Bathymetric Distribution of Soft Bottom Tropical Macrobenthos from the Exposed East Coast of Reunion Island (Southwest Indian Ocean)

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Abstract—In order to give a description of the soft bottom macrobenthic communities from Reunion Island (tropical Indian Ocean) the coastal benthic environment was investigated following a bathymetric gradient in 1994 on the Bois Rouge / St Andre sector. This baseline study of the macrobenthos will be used as part of a long-term monitoring programme focused on the impact of the industrial sugar cane processing activity. Eleven stations at 2 sites ranging from 20 to 140 m depth were surveyed once before the start of industrial outfalls, on a potential impacted area (Bois Rouge site, BR) and on a control site (St Andre, SA). Among the 81 species recorded, polychaetes, were the most abundant with more than 40 species (77 % of the abundance), followed by many cnidarians, crustacean, bivalves and sipunculans. The macrobenthic abundance, biomass and species richness showed clear bathymetric trends. The analyses conducted on the sediments and macrofauna yielded a progressive depth cline, with three macrobenthic assemblages recorded along the Eastern coastal shelf of Reunion Island. The community analysis, confirmed the progressive depth gradient in both sites. Our results contribute to the knowledge on biodiversity of tropical soft bottom macrofauna on little studied tropical coasts, and illustrate a traditional framework of the macrobenthic community composition in an Indian Ocean coastal high-energy environment.

INTRODUCTION

Marine communities vary across different spatial and temporal scales. Therefore, the quantitative description of macrobenthos patterns at several spatial and or temporal scales is a fundamental step in the scientific process from which questions and hypotheses arise and from which appropriate predictive models can be proposed (Constable, 1999; Ysebaert & Herman, 2002). In subtidal marine coastal zones, the extent of habitat gradients and macrofaunal assemblages are distributed along

a succession of benthic habitats that often cannot be easily identified (Gray, 2000; Bergen *et al.*, 2001). Available data support the fact that most macrobenthic systems are stratified by depth (Zmarzly *et al.* 1994; Bergen *et al.* 2001). Other studies show the importance of the physical soft bottom environment and suggest that the sediment type is a primary factor organizing benthic communities (Snelgrove, 1999). Moreover, Snelgrove and Butman (1994) suggest that the amount of hydrodynamic energy and the available organic matter are more likely to be the driving

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forces, with depth and sediment grain size as secondary correlates. Depth and sediment grain size probably act together on the spatial variability in the diversity of macrofauna communities, integrating effects of the hydrodynamic environment over time. Although these variables are often reported for temperate regions of the Northern Hemisphere (Oug, 1998; Ellingsen, 2002), there are few comparable studies in the Southern hemisphere. Such information is still largely lacking for sub-tropical and tropical areas and varies with ecosystem type (Alongi, 1990; Gray, 2002). Tropical open coasts have been mostly studied in continental areas (Long & Poiner, 1994; Paiva, 2001; Cruz-Motta & Collins, 2004; Currie & Isaacs, 2005), while there are few data dealing with tropical islands (Agard *et al.*, 1993; McCarthy *et al.*, 2000; Bailey-Brock *et al.*, 2002; Dreyer *et al.*, 2005). This is particularly true for the islands in the Southwest Indian Ocean, where the macrobenthic community composition in open-shore sediment habitats has been reported from the Mozambique Channel (Makarov & Averin, 1968), Madagascar (Thomassin *et al.*, 1976), Mayotte (Gout, 1991) and Seychelles (Mackie *et al.*, 2005). Inventories of soft-bottom benthic fauna for Reunion Island are only available for coral reefs or adjacent areas (Bouchon *et al.*, 1981; Faure, 1982; Saiz Salinaz, 1993; Vadon & Guille, 1984; Jangoux & Aziz, 1988; Conand & Mangion, 2002; Taddei & Frouin, 2006). Little information is available on the composition of the non-reefal benthic communities, even though human activities and coastal input have drastically increased over the past 20 years. In this context, a marine impact assessment and a long term monitoring program of the sugar cane marine outfalls was conducted on the east coast of Reunion before and after the onset of disturbance (Bigot, 2003; Martial, 2005; Bigot *et al.*, in press). Our hypothesis is that specific macrobenthic communities exist at specific depths and habitats and are composed of species characteristic of the hydrodynamic environment of Reunion east coast. In this context, the two main objectives of our study were (1) to provide a first contribution to the description of the macrobenthos in this area, and (2) to characterise the bathymetric patterns of macrobenthos assemblages in a subtidal marine sector marked by strong hydrodynamic conditions and not yet influenced by strong anthropogenic effects.

MATERIAL AND METHODS

Study area

In the framework of a long term monitoring programme conducted on the Northeast coast of Reunion Island (Southwest Indian Ocean) (Fig. 1), a baseline impact assessment study was set up in March 1994, to investigate the initial state of the coastal benthic environment before the possible changes following the onset of the discharge of agro-industrial effluents (Bigot *et al.*, in press). The study area is characterised by strong hydrodynamic conditions, and the swell generated by trade winds regularly affects subtidal environments up to 10 m depth (Piton & Taquet, 1992). This coast is also periodically subjected to hurricanes, when the wave height can reach 7-10 m and cause removal of sediment and associated macrofauna. The study area comprises the Bois Rouge (BR), and Saint Andre (SA). BR is located in front of the industrial complex, which encompasses a sugar mill, a distillery and a thermal power station (Fig. 1). The distillery was set up in 1994 and the industrial complex produced moderate loads of terrigenous particles with low organic content coming from the sugar mill and the power station. SA (Champ Borne cap) is situated approximately 5 km upstream from the main coastal currents of BR, and is a comparable site and a further control site (Fig. 1). This area is characterised by stronger hydrodynamic conditions (Southwest trade winds) than the BR site.

