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A QUANTITATIVE SURVEY OF THE BIOTA OF INTERTIDAL SOFT SUBSTRATA ON ALDABRA ATOLL, INDIAN OCEAN

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CONTENTS

Intertidal, soft substrata on the peripheral reef flat and within the lagoon of Aldabra Atoll were sampled at 24 stations chosen to represent a wide range of habitats. At each station, densities and biomass were estimated from sieving, or from samples of vegetation; by using a random series of quadrats in the case of smaller species; or searches of a wider area in the case of larger, more dispersed species. Where appropriate, the area of substratum covered by plants was recorded and samples of plant material were retained for estimating biomass. The degree of tidal emersion was noted.

Estimates of biomass were derived from laboratory determinations of the ash free dry masses of samples of each species, previously fixed in saline formalin and from their estimated densities. Biomass was finally presented as being in units of kcal m^{-2} from published energy (calorific) values for the different taxa (1 cal = 4.184 J). Very approximate estimates of secondary productivity were made by multiplying the total station animal biomass by the P/B ratio of 1.76 derived from Moore (1972).

An ordination of the stations produced a graphical display reflecting the different categories of habitat surveyed. The station groupings on the ordination diagram were derived solely from species distributions, thus lending support to our conclusions of how

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community structure was determined by the environmental conditions. The main categories of habitat were marine angiosperm beds in the lower intertidal, sand flats above the level of angiosperm growth, mobile sand bars and anaerobic mud associated with mangroves.

The faunal equitability at each station was studied by using relative abundances of species expressed as their proportional contribution to the total biomass. In all cases, most of the biomass was represented by 3–14 species which tended to have widespread distributions within the area surveyed. Species richness was minimal on the mobile sand bars, increased with the amount of plant cover, and was maximal where angiosperms were covered by a multispecific algal mat.

The group of stations with plant cover had a significantly greater animal biomass than the sandy stations. Since this greater biomass was largely distributed among a few dominant species, it was probably due to the increased primary production. In contrast, species richness increased with topographical complexity.

The mean estimate of angiosperm biomass (2172 kcal m^{-2}) was similar to the value derived from Moore *et al.* (1968) for a subtidal bed of *Thalassia testudinum* in Florida.

Secondary productivity was least on the mobile sand bars and anaerobic mud (< 10 kcal $cm^{-2}\,a^{-1}$). Sand flats were more productive (10–100 kcal $m^{-2}\,a^{-1}$) with values close to those derived from Moore (1972) for subtidal muddy sand in Florida and Massé (1972) for the sublittoral of a clear, sandy bay in the northwest Mediterranean. Secondary productivity was greatest in the angiosperm beds (100–1000 kcal $m^{-2}\,a^{-1}$) with values similar to those of intertidal angiosperm beds in Florida (from Moore 1972).

1. Introduction

This paper reports the results of the faunal survey of intertidal soft substrata carried out during April to July 1968 as phase IV of the Royal Society Expedition to Aldabra.

The survey was confined to substrata which could be sampled by coring. Our objectives were to obtain fauna lists and estimates of biomass which could be used as guides to the benthic productivity or compared with those from other marine habitats.

To obtain reliable estimates of biomass, randomized replicate sampling units were taken at each station. This procedure was time-consuming so that only 24 stations could be surveyed. Stations were selected to include a wide range of habitats.

A faunal list with authorities is given in the appendix. The numbers and biomass per m^2 of the species recorded are deposited at the Department of Zoology, British Museum (Nat. Hist.).

Collections of amphipods, isopods and tanaid crustacea remain to be examined.

2. Sampling methods

At each station a 5 m square was marked out and from within this ten 1 m squares were chosen with reference to random number tables. A 0.25 m^2 quadrat of sides 50 cm was placed centrally in each 1 m square.

A cylindrical core 14 cm deep was taken from the centre of each quadrat with a tin of 7.15 cm diameter. This core was sieved through a 0.5 mm nylon mesh. Cores taken in a similar manner from each corner of the quadrat were sieved through a coarser (1.59 mm) nylon mesh.

One core per station was retained intact in formalin for sediment analysis in the laboratory.

All animals retained by sieving were fixed in 4 % saline formalin and labelled with the code number of the quadrat whence they came.

Five of the 0.25 m^2 quadrats were excavated to about 40 cm and sieved in the field through a 2 mm metal sieve. All the animals were preserved for later analysis.

