

Biomass and trophic structure of the macrobenthos in the south-west lagoon of New Caledonia

P. Chardy¹ and J. Clavier²

¹ IFREMER, Centre de Brest, B.P. 337, F-29273 Brest cédex, France

² ORSTOM, Centre de Nouméa, B.P. A5, Nouméa, New Caledonia

Abstract



The biomass of the macrobenthic communities of the south-west lagoon of New Caledonia is analysed with special reference to tropical soft-bottom assemblages. The samples were obtained in 1986 from 350 Smith-McIntyre grabs as well as by diving over an area of 3 500 m², and covered a wide size-range of benthic organisms. The classification of the biomass data into taxonomic groups revealed the following: (1) a zoobenthic biomass (mean = 13 g ash-free dry wt m⁻²) that is high compared to values previously published for tropical systems, but fairly low compared to those recorded for medium and high latitudes; (2) a large macrophytic biomass (45% of ash-free dry wt); (3) dominance by weight of sponges, molluscs and cnidarians over the other faunal groups. The distribution of the biomass among the trophic groups revealed the following: (1) the dominance by weight of suspension-feeders, which account for 67% of the total zoobenthic ash-free dry wt; (2) the absence of trophic group amensalism between filter-feeders and deposit-feeders whatever the degree of bottom muddiness; (3) the existence of a relationship between the biomass of surface deposit-feeders and ATP at the surface layer of the sediment, suggesting that this group feeds preferentially on living particles. Differences in trophic structure between the muddy-bottom, grey-sand and white-sand communities of the lagoon reflect the functional characteristics of each bottom type.

Introduction

The purpose of this study is to outline and discuss the major features of the macrobenthos of the south-west lagoon of New Caledonia in terms of biomass and trophic structure. Previous studies on soft-bottom communities in tropical regions, recently reviewed by Maurer and Vargas (1984), support the contention of a reduced biomass in low latitudes, compared to middle and high latitudes. On the other hand, relationships between the trophic structure of com-

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munities and the sediment seem to be similar in tropical and temperate environments; in particular, the hypothesis of trophic-group amensalism developed by Rhoads and Young (1970) for northern and temperate regions, was found to be applicable to tropical communities (Bloom et al. 1972, Aller and Dodge 1974).

An estimation of the total macrobenthic biomass of the New Caledonian lagoon was made in order to compare this zone with the soft-bottom communities of high and low latitudes. The taxonomic groups dominant by weight were identified, and the distribution of the biomass by trophic group was determined in order to reveal the organisation of the benthic communities of the lagoon. An analysis of the distribution of the trophic groups in relation to sedimentary features (silt and clay, organic matter, ATP) was then attempted. This study aims to provide a quantitative basis for a functional investigation of the benthic system in the New Caledonian lagoon.

Materials and methods

The major benthic communities of muddy bottoms, grey-sand bottoms and white-sand bottoms, distinguished on the basis of numerically dominant species will be outlined in a further study (Chardy et al. in press). A map of these three bottom types was drawn up using observed fauna-sediment relations and available sedimentological data. The relative surface areas occupied by muddy, grey-sand, and white-sand bottoms throughout the whole investigation area, covering over 2 000 km², were 35, 50, and 15%, respectively. The same samples were used for the present investigation as for the above-mentioned study.

The investigation area was sampled at 35 different stations in 1986. Two types of sample were taken simultaneously at each station: ten Smith-McIntyre grab-samples covering an area of 1 m² were washed through a 2 mm sieve which retained the small-sized infauna and algae, while the large-sized epifauna (sponges, echinoderms, etc.) were col-

lected by diving over an area of 100 m². The grab samples were preserved in formalin, and the hand-collected samples were preserved by freezing. They were then sorted and the taxa identified. The dry weight (DW) of each taxon was determined after oven-drying at 80°C for 48 h (Crisp 1971) and the ash weight by further heating to 550°C for 2 h (Mason et al. 1983); the ash-free dry weight (AFDW) is the difference between these two values. The biomasses referred to and discussed in the present paper have been expressed in grams of AFDW per m² (g AFDW m²). For the main species, we have given the dry weights also, again expressed as grams per m² (g DW m²).