Sample collection and processing

Sampling stations were located along a depth gradient, ranging from 20 to 140 m depth (BR), and 20 to 120 m depth (SA). Eleven stations (6 at BR and 5 at SA) were sampled in March 1994, a period when industrial effluents were low. The last moderate hurricanes ("Colina" and "Holanda") had affected this coast 3 months before the study. The sampling is the baseline for the exposed areas.
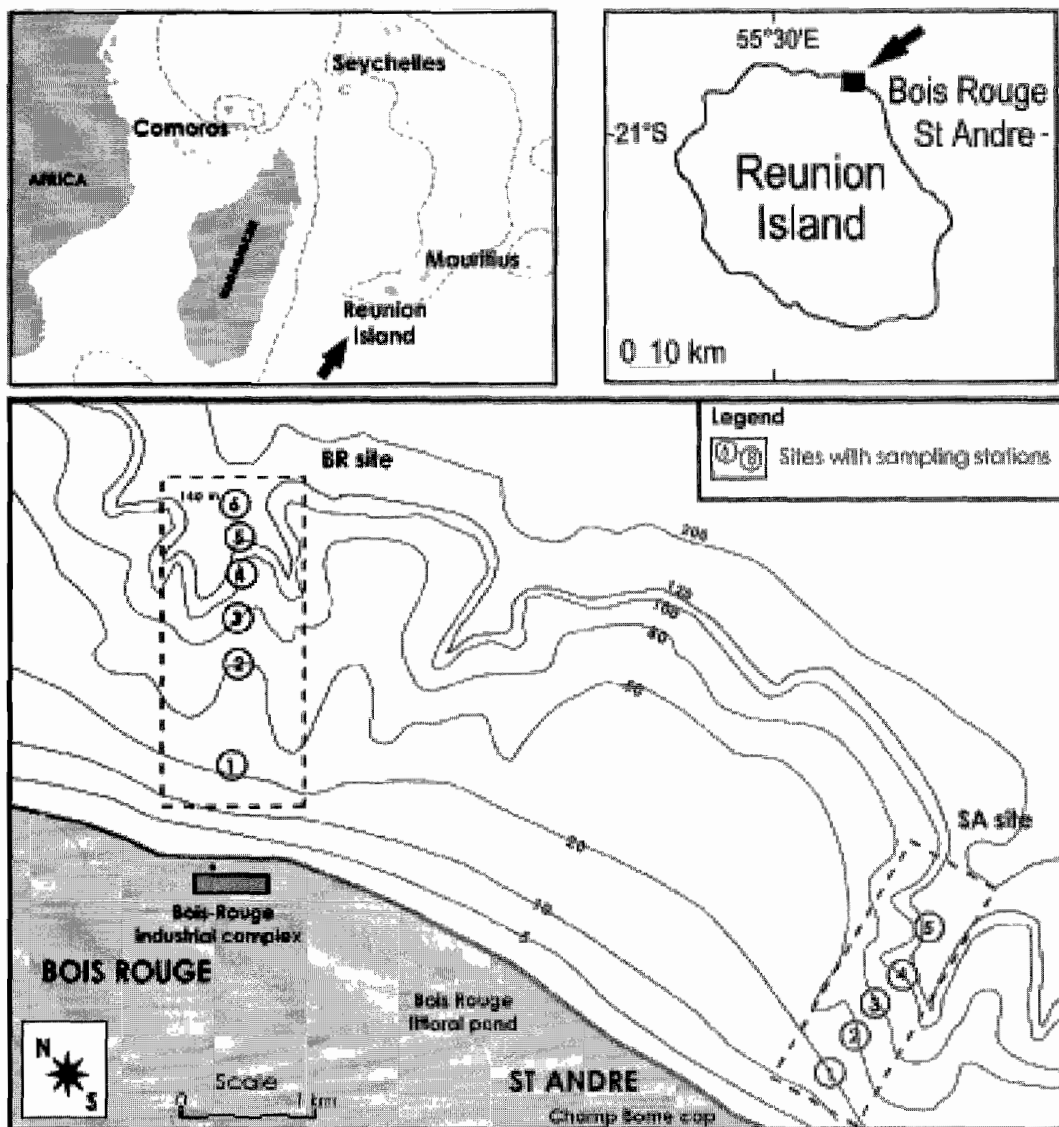
Fig. 1. Map of the study area showing the two studied sites (Bois Rouge industrial complex, BR and Saint Andre, SA) and the sampling stations

grab for macrobenthos and sediment characteristics (i.e. granulometry). At each station, 3 replicate grabs were collected for macrofauna analysis. A sub-sample of sediment was taken from one of these grabs for the analysis of sediment characteristics. Overall, 30 grabs were collected for the macrofauna analysis and 11 sub-samples for the sediment granulometry. Macrobenthic samples were sieved through a 1 mm round mesh size and the retained fauna was fixed in 5%

formalin for later identification to the lowest attainable taxonomic level. Biomass (AFDW) was assessed for each taxa by drying (100°C for 24 h) and ashing (450°C for 5 h). The results were expressed in numbers of specimens (abundance) or mg (biomass) by m^{-2}. The sediment grain size was measured by dry sieving (Folk & Ward, 1957) and classified following Wentworth (1922). The silt fraction of each sample was directly measured by wet sieving through a 63 μm mesh-sized sieve.

Statistical analyses

Bathymetric patterns in grain size distribution were analysed using Kolmogorov-Smirnov non-parametric tests. Bathymetric changes in macrofauna abundance and biomass were performed using one-way ANOVA and Levene's test was used to check for homogeneity of variance. Anova and post-hoc tests were performed using SPSS (version 7.5.2F, 1997). In a first approach, species richness (S), Shannon alpha diversity index (H'), global abundance and biomass were used to show the bathymetric fluctuations of macrobenthos. Then, changes in macrobenthic community composition were assessed using non-metric multidimensional scaling ordinations (MDS) and associated ANOSIM tests (Clarke & Warwick, 1994). The MDS was run on a Bray-Curtis dissimilarity matrix using square-root transformed data. The Index of Multivariate Seriation (IMS) (Clarke & Warwick, 1994; Brown et al., 2002) was used to assess the spatial breakdown in macrobenthos communities (seriation) between different depths. MDS and associated procedures (IMS Relate program, ANOSIM) were performed using the PRIMER(r) package (Clarke & Goorley, 2001).

RESULTS

Sediment characteristics

The sediment granulometry showed a typical bathymetric gradient with decreasing grain size from shallow to deep stations at both sites, and a clear shift after 20 m depth for BR and 50 m depth for SA (Fig. 2). The grain size did not significantly differ between stations ≥ 50 m depth at BR (Kolmogorov-Smirnov test, $p > 0.1$) and > 50 m depth at SA (K-S test, $p < 0.01$ between 50 and 80 m; K-S test, $p > 0.1$ between 80 and 120 m). A comparison between the shallow BR and SA stations (20 m) shows that sediments consisted mainly of very fine sands at BR and coarse and fine sands at SA. Shallow sediments were thus finer at BR than at SA (K-S test, $p < 0.001$), probably reflecting a higher hydrodynamic exposition at SA. Up to 50 m depth, no significant difference was

noticed between both sites (K-P test, $p > 0.1$). Deep sediments consisted mainly of silt fractions (BR) and very fine sands and silts (SA) according to the Wentworth scale.

Macrofauna characterization

One thousand six hundred and ninety nine individuals belonging to 87 taxa were collected during the study (table 1). Polychaetes were dominant both in number of taxa (40) and relative abundance (77% of total macrofauna abundance). The other dominant groups were cnidarians, crustaceans, bivalves and sipunculans (respectively 5.3, 4.7, 3.8 and 3.7% of the total macrofauna abundance). The analysis revealed 58 taxa at SA and 68 at BR. Several polychaetes of the families of Spionidae (e.g., Prionospio ehlersi, P. steenstrupi, Laonice quadridentata.), Capitellidae (e.g. Ancistrosyllis sp.), Pilargidae (e.g., Ancistrosyllis parva) and cnidarians (Heterocyathus aequicostatus, Antipathes sp.) and sipunculans (e.g., Aspidosiphon müelleri) were consistently found at both sites during the sampling (Table 1, 2).

