

Structure and temporal fluctuations of two intertidal seagrass-bed communities in New Caledonia (SW Pacific Ocean)

J. Baron^{1*}, J. Clavier¹, B. A. Thomassin²

¹ ORSTOM, Centre de Nouméa, B.P. A5, Nouméa, New Caledonia

² Station Marine d'Endoume, Rue de la Batterie des Lions, F-13007 Marseille, France

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Abstract. The structure and trophic organization of two intertidal seagrass-bed communities (*Halodule uninervis* and *Thalassia hemprichii*) were examined on the south-west coast of New Caledonia (SW Pacific Ocean), from April 1989 to March 1990. Five benthic samples were collected from each site at 2 mo intervals and various environmental parameters were simultaneously monitored. Animal:plant biomass ratios were close to 1 at both sites. Polychaetes dominated in number of species. The suspension-feeding bivalves *Gafrarium tumidum* and *Anadara scapha* constituted the greater part of the animal biomass. The evolution of the communities over an annual cycle displayed marked structural and organizational stability, resulting mainly from the absence of distinct recruitment periods for the dominant species, no mortalities during the brief low-salinity periods, and no temporal variations in the granulometry, the organic matter or the chlorophyll *a* contents of the sediments.

Introduction

As pointed out recently by Alongi (1990), anthropic pollution has increased dangerously along tropical coasts, and careful management of their littoral zones in the future is imperative. Littoral zones, particularly those covered by seagrass beds, are ecosystems of great physical, biological and economic importance, trapping sedimentary particles eroded from mangrove swamps, providing sheltered nurseries and habitats for many varied species, substrates for aquaculture, and nutritional and reproductive grounds for marketable fishes (Zieman 1987, Nienhuis et al. 1989, Moriarty et al. 1990). Unfortunately, in contrast to northern temperate zones, the effective conservation of such sites in the tropics is hindered by the lack of knowledge of structure and temporal fluctuations of the local benthic communities (Warwick and Ruswahyuni 1987, Alongi 1990). In New Caledonia,

the structure of the intertidal seagrass-bed communities is but partially known. Some harbour sizeable populations of bivalves of economic interest, such as *Gafrarium tumidum* Röding, 1798 and *Anadara scapha* (L., 1758) (Baron and Clavier 1992) and are now threatened by a number of tourism-oriented projects. Examination of the benthic communities associated with these bivalves appears of primary importance in order to provide a basis for future monitoring of human impact. The present study describes the structure and organization (*sensu* Watling 1975 and Bachelet 1981) of two such communities by examining their specific composition and their numerical and biomass distributions as a function of trophic group. Temporal fluctuations in the communities were assessed over an annual cycle and related to environmental parameters.

Materials and methods

The study was conducted in two intertidal seagrass beds (an *Halodule uninervis* bed in Tomo and a *Thalassia hemprichii* bed in Teremba), situated in Saint-Vincent and Deama bays, respectively, on the south-west coast of New Caledonia (Fig. 1). The seagrass bed at Tomo fronts a 20 m-wide sandy-muddy beach, whereas the seagrass bed in Teremba borders a dense mangrove stand. The two sites support a substantial population of the bivalves *Gafrarium tumidum* and *Anadara scapha*. In Tomo (+0.4 m above low spring tides), samples were first collected on 7 April 1989; the site was sampled again a fortnight later after Cyclone "Lili" had passed over; samples were then taken at bimonthly intervals until 26 March 1990. In Teremba (+0.2 m above low spring tides), samples were taken bimonthly from 5 June 1989 to 1 April 1990. Interstitial water temperature was measured at a depth of 2 cm with a portable thermometer, and salinity with a refractometer. Sediment was collected to a depth of 10 cm and particle size-fractions were determined according to the procedure of Folk and Ward (1957). Organic matter content was estimated for dry sediment by weighing before and after oven-heating at 550 °C for 3 h. The chlorophyll *a* content of the top 1 cm of substratum was measured by spectrophotometry after acetone extraction (Garrigue and Di Matteo 1991) on samples collected with a 5.7 cm² corer, at each sampling date in Tomo and monthly in Teremba.

