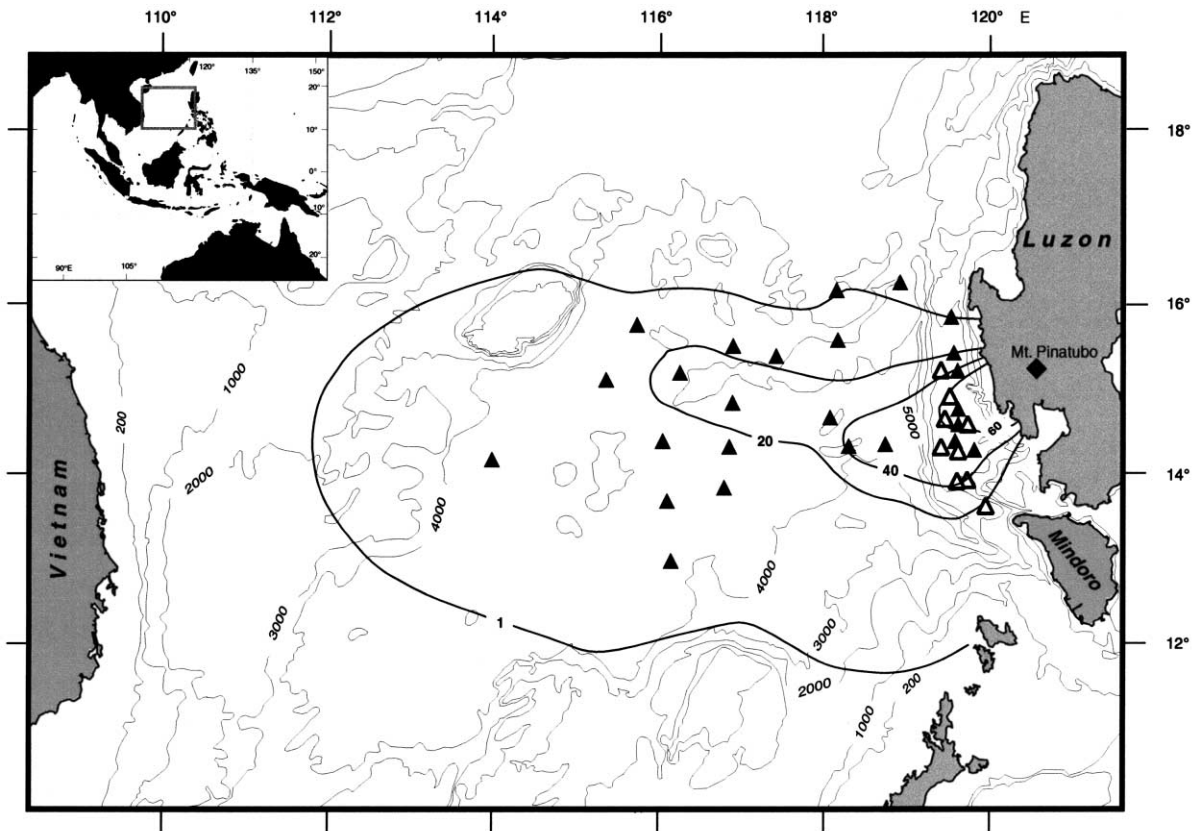


Fig. 1. Sample sites in the South China Sea. Open triangles indicate sites belonging to the transect shown in Fig. 3. The isopachs of ash in mm, modified after Wiesner et al. (unpubl. data, 2001).

elongation (Fig. 1). They were recovered along two main N–S transects, across the distal and across the proximal part of the ash lobe. The area located in the proximal part of the ash lobe east of the Manila trench and parallel to the coastline of Luzon, ranges in water depths between 2000 and 2600 m. The samples from distal areas are located west of the Manila trench in approximately 4000–4300 m water depths. The ash thickness measures between 1 and nearly 90 mm (Table 1).

The first three samples containing the 1991 Mt Pinatubo ash were collected in April 1994 (RV *Sonne* cruise 95) using a giant box corer (50 × 50 × 60 cm). Six stations were sampled during the RV *Ocean Researcher I* cruise 455 in June 1996 using a Soutar box corer (30 × 20 × 60 cm). Fifteen cores were taken in November/December 1996 (RV *Sonne* cruise 114), and 18 in June/July 1998 (RV

*Sonne* cruise 132). During both cruises, a box corer and a multicorer (12 tubes with an inner diameter of 9.5 cm) were used. Stations with position, water depth, and sample date are listed in Table 1.

Undisturbed sediment surfaces were more or less smooth, consisting of a thin fluffy layer on top of a pale fine-grained ash overlying a normally graded, relatively coarse grained, black-and-white ash layer (Salt and Pepper). The sediments below the ash were dark brown, bioturbated until they changed into lighter coloured clay.

Initial shipboard results of meio- and microfauna distribution patterns (e.g. Table 2) were mainly based on direct observation of box core surfaces on the working deck of RV *Sonne*. Box corers were examined and sampled for benthic foraminifera according to the following procedure: (1) Surface water was carefully sucked off and filtered over a 63 µm sieve.

Table 1

Position, water depth, coring device, sampling date and ash thickness of investigated sites. Replicate samples are grouped together. Ash layer thicknesses were taken from Wiesner et al. (unpubl. data, 2001). Values of questionable ash layer thicknesses are put in parentheses. Sites with a reworked ash/mud layer overlaying the primary ash are marked by an asterisk. GBC: giant box corer; BC: box corer; MUC: multiple corer

No.	Station		Coring device	Sampling date	Latitude N	Longitude E	Water depth (m)	Ash thickness (mm)
1	17920	-1	GBC	4/16/94	14°35.0'	119°45.1'	2513	62–65
	SO-114-5	-1	MUC	11/28/96				
		-2	GBC	11/28/96				
	SO-132-40	-1	GBC	7/4/98				
		-2	GBC	7/4/98				
2	17921*	-1	GBC	4/16/94	14°54.7'	119°32.3'	2514	(63–65)
	OR-455-6B*	-1	BC	6/26/96				
	SO-114-7*	-1	MUC	11/28/96				
		-2	GBC	11/28/96				
	SO-132-42*	-1	GBC	7/4/98				
3	17922	-1	GBC	4/17/94	15°22.9'	117°26.3'	4213	12–14
	SO-114-24	-1	MUC	12/4/96				
	SO-132-21	-2	MUC	6/29/98				
4	OR-455-5B*	-2	BC	6/26/96	15°12.9'	119°25.8'	2327	(27–40)
5	OR-455-7B	-1	BC	6/26/96	14°45.7'	119°38.4'	2597	85–90
	SO-114-6	-1	GBC	11/28/96				
		-2	MUC	11/28/96				
6	OR-455-9B	-1	BC	6/26/96	14°34.7'	119°38.1'	2607	(80)
7	OR-455-14B	-1	BC	6/28/96	14°39.9'	118°05.1'	4254	31–33
	SO-132-27	-1	GBC	6/30/98				
8	OR-455-17B	-1	BC	6/28/96	14°20.7'	118°45.1'	4028	50–52
	SO-132-29	-2	MUC	7/1/98				
9	SO-114-2	-3	MUC	11/27/96	13°55.6'	119°44.9'	2371	(40–50)
10	SO-114-3	-1	MUC	11/27/96	14°16.9'	119°50.1'	2414	> 35
11	SO-114-4	-2	MUC	11/28/96	14°23.0'	119°36.0'	2511	(55–60)
12	SO-114-8*	-2	MUC	11/28/96	15°12.5'	119°37.5'	2286	(>25)
13	SO-114-9*	-1	MUC	11/29/96	15°24.9'	119°35.2'	2459	> 22
	SO-132-50*	-1	MUC	7/7/98				
14	SO-114-10	-1	MUC	11/29/96	15°49.9'	119°33.2'	2498	
15	SO-114-11	-1	MUC	11/29/96	16°14.4'	118°55.7'	4007	–
16	SO-114-13	-1	MUC	11/30/96	16°09.1'	118°09.8'	3879	1–2
17	SO-114-14	-1	MUC	11/30/96	15°33.9'	118°10.8'	3686	(5)
18	SO-114-17	-1	MUC	12/1/96	14°19.6'	118°18.9'	4061	47
	SO-132-28	-2	MUC	6/30/98				
19	SO-114-27	-1	GBC	12/5/96	15°45.0'	115°45.0'	4220	2–3
20	SO-132-5	-2	MUC	6/22/98	14°10.0'	113°59.9'	4323	4–5
21	SO-132-7	-1	MUC	6/23/98	15°06.3'	115°23.1'	4265	13–16
22	SO-132-8	-2	MUC	6/24/98	14°22.9'	116°03.9'	4320	8–9
23	SO-132-9	-1	MUC	6/24/98	13°40.6'	116°07.0'	4345	5–7
24	SO-132-10	-2	MUC	6/24/98	12°58.3'	116°09.9'	4345	3–4
25	SO-132-11	-1	MUC	6/25/98	13°50.0'	116°48.3'	4249	6–7
26	SO-132-12A	-1	MUC	6/25/98	14°18.9'	116°52.0'	4320	14–18
27	SO-132-14	-1	MUC	6/26/98	14°50.1'	116°54.5'	4296	30–32
28	SO-132-15	-1	MUC	6/26/98	15°11.2'	116°16.3'	4287	31–34
29	SO-132-16	-1	MUC	6/27/98	15°29.9'	116°55.0'	4232	12–14
30	SO-132-35	-2	MUC	7/2/98	13°37.0'	119°58.4'	3322	(18–21)

Table 2

Macroscopically visible microfauna on box core surfaces of the RV *Sonne* cruise 132. Only xenophyophores larger than 1 cm in diameter were counted. Some of the sites listed ( \* ) were not used for detailed foraminiferal surface assemblage studies. Observations of replicate samples are grouped together