The mean total abundance and the biomass of macrobenthos for 1994 were very similar at BR and SA, respectively for abundance (522 ± 243 and 531 ± 118 ind. m^{-2}) and for biomass (1276 mg.$m^{-2} \pm 1775$; 1442 mg. $m^{-2} \pm 963$). Spatial changes were not significant between the two sites for abundance (one-way ANOVA, $p = 0.944$) as well as for biomass ($p = 0.948$).

At BR, the abundance of macrofauna varied significatively with depth (one-way ANOVA, $p = 0.005$) (Fig. 3A). Spatial changes were most important between BR 1 (the shallowest station) and the station BR 3 (80 m) ($p < 0.006$) and between BR 1 and BR 2 (50 m) ($p < 0.041$). The abundance increased between 20 and 50m depth and was maximal for 50 and 80 m (respectively 703 ± 221 ind.m^{-2} for BR 2 and 850 ± 144 ind.m^{-2} for BR 3). The abundance progressively decreased for depths > 100 m. The biomass of macrofauna also varied with depth, globally following the same trend.

At SA, the abundance of macrofauna also varied with depth (one-way ANOVA, $p < 0.001$) (Fig. 3B). The spatial changes were particularly
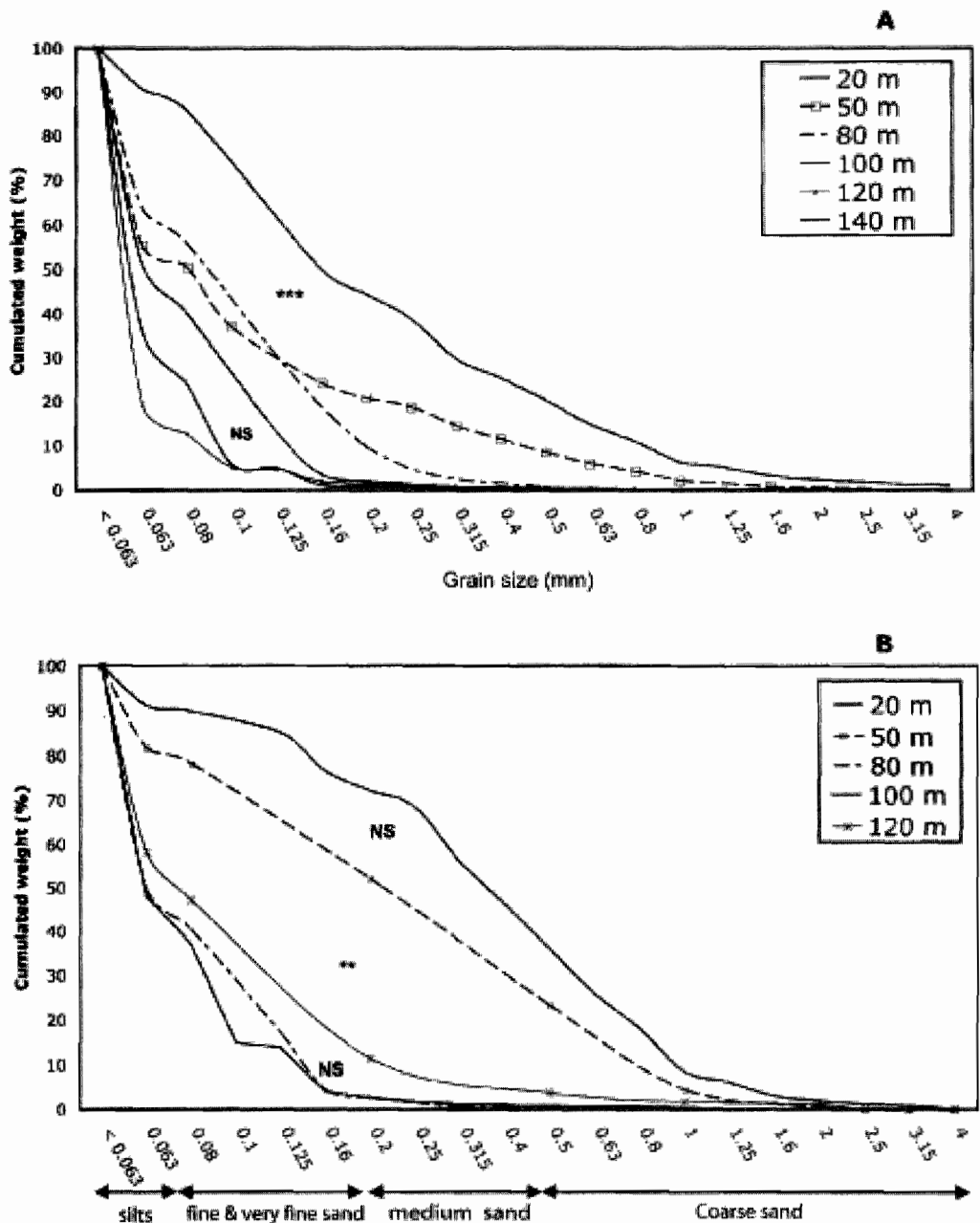
Fig. 2. Cumulated grain size curves assessed in 1994 for each sampling depth at BR (A) and SA (B). The results of the main Kolmogorov-Smirnov non-parametric test are also provided (NS: No significant; *** p < 0.001; ** p < 0.01)

significant between station SA 1 (20 m) and SA 3 (80 m), (p < 0.025) and between SA 4 and SA 5 (p < 0.004). The abundance increased with depth between 20 and 100 m and reached the highest value for this depth (SA 4: 1133 ± 255 ind.m⁻²). It drastically decreased for the deepest station (SA

5). The biomass of macrobenthos followed the same trend as the abundance.

Diversity and community analysis
The analysis of species richness for each site and depth, showed an increase between 20 m and 50

Table 1. Contribution of the main taxa at BR and SA sites in 1994. Abundances (Ab) are provided in ind.m^{-2} ±SD and absolute biomasses (AFDW) are provided in mg.m^{-2} ± SD. In bold, contribution of the main species. Mean total abundance and biomass are given for each site, respectively in ind. m^{-2} and mg. m^{-2}. ANN = polychaete, BIV = bivalve, CNI = cnidarian, CRU = crustacean, ECH = echinoderm, GAS = gastropod, NEM = nenertean, SIP = sipunculan.