The surface area covered by each plant type (angiosperms and algae) was estimated in eighths for each of the ten 0.25 m^2 quadrats. Angiosperms, *Halimeda* and algal mat (intermeshing of algae epiphytic on angiosperms) were cleared from each of the 10 quadrats, drained of excess water and weighed. A known mass of each plant type was fixed in formalin for subsequent ash free dry mass determination. A sample of angiosperm was excavated intact, followed by separation of the rhizomes from the leaves. The ratio of underground material to leaves was determined by weighing. Samples of rhizomes and roots were fixed in formalin for ash free dry mass determination.

About 100 g of each plant type were sorted for animals which were then fixed in formalin. Larger epibenthic animals, mainly gastropods, were collected by hand from a 20 m square. Since most species burrowed just beneath the surface of the substratum during the day, the 400 m^2 area was searched at night while the gastropods and decapod crustaceans were foraging.

Where certain gastropods were abundant, their size frequencies were recorded and a sub-sample retained for ash free dry mass–shell length regression. This procedure prevented unnecessary destruction of individuals and reduced the bulk of the samples.

The red burrowing prawn *Axius acanthus* was exceedingly difficult to excavate. In order to save time and to prevent undue disturbance of the habitat, the *Axius* populations were estimated by counting the holes, while population biomass was estimated by using the mean mass of three individuals.

After the identifications had been completed, all species were counted and expressed as the number per square metre.

Samples of each species were dried for 48 h at 70 °C, weighed, ashed at 550 °C for 7 h and reweighed to determine their ash free dry masses. This was necessary to overcome the effects of the widely different ash contents of different taxa and of the amount of sediment in the alimentary canal. Ash free dry masses were used to estimate biomass per m^2 for each species. The biomass of each phylum was converted to kcal m^{-2} by using the energy (calorific) equivalents given in Cummins & Wuycheck (1971). From these figures the total biomass at each station was calculated as kcal m^{-2} (1 cal = 4.184 J), thus facilitating comparisons with other ecosystems.

3. General description of the Aldabra littoral zones

Details of the climate, topography, geomorphology, biota of rocky intertidal habitats, tidal regime and previous scientific work on Aldabra are presented in Westoll & Stoddard (1971).

Aldabra lies at latitude 9° 24′ S and longitude 46° 20′ E in the path of the SE trades which blow constantly from April to December. More variable winds blow from the northwest during the remaining four months.

The atoll is slightly elevated with maximum dimensions of 34 km from east to west and 14.5 km from north to south. The land rim consists of four main islands (figure 1) separated by channels linking the shallow lagoon with the ocean. Within the lagoon are two larger islands, Ile Esprit (0.34 km^2) in the west, Ile Michel (0.4 km^2) in the east and many smaller islands, often connected to the land rim at low water, which are concentrated along the south shore of Middle Island and along the eastern shore of South Island.

Undercut reef rock cliffs rise 3.5–4.5 m above the peripheral (oceanic) reef flat. The latter is narrowest (100 m) on the eastern, windward coast and is widest (460 m) on the western, lee-ward coast, while averaging 180–280 m along the north and south coasts. The reef flat consists of reef rock planed by solutional and biological erosion. It has a thin, discontinuous cover of cobbles, gravel and sand which often supports extensive stands of algae and marine angiosperms. An intermittent boulder zone occurs at the seaward edge of the platform on the windward (east) coast, while on the leeward (west) coast, mobile sand bars are frequent on the outer half of the reef flat. The landward edge is terminated by the limestone cliffs which are highest (4–5 m) on the most exposed, east coast where the reef flat is deeper and narrower than elsewhere, and are low or poorly developed on the sheltered, west coast where they may give way to sand beaches and slabs of beach rock.

