

# Effects of anthropogenic disturbances of tropical soft-bottom benthic communities

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**ABSTRACT:** The benthic ecosystem of the lagoon surrounding Tahiti, the most populated island of French Polynesia, was investigated to assess the impacts of terrestrial runoff on these benthic communities. Five lagoonal zones based on population densities around the coast of Tahiti were identified, and within each zone a transect from the fringing reef to the barrier reef was sampled, a total of 18 stations. Only large macrofauna collected on a 2 mm sieve were considered in this study. Multivariate analysis using total biomass and environmental factors showed that the stations formed 3 main groups which were related to sediment characteristics, including percentage of silt, organic matter and phaeopigment levels. The distribution of the major feeding groups was related to the amounts of terrestrial inputs and distance from the shore. The stations on the barrier reef and those in zones adjacent to low population areas were not impacted by these terrestrial inputs. Deposit-feeding communities of capitellid polychaetes were dominant in the channel parts of the lagoon, which acted as decanting ponds. Chaetopterid polychaetes played an important role in recycling sediments of terrigenous origin in the fringing ecosystem. The patterns of diversity, density and biomass of the benthos around the lagoon revealed that some areas were impacted by moderate terrigenous inputs. It appears that the intermediate disturbance hypothesis explains the functioning of the parts of the benthic lagoonal ecosystem which are subjected to human impact. The organic enrichment by terrestrial inputs contrasts with food limitation that appears to occur in the non-disturbed areas. Despite high organic loads, the benthic communities present at the harbour station were not depauperate, as bioturbation by burrowing alpheid and callianassids prevented anoxic conditions from developing.

**KEY WORDS:** Lagoon · Macrobenthic communities · Polychaetes · Deposit-feeders · Terrestrial inputs · Tropical

## INTRODUCTION

The effects of anthropogenic inputs on coastal marine ecosystems can be quantified by studying benthic communities subjected to varying levels of input (Pearson & Rosenberg 1978). Soft-bottom macrobenthic communities have also been used to investigate levels of disturbance and human-mediated perturbations (Pearson & Rosenberg 1978, Keough & Quinn 1991, Ferraro & Cole 1992, Engle et al. 1994). Such studies are generally undertaken as part of environmental impact studies before major development is undertaken. Polychaetes, a dominant component of such communities, especially capitellids, have often been

used to assess the effects of organic enrichment (e.g. Hily 1985, Plantecun et al. 1993, Forbes et al. 1994, Heip 1995, Ellis & Schneider 1997).

In the Pacific, numerous studies have been undertaken in atoll lagoons of the Tuamotu Archipelago as well as in Moorea, French Polynesia (see Hutchings et al. 1994). Even though most of French Polynesia's population lives on Tahiti, especially in or around Papeete, which is also the location of most of the industry within the territory, its lagoonal environment is poorly known (Frouin 1996). With increasing development in the coastal zone of the island, where the majority of the population lives, impacts are certainly occurring on lagoonal communities, but the existing data were inadequate to quantify them prior to this study. It is known that in the tropics, increased rates of sedimentation and eutrophication related to terrestrially derived or-

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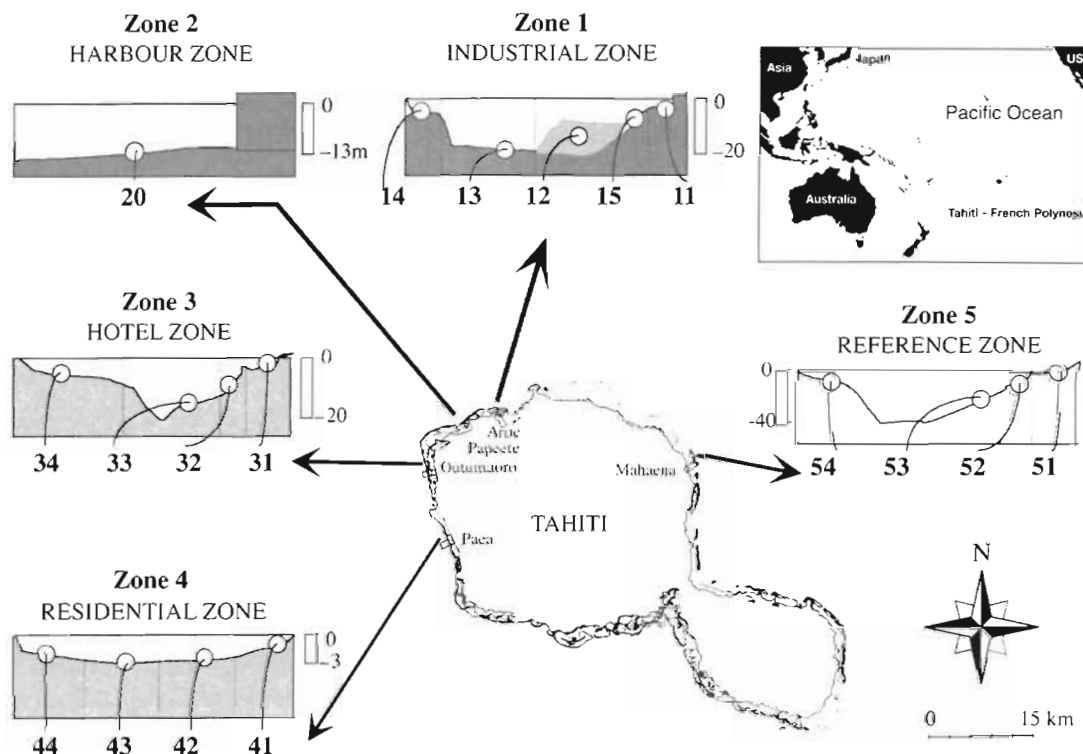


Fig. 1. Location of the 18 stations in the lagoon of Tahiti. The scale on the side of each zone shows approximate depth (m). The first digit of the station number relates to the zone, the second digit to reef morphology: 1 is for fringing reef (FR), 2 for fringing reef-channel transition (TR), 3 for channel (CH) and 4 for inner flat of the barrier reef (BR). Example: 53 is channel station in Zone 5. Characteristics of zones and stations are shown in Table 1 and described in 'Material and methods'

ganic enrichment are the most significant sources of anthropogenic impacts on coral reefs (Hatcher et al. 1989, Grigg & Dollar 1990).

The objective of this study was to investigate the soft-bottom macrobenthic communities of Tahiti lagoon and to assess the response of these communities to anthropogenic disturbances. It was assumed that these anthropogenic inputs were from the coastal zone and related to the densities of human populations around the island and associated industrial and tourist activities. As polychaetes dominated these benthic communities (Frouin & Hutchings in press), both in terms of number of species and individuals, they were primarily used to investigate the effects of increased rates of sedimentation and organic enrichment from terrestrial inputs on these communities.

## MATERIAL AND METHODS

**Study area.** Tahiti (17° S, 149° W) is the main high basaltic island in French Polynesia, south-eastern Pacific Ocean, with a population of about 200 000 inhabitants, most of whom live in and around Papeete, the capital. The majority of the wastewater is returned

to the lagoon via rivers and creeks without any treatment (Hutchings et al. 1994). Stream flow is related to rainfall, which is about 2 m annually on the coast and more than 10 m in the mountains, with the highest rainfall occurring during the wet season (December to March). About 30 floods occur annually,  $2/3$  of these occurring during the wet season (Lafforgue 1984).

Five zones (industrial, harbour, hotels, residential and reference) identified by the type of adjacent coastal development and population densities ran from the shore to the barrier reef. Four stations were sampled in each zone, fringing reef (FR), fringing reef-channel transition (TR), channel (CH) and in the inner flat of the barrier reef (BR). However, in Zone 2 (Papeete harbour) only 1 station of the CH type could be defined (Stn 20) and in Zone 1, 2 stations were sampled in the TR (Stns 12 and 15) because of the complex reef morphology, so that a total of 18 stations were sampled (Fig. 1, Table 1). The location and physical characteristics of each station are given in Table 1, together with a synopsis of the adjacent coastal development to each zone.