The biomass data were arranged according to two criteria. First we calculated the biomasses by taxonomic group (plants, sponges, molluscs, cnidarians, echinoderms, crustaceans, sipunculians and annelids). Under "others" we placed together all the minor groups by weight (plathelminthes, nemerteans, lophophorians, tunicates, cephalochords and vertebrates). The taxa were then classified by trophic group. After considering a number of possible classifications (Pearson 1971, Wolff 1973, Arntz and Brunswig 1976, Fauchald and Jumars 1979, Dauvin 1984), we chose four main groups, subdivided where necessary into sub-groups: (1) Macrobenthic primary producers (macrophytes) comprising fleshy algae, calcified algae, and phanerogams. (2) Suspension-feeders, divided into three sub-groups according to the size of the particles ingested: sponges, which retain the finest particles (<1 µm), filter-feeding bivalves, which ingest particles in the 4 to 6 µm range (Stuart and Klumpp 1984), and cnidarians, which feed on relatively large-sized organic particles, particularly zooplankton. (3) Deposit-feeders, traditionally divided into two sub-groups: the surface deposit-feeders, which take their food selectively from the water-sediment interface (bivalves, strombids, etc.), and deposit-swallowers, which ingest more or less substantial quantities of sediment (holothuroids and irregular echinoids, sipunculians, etc.). (4) Predators comprising both carnivores (muricid and conid gastropods, eunicid polychaetes, etc.) and necrophagous species (pagurid crustaceans).

Mean biomass and standard error (SE) for each taxonomic group and each trophic group were calculated for the south-west lagoon as a whole and for each macrobenthic community separately. In order to take advantage of the natural divisions (or communities) identified in this geographical area (Chardy et al. in press), the means and the standard errors of the means relating to the investigation area as a whole were calculated by the "stratified sampling" technique (Cochran 1963), whereby each community represents a stratum whose weight is proportional to the relative surface area it occupies in the zone.

At the same time, various environmental parameters were measured in order to provide a basis for interpretation of the trophic structures. The silt-clay fraction of the sediment at each sampling station was determined by washing the sample through a 63 µm-mesh sieve. In addition, the overall organic matter content and ATP were measured at five stations: three of them located on grey-sand bottoms

and one each on muddy and white-sand bottoms. At each station, two sets of 12 random sediment-samples were taken using a 5.31 cm² corer. One of the sets was frozen immediately and taken to the laboratory, where the quantity of organic matter contained in the first centimeter of sediment was estimated, using the loss of weight on ignition (550°C) method after drying for 48 h at 80°C. In the second set, the ATP present in the first centimeter of sediment was extracted less than 30 min after sampling, using the boiling NaHCO₃ method described by Bancroft et al. (1976), after which the extract was frozen. ATP determination was carried out in the laboratory by the firefly luminescence method (Strehler and Totter 1952), using a procedure already successfully applied for sediment studies on coral reefs (Charpy-Roubaud 1986).

Results

Data for biomass by station and by taxon previously published by Chardy et al. (1987) have been used as baseline values in this section.

The mean biomass of the macrobenthos in the south-west lagoon of New Caledonia, estimated by stratified sampling, is 23.6 g AFDW m⁻² (SE=15.0), or 153.9 g DW m⁻². The ash-free dry weight of plant matter accounts for 45% of the total organic biomass (10.6 g AFDW m⁻², SE=+16.5), or 34.8 g DW m⁻². The weight of animal organic matter is 13.0 g AFDW m⁻² (SE=3.2), or 119.1 g DW m⁻².

The distribution of the biomass among the main macrobenthic groups is illustrated in Fig. 1. Molluscs clearly domi-

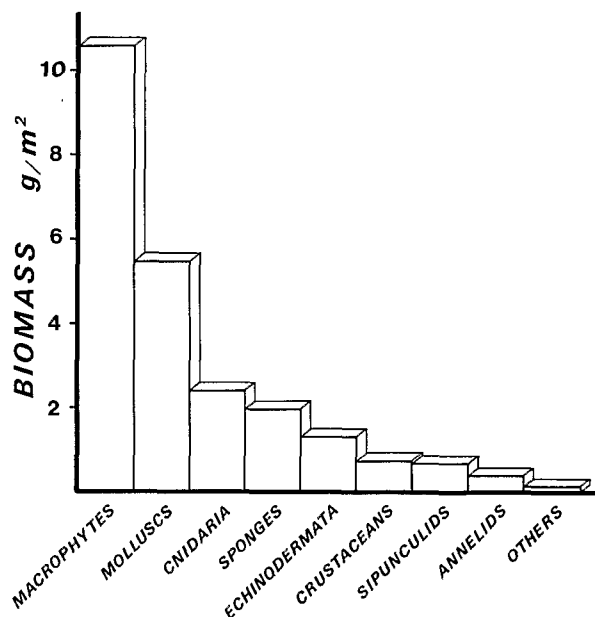


Fig. 1. Distribution of biomass among main macrobenthic groups throughout whole lagoon. Biomass in all figures is g ash-free dry wt m⁻²

nate the faunal structure by weight, accounting for 41% of the total animal biomass. Together, the group "molluscs-cnidarians-sponges" makes up 75% of the macrozoobenthic biomass, while the relative contribution of the "crustaceans-sipunculians-annelids-others" is only 9%.