Station	Latitude N	Longitude E	Water depth (m)	Visible microfauna
SO-132-3*	12°40.74	111°24.1	2435	komokiaceans, <i>Rhabdammina abyssorum</i>
SO-132-7	15°06.3	115°23.1	4265	xenophyophores
SO-132-11	13°50.0	116°48.3	4249	<i>Rhabdammina abyssorum</i> , <i>Rhizammina algaeformis</i> <i>Cibicidoides wuellerstorfi</i>
SO-132-16	15°29.9	116°55.0	4232	<i>Rhabdammina abyssorum</i> , <i>Rhizammina algaeformis</i> xenophyophores
SO-132-17*	16°06.0	116°59.6	4122	<i>Aschemonella</i> sp., <i>Rhizammina algaeformis</i> <i>Astrorhiza crassatina</i> , xenophyophores
SO-132-19*	16°25.0	117°20.0	4005	<i>Aschemonella</i> sp., <i>Rhizammina algaeformis</i> <i>Astrorhiza crassatina</i>
SO-132-21	15°22.9	117°26.3	4213	<i>Rhabdammina abyssorum</i> , <i>Rhizammina algaeformis</i> <i>Astrorhiza crassatina</i>
SO-132-23*	15°15.2	118°07.1	3714	2 xenophyophores, komokiaceans <i>Rhabdammina abyssorum</i>
SO-132-25*	15°07.3	118°25.1	4138	3 xenophyophores, <i>Rhabdammina abyssorum</i>
SO-132-26*	14°52.0	118°14.9	4207	<i>Rhizammina algaeformis</i> , komokiaceans
SO-132-29	14°20.7	118°45.1	4028	<i>Rhizammina algaeformis</i>
SO-132-30*	14°02.4	118°41.0	3936	<i>Rhizammina algaeformis</i> , komokiaceans
SO-132-33*	13°12.0	119°04.4	3390	<i>Rhizammina algaeformis</i>
SO-132-35	13°37.0	119°58.4	3322	<i>Rhizammina algaeformis</i> , <i>Bathysiphon</i> sp., xenophyophores
SO-132-36*	13°55.6	119°44.8	2370	xenophyophores, <i>Bathysiphon</i> sp.
SO-132-37*	13°54.3	119°36.8	2764	3 xenophyophores
SO-132-38*	14°15.0	119°38.1	2495	20 xenophyophores
SO-132-39*	14°18.7	119°25.5	2489	5 xenophyophores
SO-132-40	14°35.0	119°45.1	2513	30–45 xenophyophores
SO-132-41*	14°38.4	119°28.9	2603	5 xenophyophores
SO-132-42	14°54.7	119°32.3	2514	10–14 xenophyophores
SO-132-44*	15°12.9	119°25.8	2338	5 large xenophyophores, 12 smaller xenophyophores

The washing residue contained benthic foraminifera living in the fluffy layer above the sediment water interface, occasionally komokiaceans at deeper stations and other epifaunal benthic foraminifera. (2) Box core surfaces were described, photographed and examined for macroscopically visible large epifaunal benthic foraminifera and xenophyophores which were collected from the box core surface and immediately examined under a binocular microscope. (3) Metal frames of 10 × 10 or 5 × 10 cm size were placed on the sediment surface according to morphologic and sedimentologic features to obtain a defined volume of the uppermost centimetre. The sediment was removed from this frame using specially cut spoons. (4) Pushcores of 10 cm diameter were pushed into the sediment (occasionally using a hand-held piston to

avoid compaction) for examination of the vertical distribution of benthic foraminifera at stations where multicorer samples were not of adequate quality. The cores were cut into 1 cm thick slices immediately after sampling. Subsamples from the uppermost 10–15 cm of the sediment column were preserved in a methanol–seawater solution and were treated with Rose Bengal to stain organisms that were alive at the time of collection. A number of samples were washed over a 63 µm sieve in the shipboard laboratory for initial examination. (5) Surface samples from the complete surface of a second box core were taken at two monitoring stations (sites 1 and 2), to avoid bias from small-scale patchiness and washout during handling of the box corer. All surface samples were immediately preserved in a methanol–Rose Bengal solution

for identification and counts of living (stained) vs. dead specimens.

Multicorer samples for benthic foraminiferal study were examined and subsampled in the same way except for two differences: (1) The surface centimetre was mainly split in three subsamples: one subsample was taken of the sediment–water interface, including fluff and epifauna, a second sample (0–0.2 cm) contained the sediment surface and a third sample (0.2–1 cm) contained the remaining part of the uppermost centimetre of sediment. (2) Surface microfauna was examined in vivo onboard RV *Sonne* using a binocular microscope, standard 35 mm cameras equipped with a 60 mm macro lens and a digital camera (Hill, 1998).

For subsequent laboratory studies, all samples were washed over a 2 mm and a 63  $\mu\text{m}$  sieve. Fragile specimens were separately picked and stored in glycerine. The residues ( $>63 \mu\text{m}$ ) were dried at 50°C for further examination and sieved through a 250 and 150  $\mu\text{m}$  screen. Benthic foraminifera were picked from all fractions larger than 63  $\mu\text{m}$ , mounted on a slide, identified and counted. The numbers of living (stained) and dead individuals were recorded separately (see tables in the **Online Background Dataset**<sup>1</sup> Appendices). When the size of the residue was too big to be picked completely (e.g. 400 cc samples), the sample was divided using a microsplitter to obtain approximately 200 foraminifera. All slides are stored in the micropaleontological collection of the Institute of Geosciences in Kiel for documentation.

We counted living (Rose Bengal stained) and dead foraminifera separately in the size fractions 63–150, 150–250 and  $>250 \mu\text{m}$ . Primary counts are listed in **Online Background Dataset**<sup>1</sup> Appendix B Tables 1A–D and 2A–D. Subsamples of the uppermost sediment centimetre of each location were combined. Since the subsample data from each station occasionally vary substantially, we calculated the standard deviation (SD) for each data subset and used student's *t*-test to evaluate the degree of variability within each set of subsamples in comparison to the variation between samples of different location and sampling time. We express taxon abundance in the top sediment centimetre (0–1 cm) as number of individuals per 10 cm<sup>2</sup>.

The foraminiferal abundance of replicate samples varies in some cases considerably (Table 3). Often, the number of specimens is higher in multicorer than in box corer samples. The multicorer normally preserves the sediment surface perfectly. The quality of the box corer surfaces heavily depends on sea conditions. Although the box corer can be used in rougher seas than the multicorer, the water saturated upper millimetres of the sediment often go into suspension and are washed out. This was the case for many of the box core samples recovered during the RV *Sonne* cruise 114, when the weather was very rough.

Diversity was measured using Fisher's alpha index (Murray, 1991; Hayek and Buzas, 1997). Fisher's alpha values were calculated from *N* (number of individuals) and *S* (number of species) using a program written by P. Weinholz and A. Altenbach revised for Mac-Systems in FORTRAN 77 by U. Pflaumann. The resulting alpha values compare well with values given in appendix 4 of Hayek and Buzas (1997).

## 4. Results

### 4.1. Pre-ash taphocoenosis

The composition of the pre-ash taphocoenosis is comparable with that of foraminiferal assemblages known from other regions in the South China Sea (Hess and Kuhnt, 1996; Hess, 1998). The pre-ash foraminiferal assemblages are characterized by high diversity and numerous different morphotypes. Sessile suspension-feeders such as *Saccorhiza ramosa* and *Cibicides wuellerstorfi* occur along with infaunal detritus-feeders. Tubular agglutinated forms are also an important element of the fauna. Analysed surface samples containing only a very thin ash cover do not show significantly different foraminiferal assemblages than pre-ash assemblages. Diversity values are also comparable (e.g. Fisher's alpha index of 19.1 at the base of the ash layer at station 1).

### 4.2. Shipboard observations of meiofauna distribution patterns

Epifaunal benthic foraminifera (i.e. *Astrorhiza crassatina*, *komokiaceans*, *rhabdamminids*) and

<sup>1</sup> <http://www.elsevier.com/locate/marmicro>



Fig. 2. Large xenophyophores (*Syringamina* (?) *fragilissima*) which form an important element of the recolonizing fauna in the centre of the Mt Pinatubo ash fan (SO-132-44-1 BC, diameter of the specimen is approx. 4 cm).

large xenophyophores (i.e. *Syringamina* (?) *fragilissima*) already present on a few box core surfaces in the summer of 1996, were observed in larger numbers in December 1996 (RV *Sonne* cruise 114), and became one of the dominant surface recolonizers in 1998 (Fig. 2). Large tubular forms such as *Rhabdammina abyssorum*, *Astrorhiza crassatina*, *Saccorhiza ramosa*, *Rhizamina algaeformis* were mainly

observed as survivors of the ashfall in the distal part of the ash fan. In the proximal part, where the ash is coarser and thicker, large xenophyophores were observed to colonize the ash as late as five years after the ashfall (Fig. 3). These forms were absent at the same locations in 1994 (RV *Sonne* cruise 95) and only rare small individuals were observed in June 1996 during the RV *Ocean Researcher I* cruise 455. Their number and size increased dramatically between 1996 and 1998. Xenophyophores were present even on top of reworked and transported ash material and their number was highest at sites located in the middle of the ash lobe. The number of individuals larger than 1 cm in diameter was counted for all box core surfaces of the RV *Sonne* cruise 132 in 1998. The data are given in Table 2.

#### 4.3. Succession of recolonizers

##### 4.3.1. Pioneer recolonizers with high living/dead ratio in 1994

In an initial study of the Mt Pinatubo ash recolonization, Hess and Kuhnt (1996) used the ratio of living specimens to the total abundance of species to determine the succession of recolonizers, assuming that species with high numbers of dead individuals probably colonized earlier than species with higher numbers of living individuals. This method allowed the succession of earliest recolonizers to be reconstructed in the proximal area of the ash fan (Fig. 4). Small specimens of an organically cemented species of *Textularia* were probably the first colonizers followed by other opportunistic species as *Reophax*

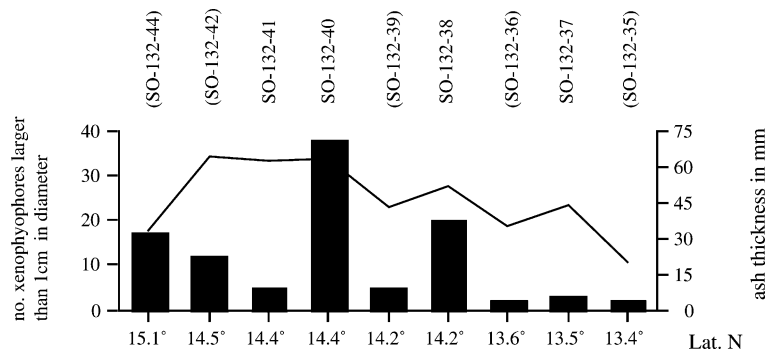


Fig. 3. Distribution of xenophyophores on box core surfaces ( $50 \times 50 \text{ cm}^2$ ) of the RV *Sonne* cruise 132 along a north–south transect across the proximal ash fan. Water depth of sites ranges between 2338 and 3322 m. Ash layer thicknesses (black line) were taken from Wiesner et al. (unpubl. data, 2001). Sites with transported material (mud/ash mixture) above the primary ash layer are in parentheses.