On the first sampling occasion, ten 0.1 m² samples of sediment were collected from each seagrass bed; after sorting the macroben-

* Present address: 42 rue de la Roche, F-17100 Saintes, France

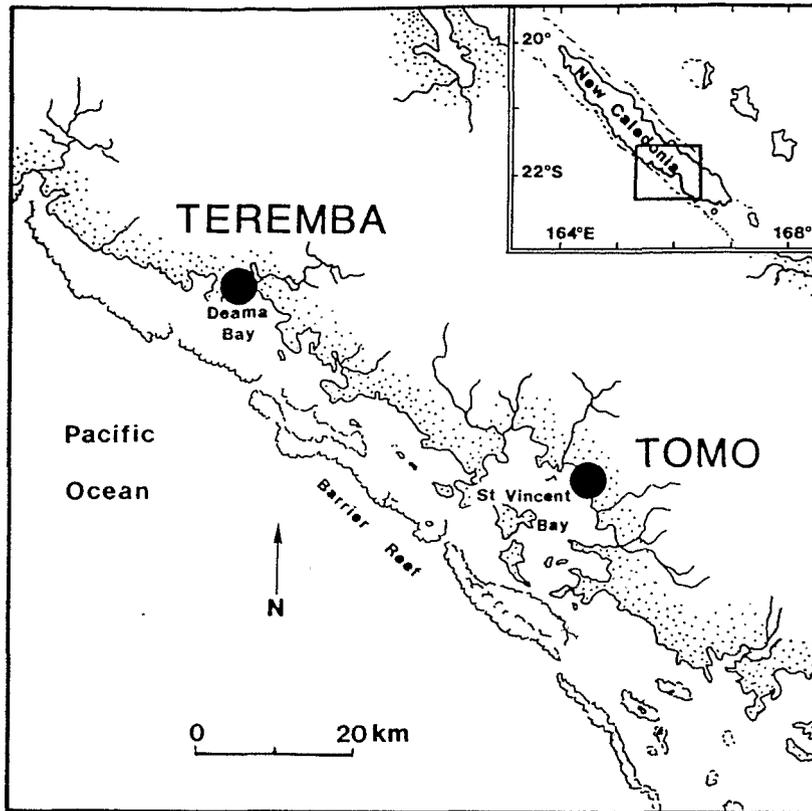


Fig. 1. Study areas on south-west coast of New Caledonia

Table 1. Mean (SE) annual variations of granulometric fractions in sediment of seagrass beds at Tomo and Teremba. Co: cobbles; PG: pebbles and granules; VCS: very coarse sand; CS: coarse sand; MS:

medium sand; F/VFS: fine and very fine sand; Md: mud. Organic (Or) and microphytobenthic chlorophyll (mg/m^2) contents are also shown

Area	% Co	% PG	% VCS	% CS	% MS	% F/VFS	% Md	% Or	Chl <i>a</i>
Tomo	9.49 (1.58)	28.55 (0.78)	20.86 (0.83)	11.52 (0.48)	8.61 (0.39)	16.20 (0.88)	4.90 (0.34)	4.03 (0.16)	38.55 (2.13)
Teremba	7.99 (4.14)	14.24 (1.99)	9.75 (1.24)	15.70 (1.06)	15.01 (0.98)	18.56 (1.32)	18.74 (1.49)	7.16 (0.37)	164.16 (8.47)

thos, the area-species curves (relating the appearance of new species to the increase in area sampled) were calculated. In Teremba, the maximum number of species was attained for an area of 0.5 m^2 ; in Tomo, for an area of 1.0 m^2 . To reduce sorting time, five 0.2 m^2 and five 0.1 m^2 samples were collected from Tomo and Teremba, respectively, on each of the subsequent sampling dates. Samples were collected along a transect parallel to the shore line, at intervals of 50 m. At low tide, sediment was removed to a depth of 10 cm, washed through a 1 mm sieve, and preserved in neutral formalin. Animals and plants $> 3 \text{ mm}$ were sorted with the naked eye, the 1 to 3 mm size-fraction was stained with Rose Bengal and sorted under a dissecting microscope. After taxonomic identification, individuals were counted, dried at 60°C for 48 h, oven-heated at 550°C for 3 h, and their ash-free dry weight (AFDW) was estimated to the nearest 0.001 g. The taxa were classified by trophic group according to Chardy and Clavier (1988): macrobenthic primary producers, suspension-feeders (passive collection of suspended particulate material), deposit-feeders (active intake of food at the surface or from the sediment), herbivores, and carnivores.