The richest bottoms as regards macrobenthic organic matter are the grey-sand bottoms, where the mean biomass is 35.7 g AFDW m^{-2} (SE=7.5), or 226.7 g DW m^{-2} . These bottoms are characterized by a high macrophytic biomass (20.9 g AFDW m^{-2} , SE=8.1) representing 58% of the total weight of organic matter (Fig. 2) and dominated by fleshy algae (50%), with phanerogams next in importance (34%) and calcified algae last (16%). From the taxonomic viewpoint, *Amansia glomerata* (8.6 g AFDW m^{-2}) is the most abundant species by weight, well ahead of the phanerogams *Cymodocea serrulata* and *C. rotundata* (5.5 g AFDW m^{-2} combined) and *Halophila ovalis* (3.4 g AFDW m^{-2}). These four species constitute more than 80% of the AFDW plant biomass in the lagoon. The macrofaunal biomass is estimated at 14.8 g AFDW m^{-2} (SE=3.0), or 158.4 g DW m^{-2} . The dominant group "molluscs-cnidarians-sponges" accounts for 73% of the macrozoobenthic biomass (Fig. 2), with the cnidarians alone contributing 31% of the animal organic matter. With regard to individual species, the cnidarian *Heteropsammia michelini* (3.9 g AFDW m^{-2}) together with the commensal sipunculian *Aspidosiphon corralicola* (1.3 g AFDW m^{-2}) dominate the zoobenthic structure, followed respectively by the bivalve molluscs *Anadara scapha* (1.7 g AFDW m^{-2}) and *Bractechlamys vexillum* (1.3 g AFDW m^{-2}), and the gastropod *Strombus erythrinus* (0.4 g AFDW m^{-2}).

The mean biomass of the macrobenthos on muddy bottoms is 12.9 g AFDW m^{-2} (SE=2.5) or 82.7 g DW m^{-2} , of which 12.7 g AFDW m^{-2} (SE=2.6) consists of animal organic matter. Molluscs, sponges and echinoderms dominate this community by weight (Fig. 2), contributing 55, 18 and 14% of the total animal organic matter, respectively. The dominant species are *Ircinia* sp. (1.2 g AFDW m^{-2}), which represents 51% of the sponge biomass on this bottom type, the bivalve molluscs *Trachycardium elongatum* (1.1 g AFDW m^{-2}), *Lioconcha* sp. (0.8 g AFDW m^{-2}) and *Crasostrea* sp. (0.6 g AFDW m^{-2}), and the echinoderms *Marettia planulata* (0.8 g AFDW m^{-2}) and *Brissopsis* sp. (0.6 g AFDW m^{-2}).

Finally, the white-sand bottoms, which have a mean macrobenthic biomass of 8.1 g AFDW m^{-2} (SE=1.7), or 77.2 g DW m^{-2} , proved to be the bottom type with lowest biomass. The macrofaunal benthos estimated at 7.9 g AFDW m^{-2} (SE=1.8), or 75.7 g DW m^{-2} , is distinctly dominated by molluscs, which account for 64% of the animal organic matter, while sponges represent only 22% (Fig. 2). The dominant species in the white-sands community are the strombid gastropods *Strombus gibberulus* (2.5 g AFDW m^{-2}) and *S. luhuanus* (0.4 g AFDW m^{-2}), associated with the bivalve *Glycymeris reevi* (1.1 g AFDW m^{-2}) and the sponge *Spirastrella* sp. (1.3 g AFDW m^{-2}) whose presence is linked to the existence of hardground areas (Thomassin and Coudray 1981) under the sediment.