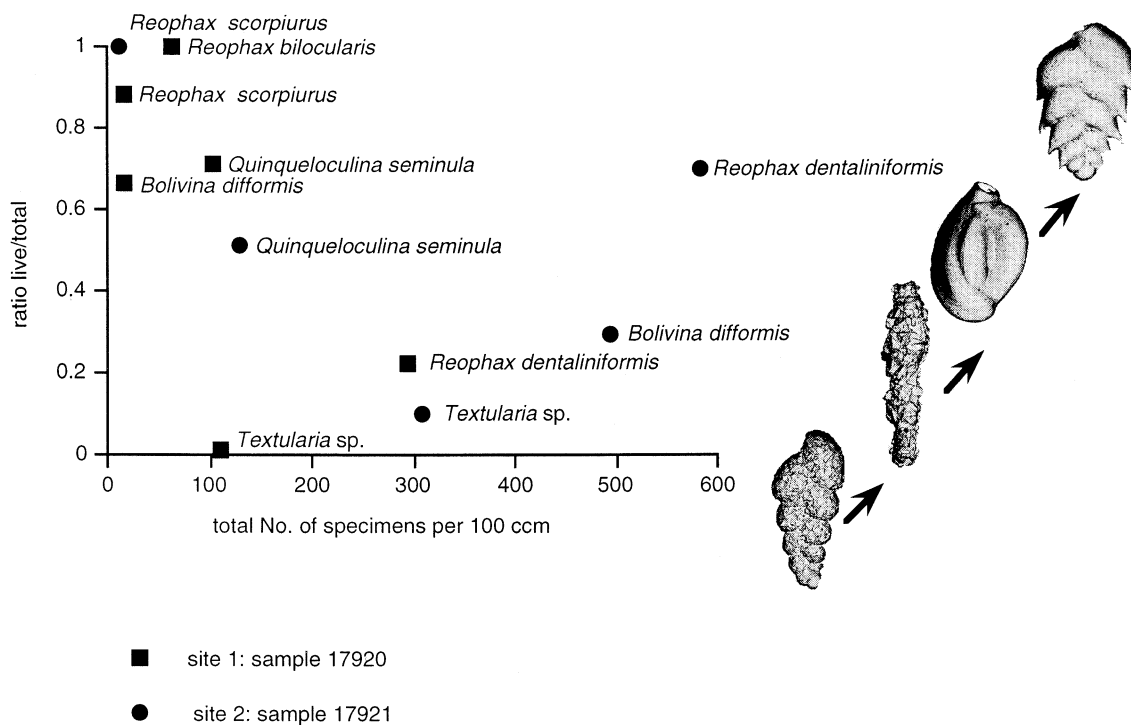


Fig. 4. Proportions of living specimens and faunal abundance for the most important recolonizers of the ash in 1994 (sites 1 and 2; modified from Hess and Kuhnt, 1996).

*dentaliniformis*. These taxa occurred in 1994 with high individual numbers, but low ratio of living to dead specimens. *Quinqueloculina seminula*, *Reophax scorpiurus* and *Reophax bilocularis* were probably later recolonizers, which showed lower individual numbers but higher portions of living individuals. These species may have recolonized the substrate just before spring 1994 and superseded the first pioneer recolonizers (**Online Background Dataset<sup>1</sup>** Appendix B, Table 1A and 2A). The low diversity fauna of April 1994 did not yet include any typical epifaunal suspension feeding forms.

The initial impression of a successive recolonization pattern was confirmed by follow-up monitoring of the same stations (Figs. 5 and 6). The individual numbers of early recolonizers mainly decreased in the living fauna and only rarely recovered to their initial population density (Fig. 5A). At the end of 1996 empty tests of early recolonizers appeared in high numbers in the top sediment centimetre at site 1, but their number decreased until July 1998 (Fig. 5B). The

main reason might be already more intensive bioturbation at this time in the upper sediment column and the relatively fast decay of thin-walled agglutinated foraminifers such as *Reophax dentaliniformis*. At site 2, the number of empty tests was mostly lower in November 1996 than in April 1994. Deposits of laminated, reworked ash/mud material on top of the primary ash layer might have influenced the fauna development at this site.

#### 4.3.2. Successive recolonizers with highest numbers of stained individuals in 1996–1998

The pioneering recolonizers were completely displaced by a ‘second wave’ of recolonizers mainly composed of the agglutinated species *Reophax scorpiurus*, *Trochammina* spp., *Adercotryma glomerata* and *Subreophax guttifer* (Fig. 6). Some of these forms, which had their maximum standing stock in November 1996 (RV *Sonne* cruise 114), again showed a decrease in the number of living individuals in July 1998 (RV *Sonne* cruise 132).

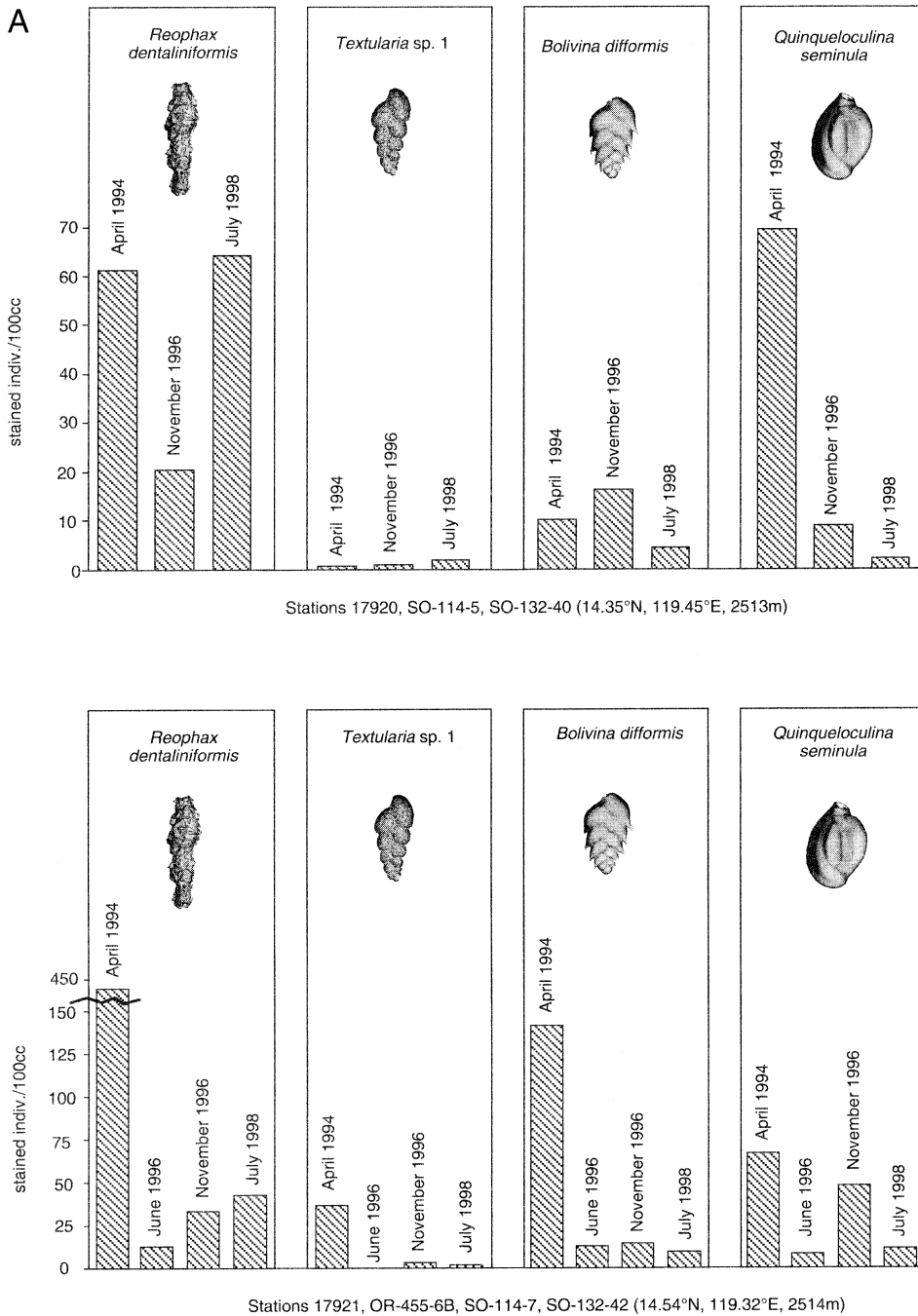


Fig. 5. (A) Temporal changes in faunal density (living fauna) observed among early recolonizers at monitoring sites 1 (14.35°N, 119.45°E, depth 2513 m) and 2 (14.54°N, 119.32°E, depth 2514 m). (B) Temporal changes in faunal density (dead fauna) observed among early recolonizers at monitoring sites 1 and 2.