**Sampling procedure.** Macrofauna of soft-bottom sediments were sampled with large PVC corers (30 cm height, 11.5 cm wide) using SCUBA and sorted on a

Table 1. General features of the stations (FR, fringing reef; TR, fringing reef-channel transition; CH, channel; BR, inner flat of the barrier reef). Values in parentheses for organic load are standard error ( $n = 8$ ; except Stn 15 with  $n = 6$  and Stn 43 with  $n = 7$ )

Zone	Zone type (population)	Stn	Station type	Depth (m)	Mean sediment grain size (mm)	Organic load (%)
1	Industrial Zone (20–40 inhab. ha <sup>-1</sup> )	11	FR	<1	0.464	4.76 (0.37)
		15	TR	6	0.074	13.40 (0.70)
		12	TR	6	0.043	5.23 (0.18)
		13	CH	18	0.048	13.31 (0.32)
		14	BR	2.5	0.682	4.09 (0.11)
2	Harbour Zone (80–220 inhab. ha <sup>-1</sup> )	20	CH	13	0.032	12.65 (0.26)
3	Hotel Zone (40–80 inhab. ha <sup>-1</sup> )	31	FR	<1	0.414	5.56 (0.54)
		32	TR	9	0.081	4.44 (0.19)
		33	CH	13	0.090	4.26 (0.24)
		34	BR	2.5	0.860	3.62 (0.06)
4	Residential Zone (5–20 inhab. ha <sup>-1</sup> )	41	FR	<1	0.397	2.65 (0.07)
		42	TR	2.5	0.630	3.76 (0.13)
		43	CH	2.5	0.352	3.56 (0.15)
		44	BR	3	0.771	4.01 (0.14)
5	Reference Zone (<5 inhab. ha <sup>-1</sup> )	51	FR	<1	0.971	5.01 (0.42)
		52	TR	9	0.287	8.75 (0.70)
		53	CH	21	0.108	8.42 (0.55)
		54	BR	2.5	0.500	4.27 (0.21)

2 mm sieve. This mesh size was used to minimise sorting and identification time. Five 0.1 m<sup>2</sup> samples were collected quarterly (April, July, October 1994 and January 1995). Animals were preserved in 5% formaldehyde, then stored in 70% alcohol. They were identified to the lowest possible taxonomic level (to species level for molluscs; as sp. 1, sp. 2, etc. for polychaetes; generally at higher levels for other taxonomic groups) and counted. As the majority of the animals had to be preserved for collections and subsequent taxonomic studies, biomass was assessed from individual ash-free dry weight (AFDW); for each species, individuals selected from replicated random samples were weighed (within 10<sup>-4</sup> g). AFDW refers to the difference between dry weight (48 h, 60°C) and ash weight (3 h, 550°C). Taxa were classified into feeding types according to Fauchald & Jumars (1979) for polychaetes and Long & Poiner (1994) for the other phyla.

The following sedimentary factors were measured: grain size, silt and clay fraction, organic load, chlorophyll and phaeopigment content, oxydo-reduction (redox) potential. The silt and clay fraction is referred to as silt in this paper. Sediment samples (3 × 0.001 m<sup>2</sup>) were collected quarterly from May 1993 to January 1995. The upper centimetre of cores was analysed. Silt fraction was expressed as dry weight after wet sieving using a 63 µm sieve. Chlorophyll pigments indicated densities of live microphytobenthos, and levels of phaeopigment indicated the amount of decaying vege-

tal material present in the sediments. Chlorophyll and phaeopigment analyses were based on Holm-Hansen et al. (1965) and Lørenzen (1967). Redox potential measurements with an Eh platinum probe were made on the boat immediately after coring (5.5 cm diameter core and repeated 3 times). Readings were performed on each core after 45 s stabilisation time. Total grain size data were determined from 1 core (100 g) collected at each station in November 1993. Sediment mean size was calculated using the formula

$$T_m = (\phi_{16} + \phi_{50} + \phi_{84})/3$$

from Folk & Ward (1957), conversion following Krumbein's formula (1936):  $x_\phi = -\log(x_{mm})/\log(2)$ .

An estimate of the amount of terrigenous sediments carried out into the lagoon by coastal runoff was calculated from the basaltic content of lagoonal sediments. All stations in

Zones 3, 4 and 5 and 2 stations in Zone 1 were sampled (total of 14 stations). Three sediment samples (each 0.001 m<sup>2</sup>) were collected in January 1995, rinsed and washed through a 63 µm mesh sieve, dried and weighed. This sediment was then added to 5% HCl, and, after 12 h, the sediment was rinsed and washed through a 63 µm mesh sieve, dried and weighed. The fraction of the sediment which dissolved in the acid was regarded as the carbonate fraction and the remaining undissolved fraction as basalt and of terrigenous origins (Hily & Frouin 1998). The island of Tahiti is composed mainly of basaltic material. The top centimetre of sediment was discarded, and sediment from 2 to 5 cm depth was analysed as 1 sample, in order to take into account the interannual temporal variation.

**Data analysis.** Two-way ANOVAs (station × date) followed by Newman-Keuls multiple range test ( $\alpha = 0.05$ ) were performed on environmental variables (log transformed) and macrofauna density —  $\log(x + 1)$  — to assess significant seasonal effects (Frouin 1996). Data were transformed because of the presence of numerous null values.

Community structure was studied using ordinations performed with non-metric multi-dimensional scaling (MDS). Groups identified from group averaging cluster analysis were superimposed on the ordination plot for better segregation (Field et al. 1982, Clarke & Green 1988). MDS analyses were performed with the

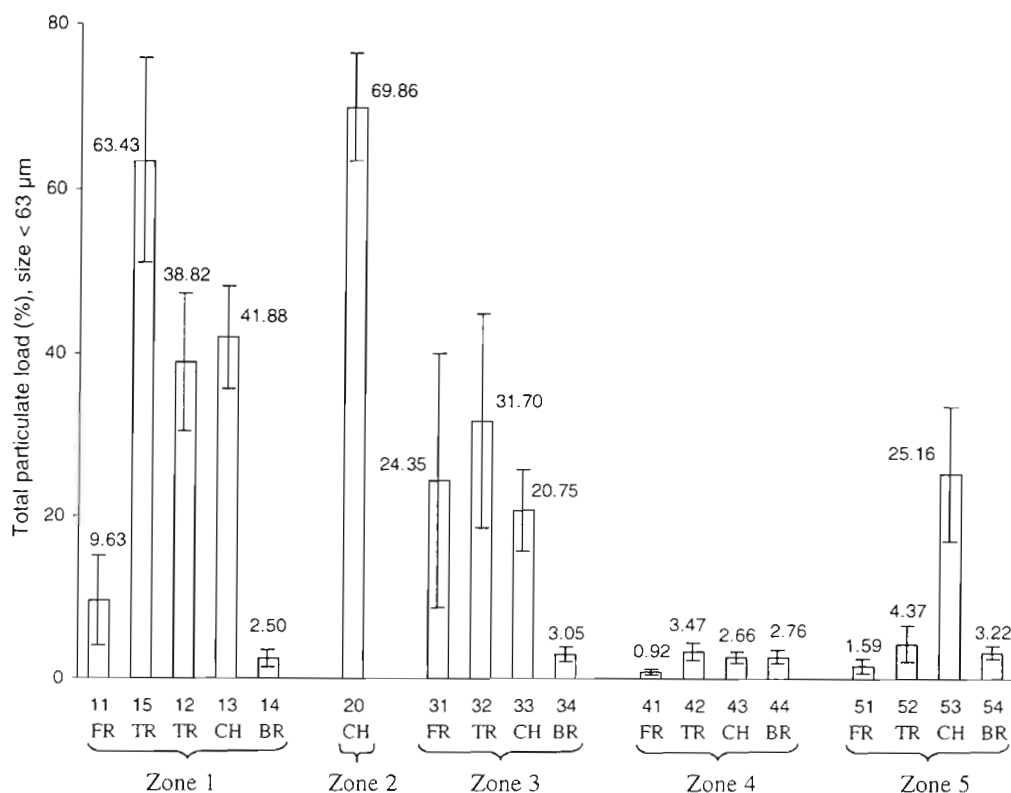


Fig. 2. Silt and clay load (particle size < 0.063 mm) in sediments. Vertical bars are standard error ( $n = 8$ ). Stations on x-axis. Highly significant differences in mean loads were highlighted with ANOVA test ( $p < 0.001$ ). Newman-Keuls tests showed several homogeneous groups of stations for silt and clay content. From the lowest to the highest load these are Stns 41, 14, 43, 51, 44, 34, 54, 42, 52 / 11 / 33, 31, 53 / 32 / 12, 13 / 15 / 20

same configuration as in cluster analyses with respect to similarity index (Bray-Curtis) and fourth root transformation. Analyses of similarity (ANOSIM, Clarke & Green 1988) were used to test differences between zones and between types of stations: the test statistic  $R$  indicates some degree of discrimination between sites. When  $R$  significantly differs from 0 and tends towards 1, intra-site similarity is higher than inter-site similarity.

Relationships between community biomass data and environmental data were investigated with a method used by Karakassis & Eleftheriou (1997) and first described by Kruskal & Wish (1978). The method consists of performing a multiple linear regression for each environmental variable, e.g. mean sediment size, redox potential, depth, phaeopigments, chlorophyll, silt and organic matter. Each environmental variable was used as the dependent variable and the MDS co-ordinates as the independent variables. Regression weights were used to plot the direction of the environmental factor in the 2-dimensional MDS plot. The adjusted multiple correlation coefficients indicated the amount of variance explained by each variable.

## RESULTS

### Seasonality

Two-way ANOVAs on phaeopigments, total organic load and silt content revealed no significant seasonal effects ( $p > 0.05$ ), whereas chlorophyll load was higher in November 1994 ( $p = 0.03$ ) than at any other time. Macrofaunal density was significantly lower in October 1994 ( $p < 0.001$ ) than at other times, but biomass showed no seasonal effect ( $p = 0.13$ ). However, for all these variables, the effect of station was always more important than time ( $F_{\text{spatial}} > F_{\text{temporal}}$ ). As low temporal variability was exhibited, the results from the quarterly samples were summed and all subsequent analyses were carried out on the total mean value of macrofauna (Zmarzly et al. 1994).