Whereas species richness was expressed as a function of the total surface area sampled, i.e., 1.0 and 0.5 m^2 at Tomo and Teremba, respectively, density and biomass were expressed per m^2 . Temporal fluctuations in density and biomass were assessed by one-way ANOVAs, after verification of the normality of the data (Shapiro

and Wilk 1965) and homogeneity of variances (Hartley 1962). The Welsch test was used to separate possible sets of homogeneous months (Sokal and Rohlf 1981). In the case of non-homogeneous variances, data were treated by the non-parametric Kruskal-Wallis test (Siegel and Castellan 1989). Temporal variations in chlorophyll *a* contents were also examined using one-way ANOVAs, and the Tukey test was used to separate possible sets of homogeneous months (Sokal and Rohlf 1981).

Results

Description of the communities

In Tomo, the substrate consists of very coarse terrigenous sand with a low mud content; in Teremba, the substrate is a fine-to-coarse terrigenous sand with a medium mud content. The organic matter concentrations are similar at both sites, but chlorophyll *a* contents are higher in Teremba (Table 1). In Tomo, 84 animal and 7 plant taxa were identified in a total sample area of 8 m^2 , whereas 69 animal and 6 plant taxa were identified in Teremba in a

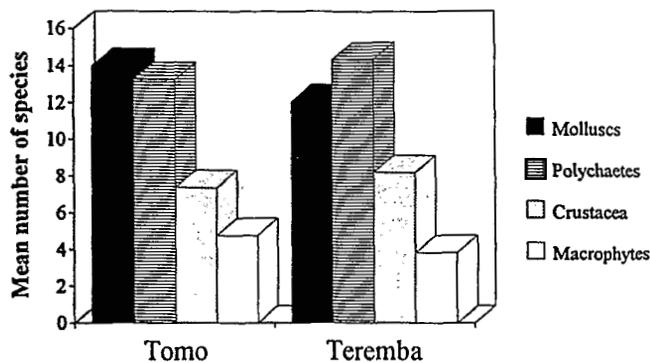


Fig. 2. Mean annual number of species of major zoological groups in *Halodule uninervis* bed at Tomo (nos./m²) and *Thalassia hemprichii* bed at Teremba (nos./0.5 m²)

total area of only 3 m². Although expressed per 0.5 m² at Teremba and per m² at Tomo, average species richness was greater in Teremba. However, when expressed per m², densities were similar at both sites and biomass was greater at Teremba (Table 2). Molluscs and polychaetes clearly dominated the faunal assemblages (Fig. 2). The brachiopod *Lingula anatina* accounted for 33% of the animals collected at Tomo; molluscs (especially the bivalve *Gafrarium tumidum* and the gastropod *Cerithium* sp.) and polychaetes (especially *Caulleriella* sp.) were also numerically abundant (Table 3). In Teremba, molluscs (especially the bivalves *Tellina* sp. and *Anadara scapha*) and polychaetes (especially *Ancystrosyllis constricta*) dominated numerically (Table 3). Suspension-feeders made up 51% of the fauna at Tomo, whereas deposit-feeders comprised 56% at Teremba and clearly dominated the trophic organization of the macrobenthic community. The fauna and flora contributed almost equally to the average biomass of the seagrass communities (33.8 g AFDW m⁻² in Tomo and 83.7 g AFDW m⁻² in Teremba), with animal:plant biomass ratios of 0.96 and 0.87 in Tomo and Teremba, respectively. The phanerogams *Halodule uninervis* (48% of plant biomass) and *H. pinifolia* (33%) dominated at Tomo, and *Thalassia hemprichii* constituted 70% of the plant biomass at Teremba. Molluscs accounted for 86 and 94% of the animal biomass at Tomo and Teremba, respectively. This was due to the marked dominance of the suspension-feeding bivalves *G. tumidum* (55% of animal biomass in Tomo) and *Anadara scapha* (72% in Teremba). In each seagrass bed, the macrophytes and suspension-feeders group (especially *H. uninervis*, *H. pinifolia* and *G. tumidum* in Tomo, and *T. hemprichii* and *A. scapha* in Teremba) accounted for >90% of the total biomass.