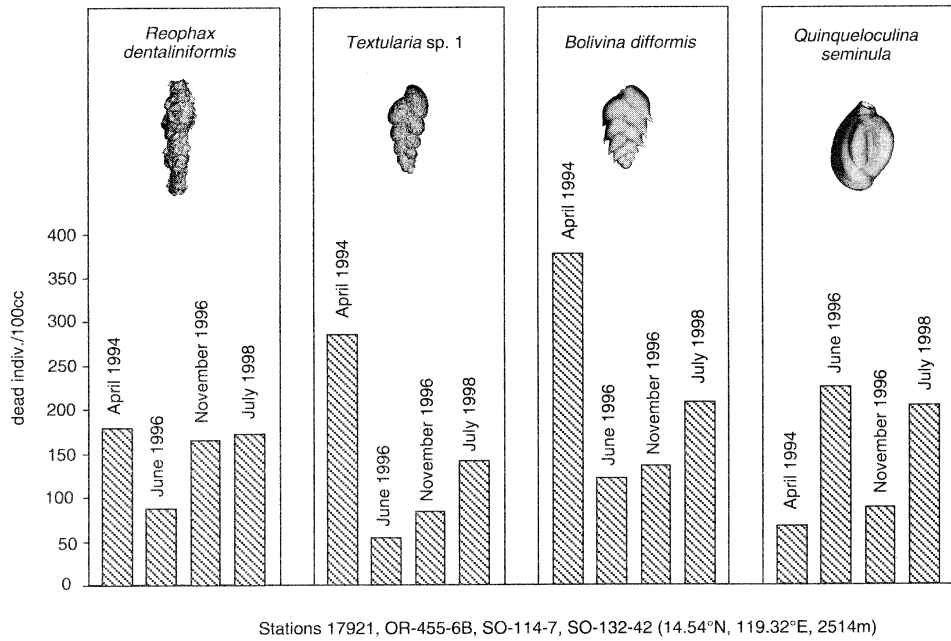
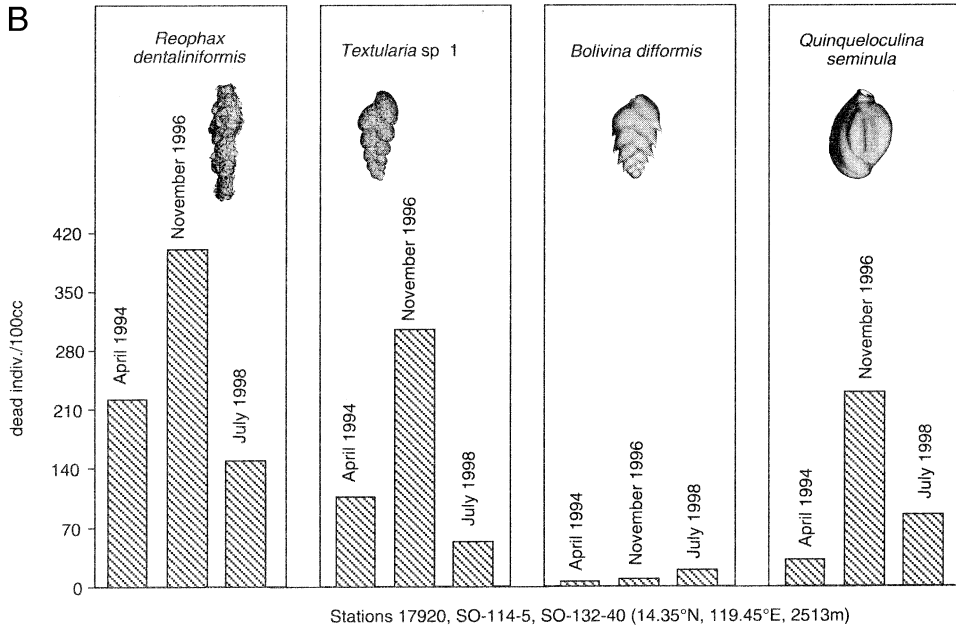


Fig. 5. (continued)

A

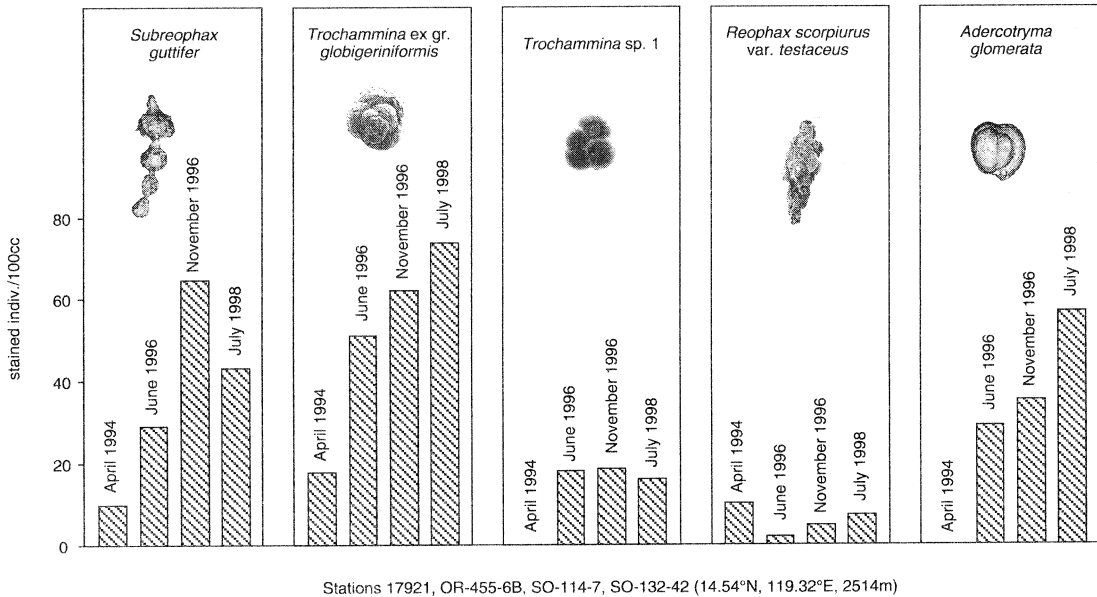
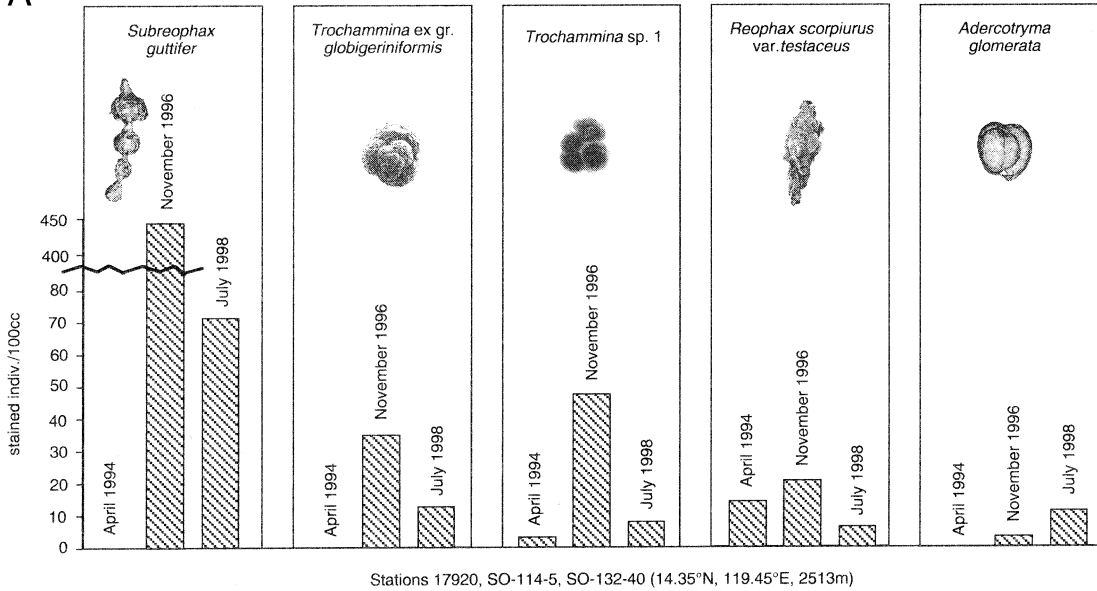


Fig. 6. (A) Temporal changes in faunal density (living fauna) observed among late recolonizers at monitoring sites 1 (14.35°N, 119.45°E, depth 2513 m) and 2 (14.54°N, 119.32°E, depth 2514 m). (B) Temporal changes in faunal density (dead fauna) observed among late recolonizers at monitoring sites 1 and 2.

B

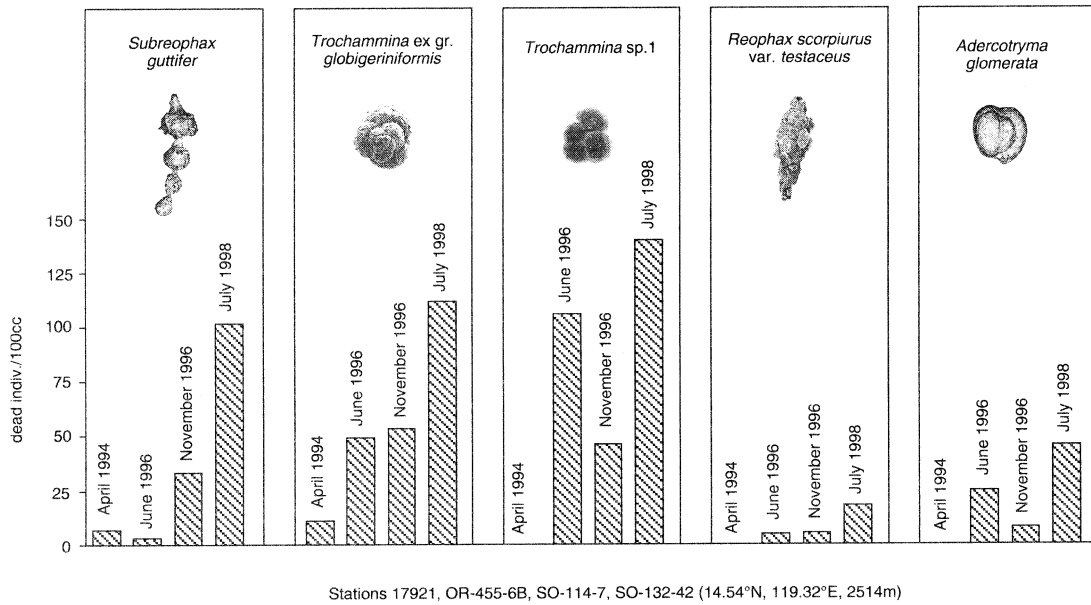
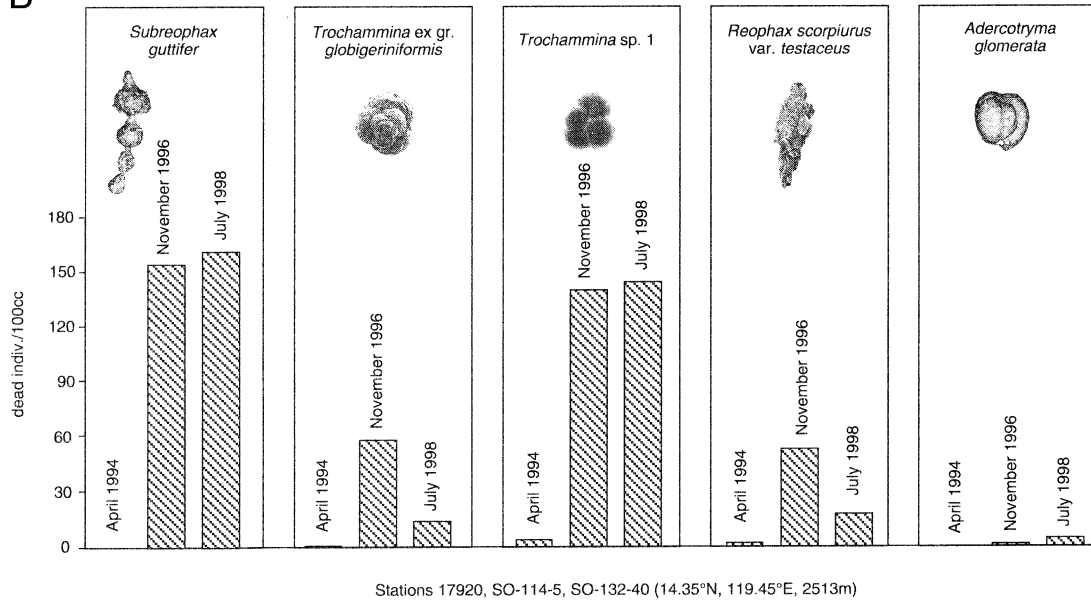