### Sediments

Mean grain size for each region of the lagoon was homogeneous, with coarse sand at BR stations, medium sand at FR stations and very fine sand to silt at TR and

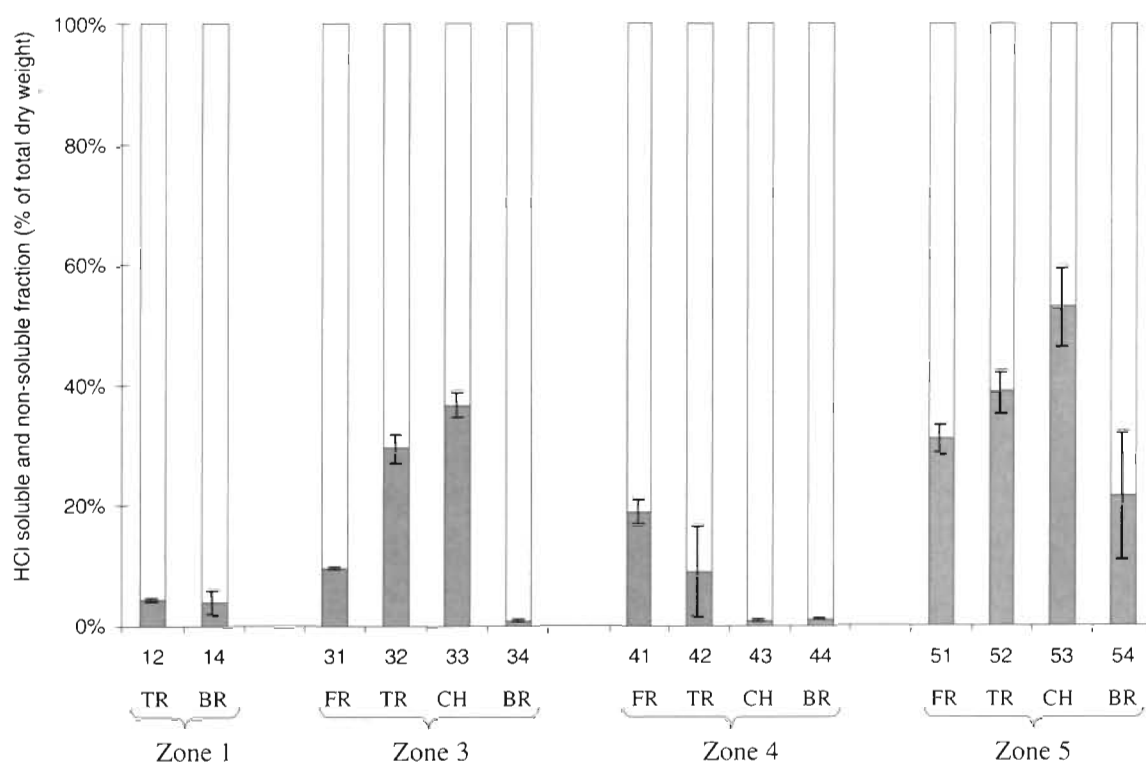


Fig. 3. Acid-soluble and non-soluble fraction in sub-surface sediments (2 to 5 cm depth, homogenised layer) as indicators of terrigenous inputs in the lagoon. Vertical bars are standard error ( $n = 3$ ). Stations on x-axis

CH stations (Table 1). The silt fraction varied significantly between stations (ANOVA,  $p < 0.001$ ), with 7 groups highlighted with the Newman-Keuls multiple range test (Fig. 2). The highest loads were recorded in the harbour (Stn 20) with  $69.9\%$  and Stn 15 with  $63.3\%$ , and the lowest loads at stations in the Residential and Reference Zones (except Stn 53) and at all BR stations (Fig. 2). All these stations with sediments containing less than  $4.5\%$  silt formed a group using the Newman-Keuls test.

The percentage of non-soluble material present in the sediment after washing in acid was used as an indicator of terrigenous inputs of basaltic origin (Fig. 3). The Residential Zone (Zone 4) showed that the percentage of terrestrially derived sediments declined from the fringing reef to the outer barrier, i.e. with increasing distance from shore. Zones 3 and 5 showed a reverse pattern with the percentage of terrestrially derived sediment increasing from the coast to the barrier reef, except for the inner barrier reef flat stations (Stns 34 and 54). Stations in the Industrial Zone (Stns 12 and 14), where runoff was limited, had low levels.

Considering total organic load of sediment, a Kruskal-Wallis test ( $p < 0.05$ ) revealed 3 groups of stations (Fig. 4). Highest organic loads were present at the TR and CH stations in the Industrial and Harbour Zones

(Stns 13, 15, 20 respectively), with up to  $13.46 \pm 0.83\%$ . All other stations had much lower levels ( $4.3 \pm 0.1\%$ ,  $n = 13$ ), except Stns 52 and 53, both in the Reference Zone, which had intermediate levels (mean  $8.6\%$ ).

Chlorophyll and phaeopigments showed heterogeneous loads (ANOVA,  $p < 0.001$ ), and no informative groupings were formed using the Newman-Keuls test. The mean value for all stations was  $1.92 \pm 0.14 \mu\text{g g}^{-1}$  ( $n = 18$ ) for chlorophyll and  $2.68 \pm 0.34 \mu\text{g g}^{-1}$  for phaeopigments. The lowest chlorophyll/phaeopigment ratios were recorded at CH stations, except for Stn 43 in the Residential Zone where the lagoon is shallow (2.5 m) and the sediment is white sand (Fig. 5). Stns 33 and 53, which were covered respectively with algae *Halimeda* spp. and seagrass *Halophila decipiens*, were not the stations with the maximum chlorophyll load in sediments. The harbour station (Stn 20) showed the highest phaeopigment load, and the lowest chlorophyll content.

Sediment cores collected for redox potential measurements did not show clear discontinuity in sediment colour. Only the harbour (Stn 20) showed a significant difference in depth for  $+100$  and  $+200$  mV potentials (ANOVA,  $p < 0.001$ ), with the redox potential higher than  $+100$  mV to depths of 20 cm.



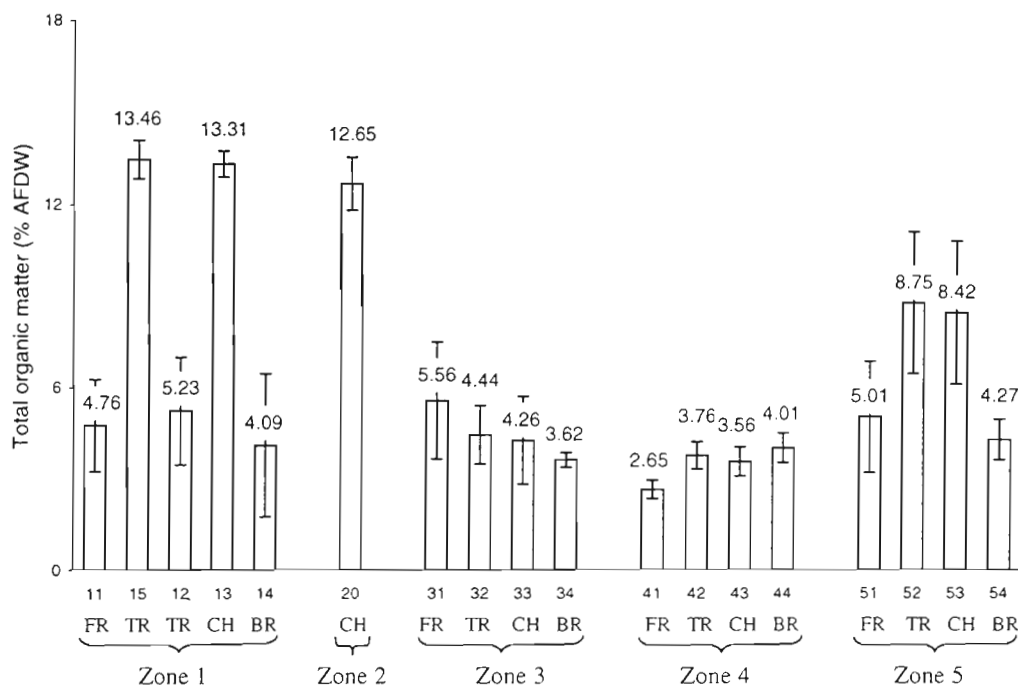


Fig. 4. Total organic content (%) in sediments. Stations on x-axis. Three homogeneous groups of stations (Kruskal-Wallis,  $p < 0.05$ ) present. Stns 13, 15 and 20 for the highest organic load; Stns 52 and 53 for intermediate values; all remaining stations for low organic content. AFDW: ash-free dry weight

### Macrofauna biomass and taxonomic structure

A total of 315 taxa were collected during the study, of which 100 were polychaetes. The mean macrofauna biomass was  $1.54 \text{ g m}^{-2} \pm 0.29$  ( $n = 18$ ), and the mean density was  $222 \pm 57 \text{ ind. m}^{-2}$  ( $n = 18$ ). SAB (for species richness, abundance and biomass) curves showed that highest values occurred in the Hotel Zone (Zone 3) (Fig. 6), a zone with intermediate levels of terrigenous input (Fig. 3).