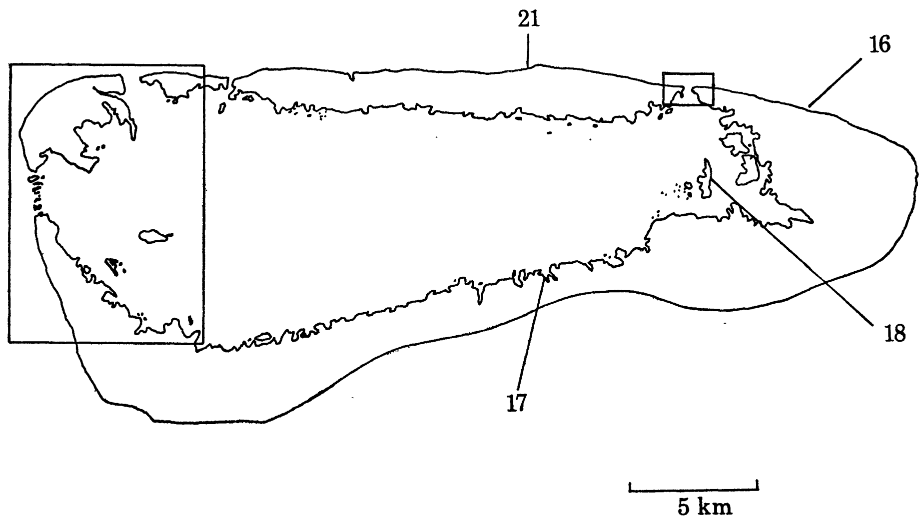
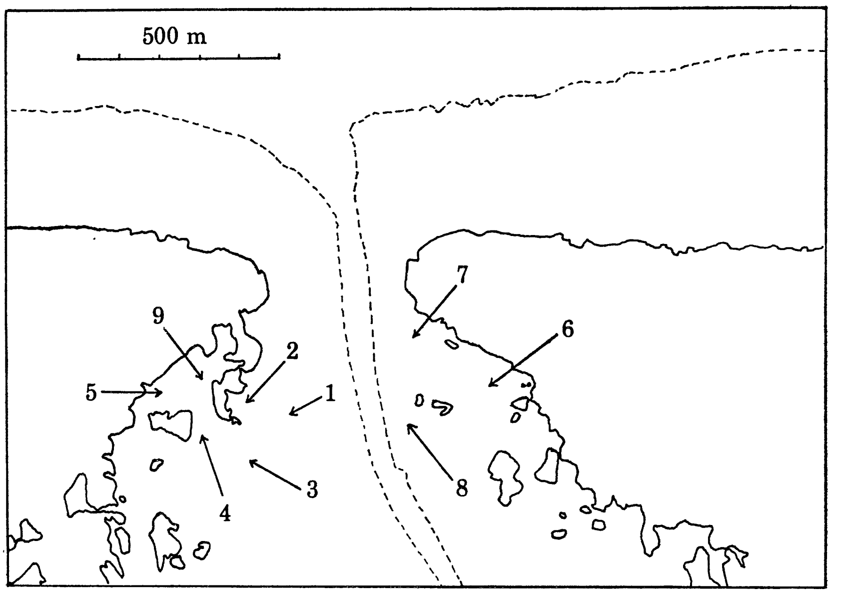


FIGURE 1. Aldabra Atoll: Locations of the sampling stations.

The lagoon varies in width from 6 to 10 km and has a smooth, rock floor thinly covered with sediment except in the vicinity of the channels where sediments are thicker.

The landward edges of the lagoon shores are terminated either by mangroves or by highly dissected, undercut limestone cliffs. The cliffs are highest (2–2.5 m) near channel entrances but decrease to 0.5 m within the lagoon as the tidal range decreases. Intertidal platforms, varying in width up to 300 m at East Channel, but elsewhere less than 50 m, have been formed by recession of the limestone cliffs. The lagoon platforms generally have a bare, smooth surface but may be covered by poorly sorted deposits at lower levels or near the channels where they tend to support extensive marine angiosperm beds.

Owing to the influence of the Moçambique Channel, tides on the peripheral reef flats of Aldabra are unusually large, with a mean spring range of 2.74 m. On passing along the channels into the lagoon the tidal range quickly decreases. Pronounced time lags interfere with lagoonal tides so that there is hardly any rise and fall on the smallest neaps. Drainage off lagoon platforms is slow and towards spring tides more water enters the lagoon through the channels than can drain away before the next tide. The water level rises until up to 30 cm remain on the lagoon platforms at low water springs. The largest periods of emersion coincide with neap tides when less water enters through the channels. On the peripheral reef flats extreme low water occurs on spring tides at midday. Emersion of the lagoon platform is longest on neap tides between 06h00 and 08h00. Consequently, the peripheral reef flats receive intense insolation during the longest periods of emersion whereas the lagoon platforms do not.