Temporal fluctuations in the seagrass communities

At both sites, maximum temperatures (27 to 30°C) were recorded from November to March and minimum temperatures (19 to 20°C) in July and August. Salinity ranged from 32 to 36‰, except in February and March when it dropped markedly (25‰ in February, 20‰ in

Table 2. Mean (SE) annual species richness (SR), density (D, nos./m²) and biomass (B, g ash-free dry wt/m²) of Tomo (*Halodule uninervis*) and Teremba (*Thalassia hemprichii*) seagrass-bed communities. SR is expressed as number of species per m² at Tomo and per 0.5 m² at Teremba

	Tomo	Teremba
SR	39.25 (1.70)	41.16 (2.81)
D	463.37 (58.18)	549.34 (25.38)
B	33.81 (3.39)	83.70 (11.34)

Table 3. Mean (SE) annual density (nos./m²), mean annual biomass (g ash-free dry wt/m²) and trophic status (SF: suspension-feeder; DF: deposit-feeder; H: herbivore; C: carnivore) of major species (density > 5 individuals/m²) in Tomo and Teremba macrobenthic communities, presented in order of decreasing numerical importance. -: biomass < 0.01 g ash-free dry wt/m²

Area and species	Density (SE)	Biomass (SE)	Trophic status
Tomo			
<i>Lingula anatina</i>	150.87 (25.47)	1.23 (0.19)	SF
<i>Gafrarium tumidum</i>	50.62 (5.95)	9.03 (0.88)	SF
<i>Caulleriella</i> sp.	49.01 (26.28)	-	DF
<i>Cerithium</i> sp.	45.87 (11.83)	0.99 (0.24)	H
Amphiurid	29.12 (5.26)	0.39 (0.07)	C
Synaptid	9.62 (0.88)	0.18 (0.03)	DF
<i>Anadara scapha</i>	8.50 (1.57)	3.22 (0.65)	SF
<i>Scoloplos</i> sp.	7.12 (1.96)	-	DF
Pagurid	6.87 (2.27)	0.08 (0.03)	C
<i>Ceratonereis</i> sp.	5.87 (5.23)	-	C
<i>Macrophtalmus</i> sp.	5.62 (1.09)	0.11 (0.02)	C
<i>Armandia leptocirris</i>	5.37 (2.19)	-	C
Caridid	5.12 (0.99)	0.15 (0.04)	C
<i>Spio</i> sp.	5.12 (1.99)	-	DF
Teremba			
<i>Tellina</i> sp.	181.66 (18.56)	1.06 (0.08)	DF
<i>Ancystrosyllis constricta</i>	43.66 (8.00)	-	DF
<i>Scoloplos</i> sp.	38.66 (10.60)	-	DF
<i>Anadara scapha</i>	38.34 (5.34)	28.00 (4.80)	SF
<i>Scolecopsis</i> sp.	26.34 (7.66)	-	DF
<i>Macoma</i> sp.	21.00 (6.26)	0.58 (0.16)	DF
Amphiurid	13.00 (2.74)	0.04 (0.01)	C
Pagurid	13.00 (4.74)	0.14 (0.04)	C
<i>Marphysa sanguinea</i>	11.66 (2.18)	0.12 (0.04)	C
Xanthid	10.66 (1.62)	-	C
<i>Loimia ingens</i>	10.34 (5.82)	0.12 (0.04)	DF
<i>Nematoneis unicornis</i>	10.34 (2.80)	0.02 (0.01)	C
Caridid	10.00 (4.66)	0.40 (0.22)	C
Tellinid	9.66 (4.04)	0.10 (0.02)	DF
<i>Gafrarium tumidum</i>	8.66 (1.38)	2.22 (0.22)	SF
<i>Ceratonereis</i> sp.	8.34 (1.52)	-	C
<i>Glycera tessellata</i>	8.34 (2.02)	0.06 (0.02)	C
<i>Thalamita</i> sp.	7.00 (1.98)	0.20 (0.10)	C
Syllid	6.34 (2.48)	-	C

March), during the passage of "Nancy" and "Hilda", two tropical depressions. Sediment structure in both seagrass beds (Fig. 3) was stable throughout the year, particularly during rainy periods, except for the two first Teremba samples which included a large cobble organic fraction (bivalve shell fragments). Organic matter content remained stable at between 3 and 5% at Tomo and