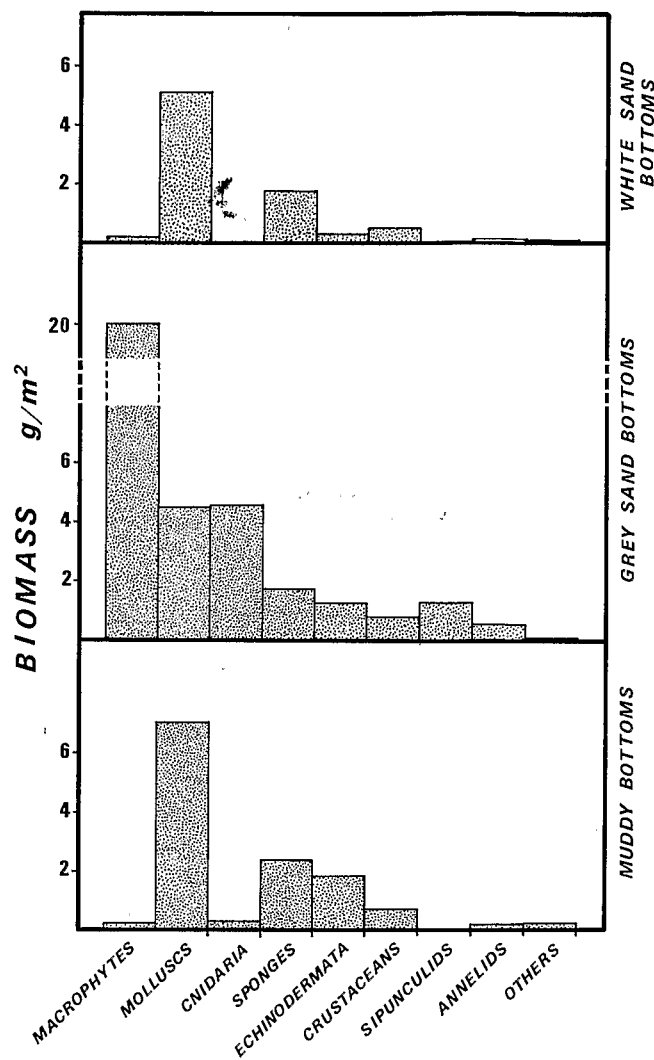


Fig. 2. Distribution of biomass among main macrobenthic groups for each of three benthic communities in lagoon

In regard to the trophic groups, the overall structure of the lagoon macrobenthos remains dominated by macrophytic primary producers (Fig. 3). Suspension-feeders represent two thirds of the total animal biomass (8.7 g AFDW m^{-2} , SE=2.7), or 94.4 g DW m^{-2} . This trophic group is clearly dominated by bivalves, with cnidarians ranking in second place, ahead of sponges. The other suspension feeders (ascidians and annelids, not illustrated) constitute an insignificant part of the biomass (1.3%). The biomass of deposit-feeders is 3.1 g AFDW m^{-2} (SE=0.1), or 18.7 g DW m^{-2} , with surface deposit-feeders and deposit-swallowers contributing about equal amounts. The carnivores together make up 9.5% of the macrozoobenthic AFDW.

This overall picture is very similar to that of the grey-sand bottoms; the only difference lies in the relative abundance of the suspension-feeding sub-groups, cnidarians, not bivalves, being predominant on grey-sand bottoms (Fig. 4). The muddy bottoms have only a small biomass of primary

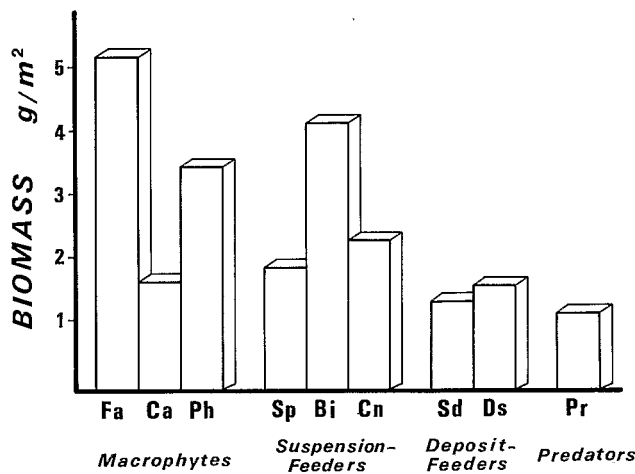


Fig. 3. Distribution of biomass among trophic groups throughout whole lagoon. Fa: fleshy algae; Ca: calcified algae; Ph: phanerogams; Sp: sponges; Bi: bivalves; Cn: cnidarians; Sd: surface deposit-feeders; Ds: deposit-swallowers; Pr: predators

producers. They are distinctly dominated by suspension-feeders (75% of the AFDW), among which the bivalves are by far the most abundant, cnidarians being rare. Deposit-feeders are less abundant here than for the investigation area as a whole, this "shortage" being almost entirely due to a lack of surface deposit-feeders which are poorly represented. The percentage of carnivores is lower than for the south-west lagoon as a whole.

The white-sand bottoms are also very poor in primary producers (Fig. 4). Unlike the muddy bottoms, they have a much lower proportion of suspension-feeders than the lagoon as a whole; this trophic group is characterized by a slight predominance of sponges over bivalves, with cnidarians being very rare. On the other hand, deposit-feeders make up almost half of this community and are distinctly dominated by the surface deposit-feeders. Lastly, the proportion of carnivores is slightly higher than for the lagoon as a whole.