Fig. 6. (continued)

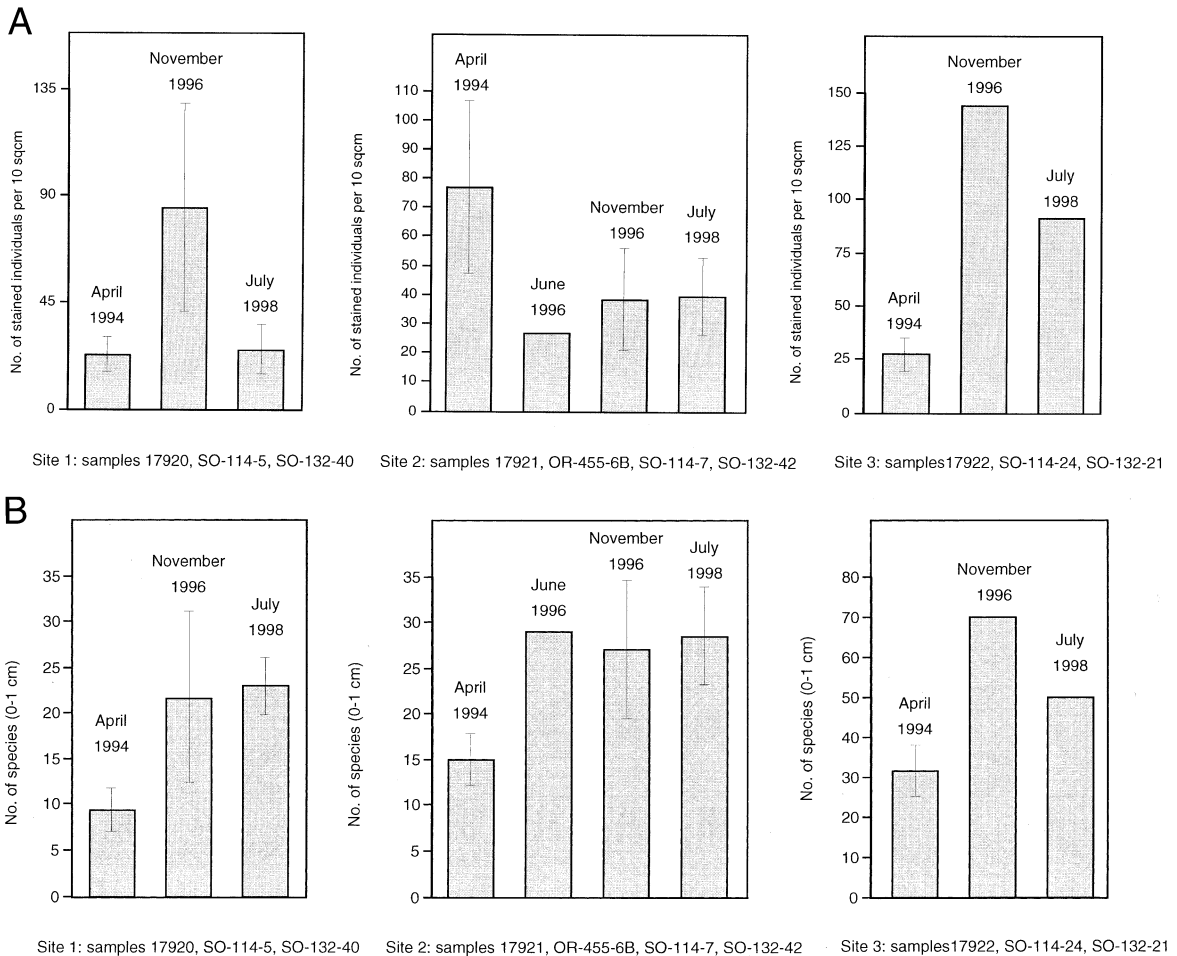


Fig. 7. (A) Number of stained individuals in the top sediment centimetre (mean values and SD for replicate samples; data without indicated that SDs are based on single samples (>260 counted individuals)) at sites 1–3 between 1994 and 1998. (B) Number of living species in the top sediment centimetre (mean values and SD for replicate samples; data without indicated that SDs are based on single samples (>260 counted individuals)) at sites 1–3 between 1994 and 1998.

#### 4.4. Population density and diversity trends

Population density changes at two main monitoring sites (1 and 3) show the same trend between 1994 and 1998 (Fig. 7A). The standing stock reached maximum values in November 1996 and decreased until July 1998. The mean number of stained specimens per 10 cm<sup>2</sup> at site 1 was 23 (SD = 7.7) in April 1994 and rose to 85 (SD = 44) in November 1996 before it decreased to 25 (SD = 10.3) in July 1998 (Table 3A). The population peak in November 1996 might reflect the reaction of the benthic fauna to the

higher seasonal nutrient input during winter monsoon conditions.

At site 2, no maximum standing stock could be observed in winter 1996. The mean value decreased from 77 (SD = 29.7) in April 1994 to 38 (SD = 17.6) in November 1996. This number remained nearly constant until July 1998 (mean number of 39.5 (SD = 13.1)). The benthic population may have been influenced by resedimentation processes at this site that might overlay the normal faunal patterns.

Diversity changes at the two main monitoring sites (1 and 2) follow a consistent trend between 1994 and

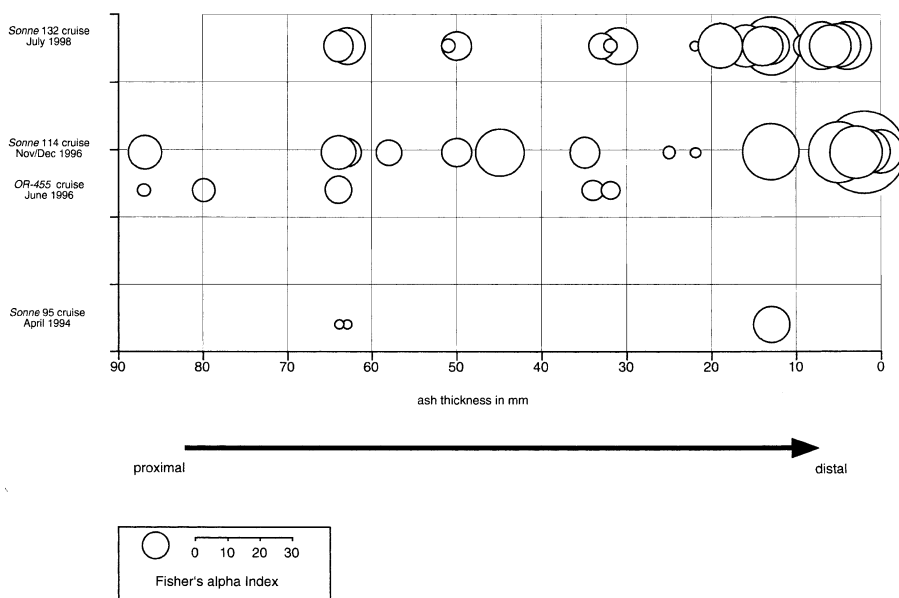


Fig. 8. Fisher's alpha diversity index of living surface assemblages of investigated stations (if replicate samples existed, a combined Fisher's alpha value was calculated). Values in the more distal area of the Mt Pinatubo ash fan (thin ash layer) show higher diversity index and are nearly constant.

1998. A significant increase in the number of living species were reached between 1994 and 1996. The mean number of living (stained) species in the samples of site 1 was 9 (SD = 2.5) in April 1994 and 22 (SD = 9.3) in November 1996 (Fig. 7B). At site 2, the mean value of diversity increased from 15 (SD = 2.8) to 27 (SD = 7.5). The numbers of species remained nearly constant until July 1998, mean value of 23 (SD = 3.2) at site 1 and 28.5 (SD = 5.3) at site 2. The Fisher's alpha diversity index showed minimum values in April 1994 (site 1 = 1.3 – 3.3; site 2 = 2.2 – 3.39), whereas the values were clearly higher in November 1996 (site 1 = 5.1 – 6.6; site 2 = 6.6 – 9.5) and July 1998 (site 1 = 6.2 – 10.3; site 2 = 6.2 – 9.0). The analysed diversity variations between 1994 and 1996 were significant (one sided *t*-distribution test with  $p = 0.045$  at site 1;  $p = 0.0525$  at site 2), but there was no significant variation observed between 1996 and 1998 (one sided *t*-distribution test with  $p = 0.397$  at site 1;  $p = 0.377$  at site 2).