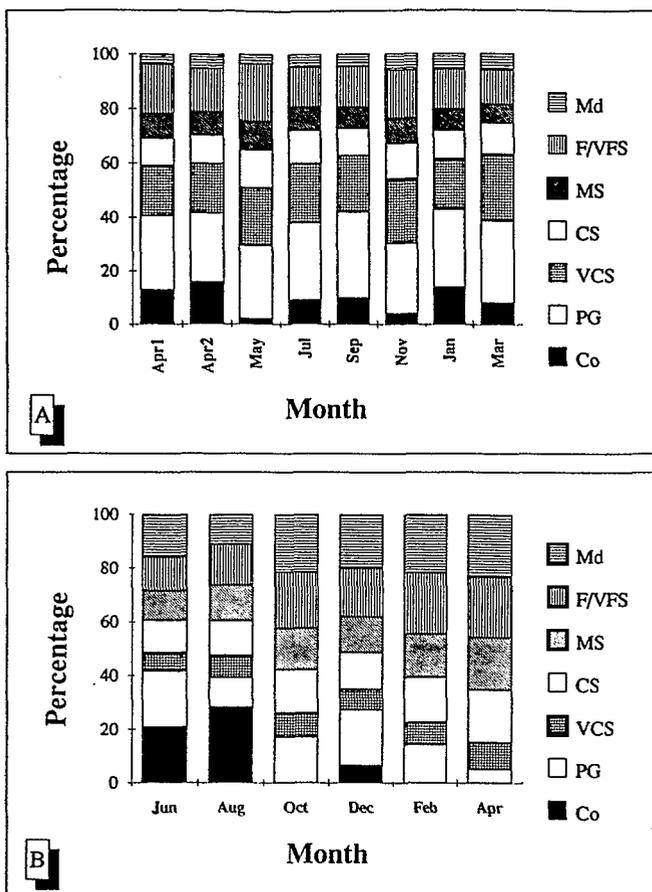


Fig. 3. Temporal evolution of mean granulometric distribution of sediment at Tomo (A) and Teremba (B). Abbreviations as in Table 1

5 and 8% at Teremba. The chlorophyll *a* content of Tomo sediments (Fig. 4) did not differ significantly between months ($F=1.96$, $P>0.05$, $df=112$); at Teremba (Fig. 4), there was an overall difference between months ($F=4.66$, $P<0.05$, $df=37$) but no seasonality, with only a higher chlorophyll content in March than during the rest of the year (Tukey test).

At Tomo (Fig. 5), faunal density varied significantly over the year ($F=2.94$, $P<0.05$), but no marked seasonality emerged, except that the January 1990 density was significantly greater than the April 1989 values (Welsch test). *Lingula anatina* and *Gafrarium tumidum* densities did not vary significantly ($F=0.51$ and $F=1.01$, $P>0.05$, respectively), whereas the density of *Caulleriella* sp. was significantly greater in November and January ($F=10.05$, $P<0.001$). Suspension-feeders consequently dominated the community numerically except in January, when deposit-feeders were numerically dominant because of the peak in the *Caulleriella* sp. population.

At Teremba (Fig. 5), overall density did not vary over the year ($F=0.81$, $P>0.05$) for either the major species, *Tellina* sp., or the rest of the community ($F=1.24$ and $F=1.03$; $P>0.05$, respectively). The trophic organization was remarkably stable, the deposit-feeders were consistently dominant and the density of all trophic group remained constant (ANOVAs).

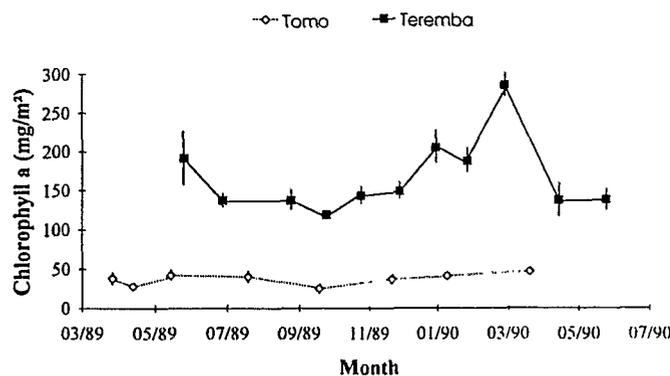


Fig. 4. Temporal evolution of microphytobenthic chlorophyll *a* contents of seagrass-bed sediments at Tomo and Teremba. Vertical bars indicate standard errors