The relationship between the trophic groups and silt-clay content of the sediment was determined using the results of the grain-size analysis made by Chardy et al. (in press). The dispersion diagram of silt and clay versus total macrobenthic AFDW per station (Fig. 5) does not reveal any interpretable trend. The absence of high biomass values for high silt and clay content should, however, be noted. Variations in the percentage biomass for the four main trophic groups of the zoobenthos in relation to the silt and clay fraction are summarised in Fig. 6, which reveals four major points: (1) The percentage of suspension-feeders, the trophic group which is dominant by weight in the lagoon whatever the proportion of silt and clay in the sediment, gradually increases up to a silt-clay content of 50%; beyond this level, the suspension-feeders make up about 90% of the zoobenthic organic matter. (2) The surface deposit-feeders constitute the second-largest trophic group by weight up to a silt-clay content of 20%; beyond this level their contribution to the total biomass sharply decreases to about 5%.

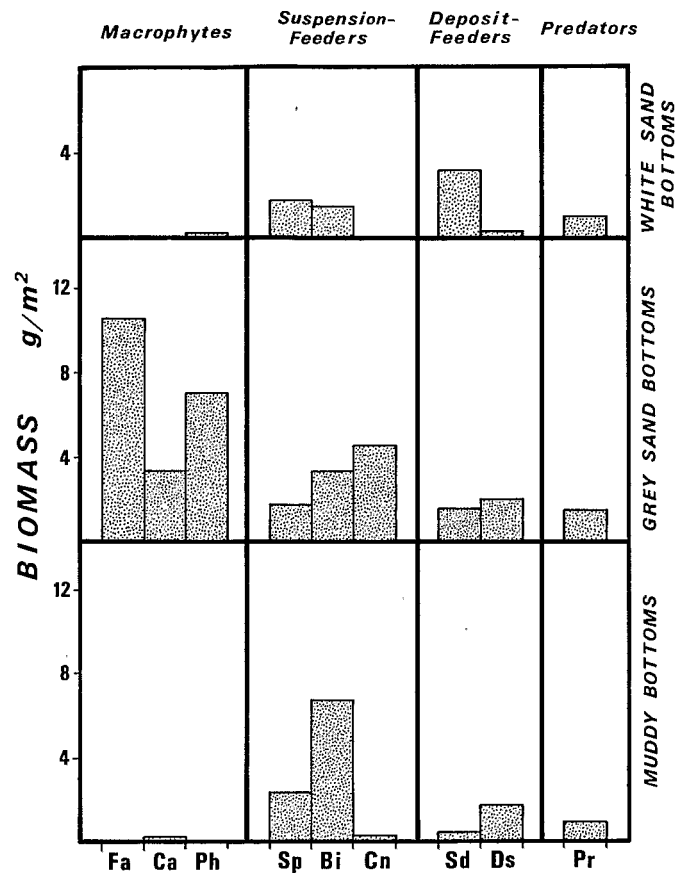


Fig. 4. Distribution of biomass among trophic groups in three benthic communities of lagoon. Abbreviations as in Fig. 3

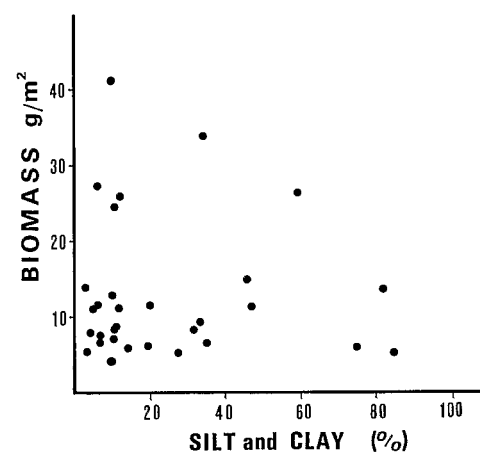


Fig. 5. Dispersion diagram of silt and clay vs total macrobenthic ash-free dry weight for stations sampled

(3) The biomass of deposit-swallowers steadily increases up to silt-clay content of approximately 35% and then suddenly decreases; at a silt-clay content of between 20 and 30% the deposit-swallowers take over from the surface deposit-feeders in importance of contribution to the total biomass. (4) The relative biomass of the carnivores is practically constant for low or medium silt-clay levels, but decreases sharply as soon as the silt-clay content reaches 50%; beyond this

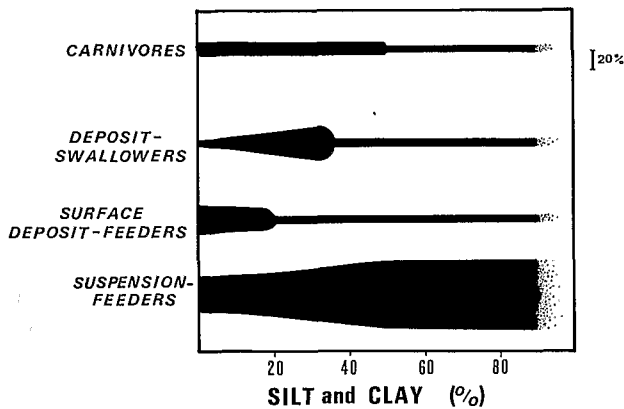


Fig. 6. Variations in percentage biomass of four main trophic groups of zoobenthos in relation to silt and clay fraction