MDS ordination based on annual biomass showed 3 groups of stations and 3 isolated stations (Fig. 7). Group I included TR and CH stations from the Industrial Zone (Stns 15 and 13) and the harbour station (Stn 20), and was characterised by a dominance of

polychaetes (Table 2). The dominant species were the capitellid *Dasybranchus* sp. 1 (28.1 to 72.3% of the total biomass), and callianassid and alpheid decapods (5.3 to 24.2%).

Group III included all BR stations and stations from the Residential Zone, except Stn 41; it was dominated by bivalves and gastropods (79.0% of the total biomass), including the bivalves *Tellina* spp. and *Terebra* spp. and the gastropods *Conus* spp. and *Rhinoclavis diadema*. Polychaetes accounted for only 10.2% of total biomass.

Group II showed an intermediate pattern, with Stns 11 and 12 (FR and TR for Industrial Zone), 31 to 33 (Hotel Zone except BR station) and 53 (Reference CH station). Polychaetes and gastropods dominated the biomass (Table 2), with bivalves also well represented (22.0% of the total biomass).

Stns 41, 51 and 52 were not grouped and showed unique macrofaunal assemblages. Stn 41 was dominated by chaetopterid polychaetes *Spiochaetopterus* sp. 1 and *Phyllochaetopterus* sp. 1, Stn 51 by the decapod *Hippa* cf. *pacifica*, and Stn 52 by molluscs (84.9%), especially *Venus toreuma*, *Tellina rhomboides*, *Nassarius rehderi*, *Terebra affinis* and *Nassarius* spp. (Table 3).

Table 2. Contribution of the main taxonomic groups to the total biomass. Each group of homogeneous stations was defined from the data analysis. Values are expressed as percent of the total biomass (AFDW). Group I: Stns 13, 15, 20; Group II: Stns 11, 12, 31–33, 53; Group III: Stns 14, 34, 42–44, 54

Taxon	Group I	Group II	Group III	Stn 41	Stn 51	Stn 52
Polychaeta	50.8	27.6	10.2	58.4	13.3	3.9
Gastropoda	6.5	28.3	39.4	14.2	20.8	47.4
Bivalvia	8.0	22.0	29.5	4.3	5.3	37.5
Decapoda	18.9	13.3	7.0	7.1	57.0	8.7
Sipuncula	9.9	5.7	8.3	0.0	0.0	0.3
Others	6.0	3.1	5.6	16.0	3.6	2.2

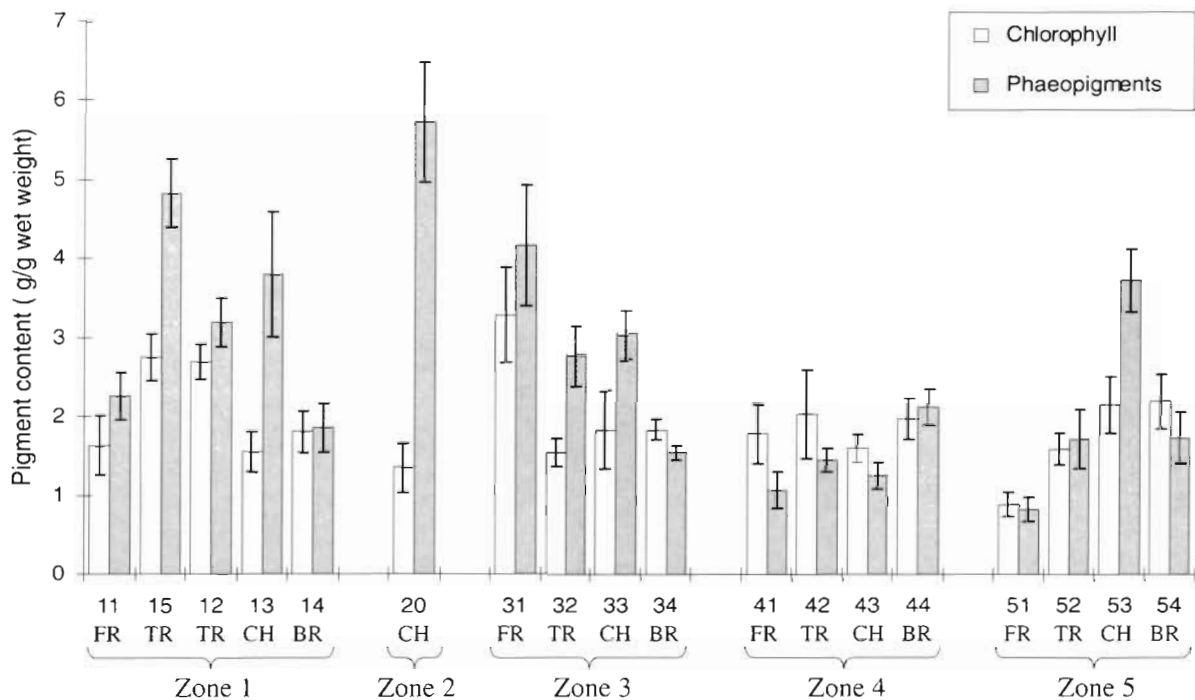


Fig. 5. Pigment load in sediments. Vertical bars represent standard error ( $n = 8$ ). Stations on x-axis

Differences between zones and between types of stations were highlighted by ANOSIM tests on the total density of macrofauna present. Variability between zones was higher than variability between types of stations: respectively  $R = 0.287$ ,  $p = 0.008$  and  $R = 0.132$ ,  $p = 0.086$ . The same trend was observed for biomass:  $R = 0.254$ ,  $p = 0.014$  between zones and  $R = 0.201$ ,  $p = 0.024$  between stations. The highest dissimilarity was found between Zone 1 and Zone 4, indicating that the zones identified were more important in determining benthic community patterns than the type of station sampled across the lagoon.

### Trophic structure

MDS ordination highlighted the trophic structure for the total macrofauna (Fig. 8A). The low spatial variability of feeding types revealed few distinct groups of stations (87 to 89 % similarity level). The first group (Group A1) included the 3 stations from the Harbour and Industrial Zones, also defined as Group I in Fig. 7. In this group, the dominant trophic type was deposit-feeding. The non-selective deposit-feeder *Dasybranchus* sp. 1 dominated the group, particularly at Stns 15 and 20, which were closest on the MDS plot with a similarity of about 92 % (Fig. 8A). The second group (Group A2) included the rest of the stations, except Stns 51 to 53 from the Reference Zone (Zone 5). Within that group carni-

vores were dominant, although suspension-feeders characterised FR stations and selective deposit-feeders were present at Stns 14, 42 and 43. Stns 51, 52 and 53 in the MDS plot indicated distinctive trophic structure, all consisting of a range of feeding types. Stn 51 included 73.4 % carnivores, 19.6 % selective deposit-feeders, 4.1 % herbivores and 2.7 % suspension-feeders. Stn 52 included 53.5 % carnivores, 26.7 % selective deposit-feeders and 17.6 % suspension-feeders. Stn 53 included 38.6 % selective deposit-feeders, carnivores and suspension-feeders being represented by 26.9 and 31.3 % respectively, and herbivores and non-selective deposit-feeders representing less than 2.5 % of total biomass.

Using biomass of polychaete trophic groups, the MDS plot (Fig. 8B) revealed a greater number of cohesive groups of stations. The FR stations (Stns 11, 31, 41 and 51) showed the highest variability and were dominated by suspension-feeding chaetopterid polychaetes. The strongest similarity was between Stns 11 and 31 in the Industrial and Hotel Zones (Group B1). However Stn 51 was dominated by carnivores (including *Glycera* spp., *Pisione* sp. 1, amphinomids, arabelids). Stn 51 resembled Stn 52 (Group B4) in also having non-selective deposit-feeding species (dominated by capitellids and cirratulids). The CH stations (Stns 13, 20 and 33) and 1 TR station (Stn 15), formed a distinct group (Group B2) dominated by non-selective deposit-feeders especially capitellid species *Dasybranchus* sp. 1. The largest group of stations (B3) included

Table 3. Distribution of taxa at 18 stations, according to biomass ranking. Only taxa accounting for 2% of total biomass or more are presented (SF, suspension feeders; CAR, carnivores; SDF, selective deposit-feeders; NSDF, non-selective deposit-feeders; HER, herbivores; —, indeterminate)