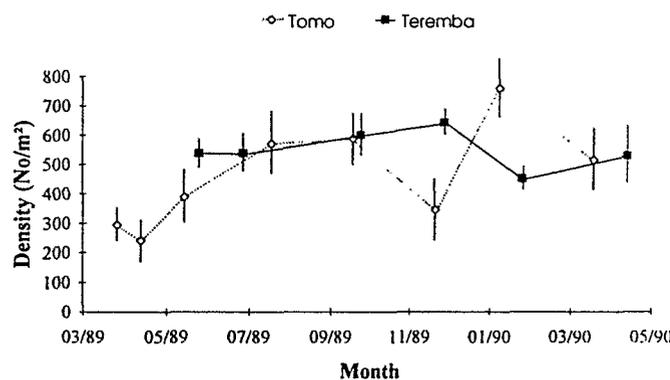


Fig. 5. Temporal evolution of density of macrobenthic communities (nos./m²) during study period. Vertical bars indicate standard errors

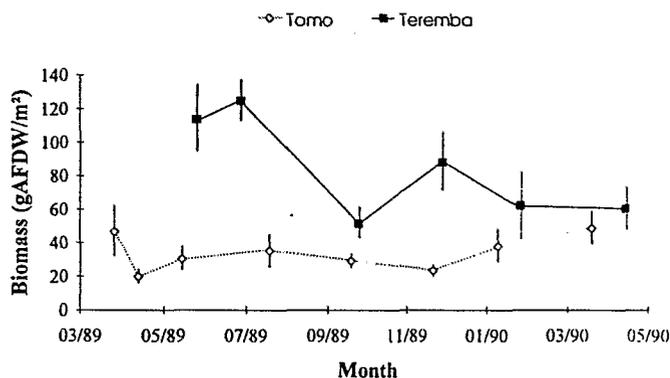


Fig. 6. Temporal evolution of total biomass of seagrass-bed communities (g ash-free dry wt/m²) during study period. Vertical bars indicate standard errors

Fig. 6 shows the annual patterns for the total biomass of the seagrass communities. At Tomo, total biomass did not vary significantly throughout the year ($F=1.05$, $P>0.05$). The absence of temporal fluctuations observed for animal and plant biomasses ($F=5.52$ and $F=0.73$, $P>0.05$, respectively) was particularly notable for *Gafrarium tumidum*. The macrophytes and suspension-feeders' group constituted $>90\%$ of the total biomass, the biomass of each trophic group being constant throughout the year (ANOVAs). In the Teremba commu-

nity, on the other hand (Fig. 6), biomass varied significantly ($F=3.00$, $P<0.05$) because of a significantly greater biomass in August than in October (Welsch test). The total animal biomass remained constant as did that of *Anadara scapha* ($F=1.73$ and $F=1.79$, $P>0.05$, respectively). Plant biomass varied significantly ($F=4.20$, $P<0.05$), with the biomass in June being greater than during the rest of the year, except August (Welsch test). This greater biomass during the cool season arose from the contribution of rare phanerogams (*Halodule uninervis* and *Cymodocea rotundata*); *Thalassia hemprichii* biomass remained constant (ANOVAs). Finally, the macrophytes and suspension-feeders' group always accounted for >95% of the total biomass.

Discussion

The Tomo community was dominated by the brachiopod *Lingula anatina*, which occurred in highest densities on vegetationless areas within the seagrass bed. Apart from *L. anatina* at Tomo, the seagrass communities at both Tomo and Teremba were clearly dominated by molluscs and polychaetes. Broom (1982) reported the dominance of molluscs on intertidal mud-flats of Malaysia coincident with an absence of polychaetes. However, polychaetes are generally dominant in tropical sandy-muddy bottoms, along with crustaceans (Ledoyer 1967, Thomassin 1978, Grelet et al. 1987, Vargas 1987, Alongi 1990). Swennen et al. (1982) recorded a dominance of isopods and amphipods on the intertidal mud-flats of Surinam. The almost complete absence of these organisms from the seagrass beds of Tomo and Teremba is most probably due to the low mud content of the sediments in these areas.