Table 1. Mean values and standard deviations of total organic matter (AFDW) and ATP in sediment at five sampling stations related to three communities

Sediment type	$\mu\text{g cm}^{-2}$ of:			
	AFDW		ATP	
Muddy bottoms	57.37	(6.63)	0.15	(0.03)
Grey-sand bottoms	62.19	(13.54)	0.34	(0.17)
	54.27	(6.63)	0.33	(0.17)
	49.83	(10.75)	0.37	(0.13)
White-sand bottoms	53.02	(6.63)	0.52	(0.26)

point, the carnivores make up only a few per cent of the total animal organic matter.

In addition to silt-clay levels, the total amount of organic matter and the total amount of living organic matter can also affect the relative abundance of the trophic groups in the different communities. We measured total organic matter and ATP at five sampling stations and shall confine ourselves to general comparisons. The weight of the total organic matter in the sediment (Table 1) does not significantly differ between the communities (Mann-Whitney *U*-test, $P > 0.05$), and cannot therefore be regarded as useful for interpreting the trophic structures observed. On the other hand, ATP (Table 1) per unit surface area, which is assumed to be proportional to the biomass of living organic matter, differs significantly between the bottoms corresponding to each community (Mann-Whitney *U*-test, $P < 0.05$). Use of a one-tailed *t*-test demonstrated that white-sand bottoms are richer in living organic matter than grey-sand bottoms which, in turn, are richer than muddy bottoms.

Discussion

Comparison of our findings with the biomass values in the literature is rendered difficult by incompatibility of units used, heterogeneity of sampling techniques and scales, di-

versity of the communities studied, etc. As a rough basis for comparison, we therefore chose, just a few studies pertaining to the macrozoobenthic communities of coastal systems, wherein results are given as mean values determined for large areas (estuaries, bays, inland seas, continental shelf). The results have been compared by assuming that carbon represents 40% of the ash-free dry weight (Steele 1974), that 1 g of carbon is equal to 11.4 kcal (Platt and Irwin 1973) and that 1 g wet weight is equal to 0.6 kcal (Mills and Fournier 1979).

For coastal tropical areas, the mean macrofaunal biomass of the south-west lagoon of New Caledonia (13 g AFDW m^{-2}) is greater than most values in the literature, notably in the following instances: 3.5 g m^{-2} dry wt after decalcification in Kingston Harbour, Jamaica (Wade 1972), $7.68 \text{ g AFDW m}^{-2}$ in a Florida estuary (Bloom et al. 1972), 10.98 g m^{-2} wet wt in the Gulf of Nicoya, Costa Rica (Maurer and Vargas 1984), 10 g m^{-2} wet wt off the Malabar Coast, India (Seshappa 1953), 30 to 40 g m^{-2} wet wt off Volta and Congo (Sparck 1951), 6.73 to 74.23 g m^{-2} wet wt off West Africa (Longhurst 1959), 32.2 g m^{-2} wet wt off Hong Kong (Shin and Thompson 1982), 28 to 120 g m^{-2} wet wt off Ghana (Buchanan 1958). Two results are higher than that found in the present study: 137 g m^{-2} wet wt in a Guinea estuary (Longhurst 1959) and 540 g m^{-2} wet wt in a sandy silt bottom off Ghana (Buchanan 1958).

Compared with the biomass values for benthic communities of northern and temperate zones recorded by Mann (1982), the south-west lagoon of New Caledonia is very much poorer than the Severn estuary, UK, with 17 g C m^{-2} (Warwick et al. 1978), and the Gravelingen estuary, Netherlands, with 10 g C m^{-2} (Wolff and de Wolff 1977). On the other hand, our results are of the same order of magnitude as the 4.8 g C m^{-2} recorded by Sanders (1956) at Long Island Sound, USA, and very much higher than the biomasses recorded in the North Sea (1.7 g C m^{-2}) and the Baltic Sea (1.7 g C m^{-2}) by Buchanan and Warwick (1974) and Cederwall (1977). All in all, the biomass of the New Caledonian lagoon is among the higher recorded tropical zone values and near the middle of the range of values for the northern and temperate zones. The biomass of our grey-sands community (5.92 g C m^{-2}) is of the same order of magnitude as that of the Lynher estuary, Cornwall, England (Warwick and Price 1975) and of Morlaix Bay, France (Dauvin 1984), while that of our white-sands community (3.16 g C m^{-2}) is consistent with the low biomass values recorded in tropical systems or in high- and medium-latitude open-systems. The algal biomass of our lagoon is however remarkable compared with the other soft-bottom communities described to date. Macrophytic primary producers by weight constitute the main compartment within the south-west lagoon. The value we obtained is comparable to the plant biomass of the reef ecosystem at French Frigate Shoals, Hawaii, estimated from the benthic primary production data given by Atkinson and Grigg (1984) and from the ECOPATH model proposed by Polovina (1984).