Taxon	Total biomass (%)	Cum. (%)	Trophic type	Taxon	Total biomass (%)	Cum. (%)	Trophic type
<b>Stn 11</b>				<i>Phascolosoma</i> sp. 5	2.9	81.1	SDF
<i>Phyllochaetopterus</i> sp. 1	37.3	37.3	SF	<i>Glycera</i> cf. <i>lancadivae</i>	2.4	83.5	CAR
<i>Conus pulicarius</i>	8.4	45.7	CAR	<i>Alpheus</i> sp. 1	2.2	85.7	SDF
<i>Alys parallelus</i>	5.6	51.3	CAR	<b>Stn 31</b>			
<i>Paraspidosiphon</i> sp. 1	5.6	56.8	SDF	<i>Mesochaetopterus</i> sp. 2	32.6	32.6	SF
<i>Conus eburneus</i>	4.5	61.3	CAR	<i>Diopatra</i> sp. 1	8.5	41.2	CAR
<i>Dasybranchus</i> sp. 1	3.8	65.1	NSDF	<i>Dasybranchus</i> sp. 1	7.7	48.8	NSDF
<i>Phascolosoma</i> sp. 5	3.6	68.7	SDF	<i>Conus coronatus</i>	6.9	55.7	CAR
<i>Arcopagia robusta</i>	2.6	71.3	SDF	<i>Thalamita</i> sp. 1	4.2	59.9	CAR
<b>Stn 12</b>				Actinians	4.0	64.0	SF
<i>Conus eburneus</i>	27.1	27.1	CAR	<i>Phyllochaetopterus</i> sp. 1	3.5	67.4	SF
<i>Venus toreuma</i>	11.1	38.1	SF	<i>Macrophthalmus</i> sp. 1	3.0	70.4	SDF
<i>Corculum fragum</i>	4.4	42.6	SF	<i>Phyllochaetopterus</i> sp. 2	3.0	73.4	SF
<i>Phascolosoma</i> sp. 5	3.8	46.3	SDF	<b>Stn 32</b>			
<i>Nassarius tabescens</i>	3.7	50.1	CAR	<i>Conus eburneus</i>	11.0	11.0	CAR
<i>Clavus pusilla</i>	3.5	53.6	CAR	<i>Dasybranchus</i> sp. 1	10.8	21.8	NSDF
<i>Arcopagia robusta</i>	3.0	56.6	SDF	<i>Tellina tithonia</i>	6.9	28.7	SDF
<i>Strombus gibberulus</i>	2.8	59.5	SDF	<i>Cancilla filaris</i>	6.2	34.9	CAR
<i>Dasybranchus</i> sp. 1	2.5	62.0	NSDF	<i>Thalamita</i> sp. 3	4.9	39.8	CAR
<i>Terebra undulata</i>	2.5	64.4	CAR	<i>Venus toreuma</i>	4.4	44.2	SF
<i>Cancilla filaris</i>	2.3	66.7	CAR	<i>Arcopagia robusta</i>	4.2	48.4	SDF
<i>Glycera</i> cf. <i>lancadivae</i>	2.2	68.9	CAR	<i>Macrophthalmus</i> sp. 1	3.7	52.1	SDF
<b>Stn 13</b>				<i>Anodonta edentula</i>	3.2	55.3	SDF
<i>Dasybranchus</i> sp. 1	28.1	28.1	NSDF	<i>Callianassa</i> sp. 3	3.1	58.4	SDF
<i>Paraspidosiphon</i> sp. 1	20.1	48.2	SDF	<i>Glycera</i> cf. <i>lancadivae</i>	3.0	61.5	CAR
<i>Anodonta edentula</i>	8.0	56.2	SDF	Actinians	3.0	64.5	SF
<i>Venus toreuma</i>	4.9	61.2	SF	<i>Paraspidosiphon</i> sp. 2	2.7	67.2	SDF
<i>Syndesmia seurati</i>	3.6	64.7	SDF	<i>Strombus mutabilis</i>	2.3	69.5	SDF
<i>Terebra undulata</i>	2.5	67.2	CAR	<i>Callianassa</i> indet.	2.1	71.5	SDF
<i>Glycera</i> cf. <i>lancadivae</i>	2.5	69.7	CAR	<b>Stn 33</b>			
<b>Stn 14</b>				<i>Dasybranchus</i> sp. 1	19.6	19.6	NSDF
<i>Rhinoclavis diadema</i>	17.8	17.8	SDF	<i>Cerithium rostratum</i>	9.7	29.3	SDF
<i>Phascolosoma</i> sp. 3	16.3	34.1	SDF	<i>Thalamita</i> sp. 1	7.2	36.5	CAR
<i>Phascolosoma</i> sp. 8	16.1	50.3	SDF	<i>Glycera</i> cf. <i>lancadivae</i>	4.3	40.8	CAR
<i>Conus tessulatus</i>	7.0	57.3	CAR	<i>Anodonta edentula</i>	3.7	44.5	SDF
<i>Terebra affinis</i>	5.2	62.5	CAR	<i>Alys parallelus</i>	3.4	47.9	CAR
<i>Conus vitulinus</i>	3.5	66.1	CAR	<i>Portunus</i> cf. <i>longispinosus</i>	3.2	51.1	CAR
<i>Imbricaria olivaeformis</i>	3.1	69.2	CAR	<i>Natica gualteriana</i>	2.3	53.4	CAR
<i>Eurythoe</i> sp. 1	2.3	71.5	CAR	<i>Strombus mutabilis</i>	2.3	55.6	SDF
<i>Rhinoclavis sinensis</i>	2.1	73.6	SDF	<i>Thalamita</i> sp. 3	2.0	57.7	CAR
<b>Stn 15</b>				<b>Stn 34</b>			
<i>Dasybranchus</i> sp. 1	36.2	36.2	NSDF	<i>Terebra affinis</i>	10.2	10.2	CAR
<i>Brachyura</i> indet.	8.4	44.5	CAR	<i>Tellina rhomboides</i>	9.5	19.7	SDF
<i>Callianassa</i> sp. 1	6.7	51.3	SDF	<i>Chiridota</i> sp. 1	6.3	26.1	NSDF
<i>Alpheus</i> sp. 1	6.4	57.7	SDF	<i>Conus eburneus</i>	6.2	32.3	CAR
<i>Blenniidae</i> indet.	6.3	64.0	CAR	<i>Eurythoe</i> sp. 1	6.0	38.2	CAR
<i>Callianassa</i> sp. 2	5.7	69.7	SDF	<i>Spatangidae</i> indet.	5.9	44.1	NSDF
<i>Nassarius tabescens</i>	3.2	72.8	CAR	<i>Nassarius graniferus</i>	4.6	48.7	CAR
<i>Terebra longiscata</i>	2.7	75.5	CAR	<i>Tellina oahuana</i>	3.9	52.6	SDF
<i>Callianassa</i> indet.	2.4	78.0	SDF	<i>Vexillum cadaverosum</i>	3.9	56.5	CAR
<i>Glycera</i> cf. <i>lancadivae</i>	2.3	80.3	CAR	<i>Aspidosiphon</i> sp. 1	3.9	60.4	SDF
<i>Paraspidosiphon</i> sp. 1	2.1	82.4	SDF	<i>Glycera</i> cf. <i>lancadivae</i>	3.2	63.6	CAR
<b>Stn 20</b>				<i>Callianassa</i> sp. 1	2.9	66.5	SDF
<i>Dasybranchus</i> sp. 1	72.3	72.3	NSDF	<i>Cerithium salebrosum</i>	2.5	69.1	SDF
<i>Blenniidae</i> indet.	5.9	78.2	CAR	<i>Phyllochaetopterus</i> sp. 1	2.1	71.2	SF
				<i>Portunus</i> cf. <i>longispinosus</i>	2.1	73.3	CAR



all BR stations (Stns 14, 34, 44, 54), stations of the Residential Zone (Stns 42, 43 and 44) and Stns 12, 32 and 53. Carnivores and non-selective deposit-feeders were the dominant trophic types present at these stations. Non-selective deposit-feeders such as *Dasybranchus* spp. were also dominant species at TR stations (Stns

12, 32, 42 and 52), whereas carnivores and selective deposit-feeding amphinomids (*Eurythoe* sp. 1 and *Linopherus* sp. 1) dominated BR stations (Stns 14, 34, 44 and 54). *Phyllochaetopterus* spp. and *Mesochaetopterus* spp. (suspension-feeding chaetopterids) were also present (Fig. 8B).

Table 3. (continued)