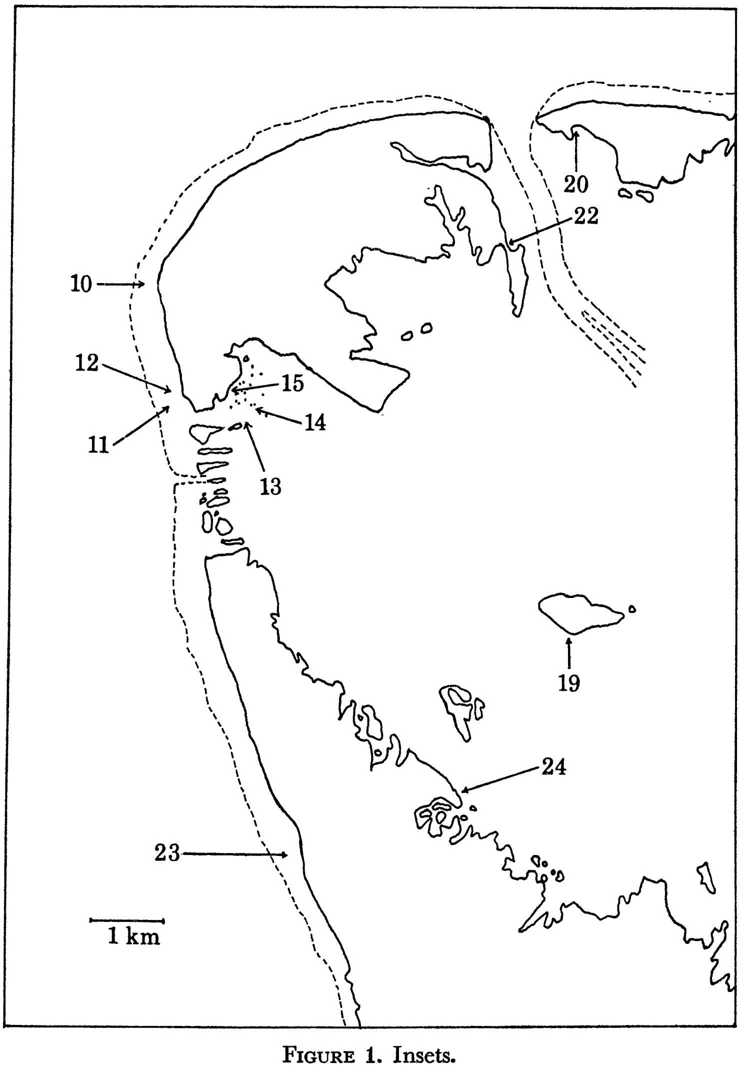


FIGURE 1. Insets.

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4. Description of stations

(and a brief review of their fauna and flora) (figure 1))

Locality: East Channel (*Passe Houareau*)

Stations 1–9 were chosen to represent the full range of intertidal soft substrata found on either side of East Channel immediately within the lagoon. The tidal characteristics and substratum types of this extensive intertidal area, called the Marquoix Platform, have been studied by Farrow & Brander (1971).

Station 1 lay 150 m perpendicular to the sand beach at Middle Camp. Due to time lags in the lagoon drainage system, the water level fell lower on neap tides than on springs. At low water neap, the tips of the angiosperm foliage just became emersed, but were covered by about 9 cm of water during low water springs.

A mixed stand of *Thalassodendron ciliatum* (Forsk.) den Hartog (formerly *Cymodocia ciliata* Ehrenb. ex Aschers., see den Hartog, 1970) and *Thalassia hemprichii* (Ehrenb.) Aschers. covered about seven eighths of the surface area. Tufts of *Halimeda* sp. occurred among the angiosperms while the latter were covered by a multispecific algal-mat in half the sampling units. This algal-mat contained an intricate intermeshing of species such as *Acanthophora* spp., *Laurencia* spp., *Gracilaria* spp., *Dictyosphaeria* spp. such as described by Price (1971).

Expressed as percentage contribution to the total biomass (ash free g per m^2), the following species were the most important. (In all subsequent station descriptions, only those species accounting for at least 1.5 % of the total biomass will be listed. The numbers in parentheses are the percentage contributions, i.e. relative abundance.)

Typhlocarcinodes piroculatus (26.8), Pagurid (23.3), *Chlorodiella laevissima* (9.6), *Eurythoe complanata* (3.4), *Chlorodopsis negrocrinita* (3.2), *Hesione splendida* (3.1), *Brissus latecarinatus* (2.9), *Menaethius monoceros* (2.0), *Ophiocoma valenciae* (1.6).

All these speceis except the burrowing *Brissus latecarinatus* move actively among the angiosperms, especially within the algal-mat.