As pointed out by Fauchald and Jumars (1979) in their study on the diet of worms, there are various ways of group-

ing species into functional units (e.g. by degree of opportunism, by reproductive behaviour). Discrimination according to feeding patterns however seems appropriate as a basis for analysis of energy transfers within an ecosystem. It is not always easy to assign a species to a particular trophic group, and therefore necessary to indicate the criteria that guided our choice.

The macrobenthic primary producers group was considered exclusively as consisting of macrophytes (algae and phanerogams). Other organisms, such as bivalve molluscs (Trench et al. 1981), cnidarians (Muscatine et al. 1981) and certain sponges (Wilkinson 1983) could also have been included, at least in part, in the primary producers in our scheme. However, among these taxa, only the cnidarian *Heteropsammia michelini* appeared in our study as significant by weight. Association of this cnidarian with zooxanthellae is not consistent at our study site (M. Pichon personal communication) and we have disregarded its contribution to primary production.

The suspension-feeders group, as defined by J rgensen (1966), was divided into three sub-groups. Sponges (1) and lamellibranch molluscs (2) are filter-feeders *sensu stricto* (Marshall and Orr 1960), which cause the surrounding water to pass through a filter that selects particles according to their size and shape. The sponges feed on very small particles – bacteria (Gili et al. 1984) or phytoplankton (Frost 1981) – and thus largely avoid competition with the bivalves which generally absorb larger particles (Stuart and Klumpp 1984), although some species are able to use bacteria and phytoplankton as a source of carbon (Amouroux 1986). The sponges and bivalve molluscs can also be differentiated on the basis of their respective effects on the economy of the benthic compartment. The particles pumped in by the sponges but not absorbed are ejected through the oscula and carried away by the resulting water turbulence (J rgensen 1966); these particles are thus re-suspended in the surrounding water. On the other hand, the bivalves aggregate non-ingested particles in the form of pseudofaeces and thus effect retention of organic matter in the benthic compartment. Vahl (1980) estimated that 87% of the organic matter thus retained by the pectinid bivalve *Chlamys islandica* became available for use by other benthic organisms. Recent studies have shown that some sponges can exude organic matter in coral reef environments (Hammond and Wilkinson 1985), but the quantitative impact of this phenomenon is as yet unknown. The third sub-group of suspension-feeders comprises all the cnidarians. Cnidarians (3) possess polytrophic feeding capacities including endocytosis of particulate food, absorption of dissolved organic material, and utilisation of assimilates from zooxanthellae (Schlichter 1982). To simplify our scheme, we assumed the main source of energy for cnidarians to be suspended particles, particularly zooplankton (Lewis 1982, Patterson 1984). Their food-capture method enables them to be separated from filter-feeders *sensu stricto* (Muscatine 1973).

Deposit-feeders were divided into two sub-groups. The deposit-swallowers differ from the deposit-feeders by the presence of substantial amounts of sediments in their diges-

tive tract. This fact reflects a difference in selectivity as regards particles ingested: a high-degree of selectivity is believed to occur in the surface deposit-feeders (Self and Jumars 1978); it is less marked in the deposit-swallowers, although preferential ingestion of sediment rich in organic materials has been observed in certain echinoderms (Moriarty 1982, Hammond 1983). This general pattern must however be regarded as a considerable simplification of the biological reality, since numerous species in fact display both types of feeding behaviour (Taghon et al. 1980, Maurer and Leathem 1981, Harvey and Luoma 1984). The contribution of resuspended bottom material to the nutrition of filter-feeders must also be taken into account (Ki rbe et al. 1981, Bricelj and Malouf 1984).

The last of the trophic groups we considered comprises carnivores only. In this group we lumped together all macrophagous organisms, without making a distinction between predatory and necrophagous species. In our samples, the biomass of grazers was so insignificant that this category has not been taken into account.

Our study revealed very marked changes in the trophic composition of the communities related to changes in the silt-clay content of the bottom substrate. For the whole south-west lagoon of New Caledonia, bottoms with a silt-clay content of less than 15%, i.e., all the grey-sand and white-sand bottoms, cover 65% of the total soft-bottom surface-area (Chardy et al. in press). Within this soft-bottom system, the main changes in trophic structure associated with an increase in silt-clay content consist of an increase in the biomass of suspension-feeders together with a sharp decrease in the biomass of deposit-feeders above a 35% silt-clay threshold.