Taxa	Family	Species	BR		SA	
			Abundance	Biomass (AFDW)	Abundance	Biomass (AFDW)
ANN	Pilargidae	**Ancistrosyllis parva**	**16.5 ± 5.1**	7.22 ± 2.2	**41.3 ± 9.5**	20.59 ± 3.7
ANN	Spionidae	Aonides oxycephala	-	-	5 ± 3.0	0.79 ± 0.5
ANN	Eunicidae	Diopatra cuprea cuprea	4.7 ± 1.2	4.63 ± 1.2	-	-
ANN	Serpulidae	Ditrupa gracillima	6.6 ± 2.7	0.95 ± 0.4	4 ± 2.7	0.61 ± 0.4
ANN	Glyceridae	Glycera prashadi	5.5 ± 1.2	4.87 ± 1.0	2.6 ± 0.7	2.87 ± 0.5
ANN	Spionidae	**Laonice quadridentata**	**29.3 ± 8.8**	17.20 ± 5.0	**10 ± 3.8**	5.95 ± 2.1
ANN	Eunicidae	Lumbrinereikatreilli	20.2 ± 4.0	5.07 ± 1.0	15 ± 4.6	4.02 ± 1.1
ANN	Chaetopteridae	Mesochaetopterus minutus	8.3 ± 6.1	3.93 ± 2.9	-	-
ANN	Nephthyidae	Nephthys (Agloa.) dibranchis	0.6 ± 0.4	4.33 ± 3.2	7.66 ± 4.6	117 ± 44.8
ANN	Capitellidae	**Notomastus sp**	**28.7 ± 5.4**	23.79 ± 4.5	**16 ± 5.1**	14.19 ± 4.2
ANN	Eunicidae	Oenonfulgida	7.2 ± 2.4	7.94 ± 2.6	6.3 ± 2.4	7.46 ± 2.7
ANN	Eunicidae	Onuphisremita	3.75 ± 1.5	2.15 ± 0.9	3.3 ± 1.4	2.05 ± 0.8
ANN	Phyllodocidae	Phyllodoce malmgreni	2.2 ± 1.2	1.20 ± 0.6	2 ± 0.8	1.55 ± 0.4
ANN	Spionidae	**Prionospio ehlersi**	**163.6 ± 50.2**	25.53 ± 7.7	**208 ± 80.1**	34.62 ± 12.4
ANN	Spionidae	**Prionospio steenstrupi**	**71.5 ± 19.3**	121.42 ± 32.4	**38 ± 14.0**	90.07 ± 23.3
ANN	Spionidae	Spio pacifica	-	-	1.7 ± 0.7	0.41 ± 0.1
ANN	Amphinomidae	Pseudoeryhtoe parvecarunculata	1.6 ± 0.8	6.0 ± 3.0	5.6 ± 2.5	21.85 ± 8.9
ANN	Ampharetidae	Samytha sp	13.6 ± 6.0	3.08 ± 1.4	0.6 ± 0.4	-
ANN	Aphroditidae	Sigalion mathildae	1.1 ± 0.9	0.61 ± 0.4	-	-
BIV	Mytilidae	Amygdalum soyoae	2.2 ± 1.2	12.47 ± 6.8	6.6 ± 1.8	24.05 ± 9.2
BIV	Veneridae	Lioconcha philipinarum	4.4 ± 1.4	2.52 ± 0.7	1 ± 0.6	2.43 ± 1.1
BIV	Cuspidaridae	Pseudonearea thomasya	3.7 ± 0.9	1.18 ± 0.3	2 ± 1.3	0.92 ± 0.3
BIV	Tellinidae	Tellina sp	3.5 ± 1.3	0.59 ± 0.2	6.3 ± 2.1	30.30 ± 18.5
BIV	Veneridae	Timocleaoncinua	1.2 ± 0.9	0.16 ± 0.1	1 ± 0.7	0.33 ± 0.1
CNI	Antipatharian	Antipathes sp.	**23.8 ± 16.1**	438.24 ± 308.9	**19.6 ± 8.7**	495.44 ± 247.5
CNI	Dendrophyllidae	**Heterocyathus aequicostatus**	**1.6 ± 1.2**	75.36 ± 55.37	**5 ± 2.1**	117.63 ± 88.1
CRU	Alpheidae	**Alpheidae sp**	**5.4 ± 2.3**	1.86 ± 0.8	**16 ± 3.6**	5.90 ± 1.2
CRU	Caridae	Ogyridesp	7.7 ± 5.7	0.77 ± 0.6	-	-
CRU	Corophiidae	**Siphonoecetes sp**	-	-	**69 ± 46.5**	3.18 ± 14.2
ECH	Lovenidae	Lovenia elongata	2.7 ± 1.3	226.12 ± 105.1	3 ± 1.3	327.07 ± 136.5
ECH	Brissidae	Brissopsis luzonica	-	-	2.7 ± 1.8	0.59 ± 0.2
GAS	Terebridae	Hastulla matheroniana	7.2 ± 9.2	3.13 ± 2.3	-	-
GAS	Actaeocinidae	Cylichna collyra	1.5 ± 0.5	0.15 ± 0.05	1 ± 0.7	0.11 ± 0.06
NEM	Anopla	Baseodiscus sp	**15.4 ± 5.2**	5.82 ± 1.9	**9.7 ± 2.5**	3.91 ± 0.9
SIP	Aspidosiphonidae	**Aspidosiphon muelleri**	**20.2 ± 5.7**	3.87 ± 1.1	**11.6 ± 4.7**	0.75 ± 0.1
		MEAN TOTAL	**522 ± 243**	1276 ±1775	**531 ± 118**	1442 ± 963

m at the both sites (Fig. 4). Between 50 and 100 m, the species richness showed a relative stability and decreased steadily for the deepest area (> 100 m). At the same time, the diversity (H') was similar in the shallow environment (H' > 2 for BR and SA at 20 m), and progressively decreased after 50 m. At both sites, the diversity followed the same trend as the bathymetry. A more structured community composition was found for the intermediate depth (50 - 80 m), where the diversity reached a maximum value (H' = 2.8 for SA and H' = 2.5), and then decreased gradually after 100 m. Below 190 m, other samplings at BR and SA sites (not shown here) confirmed the very low species richness and abundance (often less than 10 species, 200 ind.m^{-2}).