Although not important members of the biomass, 21 species of gastropod were recorded. Most of these were small forms living among the plants. As in all stations containing angiosperms, large numbers of the tiny neritid *Smaragdia rangiana* were found grazing over the *Thalassia* and *Thalassodendron* leaves. Those found on *Thalassia* were always of a light green colour while those on *Thalassodendron* tended to be larger and of a reddish hue in accordance with the colour of the host plant. Dead *Smaragdia* shells were exceedingly numerous on the surface of the sediment or trapped among the algal-mat, making the counting of live individuals more difficult.

Small polychaetes belonging to the Syllidae, Nereidae and Hesionidae swarmed within the algal-mat which also harboured large numbers of polyclads, juvenile *Thalamita* spp., small xanthid species, hermit crabs, tanaids and amphipods.

Station 2 lay 50 m out from the beach at Middle Camp. Tidal emersion was similar to that of station 1. About seven eighths of the surface area was covered by a pure stand of *Thalassia*. The density of the leaves of *Thalassia* always seemed less than that of *Thalassodendron* in that more of the substratum could be seen between the former. The *Thalassia* was almost completely covered by a thick, brown algal-mat.

Important members of the biomass were: *Typhlocarcinodes piroculatus* (24.8), *Axius acanthus* (21.7), *Dasybranchus caducus* (6.8), *Codakia tigerina* (6.3), *Chlorodopsis granulata* (5.8), *Thalamita* *integra* (4.6), *Ochetostoma* sp. 1 (4.2), *Lumbrinereis latreilli* (4.0), *Ceratonereis mirabilis* (3.1), *Phymodius ungulatus* (3.0), Pagurid (2.5), *Ophiocoma brevipes* (2.2), *Conus arenatus* (1.8), *Etisus electra* (1.5).

The algal-mat teemed with small epifauna typical of angiosperm–algal mat communities, notably *Cerithium rostratum*, *Pyrene dautzenbergi*, *Columbella varians*, *C. turturina*, *Phasionella aethiopica*, *Leptothyra candida*, *Smaragdia rangiana*, Syllidae, Nereidae, *Amphipholis squamata*, polyclads, *Thalamita* spp., and small xanthidae.

This station supported a good population of the red Thalassinid prawn *Axius acanthus* whose burrows were a conspicuous feature of most angiosperm beds.

Station 3 was about 170 m SSE of Middle Camp, being covered by 2–3 cm of water at low water neaps. The substratum was completely covered by a thick stand of *Halimeda* sp., among which were found occasional leaves of *Thalassia* and *Thalassodendron*. Beneath the *Halimeda* were large quantities of rotten rhizomes suggesting that a once thriving angiosperm bed was giving way to *Halimeda* in a kind of succession.

Dominant species (biomass) were: *Hesione splendida* (35.9), *Syllis exilis* (16.7), *Lumbrinereis latreilli* (7.1), *Chlorodiella laevissima* (5.4), *Lophozozymus dodone* (3.6), *Typhlocarcinodes piroculatus* (3.6), *Eurythoe complanata* (3.4), *Etisus electra* (2.9), *Ophiocoma dentata* (2.3), *Ophionereis dubia* (2.1).

Small specimens of the pearl oyster *Pinctada margaritifera* were relatively abundant in this area but the population was probably limited by the local fishermen who searched the area for *Pinctada*. Most of the *Pinctada* harboured a pair of the commensal Pontonid crustaceans *Conchodytes tridacnae*.

The interstices of the *Halimeda* provided suitable habitats for small epifaunal species, many of them typical of algal-mats. Particularly favoured were small bivalves such as *Lasaea rubra*, *Lima natans*, *Chlamys cuneolus*, *Galeomma ambigua*; Syllidae, Nereidae, Hesionidae, the small, orange aphroditid *Iphione muricata*, the amphinomid fire worms *Eurythoe complanata* and *Pherecardia striata*, *Glycera lancadivae*, Spionidae, Eunicidae, Capitellidae, Terebellidae; *Ophionereis dubia*, *Ophiactis savignyi*; polyclads and xanthids. A small anemone was commonly attached to the blades of *Halimeda*.

Station 4 was about 120 m SW of Middle Camp in a sheltered situation between the Middle Camp peninsula and a small mangrove covered island. The substratum was emersed at low water neaps but much of the area retained a 2–3 cm layer of standing water.