Even the more distal site 3 with an ash thickness of only 12–14 mm and only small obvious faunal changes shows a comparable trend (Fisher's alpha diversity values of 8.1–11.3 in April 1994 increased

to 17.4 in November 1996 and 17.9 in July 1998; Table 3A).

Diversity trends in a geographically more widespread area are given in Table 3A and B and Fig. 8. Diversity depends somewhat on ash thickness (logarithmic correlation of the Fisher's alpha diversity index of samples from all cruises is  $r^2 = 0.54$  with  $n = 29$  (by turbidites influenced samples and samples with questionable ash thicknesses were excluded)). Comparisons of diversity values between samples from the proximal part (ash thicknesses > 30 mm) and the distal part of the ash lobe showed significant differences ( $p < 0.0001$ ) in 1996 and 1998. Ash thinner than 2 cm did not significantly influence benthic faunas and Fisher's alpha index reaches values of 20 at these stations (e.g. SO-114-10 and SO-132-10).

We recognized a general trend in the temporal succession of species diversity from the distal to the proximal part of the ash lobe (Fig. 8). In the early stage of the recolonization process, a strong diversity gradient existed between the proximal part of the ash fan (Fisher's alpha values around 3) that experienced total mass mortality and the distal area (Fisher's alpha values above 11), where a large number of individuals survived. With time this gradient became less

Table 3

(A) Faunal data of living assemblages in surface sediments of the Mt Pinatubo ash layer. Listed are the number of counted individuals and species, Fisher's alpha index from each sample and from the combined dataset of one site and the number of individuals per 10 cm<sup>2</sup>. (B) Faunal data of dead assemblages in surface sediments of the Mt Pinatubo ash layer. Listed are the number of counted individuals and species, Fisher's alpha index from each sample of one site and the number of individuals per 10 cm<sup>2</sup>. GBC: giant box corer; BC: box corer; MUC: multiple corer

No.	Station	Sample (volume)	Sampling date	No. of counted:		Mean species no. (SD)	Fisher's $\alpha$ index	Combined Fisher's $\alpha$ index	No. of individuals/ 10 cm <sup>2</sup>	Mean no. of individuals/ 10 cm <sup>2</sup> (SD)	
				Individuals	Species						
1	17920	GBC	I; 0–1 cm (80 cc)	April 1994	120	12	9.3 (2.5)	3.3	3	15	22.6 (7.7)
		GBC	II; 0–1 cm (80 cc)	April 1994	180	9	9.3 (2.5)	2	3	22.5	22.6 (7.7)
		GBC	A; 0–1 cm (100 cc)	April 1994	304	7	9.3 (2.5)	1.3	3	30.4	22.6 (7.7)
	SO-114-5	MUC-A	0–1 cm (64 cc)	Nov. 1996	848	32	21.7 (9.3)	6.6	8.5	119.4	84.8 (44.0)
		BC-A	0–1 cm (100 cc)	Nov. 1996	115	19	21.7 (9.3)	6.5	8.5	99.8	84.8 (44.0)
		BC-D	0–1 cm (100 cc)	Nov. 1996	74	14	21.7 (9.3)	5.1	8.5	35.2	84.8 (44.0)
	SO-132-40	BC-1:	0–1 cm (200 cc)	July 1998	124	25	23 (3.2)	9.4	11.4	31	24.9 (10.3)
		BC-1:	R4: 0–1 cm (400 cc)	July 1998	126	19	23 (3.2)	6.2	11.4	35	24.9 (10.3)
		BC-2:	0–1 cm (100 cc)	July 1998	119	26	23 (3.2)	10.3	11.4	11.9	24.9 (10.3)
		MUC-J:	0–1 cm (64 cc)	July 1998	154	22	23 (3.2)	7	11.4	21.7	24.9 (10.3)
2	17921	GBC	I; 0–1 cm (80 cc)	April 1994	783	13	15 (2.8)	2.2	2.9	97.9	76.8 (29.7)
		GBC	A; 0–1 cm (100 cc)	April 1994	558	17	15 (2.8)	3.3	2.9	55.8	76.8 (29.7)
	OR-455-6B	KG	0–1 cm (100 cc)	June 1996	266	29		8.3	8.3	26.6	
		SO-114-7	MUC-A	0–1 cm (64 cc)	Nov. 1996	453	37	27 (7.5)	9.5	10.6	63.8
	SO-132-42	MUC-B	0–1 cm (64 cc)	Nov. 1996	254	27	27 (7.5)	7.6	10.6	35.8	38.2 (17.6)
		BC-A	0–1 cm (100 cc)	Nov. 1996	282	25	27 (7.5)	6.6	10.6	28.2	38.2 (17.6)
		BC-C	0–1 cm (100 cc)	Nov. 1996	79	19	27 (7.5)	7.9	10.6	25.2	38.2 (17.6)
		BC-1:	0–1 cm (100 cc)	July 1998	195	28	28.5 (5.3)	9	9.2	49.5	39.5 (13.1)
		BC-3:	0–1 cm(200 cc)	July 1998	396	26	28.5 (5.3)	6.2	9.2	30.6	39.5 (13.1)
		BC-3:	R1: 0–1 cm (400 cc)	July 1998	223	24	28.5 (5.3)	6.8	9.2	26	39.5 (13.1)
3	17922	BC-3:	R4: 0–1 cm (400 cc)	July 1998	697	36	28.5 (5.3)	8	9.2	51.9	39.5 (13.1)
		GBC	I; 0–1 cm (80 cc)	April 1994	262	36	31.5 (6.4)	11.3	11.4	32.7	27.2 (7.8)
	SO-114-24	GBC	C; 0–1 cm (100 cc)	April 1994	217	27	31.5 (6.4)	8.1	11.4	21.7	27.2 (7.8)
		MUC-A	0–1 cm (64 cc)	Dec. 1996	961	70		17.4	17.4	143.4	
SO-132-21	MUC-G:	0–1.5 cm (96 cc)	June 1998	276	50		17.9	17.9	90.8		
4	OR-455-5B	KG	0–1 cm (100 cc)	June 1996	118	19		6.4	6.4	11.8	



Table 3 (continued)

No.	Station		Sample (volume)	Sampling date	No. of counted:		Mean species no. (SD)	Fisher's $\alpha$ index	Combined Fisher's $\alpha$ index	No. of individuals/ 10 cm <sup>2</sup>	Mean no. of individuals/ 10 cm <sup>2</sup> (SD)
					Individuals	Species					
5	OR-455-7B	KG	0–1 cm (100 cc)	June 1996	19	7		4	10.5	1.9	
	SO-114-6	MUC-A	0–1 cm (64 cc)	Nov. 1996	416	38	31.5 (9.2)	10.2	10.5	58.6	78.5 (28.1)
		MUC-AR	0–1 cm (64 cc)	Nov. 1996	195	25	31.5 (9.2)	7.6	10.5	98.4	78.5 (28.1)
6	OR-455-9B	KG	A; 0–1 cm (80 cc)	June 1996	75	17		6.9	6.9	9.4	
7	OR-455-14B	KG	1; 0–1 cm (100 cc)	June 1996	90	16		5.7	5.7	9	
	SO-132-27	BC	0–1 cm (100 cc)	June 1998	122	14		4.1	4.1	21.2	
8	OR-455-17B	KG	A; 0–1 cm (50 cc)	June 1996	3	1		0.5	0.5	0.6	
	SO-132-29	MUC-J:	0–1 cm (64 cc)	July 1998	752	22		4.2	4.2	193.7	
9	SO-114-2	MUC-A	0–1 cm (64 cc)	Nov. 1996	1097	64		14.8	14.8	154.5	
10	SO-114-3	MUC-A	0–1 cm (64 cc)	Nov. 1996	570	38		9.2	9.2	80.3	
11	SO-114-4	MUC-A	0–1 cm (64 cc)	Nov. 1996	347	30		7.9	7.9	48.9	
12	SO-114-8	MUC-D	0–1 cm (64 cc)	Nov. 1996	135	14		3.9	3.9	19	
13	SO-114-9	MUC-A	0–1 cm (64 cc)	Nov. 1996	489	16		3.2	3.2	68.9	
	SO-132-50	MUC-I:	0–0.2 cm (13 cc)	July 1998	2258	20		3	3	318	
14	SO-114-10	MUC-A	0–1 cm (64 cc)	Nov. 1996	421	73		25.5	25.5	59.3	
15	SO-114-11	MUC-B	0–1 cm (64 cc)	Nov. 1996	237	39		13.3	13.3	41.8	
16	SO-114-13	MUC-B	0–1 cm (64 cc)	Nov. 1996	454	48		13.2	13.2	108.7	
17	SO-114-14	MUC-A	0–1 cm (64 cc)	Nov. 1996	708	68		18.5	18.5	150.4	
18	SO-114-17	MUC-A	0–1 cm (64 cc)	Dec. 1996	418	20		4.4	9	65.2	
	SO-132-28	MUC-G:	0–1 cm (64 cc)	June 1998	226	26	24 (2.8)	7.6	9	63.5	53.6 (14)
		MUC-J:	0–1 cm (64 cc)	June 1998	310	22	24 (2.8)	5.4	9	43.7	53.6 (14)
19	SO-114-27	BC-A	0–1 cm (100 cc)	Dez. 1996	219	43		16	16	81.6	
20	SO-132-5	MUC-F:	0–1 cm (64 cc)	June 1998	307	48		16	16	76.2	
21	SO-132-7	MUC-H:	0–1.5 cm (96 cc)	June 1998	621	51		13.2	13.2	133.9	
22	SO-132-8	MUC-I:	0–1.5 cm (96 cc)	June 1998	607	48		12.2	12.2	103.2	
		MUC-J:	0–1 cm (64 cc)	June 1998	165	23		7.3	7.3	48.6	
		MUC-H:	0–1.5 cm (96 cc)	June 1998	378	44		12.9	12.9	103.9	
23	SO-132-9	MUC-H:	0–1.5 cm (96 cc)	June 1998	378	44		12.9	12.9	103.9	
24	SO-132-10	MUC-I:	0–1 cm (64 cc)	June 1998	282	44		14.6	14.6	51.8	
25	SO-132-11	MUC-I:	0–1 cm (64 cc)	June 1998	373	47		14.2	14.2	74.2	
26	SO-132-12A	MUC-I:	0–1 cm (64 cc)	June 1998	98	28		13.1	13.1	16.5	
27	SO-132-14	MUC-I:	0–1 cm (64 cc)	June 1998	148	30		11.4	11.4	48.4	
28	SO-132-15	MUC-I:	0–1 cm (64 cc)	June 1998	161	24		7.8	7.8	27.6	
29	SO-132-16	MUC-I:	0–1 cm (64 cc)	June 1998	520	44		11.5	11.5	90.1	
30	SO-132-35	MUC-I:	0–1 cm (64 cc)	July 1998	452	48		13.6	13.6	63.7	