The most important species of these communities were often the same at both sites (Table 1). At BR site, the macrobenthos assemblages were dominated by polychaetes belonging to the families of Spionidae (*Prionospio ehlersi, P. steenstupi*) and to a lesser extent the Spionidae (*Laonice quadridentata*), Capitellidae (*Notomastus* spp.), Pilargidae (*Ancistrosyllis parva*), by cnidarians, nemerteans and sipunculans (e.g. *Aspidosiphon muëlleri*). Spionidae were mostly represented at intermediate (50 to 100 m) and deep stations (> 100 m), whereas shallow stations (20 m) were mostly characterized by crustaceans (Caridea, Amphipoda) and gastropods (*Hastulla matherioniana*). At the SA site, the macrobenthos composition was similar for the

Table 2. List of species and taxas recorded during the study at each station and sites (presence / absence). ▨▨▨ SA site; ▬▬▬ BR site * new record for Reunion island. See Table 1 for taxa

Taxa	Family	Species	Stations						
			1	2	3	4	5	6
ANN	Ampharetidae	* Ampharete cf. acutifrons (Grube, 1860)						
ANN	Ampharetidae	Samytha sp (Malmgrem, 1866)						
ANN	Ampharetidae	* Samythella affinis (Day, 1963)						
ANN	Amphinomidae	* Euryhtoe parvecarunculata (Horst, 1912)						
ANN	Aphroditidae	Pareulepsis gaeyi (Fauvel, 1918)						
ANN	Aphroditidae	* Sigalion mathildae (Audouin & Milne Edwards, 1832)						
ANN	Aphroditidae	* Sthenelaïs boa (Johnston, 1839)						
ANN	Aphroditidae	* Sthenelais limicola (Ehlers, 1864)						
ANN	Capitellidae	Notomastus sp (Sars, 1851)						
ANN	Capitellidae	* Dasybranchus caducus (Grube, 1846)						
ANN	Capitellidae	Notomastus sp (Sars, 1851)						
ANN	Chaetopteridae	* Mesochaetopterus minutus (Potts, 1914)						
ANN	Eunicidae	* Diopatra cuprea cuprea (Bosc, 1802)						
ANN	Eunicidae	* Lumbrinereis latreilli (Audouin & Milne Edwards, 1834)						
ANN	Eunicidae	* Oenone fulgida (Savigny, 1818)						
ANN	Eunicidae	* Onuphis eremita (Audouin & Milne Edwards, 1833)						
ANN	Glyceridae	* Glycera prashadi (Fauvel, 1932)						
ANN	Glyceridae	* Goniada emerita (Audouin & Milne Edwards, 1833)						
ANN	Mageloniidae	* Magelona cf. americana (Müller, 1858)						
ANN	Nephthyidae	Nephthys (Aglaophamus) dibranchis (Grube, 1877)						
ANN	Orbinidae	* Scoloplos madagascariensis (Fauvel, 1919)						
ANN	Owenidae	* Myriochele cf. picta (Southern, 1921)						
ANN	Owenidae	undet. Sp						
ANN	Paralacydoniidae	* Paralacydonia paradoxa (Fauvel, 1913)						
ANN	Phyllodocidae	* Phyllodoce malmgreni (Gravier, 1900)						
ANN	Pilargidae	* Ancistrosyllis parva (Day, 1963)						
ANN	Sabellidae	* Potamilla linguicollaris (Day, 1961)						
ANN	Serpulidae	* Ditrupa gracillima (Grube, 1878)						
ANN	Serpulidae	* Serpulavermicularis vermicularis (Linnnaeus, 1767)						
ANN	Serpulidae	* Vermiliopsis babylonia (sp. nov.)						
ANN	Spionidae	* Aonides oxycephala (Sars, 1862)						
ANN	Spionidae	* Laonice cirrata (Sars, 1851)						
ANN	Spionidae	* Laonice quadridentata (Blake & Kudenov, 1978)						
ANN	Spionidae	* Malacoceros indicus (Fauvel, 1928)						
ANN	Spionidae	* Prionospio cf. pinnata (Ehlers, 1901)						
ANN	Spionidae	* Prionospio ehlersi (Fauvel, 1928)						
ANN	Spionidae	* Prionospio steenstrupi (Malmgren, 1867)						
ANN	Spionidae	* Spiopacifica (Blake & Kudenov, 1978)						
ANN	Syllidae	* Syllis (Typosyllis) variegata (Grube, 1860)						
ANN	Terebellidae	Melinna sp (Malmgren, 1866)						
ANN	Terebellidae	* Thelepus ehrembergi (Leuckart, 1849)						
ANN	Terebellidae	* Terrebellides stroemi (Sars, 1835)						
ANN	Trophiochaethidae	* Poecilochaetus serpens (Allen, 1904)						
CRU	Nannastacidae	Campilaspis sp (Sars, 1865)						
CRU	Portunidae	undet. Sp						
CRU	Processidae	Processa sp (Leach, 1815)						
CRU	Thallassinidae	Upogebia sp (Leach, 1814)						
CRU	Alpheidae	Alpheus sp (Fabricius, 1798)						
CRU	Ampeliscidae	Ampelisca sp (Kroyer, 1842)						
CRU	Anthuridae	Calathurasp (Nordman & Stebbing, 1886)						
CRU	Caprellidae	Phtisica sp (Slabber, 1749)						
CRU	Caridae	Ogyrides sp (Stebbing, 1914)						
CRU	Corophiidae	* Erichthonius brasiliensis (Dana, 1852)						
CRU	Corophiidae	Siphonoecetes sp (Koyer, 1845)						
CRU	Goneplacidae	* Xenophthalmodes moebi (Richters, 1880)						
CRU	Hippidae	Albunea sp (Weber, 1795)						
CRU	Isaidae	* Photis cf. longicaudata (Bate & Westwood, 1862)						
CRU	Gammaridae	undet. sp						
CRU	Lysiosquillidae	Lysosquilla sp						

Table 2 contd.

| Taxa	Familly	Species	Stations 1 2 3 4 5 6
BIV	Cardiidae	Frigidocardium centumliratum (Mellvill & Standen, 1899)	
BIV	Cuspidaridae	Pseudonearea thaumasya (Sturany, 1902)	
BIV	Lucinidae	Pillucina neglecta (Habe, 1960)	
BIV	Modiolidae	Amygdalum soyoae (Habe, 1958)	
BIV	Cardiidae	Microcardium sp	
BIV	Poromyidae	Poromya (tenuiconcha) soyoa (Kira, 1952)	
BIV	Tellinidae	Tellina sp	
BIV	Veneridae	Dosinia minor (Deshaye, 1863)	
BIV	Veneridae	Lioconcha philipinarum (Hanley, 1844)	
BIV	Veneridae	Timoclea concinna (Viader, 1951)	
GAS	Actaeocinidae	Cylichna collyra (Melvill, 1906)	
GAS	Cerithidae	Cerithium sp	
GAS	Nassaridae	Cyllene concinna (A. Adams, 1851)	
GAS	Nassaridae	Nassarius novaehollandiae (Reeve, 1845)	
GAS	Naticidae	Naticarius sp	
GAS	Terebridae	Cancilla salisburyi (Drivas & Jay, 1990)	
GAS	Terebridae	Hastulla matheroniana (Deshayes, 1859)	
GAS	Turitellidae	Turitella auricincta (Von Martens, 1875)	
CNI	Antipatharian *	Antipathes sp	
CNI	Actiniairia	undet. Sp	
CNI	Dendrophyllidae	Heterocyathus aequicostatus (Milne Edwards & Haime, 1848)	
CNI	Pennatulidae *	Pennatula inflata (Kükenthal, 1910)	
ECH	Amphiuridae	Amphiura sp	
ECH	Brissidae *	Brissopsis luzonica (Gray, 1851)	
ECH	Loveniidae *	Lovenia elongata (Gray, 1845)	
ECH	Goniasteridae	Ogmaster capella (Müller & Troschel, 1842)	
NEM	Anopla	Baseodiscus sp	
SCA	Siphonodentallidae	Polychides arnaudi (Scarabino, 1995)	
SIP	Aspidosiphonidae	Aspidosiphon (Aspidosiphon) müelleri (Diesing, 1851)	
SIP	Golfingiidae	Phascolion sp. (Théel, 1875)	