Taxon	Total biomass (%)	Cum. (%)	Trophic type	Taxon	Total biomass (%)	Cum. (%)	Trophic type
<b>Stn 41</b>				<b>Stn 51</b>			
<i>Spiochaetopterus</i> sp. 1	21.8	21.8	SF	<i>Hippa</i> cf. <i>pacifica</i>	46.1	46.1	CAR
<i>Phyllochaetopterus</i> sp. 1	17.6	39.4	SF	<i>Rissoina ambigua</i>	7.6	53.7	SDF
Enteropneusta indet.	9.9	49.3	NSDF	<i>Rhinoclavis sinensis</i>	5.6	59.3	SDF
Patellidae indet.	9.5	58.8	HER	<i>Codakia divergens</i>	5.3	64.6	SDF
Actinians	5.2	64.0	SF	<i>Leptodius</i> sp. 1	4.1	68.7	HER
<i>Tellina rhomboides</i>	3.5	67.5	SDF	Brachyura indet.	4.1	72.8	—
<i>Phyllochaetopterus</i> sp. 2	3.4	70.9	SF	<i>Pyramidella sulcata</i>	3.8	76.6	CAR
<i>Phyllochaetopterus</i> indet.	3.4	74.2	SF	<i>Rissoina</i>	3.8	80.4	SDF
<i>Calappa hepatica</i>	2.5	76.8	CAR	Chaetopteridae indet.	2.7	83.1	SF
<i>Huenia</i> sp. 1	2.5	79.3	HER	Gobiidae indet.	2.6	85.6	CAR
<i>Otopleura mitralis</i>	2.4	81.7	CAR	<b>Stn 52</b>			
<i>Nerita morio</i>	2.4	84.1	HER	<i>Venus toreuma</i>	17.3	17.3	SF
<i>Linopherus</i> sp. 1	2.3	86.4	SDF	<i>Tellina rhomboides</i>	13.0	30.4	SDF
<b>Stn 42</b>				<i>Nassarius rehderi</i>	10.5	40.9	CAR
<i>Tellina oahuana</i>	26.4	26.4	SDF	<i>Terebra affinis</i>	6.7	47.6	CAR
<i>Tellina donaciformis</i>	11.7	38.1	SDF	<i>Nassarius graniferus</i>	5.3	52.8	CAR
<i>Tellina crebrimaculata</i>	10.8	48.9	SDF	<i>Nassarius tabescens</i>	5.3	58.1	CAR
<i>Tellina rhomboides</i>	7.9	56.8	SDF	<i>Albunea speciosa</i>	5.2	63.3	CAR
<i>Arcopagia robusta</i>	7.2	64.0	SDF	<i>Terebra langfordi</i>	4.4	67.8	CAR
<i>Conus eburneus</i>	5.7	69.7	CAR	<i>Cancilla filaris</i>	3.7	71.5	CAR
<i>Aspidosiphon</i> sp. 1	2.8	72.5	SDF	<i>Tellina donaciformis</i>	3.1	74.6	SDF
<i>Portunus</i> cf. <i>longispinosus</i>	2.8	75.4	CAR	<i>Nassarius splendidulus</i>	2.6	77.2	CAR
<i>Terebra affinis</i>	2.2	77.6	CAR	<i>Philyra</i> sp. 1	2.4	79.6	HER
Enteropneusta indet.	2.2	79.8	NSDF	<i>Atys cylindricus</i>	2.2	81.8	CAR
<b>Stn 43</b>				<i>Nassarius</i> indet.	2.2	84.0	CAR
<i>Tellina oahuana</i>	13.6	13.6	SDF	<i>Terebra</i> indet.	2.2	86.3	CAR
<i>Conus eburneus</i>	11.8	25.4	CAR	Strombidae indet.	2.2	88.5	SDF
<i>Conus pulicarius</i>	11.8	37.1	CAR	<b>Stn 53</b>			
<i>Tellina rhomboides</i>	7.2	44.3	SDF	<i>Corbula tahitensis</i>	18.7	18.7	SDF
<i>Arcopagia robusta</i>	6.8	51.1	SDF	<i>Chlamys elegantissima</i>	15.7	34.4	SF
<i>Terebra affinis</i>	6.0	57.1	CAR	<i>Venus toreuma</i>	15.0	49.4	SF
<i>Corculum fragum</i>	5.1	62.3	SF	<i>Anodontia edentula</i>	6.7	56.0	SDF
<i>Tellina crebrimaculata</i>	3.4	65.7	SDF	<i>Terebra longiscata</i>	4.2	60.3	CAR
<i>Strombus gibberulus</i>	3.1	68.7	SDF	<i>Philyra</i> sp. 1	3.0	63.2	HER
<i>Aspidosiphon</i> sp. 1	2.9	71.7	SDF	<i>Natica gualteriana</i>	2.6	65.8	CAR
<i>Dasybranchus</i> sp. 1	2.2	73.8	NSDF	<i>Nassarius coronatum</i>	2.0	67.8	CAR
<i>Rhinoclavis diadema</i>	2.1	75.9	SDF	<b>Stn 54</b>			
<b>Stn 44</b>				<i>Tellina oahuana</i>	15.4	15.4	SDF
<i>Terebra affinis</i>	14.7	14.7	SDF	<i>Terebra affinis</i>	12.2	27.5	CAR
<i>Tellina oahuana</i>	11.9	26.5	SDF	<i>Conus pulicarius</i>	11.2	38.7	CAR
<i>Cerithium salebrosum</i>	10.2	36.7	SDF	<i>Tellina rhomboides</i>	10.3	49.0	SDF
<i>Tellina rhomboides</i>	9.1	45.8	SDF	<i>Nassarius graniferus</i>	9.1	58.2	CAR
<i>Conus striatus</i>	6.1	51.9	CAR	<i>Dasybranchus</i> sp. 1	6.2	64.4	NSDF
<i>Terebra maculata</i>	5.0	56.9	CAR	<i>Conus tessulatus</i>	5.6	70.0	CAR
<i>Portunus</i> cf. <i>longispinosus</i>	4.8	61.7	CAR	Actinians	2.5	72.4	SF
<i>Tellina crebrimaculata</i>	3.5	65.2	SDF	<i>Vexillum cadaverosum</i>	2.3	74.7	CAR
<i>Cerithium nesioticum</i>	3.1	68.3	SDF				
<i>Rhinoclavis diadema</i>	2.3	70.6	SDF				

### Environmental effects

All environmental variables were significantly correlated with grain size (Tm), except for chlorophyll content (Chl). Silt, total organic matter (OM) and phaeopigment (Phaeo) variables showed the most significant

correlations (Table 4). The use of multiple regression analysis to show environmental effects was then possible as this method is best fitted for correlated factors (Karakassis & Eleftheriou 1997). Using this analysis showed that the amount of chlorophyll present in the sediment was not a significant factor in explaining macrofaunal distributional patterns ( $p = 0.53$ ) (Table 5), and was therefore not included in Fig. 7. Redox potential at 5 cm depth in sediments (Eh5) also had little effect on the community structure. The other environmental variables, grain size (Tm and Silt), Phaeo and OM best explained the variance exhibited by the macrofauna data (Fig. 7). Silt and Phaeo were responsible for the gradient in communities from Group III to Group I. Stations of Group III showed high grain size and no silt or phaeopigment enrichment, whereas in the opposite direction of that gradient Group I homogeneity was related to highest loads in Silt and Phaeo, and OM to a lesser extent.

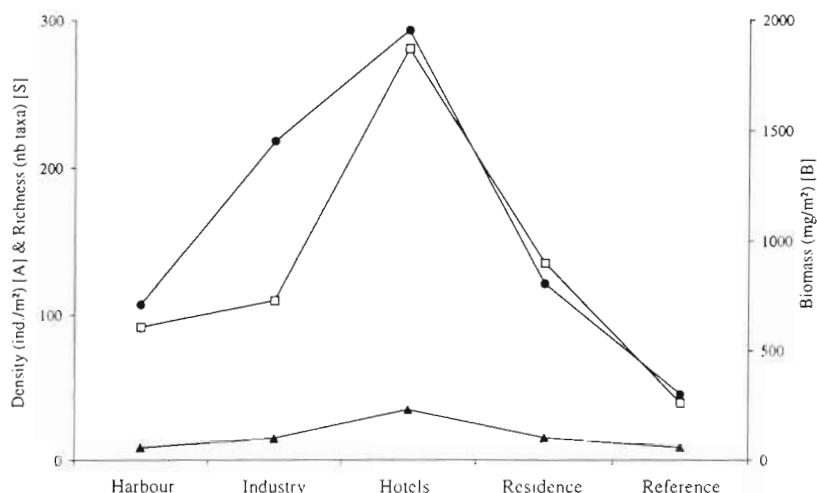


Fig. 6. SAB curves of total macrofauna data. x-axis shows the 5 zones, sorted by particulate load in sediment (organic matter and silt). Plots represent median values for all the stations of the zone, except BR stations. ( $\blacktriangle$ : species richness;  $\square$ : density;  $\bullet$ : biomass)

### DISCUSSION

Shallow coastal ecosystems in the tropics depend on nutrients derived from terrigenous inputs (Chardy & Clavier 1988, Alongi 1990). In Tahiti, coastal, and river runoff is responsible for transporting large amounts of terrestrially derived sediments into the lagoon. Lafforgue (1994) estimated that up to 61 t of particulate matter may be transported by a small river into the lagoon of Tahiti during a cyclone lasting 4 d. Using estimates of the basaltic content of lagoonal sediments, as an indication of terrestrially derived particles, it is clear that they can be transported to the barrier reef sites, even when a large channel is present. This is clearly shown in the Reference Zone (Zone 5). However such terrestrially derived particles mostly settled in the channel part, with minimum sedimentation on fringing reefs and inner flats of the barrier reef. The high levels of silt and associated high organic loads, as a result of