Table 3 (continued)

(B)									
No.	Station	Sample	Sampling date	No. of counted:		Fisher's $\alpha$ index	No. of individuals/ 10 cm <sup>2</sup>		
				Individuals	Species				
1	17920	GBC	I; 0–1 cm (80 cc)	April 1994	286	14	3.1	35.7	
		GBC	II; 0–1 cm (80 cc)	April 1994	251	7	1.3	31.4	
	SO-114-5	GBC	A; 0–1 cm (100 cc)	April 1994	536	12	2.2	53.6	
		MUC-A	0–1 cm (64 cc)	Nov. 1996	1599	26	4.4	225.2	
		BC-A	0–1 cm (100 cc)	Nov. 1996	186	14	3.5	205.8	
	SO-132-40	BC-D	0–1 cm (100 cc)	Nov. 1996	237	19	4.9	130.4	
		BC-1:	0–1 cm (200 cc)	July 1998	254	20	5.1	89.3	
		BC-1:	R4: 0–1 cm (400 cc)	July 1998	182	15	3.9	81.2	
		BC-2:	0–1 cm (100 cc)	July 1998	345	18	4	34.5	
		MUC-J:	0–1 cm (64 cc)	July 1998	722	25	5	101.7	
2	17921	GBC	I; 0–1 cm (80 cc)	April 1994	1361	20	3.3	170.1	
		GBC	A; 0–1 cm (100 cc)	April 1994	563	18	3.5	56.3	
	OR-455-6B	KG	0–1 cm (100 cc)	June 1996	919	73	18.6	91.9	
		MUC-A	0–1 cm (64 cc)	Nov. 1996	916	39	8.3	129	
		MUC-B	0–1 cm (64 cc)	Nov. 1996	815	43	9.7	114.8	
	SO-114-7	BC-A	0–1 cm (100 cc)	Nov. 1996	433	29	7	60.9	
		BC-C	0–1 cm (100 cc)	Nov. 1996	37	11	5.3	17.5	
		SO-132-42	BC-1:	0–1 cm (100 cc)	July 1998	923	51	11.6	245
			BC-3:	0–1 cm(200 cc)	July 1998	621	31	6.9	55.5
			BC-3:	R1: 0–1 (400 cc)	July 1998	948	45	9.8	152.8
BC-3:	R4: 0–1 cm (400 cc)	July 1998	1550	41	7.7	113.1			
3	17922	GBC	I; 0–1 cm (80 cc)	April 1994	209	36	12.5	26.1	
		GBC	C; 0–1 cm (100 cc)	April 1994	95	30	15.1	9.5	
	SO-114-24	MUC-A	0–1 cm (64 cc)	Dec. 1996	647	58	15.4	123	
	SO-132-21	MUC-G:	0–1.5 cm (96 cc)	June 1998	158	32	12.1	57.7	
4	OR-455-5B	KG	0–1 cm (100 cc)	June 1996	155	17	4.9	15.5	
5	OR-455-7B	KG	0–1 cm (100 cc)	June 1996	127	13	3.6	12.7	
		MUC-A	0–1 cm (64 cc)	Nov. 1996	1130	50	10.7	159.2	
	SO-114-6	MUC-AR	0–1 cm (64 cc)	Nov. 1996	460	28	6.6	273.8	
6	OR-455-9B	KG	A; 0–1 cm (80 cc)	June 1996	46	11	4.6	5.7	

Table 3 (continued)

No.	Station	Sample	Sampling date	No. of counted:		Fisher's $\alpha$ index	No. of individuals/ 10 cm <sup>2</sup>	
				Individuals	Species			
7	OR-455-14B	KG	1; 0–1 cm (100 cc)	June 1996	8	4	3.2	1
	SO-132-27	BC	0–1 cm (100 cc)	June 1998	18	9	7.2	9.3
8	OR-455-17B	KG	A; 0–1 cm (50 cc)	June 1996	11	8	13.2	1.1
	SO-132-29	MUC-J:	0–1 cm (64 cc)	July 1998	153	10	2.4	56
9	SO-114-2	MUC-A	0–1 cm (64 cc)	Nov. 1996	695	71	19.8	97.9
10	SO-114-3	MUC-A	0–1 cm (64 cc)	Nov. 1996	390	48	14.4	54.9
11	SO-114-4	MUC-A	0–1 cm (64 cc)	Nov. 1996	319	19	4.4	44.9
12	SO-114-8	MUC-D	0–1 cm (64 cc)	Nov. 1996	31	18	17.9	4.4
13	SO-114-9	MUC-A	0–1 cm (64 cc)	Nov. 1996	38	12	6	5.3
	SO-132-50	MUC-I:	0–0.2 cm (13 cc)	July 1998	66	6	1.6	9.3
14	SO-114-10	MUC-A	0–1 cm (64 cc)	Nov. 1996	1000	101	28	140.8
15	SO-114-11	MUC-B	0–1 cm (64 cc)	Nov. 1996	1558	54	10.9	313.2
16	SO-114-13	MUC-B	0–1 cm (64 cc)	Nov. 1996	740	57	14.4	185.8
17	SO-114-14	MUC-A	0–1 cm (64 cc)	Nov. 1996	953	74	18.7	299.3
18	SO-114-17	MUC-A	0–1 cm (64 cc)	Dec. 1996	97	19	7.1	36.2
	SO-132-28	MUC-G:	0–1 cm (64 cc)	June 1998	190	24	7.3	73.2
		MUC-J:	0–1 cm (64 cc)	June 1998	151	19	5.7	21.3
19	SO-114-27	BC-A	0–1 cm (100 cc)	Dec. 1996	251	45	16	25.1
20	SO-132-5	MUC-F:	0–1 cm (64 cc)	June 1998	109	30	13.7	18.7
21	SO-132-7	MUC-H:	0–1.5 cm (96 cc)	June 1998	299	48	16.2	82.3
22	SO-132-8	MUC-I:	0–1.5 cm (96 cc)	June 1998	227	48	18.6	56.6
		MUC-J:	0–1 cm (64 cc)	June 1998	58	21	11.8	29.3
23	SO-132-9	MUC-H:	0–1.5 cm (96 cc)	June 1998	177	44	18.8	60.8
24	SO-132-10	MUC-I:	0–1 cm (64 cc)	June 1998	146	45	22.2	32
25	SO-132-11	MUC-I:	0–1 cm (64 cc)	June 1998	259	47	16.8	60.1
26	SO-132-12A	MUC-I:	0–1 cm (64 cc)	June 1998	150	45	21.8	30.4
27	SO-132-14	MUC-I:	0–1 cm (64 cc)	June 1998	123	29	12	39
28	SO-132-15	MUC-I:	0–1 cm (64 cc)	June 1998	51	25	19.4	8.7
29	SO-132-16	MUC-I:	0–1 cm (64 cc)	June 1998	268	37	11.6	50.4
30	SO-132-35	MUC-I:	0–1 cm (64 cc)	July 1998	552	39	9.6	77.7

pronounced. The largest increase in diversity values was observed in the proximal part of the ash fan between 1994 and 1996. However, this increase may have been partly caused by the downslope displacement of specimens. Generally, multicore samples show higher diversity values than box core samples. We suspect that box core samples experienced some washout during core retrieval.

## 5. Discussion

### 5.1. Disturbance of the original environment

The Mt Pinatubo ashfall, resulting in the accumulation of an ash layer exceeding 8 cm thickness, was lethal for large parts of the benthic community. The original sea floor surface was covered within a few days by ash that prevented the supply of organic matter, oxygen, and nutrients (Haeckel et al., unpubl. data, 2001). Some of the Rose Bengal stained benthic foraminifera, which we observed below the ash layer in 1994, may have survived until the last oxygen was consumed. The extremely good preservation of some agglutinated foraminifera with organic cement below the ash layer confirms that bacterial decay of organic linings and cements slowed-down below the seal of volcanic ash (Hess and Kuhnt, 1996; Düffel, 1999).

Although the composition of the benthic foraminiferal assemblages was affected by ash deposition at sites, where this layer is only 15–25 mm thick, a significant number of benthic foraminifera survived the event. Most species of the pre-ashfall foraminiferal community are also found after the ashfall. As expected, epifaunal and especially sessile suspension-feeders (e.g. *Saccorhiza ramosa* and *Cibicidoides wuellerstorfi*) and tubular agglutinated morphotypes or grazing detritus-feeding foraminifera (i.e. ammodiscids) were reduced in number even by this comparatively thin ash cover. Infaunal benthic morphotypes such as *Reophax* and mobile taxa survived the event. Living individuals of this group occur within the ash layer and in the undisturbed sediment below the ash layer.

### 5.2. Recolonization of the new environment

Most of the pioneering and successive recolonizing species observed on the Mt Pinatubo ash layer in 1994 were absent from the pre-ash assemblages and from

undisturbed areas outside the ash lobe (Hess and Kuhnt, 1996; Hess, 1998). Obviously the first recolonizers were species characterized by the capability of rapid dispersion. Owing to lacking predation and competition in the newly occupied habitat they rapidly reached high standing stocks, indicating rapid reproduction rates and short life cycles (*r*-strategists). Typical representatives of these opportunistic taxa are *Reophax bilocularis*, *Reophax dentaliniformis*, *Textularia* sp., *Bolivina difformis* and *Quinqueloculina seminula*. All these species are regarded as mobile, infaunal detritivores, some of which have been previously reported from physically disturbed deep sea environments (Kaminski et al., 1988). In a study of the deep San Pedro Basin off southern California, an area that experiences seasonal anoxia, Kaminski et al. (1995) reported a remarkably similar faunal assemblage consisting of *Psammosphaera*, *Reophax dentaliniformis*, *Reophax* spp. and a minute organically cemented species of *Textularia* that was interpreted as opportunistic. Many of the species were the same as those found in recolonization trays in the Panama Basin (Kaminski et al., 1988), suggesting that different types of disturbance may result in similar benthic foraminiferal communities.