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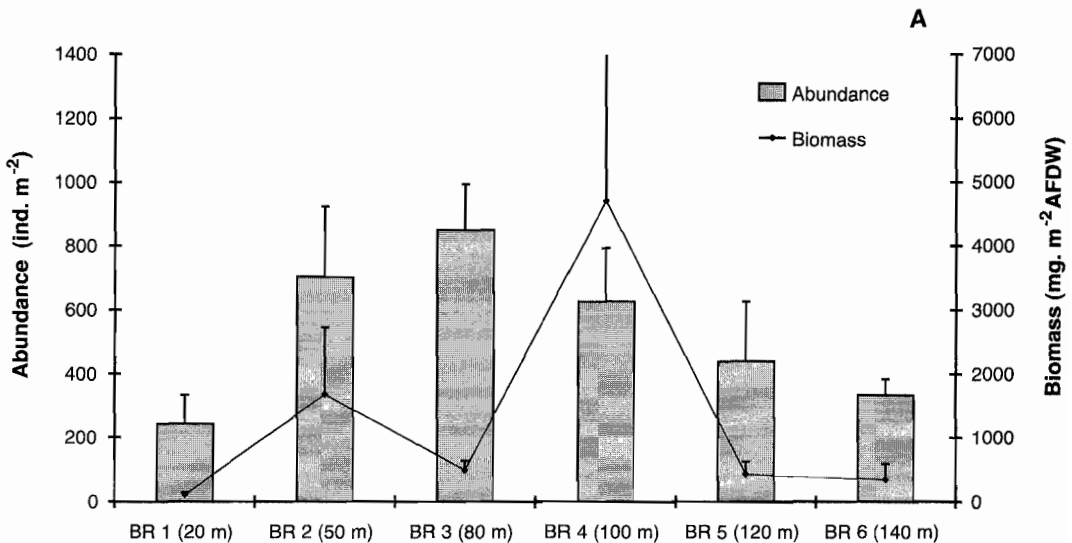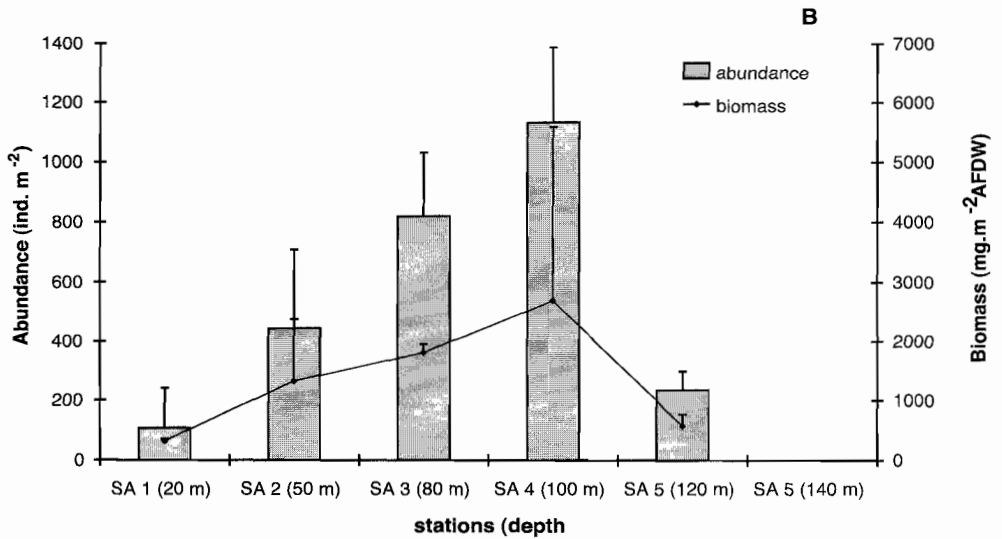
Fig. 3. Spatial patterns of the mean abundance (± SD) and mean biomass (± SD) of the total macrofauna at BR (A) and SA (B)
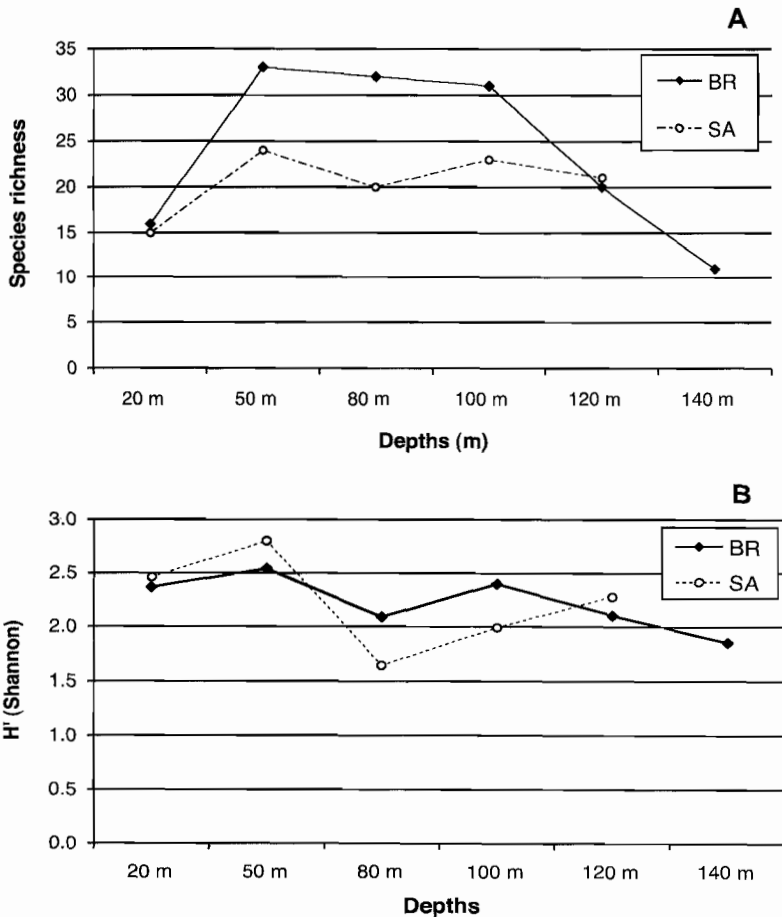
Fig. 4. Spatial patterns of species richness (A) and diversity Shannon index (B) across a depth profile at BR and SA

intermediate and deep stations. The local abundance of crustaceans, such as amphipods belonging to the Corophiidae (Siphonoecetes sp.), have been recorded at intermediate depth (50 m).