Tropical seagrass beds generally have animal:plant biomass ratios of <1. On the Aldabra atoll (Indian Ocean), mixed seagrass beds (*Thalassodendron ciliatum*, *Thalassia hemprichii* and *Cymodocea ciliata*) are characterized by average plant biomasses of 600 g AFDW m^{-2} (Hughes and Gamble 1974), and animal biomasses (<30 g AFDW m^{-2}) are dominated by motile fauna (crustaceans, polychaetes and echinoderms). In intertidal and subtidal Indonesian seagrass beds, Nienhuis et al. (1989) measured plant biomasses of 2000 g AFDW m^{-2} , of which the *T. hemprichii* biomasses equalled 500 g AFDW m^{-2} . Nienhuis et al. also reported animal biomasses from 40 to 60 g AFDW m^{-2} , with poriferans and holothurians as dominants. Compared to those values, the plant biomass recorded in the present study for Tomo and Teremba (17 and 45 g AFDW m^{-2} , respectively) are relatively low. These low biomasses (particularly the low rhizome and root biomasses) would appear to favour an abundant non-motile macroinfauna, such as the bivalves *Gafrarium tumidum* and *Anadara scapha* because of sufficient space to develop. This bivalve dominance among the fauna, in low-biomass seagrass beds, would appear to be similar to those previously observed for other bivalves in temperate and tropical unvegetated intertidal zones by many authors, including Squires et al. (1973), Beukema (1976), Hibbert (1976), Broom (1982), Borrero (1986) and Wolff et al. (1987).

As pointed out by Rhoads and Young (1970), intertidal seagrass beds are mixed places where suspension-feeders and deposit-feeders coexist regardless of the mud content of the sediment. As far as biomass is concerned, suspension-feeders clearly dominate the fauna in the two seagrass beds of the present study area. Epibenthic suspension-feeders have been shown to constitute the major trophic group in the New Caledonian south-west lagoon (Chardy and Clavier 1988), even in muddy substrates. However, Broom (1982) reported deposit-feeders to dominate, in terms of biomass, on Malaysian intertidal mud-flats. This obvious contradiction with our Teremba results is explained by the fact that Broom classified bivalves of the genus *Anadara* as facultative surface deposit-feeders.

Studies dealing with temporal fluctuations of tropical macrobenthos are scarce in the literature. In monsoon-affected regions, changes in substrate granulometry and/or decreases in salinity after heavy rains cause a decline in the number of species and density of the macrofauna (Ansell et al. 1972, Le Fur 1978, Ansari et al. 1986). In other regions not subject to important erosion, faunal response to environmental perturbations occurs mainly at the species level, and the response of the community as a whole depends on the intensity, duration and time of occurrence of the environmental change (Alongi 1990). In Malaysia, fluctuations in the densities of macrobenthic communities over the year reflect recruitment synchronism of major species (Broom 1982). In the intertidal mud-flats of Costa-Rica, seasonality in the density of such communities observed by Vargas (1987) resulted from fluctuations in the densities of the four major species after reproduction. In the present study, the macrobenthic community of Tomo displayed a fairly constant species richness and biomass throughout the year, but a greater density during the hot season arising from a peak in abundance of one polychaete (*Caulleliella* sp.). The abundances of other major species in Tomo did not vary significantly over the year; in the Teremba community also, no major species displayed significant numerical variations. The absence of mortalities during the brief low-salinity periods and of distinct recruitment periods enabled a stable community structure and trophic organization to be maintained throughout the year. Riddle et al. (1990) explained the absence of seasonal variations in tropical benthic communities by (1) constant food availability throughout the year, and (2) non food-limited fauna. The microphytobenthic chlorophyll *a* contents of Tomo and Teremba sediments, which represent an important part of the available food for suspension-feeders after resuspension, and for deposit-feeders *sensu stricto*, are high and constant throughout the year. Neither the organic matter content of the sediment nor the biomass of the major macrophytes display temporal fluctuations. The seagrasses constitute a relatively stable habitat for the macrofauna and produce constant amounts of dissolved organic carbon (Duarte 1989). The sedimentary structure does not change seasonally, it is stabilized by the macrophytes, and the seagrass beds are additionally in sheltered positions. However, the fine-fraction content of the sediments would have been expected to increase

after heavy rains. The lack of such increase is more easily explained for Tomo, which is near a sandy-muddy beach, than for Teremba, which would have received deposits from the adjacent mangroves. In Australian lagoons, the composition of macrobenthic communities changed after Cyclone "Winifred" had passed over (Riddle 1988), but the communities displayed no seasonality (Riddle et al. 1990). In Tomo, the sedimentary structure was stable, even after the passing of Cyclone "Lili". The absence of community changes is therefore not surprising, since Riddle (1988) demonstrated the close relationship between changes in macrobenthic communities and substrate granulometry in tropical areas.

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