A second succession of colonizers appeared between 1994 and 1996. *Subreophax guttifer*, *Trochammina* spp. and *Adercotryma glomerata* were then the dominant species in the living fauna while dead assemblages were dominated by pioneer recolonizers. As the diversity significantly increased during this time, competition for space and resources grew and pioneering species started to be replaced by *K*-strategists. Benthic foraminifera living on the sediment surface (including epifaunal small specimens of *Cibicidoides wuellerstorfi* and tubular forms such as *Rhabdammina abyssorum*) appeared regularly and xenophyophores, large agglutinated protozoans, started to flourish on the sediment surface. In winter 1996 and summer 1998 we observed specimens of the xenophyophoria genus *Syringamina* with diameters larger than 50 mm in areas with a maximum ash thickness. Large xenophyophores are known to be abundant in deep sea areas with enhanced food supply (Tendal, 1972; Tendal and Gooday, 1981). Gooday et al. (1993) observed rapid and episodic growth of the xenophyophoria *Reticulammina labyrinthica* on the Madeira abyssal plain: three specimens increased their test

volume by three to ten times in eight months. These in situ observations of rapid growth may explain the sudden appearance of large xenophyophores on the Mt Pinatubo ash layer in the South China Sea.

Changes in the foraminiferal community were not extremely pronounced between 1996 and 1998. Surprisingly, the standing stock was even slightly lower in 1998, while the diversity remained almost constant (Table 3A). Changes in assemblage composition occurred. Some of the dominant forms in the living assemblages of 1996, such as *Subreophax guttifer*, were a main component of the dead assemblages in 1998, while others such as *Trochammina* spp. were still abundant in the living fauna.

Lowered abundance of benthic foraminifera observed in 1998 are consistent with the idea that predator–prey relationships were beginning to be reestablished. At one of the stations (SO-132-39), we observed a cache of post-ash foraminifera and xenophyophores within an onion-shaped burrow, indicating predation by some macrofaunal invertebrate (Kaminski and Wetzel, 2001). Abundant metazoan traces were observed on the surfaces of cores in 1998. Predator-exclusion experiments carried out by Buzas (1978), and Buzas et al. (1989), using protected sediment boxes have demonstrated that benthic foraminifera densities significantly increased when predators were excluded. When the density of predators is low and their foraging areas non-overlapping, the patchiness of surface-dwelling foraminiferal populations can also be expected to increase.

An additional explanation for the decrease in standing stock observed in summer 1998 may be naturally fluctuating primary production leading to a lowered carbon flux to the sea floor. The 1996 samples were collected in winter, when the winter monsoon creates upwelling in the area north-west of Luzon. High food abundance at the sea floor may have been influential, leading to higher foraminiferal standing stocks. Population densities in July 1998 may simply have been lower because more time had elapsed since the last organic detritus deposition event.

### 5.3. Spatial distribution patterns of the recolonization fauna

The environmental conditions for the benthic foraminiferal fauna in the proximal area of the ash

lobe changed completely after the Mt Pinatubo eruption. To the north, south and west of the areas with the thickest ash, the ash layer thins out and becomes more fine-grained. The degree of disturbance of the original environment and fauna also decrease towards the margin of the ash lobe; where the ash is thinner than 2 cm, most of the infaunal and mobile benthic foraminifera survived (Hess and Kuhnt, 1996).

The ash accumulated quite rapidly. The thick ash cover in the central part of the ash lobe was lethal for the entire existing benthic fauna. So, the ensuing recolonization process had to be initiated by immigrating species. Because of the vast extension of the ash deposit it is doubtful if immigrant species moved actively to their new environment. The distance to undisturbed ‘source’ areas was quite large and most recolonizing specimens probably reached the new environment by lateral dispersal (possibly in a larval stage, see Alve, 1999). The common occurrence of several species (*Textularia* sp. 1, *Bolivina difformis*, *Trochammina* sp. 1) in the recolonization fauna and their near absence in surrounding natural populations supports this scenario.

The coarse grain size of the ash compared to the background sediment might provide another explanation for the relatively slow colonization process. The well-sorted, coarse ash has a higher resistance against displacement than the slowly accumulated hemipelagic sediments, which made it difficult for benthic foraminifera to dig and move through the event layer. With the increasing activity of burrowing macroorganisms, observed in 1998, new ecological niches for more specialized forms appeared.

Our observations of replicate samples from the same site sometimes show a significant variability (compare site 1 or 2 in Table 2). Small-scale patchiness may be artificial (e.g. handling of the core) or natural (small environmental changes). The presence of a macrofaunal burrow can readily influence foraminiferal composition in the surrounding substrate because of stronger small-scale turbulences, ventilation effects or the preying behaviour of the occupant of the burrow (Kaminski and Wetzel, 2001).

## 6. Conclusions

The continuous monitoring of benthic foraminiferal communities from the 1991 Mt Pinatubo ash layer in

the South China Sea resulted in the following reconstruction of the recolonization process (Fig. 9):

The undisturbed benthic foraminiferal population prior to the ashfall of Mt Pinatubo consisted of a broad variety of morphotypes with different habitat preferences and feeding strategies. All ecological niches were occupied (Fig. 9A). This thriving deep sea assemblage was drastically decimated by the Mt Pinatubo ashfall in June 1991. For large parts of the benthic foraminiferal community this event was lethal (Fig. 9B).

The first wave of colonizers consisted of only a few species, considered to be infaunal detritus feeders. They still represented the living fauna in April 1994, three years after the eruption (with the exception of an organically cemented *Textularia* at site 1) (Fig. 9C).

The abundance, diversity, and complexity of the community structure increased with time. Between 1994 and 1996, species with different feeding modes such as suspension feeders appeared on top of the ash layer. At the same time, many of the early recolonizers disappeared and were only present in dead assemblages, but new taxa such as *Trochammina* species occurred in the sediment (Fig. 9D).

In 1998, large epifaunal foraminifera and xenophyophores on top of the ash layer were visibly more abundant on box core surfaces than in 1996, although the total abundance of living foraminifera was slightly lower than in 1996. Suspension-feeders, such as *Cibicoides wuellerstorfi* and xenophyophores were becoming common components of the post-ash surface fauna (Fig. 9E). Metazoan burrowers were also increasing their activity following the ashfall.

### 6.1. And the future?

The main question as to whether and when a 'normal' comparable to the pre-ash situation marine environment will reestablish itself remains open. Three problems arise:

1. Differences in substrate composition after the emplacement of the 1991 ash layer may lead to a different equilibrium fauna than on the soft substrate before the ashfall.

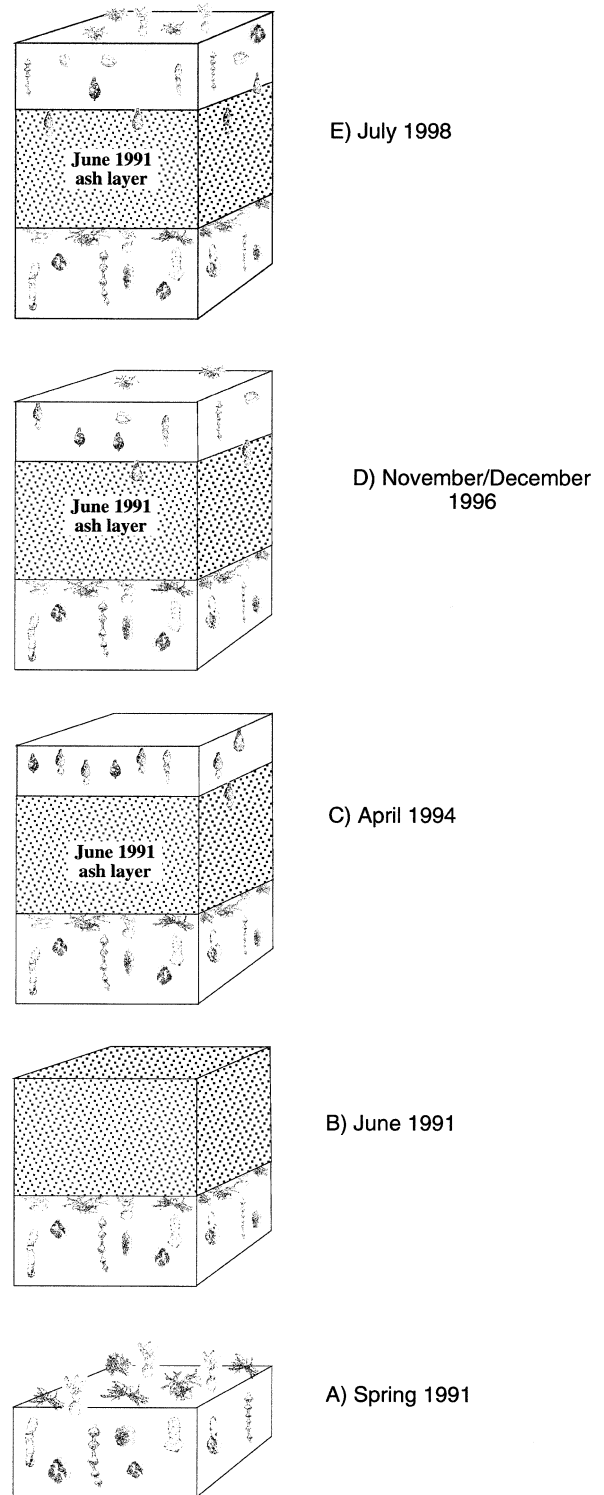


Fig. 9. Model of the recolonization process by benthic foraminifera.

2. During the timescale of our study, we observed secondary ash deposition by sediment gravity transport at several sites. The emplacement of re-deposited ash in the form of turbidites of up to 20 cm in thickness creates subsequent disturbances.
3. With the establishment of new predator–prey relationships and the selective predation of epifaunal taxa, we expect to observe increased patchiness in the post-ash fauna. Future sampling strategies have to take account of the fact, that patchiness may be on a larger scale than sampling area using standard sampling devices.

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