Depth gradient

The MDS indicates the existence of three groups of stations (Fig. 5): the first corresponds to the shallow stations (BR 1 and SA 1), the second to the intermediate (50 - 100 m depth) stations BR 2, 3, 4 and SA 2, 3, 4, and the third group to the deep (120 - 140 m depth) stations BR 5, 6 and SA 5. MDS configurations indicated that benthic communities changed following a gradual depth pattern, particularly marked for the BR site between 20 and 50 m and after 100 m.

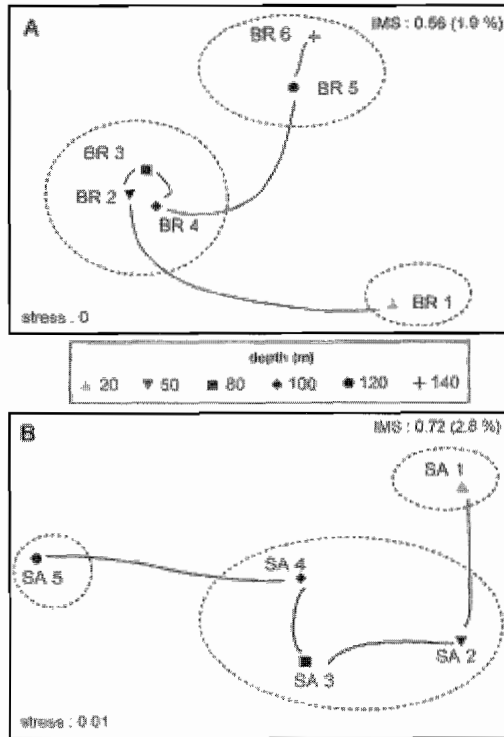The Index of Multivariate Seriation (IMS) measures the degree to which the community

Fig. 5. MDS plots for square root transformed macrobenthos taxa/abundance data at BR (A) and SA (B) with the distinction of 3 groups of stations (shallow, intermediate, deep). The lines indicate the degree of seriation by linking successive points along the depth transect from shallow station (20 m) to deep station (>100 m). Index of Multivariate Seriation (IMS) values are at the top right. (Values) are the % significance levels in a permutation test for absence of seriation (T = 999)

changes (the breakdown of seriation between the different depths) conform to a linear standardised sequence. The values of IMS are consequently high on both sites and show a significant correlation with a linear sequence at BR (Rho = 0,56; p < 0.019) and SA (Rho = 0.72; p < 0.028). Both BR and SA stations show significant depth patterns in the composition of macrobenthos assemblages (ANOSIM tests, p < 0.001 in both cases). More specifically, significant spatial patterns in the macrobenthos were noticed between BR 1 (20 m) and BR 2 (50 m) (ANOSIM pairwise tests, p < 0.040), and after 100 m (BR 5, p < 0.029).

DISCUSSION

The two main objectives of the present study were to: (1) provide a first contribution on the knowledge soft-bottom subtidal communities off the East coast of Reunion Island, (2) describe their main bathymetric patterns in an open shore environment, before the onset of land based agro-industrial inputs.

Description of soft-bottom communities

In the Southern hemisphere, few studies describe the macrobenthic composition of sub-tropical and tropical open shore areas (Hylleberg & Nateewathana, 1984; Warwick & Ruswahyuni, 1987; Alongi 1990; Gray, 2002). In the Southwest Indian Ocean, studies on the composition of soft bottom macrobenthic communities around islands are reported mainly for coral reefs from Madagascar (Thomassin *et al.*, 1976; Pichon, 1967), Mayotte (Gout, 1991) and Mauritius (Rullier, 1962). Recently, studies have been reported on the mollusc communities of the Seychelles (Mackie *et al.*, 2005), East Africa open shore coasts (Mgaya *et al.*, 2005, Samaai *et al.*, 2005), and South African tidal flats and estuaries (Boer & Prins, 2002; Teske & Wooldrigde, 2001). Inventories and quantitative descriptions of the soft-bottom macrobenthic assemblages in Reunion Island were previously limited to a few taxa: sipunculans (Saiz Salinas, 1993) echinoderms (Vadon & Guille, 1984; Jangoux & Aziz, 1988; Conand & Mangion, 2002), cnidarians and

polychaetes (Bouchon *et al.*, 1981; Faure, 1982), crustacean (S. Ribes, pers. com.) and molluscs (M. Jay, pers. com.; Deshayes, 1863) and a short term temporal sampling of coral reef communities (Taddei & Frouin, 2006). The present study recorded 81 taxa, 45 of them being new records for Reunion Island. The macrobenthic assemblages are dominated by polychaetes (40 species, 77% in abundance), but cnidarians, crustaceans, bivalves and sipunculans are also common. The dominance of polychaetes in tropical macrobenthos composition has already been described for coral reefs (Alongi, 1990; Frouin, 2000) or subtidal areas (McCarthy *et al.*, 2000; Lancellotti & Stotz, 2004; Shin & Ellingsen, 2004). The abundance of cnidarians such as antipatharian (*Antipathes* sp) or free-living corals (*Heterocyathus aequicostatus*) are new observations for Reunion Island and have mainly been described for other Indian Ocean locations such as Indonesia (Hoeksema & Best, 1991).

The community composition shows a traditional scheme assemblage with 20 to 30 common and abundant species (mainly polychaetes), widely distributed spatially, while species with low abundance represent an important part of the species richness, as described elsewhere (Ellingsen, 2002). The mean abundances recorded during the present study vary between 107 (SA 1, 20 m) and 1133 ind. m^{-2} (SA 4, 100 m) with a mean total abundance of 515 ind.m^{-2}. These values are higher than those reported by Makarov & Averin (1968) for the Mozambique Channel (32 - 333 ind. m^{-2}). Similar abundances were reported by Long & Poiner (1994) and Currie & Isaacs (2005) for open shore reference areas in Australia and by Warwick & Ruswahyuni (1987) for a subtidal area in Indonesia (422 ind. m^{-2}). Frouin (2000) also reported a similar range of mean abundance for Tahiti (222 ind. m^{-2}) for macrofauna sorted on a 2 mm mesh. These abundances are in the lower range of the values reported by Taddei & Frouin (2006) for the Reunion fringing reef (1160 - 2810 ind. m^{-2}), or obtained for non-perturbed tropical benthic communities. Other studies reported much higher maximum abundances: up to 4000 ind. m^{-2} in Hawai (McMarthy *et al.*, 2000; Dreyer *et al.*,