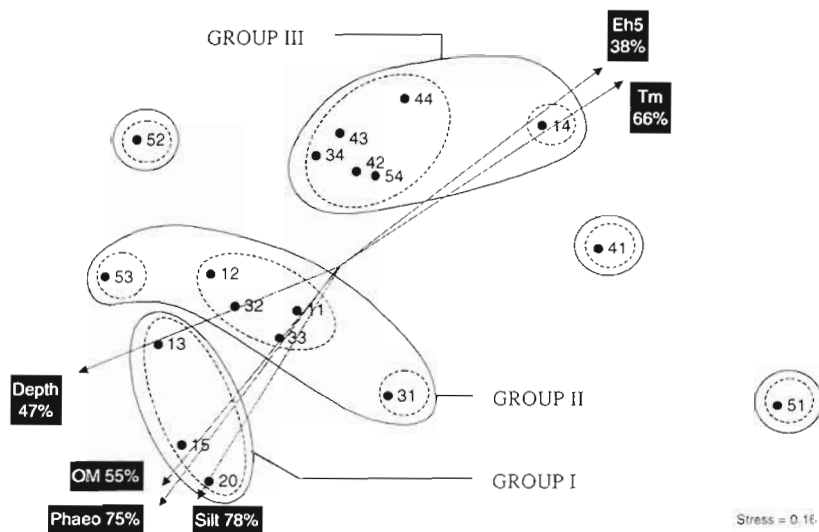


Fig. 7. Two-dimensional MDS ordination for macrofauna biomass with superimposed cluster groups (solid lines, 21 to 24 % similarity; dashed lines, 34 to 40 % similarity). Arrows show directions of increase for each significant environmental variable. Numbers following variable designation indicate the percentage of variance explained by each variable and defined with the multiple regression. Groups cited in the text are numbered from I to III (Tm, mean grain size; Eh5, redox potential at 5 cm depth in sediment; Phaeo, phaeopigment content; Silt, percentage of silt and clay; OM, total organic matter load)

land runoff were most evident in the populated zones (Zones 1, 2 and 3), while BR areas and sparsely populated zones (Zones 4 and 5) were not subjected to high organic matter, silt and basaltic loads. In the silt-enriched zones, the maximum loads were recorded at CH and TR stations. An exception to this was found at Stn 53, where the high silt content was probably related to the presence of a *Halophila* seagrass bed, which increased depositional rates (e.g. Curras et al. 1994, Everett 1994). Levels of phaeopigment were strongly correlated with silt content, but not with chlorophyll content, with maximum values being recorded

in channels. This suggests that the silt and phaeopigments present in the sediments may have similar origins, probably terrestrial sources. The terrigenous inputs were identified by Harris (1998) by measurements of metals (Cr, Ni, Al, Fe, Mn) and polycyclic aromatic hydrocarbons. In summary the channel areas were highly impacted by terrestrially derived sediments, as shown by organic matter, silt and basaltic loads.

A schematic figure based on the trophic groups of the total macrofauna and polychaete communities (Fig. 9) illustrates the different feeding patterns of the

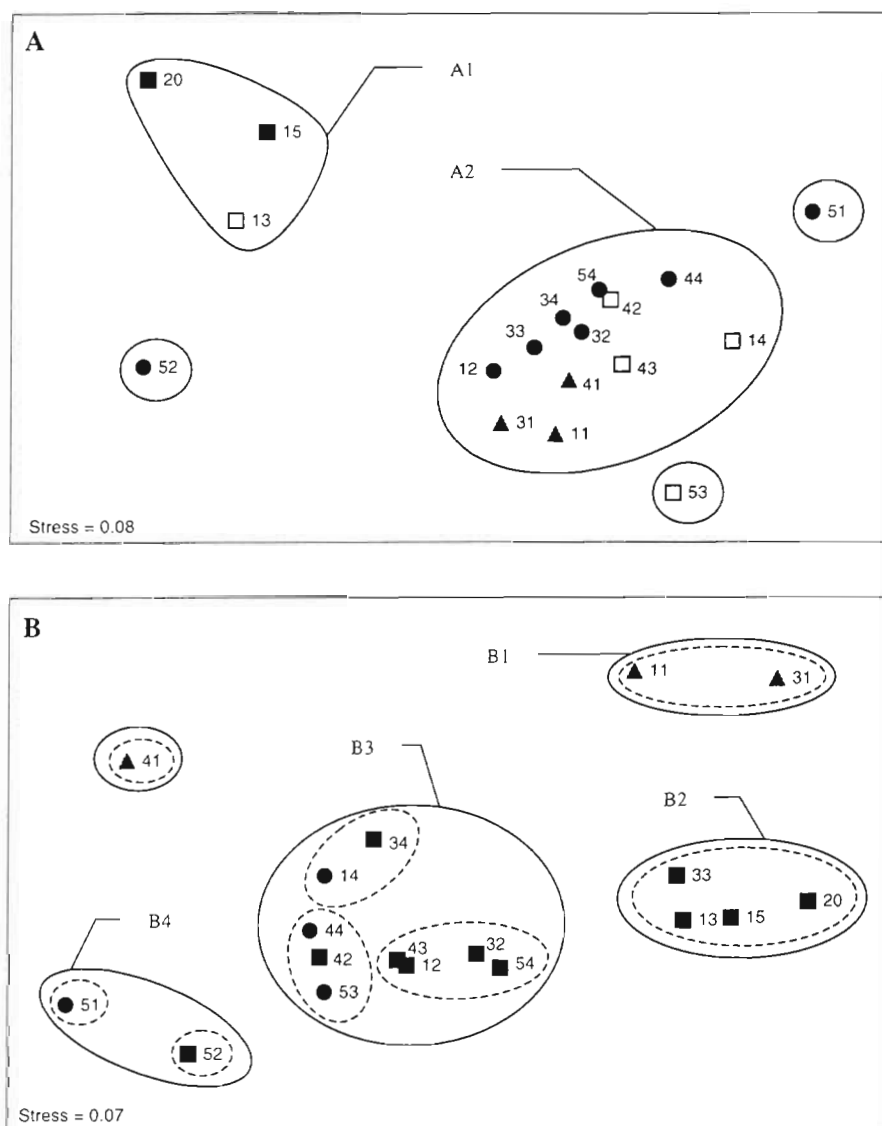


Fig. 8. Two-dimensional MDS ordination on biomass data for the 18 stations. (A) Ordination for trophic types of all macrofauna. Solid lines show cluster groups with 85% similarity (Bray-Curtis index). Groups cited in the text are labelled A1 and A2. (B) Ordination for polychaete trophic types. Solid lines are for cluster groups with 35 to 50% similarity, dashed lines for groups with 65% similarity. Groups cited in the text are labelled from B1 to B4 (symbols for the dominant trophic type in the station are: ■, non-selective deposit-feeders; □, selective deposit-feeders; ▲, suspension feeders; ●, carnivores)

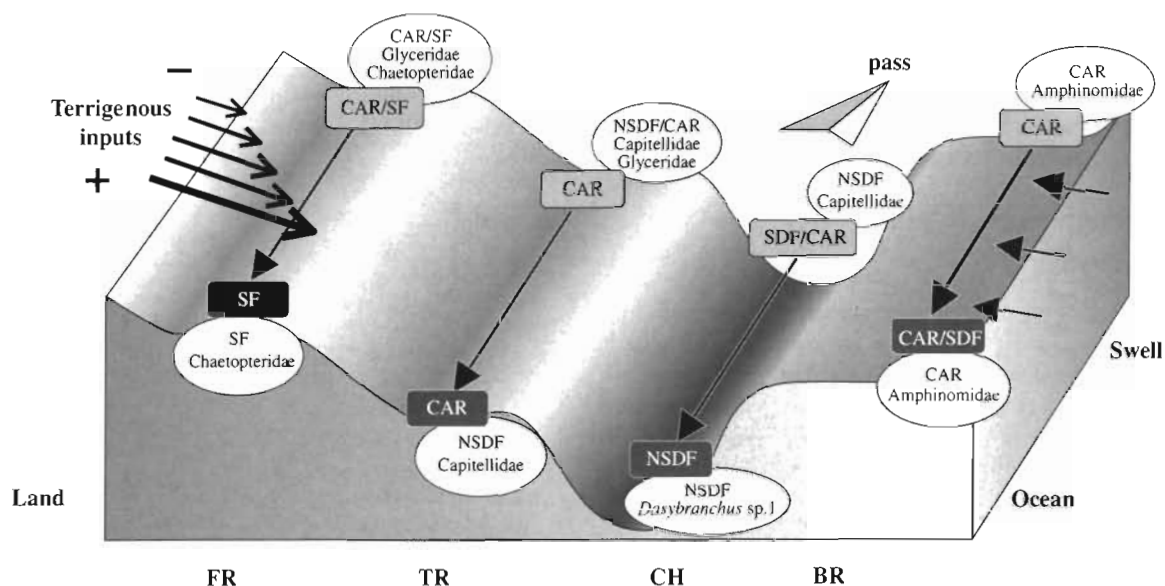


Fig. 9. Idealised functioning of a reef complex section from shore to barrier reef (FR, fringing reef; TR, fringing reef-channel transition; CH, channel; BR, barrier reef), for a high island subjected to increasing terrigenous inputs. On the landward side, terrigenous inputs increase from background to foreground and control the communities down to the channel. On the seaward side, swells protect the inner flats of the barrier reef from terrigenous influences. Within boxes are the dominant trophic groups for total macrofauna, encircled are those for polychaete taxa, with specification of dominant taxa (CAR, carnivores; SF, suspension-feeders; SDF, selective deposit-feeders; NSDF, non-selective deposit-feeders). Black arrows represent the shift from non-impacted ecosystem to impacted ecosystem with terrigenous elements