Our results confirm the importance of silt-clay levels on the trophic structure of benthic communities (Salen-Picard et al. in preparation). However, the proportion of the two key feeding-groups, i.e., suspension-feeders and deposit-feeders, in relation to silt-clay content is totally inconsistent with the pattern established for soft-bottom communities in northern and temperate regions (Sanders 1958, Rhoads and Young 1970, Levinton 1972, Hartley 1984). The common concept in benthic animal-sediment relationships assumes that suspension-feeders and filter-feeders are dominant in sand and mud sediments, respectively. In their hypothesis of trophic group amensalism, Rhoads and Young (1970) assume that the resuspended sediment produced by deposit-feeders inhibits suspension-feeders by clogging filtering mechanisms, and by providing physical instability unsuitable for larval settlement and maintenance. The results of the present study indicate that the soft-bottom fauna of the south-west lagoon of New Caledonia does not fit the concept of the effect of amensalism upon suspension-feeders in mud, this group always being dominant by weight (67% of the total zoobenthos biomass of the lagoon), whatever the degree of muddiness (i.e., silt-clay content).

There are two possible explanations for this absence of amensalism. Firstly, the conventional pattern is usually established on the basis of population densities, whereas in this paper results are expressed in terms of biomass. Thus,

the fact that sponges are counted as colonies and not as individuals changes the biomass: density ratio of the filter-feeders. Inversely, the annelid polychaetes that account for over 50% of the living organisms only constitute 3% of the biomass. Secondly, the common pattern is mainly established on soft-bottom infauna (Levington 1972), whereas the trophic groups of the New Caledonian lagoon, particularly the suspension-feeders, are markedly dominated by epifaunal organisms (sponges, pectinid, mytilid and ostreid bivalves and cnidarians). Lastly, the existence of a mode in the gravel fraction of the grain-size distribution of the muddy-bottom (Chardy et al. in press) is probably conducive to larval settlement and maintenance of the observed suspension-feeding organisms. An alternative to the hypothesis of trophic-group amensalism proposed by Wildish and Kristmanson (1979) suggests that both groups are food-limited and controlled by the turbulent mass-transfer of seston, current velocity and bottom roughness being the main physical factors controlling the proportion of filter-feeders to deposit-feeders. In the absence of hydrodynamic data, it is not possible to interpret the distribution of suspension-feeders in the New Caledonian lagoon on this basis. We can merely assume that, at the water-sediment interface of the muddy bottoms, as on all the bottom types of the lagoon, there is enough turbulence to create trophic conditions favourable to the development and maintenance of suspension-feeding organisms.

As regards the positive correlation between mud- and deposit-swallowers up to the 35% threshold, our observations are consistent with the findings of Hartley (1984) on the benthic community of the Forties Oilfield (North Sea). Similarly, the observed decrease in the proportion of carnivores above the 50% silt-clay threshold is consistent with the findings of Salen-Picard et al. (in preparation).

Our results do not lend themselves to a thorough analysis of the relationships between the trophic groups and total organic matter or living organic matter. On the other hand, the biomass of living organic matter, as indicated by ATP measurements, was seen to vary with bottom type. There is a relationship between the biomass of this living organic matter and the biomass of surface deposit-feeders, the latter being seven times higher on white-sand bottoms than on muddy bottoms, with the grey-sand bottoms occupying an intermediate position. This relationship suggests that surface deposit-feeders feed preferentially on the meio- and microbenthos, regardless of the total amount of organic material available.

These results, achieved on the basis of biomass weight and trophic groups, confirm identification of the communities of the south-west lagoon of New Caledonia, made on the basis of numerically dominant species (Chardy et al. in press). The characteristics of the trophic structure within the three previously identified assemblages suggest different functional patterns. Our study indicates that the energy entering the white-sand community passes through an abundant meio- and microbenthic compartment which ensures its preferential transfer to the surface deposit-feeders. The muddy bottoms, on the other hand, are distinctly dominated

by the filter-feeders, which absorb the organic material entering the benthos either directly or after resuspension. This phenomenon is associated with a relatively small meio- and microbenthic biomass. The grey-sand community, identified as a quite separate unit on the basis of faunal composition (Chardy et al. in preparation) lies, on the basis of its trophic structure, mid-way between these two poles. This third unit, however, possesses a large macrophytobenthic biomass whose production, in the absence of grazers, probably constitutes a source of organic material and hence an enrichment factor for the whole of the lagoon.

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