2005), but for macrofauna sorted on a 0.5 mm mesh; up to several thousands ind.m^{-2} were found in Chile and Australia (Lancellotti & Stotz, 2004; Cruz-Motta & Collins, 2004; Alongi, 1990). The mean biomasses recorded during the present study ranged from 107 (BR 1, 20 m) to 4711 mg AFDW m^{-2} (BR 4, 100 m). These values are in the same range as those reported by Makarov & Averin (1968) for the Mozambique Channel (0.7 - 3 g AFDW m^{-2}), by Alongi (1989) in the North-East Australia (0.9 - 3.4 g AFDW m^{-2}) or by McCarthy al. (2000) in Hawai (0.3 - 0.5 g. m^{-2}) for a shallow area (10 m). In comparison to temperate areas, tropical communities are generally lower in abundance and biomass (Maurer & Vargas, 1984; Warwick & Ruswahyuni, 1987; Alongi, 1989, 1990). In this sense, abundances and or biomasses are in a lower range of the values reported for the same depths by Gremare *et al.* (1998) for the Mediterranean coast (respectively, 3448 ind. m^{-2}; 4.13 g. m^{-2}), by Rosenberg *et al.* (2002) for the Gullmarfjord in Sweden (respectively, 3610 ind. m^{-2} ; 10 g. m^{-2}) or by Warwick *et al.* (2002) for the Tees Bay, England (5000 to 60000 ind. m^{-2}). Our results support this in undisturbed conditions, though high diversities can be locally found in specific habitats such coral reefs, seagrasses or mudflats (Alongi, 1990). The explanation why such Reunion island macrobenthic parameters (abundance, biomass) are not higher is complex and should be linked to different kinds of indicators of environmental conditions (biological response variables, exposure variables or watershed variables) (Dauer *et al.*, 2000). In this context, one hypothesis could be proposed in relation to the exposure variables of the water column. Our results should be interpreted according to the oligotrophic conditions of Reunion island coastal waters (mean annual value of 0.4 µMol.l^{-1} for water column concentration of total nitrogen; 0.2 µg.l^{-1} for chlorophyll a in 2001-2002) as reported by a recent monitoring study (Ecomar / Arvam, unpublished data). Such exposure variables are known to measure the occurrence or magnitude of physical, chemical or biological stress, and are commonly used as indicators of eutrophication for higher values.

Bathymetric spatial patterns of sediment and macrobenthos

The spatial analysis clearly shows the role of depth as one of the primary factor organizing the coastal macrofauna assemblage, which is often the case in other contexts (Snelgrove, 1999). It also integrates the effects of the hydrodynamism, the importance of sediment grain size and the amount of available organic materials in sediment, which act as primary driving forces structuring the macrofaunal communities (Snelgrove and Butman, 1994; Rosenberg, 1995; Karakassis & Eleftheriou, 1997; Ellingsen, 2002). Although the role of these variables is often reported for the Northern Hemisphere (Oug, 1998; Ellingsen, 2002), few studies exist to confirm this for the Southern hemisphere (Gray *et al.*, 1997). In Reunion, the strong hydrodynamic conditions together with the narrow insular shelf and steepness of the slope result in a marked sorting of sediments with a strong granulometric gradient, with mixed coarse and fine sand fractions in shallow sediments and a progressive increase of silts below 50 m depth. This pattern is fully coherent with the faunal distinction between shallow, intermediate and deep station groups resulting from the MDS. A similar pattern has been described in the Southern Californian coast with a shallow water assemblage (10-32 m), a mid-depth assemblage (32 to 115 m) and a deep-water assemblage (115 - 200 m) (Bergen *et al.*, 2001). At Reunion Island, changes in the macrobenthos composition relative to depth seem clearly related to changes in sediment granulometry. A Canonical Correspondences Analysis ordination (CCA) on BR-SA macrobenthos data shows that 16.3 % of faunistic variance is explained by the environmental variables (depth, medium sediment grain size, silt-clay fraction and total organic matter) (Bigot *et al.*, in prep). Similar values were described for other North hemisphere sites by Ysebaert & Herman (2002). The shallow assemblage is characterized by a pool of species including many carnivores and / or scavengers such as gastropods (*Hastula matheroniana*), crustaceans (*Ogyrides sp, Leptochelia sp*), many Corophiidae (*Siphonoecetes sp.*), nemerteans and few polychaetes (*Phyllodoce malmgreni, Sthenelais boa, Sigalion mathildae*).

These groups are often found in sandy habitats where strong hydrodynamic conditions prevail (Alongi, 1990; Frouin, 2000; Bergen *et al.*, 2001). Low species richness and abundance were found here in shallow areas subjected to constantly fluctuating environmental conditions or stress conditions, swell generated by high trade winds or hurricanes, important back-wash and sediment removal as described in other areas (Gray, 2002). Such hydrodynamic conditions generated poor food availability in sediments and did not favour the establishment of sustainable macrobenthic communities. From our results, and according to Taddei & Frouin (2005) for Reunion fringing reefs, we suggest that the resistance of such assemblages is an important factor in the global stability of the macrobenthos in these shallow and stressful ecosystems. In such context, species-poor systems were both more resistant and more resilient than species-rich systems (Pfisterer & Schmid, 2002). In the intermediate and deep station groups, macrofauna abundance and diversity were higher and generally dominated by surface deposit feeders, this also being consistent with previous observations by Bergen *et al.* (2001) for the Southern Californian coast. In Reunion Island, these deposit feeders were mainly polychaetes of the families of Spionidae (e.g *Prionospio steenstrupi, P. ehlersi, Laonice quadridentata*), Capitellidae (e.g *Notomastus* spp.), Ampharetidae (e.g *Samytha* sp.); sipunculans of the Aspidosiphonidae (*Aspidosiphon muëlleri*) and echinoderms (*Lovenia elongata*). Carnivorous species belonging to Pilargidae (*Ancistrosyllis parva*), Glyceridae (*Glycera prashadi, Goniada emerita*) and Eunicidae (e.g *Lumbrineris* spp, *Diopatra cuprea, Oenone fulgida*) were also well represented. Moreover, suspension feeders such as the free-living corals *Heterocyathus aequicostatus* and the cnidarians (*Antipathes* sp.) were characteristic of the intermediate depth group (50 to 100 m). In the deepest and muddy habitats (>140 m), the faunal diversity and biomass were the lowest, probably because of lower food resources or food availability (Rosenberg, 1995), which support smaller population sizes compared with the shallowest coastal areas (Gray, 2002).

This study has shown the occurrence of a classic pattern of species assemblages recorded

along the depth gradient off the coast of a tropical Indian Ocean island, exposed to strong hydrodynamic conditions. It also contributes to the knowledge of soft-bottom macrobenthos for south-western Indian Ocean islands and provides relevant informationfor further biodiversity studies and monitoring programmes in such open tropical environments.

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