macrobenthos and how these relate to terrigenous inputs, across the lagoon from the fringing to the barrier reef. It is suggested that the type of sediment present as well as terrigenous inputs, and the type of reefal habitat all play major roles in determining the community structure. This is consistent with conclusions from many macrobenthic studies which show that community structure is largely dependent on sediment grain size (Alongi 1986, Riddle 1988, Agard et al. 1993, Long & Poiner 1994, Karakassis & Eleftheriou 1997, Harvey et al. 1998). Fig. 9 illustrates how inputs flow out over the FR part of the lagoon where low rates of sedimentation were observed. In FR areas, chaetopterid communities trap suspended sediments in the water col-

umn and their high density of tubes stabilises the sediments (Bailey-Brock 1979). Such behaviour by suspension-feeders (chaetopterids) plays an important facilitation role for associated communities in the FR subsystem (Bailey-Brock 1979, Gallagher et al. 1983). Chaetopterids tended to dominate FR communities in Tahiti lagoon, which were subjected to high levels of terrigenous inputs. This is consistent with studies by Heip (1995) that increasing rates of suspended matter in the water column increase the abundance of suspension-feeders. Pastorok & Bilyard (1985) showed that moderate sewage inputs may mimic nutrient enrichment and promote rapid growth of benthic organisms and domination by benthic suspension-feeders. Towards the CH part of the lagoon, as sedimentation rates increased, macrobenthic communities shifted from a carnivore-dominant mode (TR) to a non-selective deposit-feeding mode (CH). Driscoll (1975) noted that deposit-feeding benthos was favoured by fine-grained sediments characterised by high organic content. For polychaete communities (Fig. 9), non-selective deposit feeding was the dominant mode in TR and CH parts, with capitellids and particularly *Dasybranchus* sp. 1 contributing most to the biomass of the communities in the CH zone. At this point, a convergence of waters from the land with oceanic waters transversing the inner flat of the barrier reef occurs,

Table 4. Correlation between environmental variables (Tm, mean grain size; Eh5, redox potential at 5 cm depth in sediment; Phaeo, phaeopigments; Chl, chlorophyll; Silt, silt and clay; OM, total organic matter). \*p < 0.05, \*\*p < 0.01, \*\*\*p < 0.001

	Tm	Eh5	Depth	Phaeo	Chl	Silt
Eh5	0.71**	1				
Depth	-0.70**	-0.43	1			
Phaeo	-0.71**	-0.52*	0.59*	1		
Chl	-0.24	-0.40	-0.10	0.39	1	
Silt	-0.75***	-0.53*	0.54*	0.93***	0.24	1
OM	-0.58*	-0.36	0.63**	0.77***	0.05	0.80***

enhancing sedimentation rates in the channel area. The resulting current is then directed toward the passes (pers. obs.). Wolanski et al. (1993) studied the hydrodynamics of the lagoon of Moorea, which is a high island close and similar to Tahiti, and found a similar pattern. On the ocean side, the BR system, isolated from terrigenous influence by swell effect, exhibited structured macrobenthic communities dominated by carnivores, suggesting that carnivores are the dominant group where terrigenous inputs are minimal. However, in non-impacted zones polychaetes were more responsive to the reefal structure, with non-selective deposit-feeders being best represented in CH locations, which act as settlement pools for particles.

The increased particulate enrichment from the non-urbanised zones to the harbour area did not cause a linear reaction from the macrobenthos. If the SAB curves (Fig. 6) are considered, the response of communities represented a bell-shaped line, with maximum SAB values corresponding to intermediate levels of enrichment. The response of the Tahitian ecosystem to increasing terrestrial inputs corresponds to the intermediate disturbance hypothesis proposed by Connell (1978), in which high diversity is maintained by disturbance operating at intermediate levels. Our results from Tahiti can be compared to those of several authors who have applied this hypothesis to explain the functioning of tropical ecosystems (e.g. Warwick & Ruswahyuni 1987, Grigg & Dollar 1990, Dollar & Tribble 1993). A complementary study on microbenthos in Tahiti lagoon (Torréton et al. 1997) supported the hypothesis that these communities are food limited. The increasing SAB values found in this study support this hypothesis (Fig. 6). Some authors argue that biogenic disturbance (Riddle et al. 1990) or low metabolic rates (Grigg et al. 1984) play a major role in community limitation compared to nutrient depletion. However, food limitation in tropical systems was suggested in several cases (Alongi & Christoffersen 1992, Edgar 1993, Long & Poiner 1994). In the Tahitian lagoon, terrigenous inputs may minimise this limitation.

The mean organic content of sediments of 4.3% ( $60.72 \pm 2.43 \mu\text{g AFDW cm}^{-2}$ ) for a major group of 13 stations (Fig. 4) was close to the value of  $53.02 \mu\text{g AFDW cm}^{-2}$  recorded from the white sand sediments of the New Caledonian lagoon by Chardy & Clavier (1988) and slightly higher than recorded from some French Polynesian atoll lagoons (2.47 to 3.80% from Hily & Frouin 1998) or from isolated carbonate reefs (0.1 to 0.7% of organic carbon in Hansen et al. 1987, Riddle 1988, Alongi 1989). The high total organic content recorded at Stn 53 in Tahiti was directly related to the presence of a seagrass bed (see Everett 1994). Sub-surface roots and leaves incorporated into the sediments increased the organic matter content of the sedi-

Table 5. Multiple regression analysis between environmental factors and MDS scores. Adjusted coefficient of determination accounts for the part of variance explained by the variable.  $R^2$  was tested with ANOVA ( $df = 2, 15$ ) (Tm, mean grain size; Eh5, redox potential at 5 cm depth in sediment; Phaeo, phaeopigment content; Chl, chlorophyll content; Silt, percentage of silt and clay; OM, total organic matter load)

Variable	Direction cosines		Adjusted $R^2$	F	p-values
	x	y			
Tm	0.839	0.543	0.658	17.374	0.000
Eh5	0.796	0.605	0.383	6.287	0.010
Depth	-0.925	-0.379	0.472	8.580	0.003
Phaeo	-0.581	-0.814	0.751	26.694	0.000
Chl a	-0.979	-0.202	0.040	0.6713	0.526
Silt	-0.508	-0.861	0.782	31.457	0.000
OM	-0.629	-0.778	0.547	11.253	0.001

ment. It is suggested that Stn 52 was subjected to enrichment by plant material and detritus imported from Stn 53 during periodic heavy swell or wind events. However, terrestrially derived organic inputs cannot be excluded as Zone 5 had a high percentage of basaltic sediments. High levels of organic matter present at Stns 13, 15 and 20 appear to be related to anthropogenic organic inputs from sewage and polluted rivers. Also at Stns 15 and 20, sediments contained 60 to 70% of silt. Generally, such conditions result in low oxygen levels leading to defaunation (Nilsson & Rosenberg 1994), but in the Tahitian ecosystem diverse communities occurred in these highly enriched sediments. Actually redox measurements showed that muddy sediments were oxygenated (redox > 200 mV; Fenchel 1969) down to depths of 20 cm, the length of the cores. It is suggested that this is because of bioturbation of sediments and irrigation of burrows by *Callianassa* spp. and *Alpheus* spp. Burrow densities of these decapods were up to  $436 \pm 21$  burrow openings per square metre (Stn 20;  $n = 12$ ), and these species are known to have complex burrows, which may be 1 to 2 m in depth (Vaugelas de 1985, Nickell & Atkinson 1995). Such complex burrows and the high mobility of these organisms were probably responsible for them being poorly represented in benthic samples (Ansell et al. 1972, Chardy et al. 1988, Frouin et al. 1998). Water flux in burrows generated by ventilation associated with interstitial water circulation due to sediment-reworking greatly contributes to the oxygenation of sediments (Forster & Graf 1992, Ziebis et al. 1996) and favours the persistence or the settlement of other macrobenthic populations. Moreover, their activity is also important in incorporating organic matter into deeper layers of the sediment and recycling in relation to the bacterial loop (Driscoll 1975, Anderson & Meadows 1978, Daumas 1990, Ebenhöf et al. 1995). In the highly impacted Harbour Zone, it is suggested that decapod activity is the key element in maintaining the di-



verse macrofaunal community. It appears that no equivalent ecological process has been recorded from temperate systems.

It is strongly recommended that additional studies are carried out to confirm this important role, and the possible risks if decapod populations are not maintained. Reductions of the decapod population, or even loss of them, could lead to anoxic conditions developing and under such conditions, loss of the macrobenthic communities. This could have major impacts on the marine ecosystem of this region.

In conclusion, this study has shown that the lagoon of Tahiti is ideally suited for studying disturbance, with enhanced effects on a small spatial scale (the lagoon never exceeds 2 km in width). Inputs from terrestrial sources into the lagoon were composed of fine terrigenous elements (silt and clay) and organic matter, and the amount of these inputs was related to coastal population densities. Lagoonal hydrodynamic patterns also played an important role in the functioning of the ecosystem. Particulate organic and inorganic enrichment leads to a simplified trophic structure dominated by non-selective deposit-feeders, *Dasybranchus* sp. 1. In areas of high sedimentation bioturbation by decapods ensures that the sediments remain aerated and that diverse benthic communities are maintained.

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