About six eighths of the fine, sandy substratum was covered by a pure stand of *Thalassia*. Occasional clumps of algal-mat had drifted into the *Thalassia* leaves.

The patchwork of sandy areas among *Thalassia* seemed to favour more species of *Conus* and *Cypraea*. Small gastropods typical of plant cover such as *Cerithium rostratum*, *Mitrella blanda*, *Phasionella aethiopica*, *Smaragdia rangiana* occurred among the *Thalassia* while the sandy areas supported burrowing species such as *Natica marochiensis*, *Polynices mammilla*, and those which hide just beneath the surface by day while moving over the substratum at night to hunt or graze, e.g. *Conus lividus*, *C. arenatus*, *C. tessulatus*, *C. quercinus*, *Cypraea annulus*, *C. moneta*.

Sedentary polychaetes, sipunculids and holothurians became more important among the sand patches. 96.1 % of the biomass was represented by: *Chiridota violacea* (23.8), Pagurid (16.3), *Thalamita chaptali* (11.7), *Menaethius monoceros* (11.0), *Thalamita integra* (6.8), *Conus arenatus* (5.5), *Dasybranchus caducus* (4.3), *Smaragdia rangiana* (3.9), *Pinna muricata* (3.3), *Dardanus deformis* (3.1), *Siphonosoma cumanense* (2.5), *Clibanarius* sp. (2.3), *Ochetostoma* sp. (1.6).

Station 5 was in a sheltered situation about 100 m east of Middle Camp. Apart from shallow pools, the substratum was emersed for about 2 h at low water neaps. Only about one eighth of the surface area was covered by *Thalassia*.

Although the sandy substratum appeared rather barren during the day, night collecting revealed a rich gastropod fauna. Small pools occurred as depressions between wide mounds of sand thrown up by the long red holothurian *Chiridota violacea*, which was therefore not only the dominant species but also responsible for major structural features of the habitat.

Because of their abundance, about 20 specimens each of *Conus arenatus*, *Conus tessulatus*, *Cypraea annulus*, and *Bulla ampulla* were taken for ash free dry mass–shell length regressions, to be used for estimating biomass.

85.8 % of the biomass was due to the following species: *Chiridota violacea* (56.6), *Axius acanthus* (8.6), *Siphonosoma vastum* (5.4), *Conus arenatus* (2.8), *Tellinella crucigera* (2.3), *Scolelepis squamata* (2.1), *Siphonosoma cumanense* (2.1), *Nassarius horridus* (2.1), *Bulla ampulla* (1.9), *Codakia tigerina* (1.9).

Station 6 was situated close to the fossilized coral cliffs on the east side of the Channel. The site was one of extreme shelter, being protected by the *Casuarina* trees and raised coral cliffs from SE trades and by small islands towards the Channel. A very soft, 30–60 cm layer of sediment lay over muddy rock and was seven eighths covered by a mixed stand of equal proportions of *Thalassia* and *Thalassodendron*. The western half of the angiosperm bed was slightly higher than the rest, with no residual layer of water at low tide. It was covered by a silt-laden algal-mat, composed mainly of *Ceramium* sp., which harboured multitudes of small amphipods and tanaids.

Samples of *Conus lividus* and *Strombus mutabilis* were retained for ash free dry mass–shell length regression.

The following species comprised 88.8 % of the biomass: *Dardanus deformis* (53.2), *Thalamita chaptali* (12.4), *Menaethius monoceros* (8.6), *Siphonosoma cumanense* (4.1), *Ebalia erosa* (3.5), *Thalamita integra* (2.4), *Dasybranchus caducus* (2.3), *Bulla ampulla* (2.3).

The fine, silt-laden algal-mat did not support the large numbers of small gastropods, errant polychaetes and xanthids typical of other algal-mats. This station, however, was particularly rich in larger gastropods, e.g. 6 species of *Conus*, 3 *Cypraea*, 2 *Terebra* and 4 *Strombus*.

Station 7 was situated further towards the mouth of East Channel in a slightly less sheltered situation than station 6. The site was a long, mobile sand bar with pronounced ripples of about 30 cm from crest to crest, about 5 cm in height and oriented transversely to the length of the sand bar. Evidently the well sorted coarse sand bar was produced by the strong tidal currents converging towards the mouth of East Channel. The sand was emersed for 2–3 h at low water springs and formed a layer about 10 cm deep over rock. Coarser sand lay in the troughs than on the ridges of the ripples and many stones were hidden beneath the surface.

The sparse fauna had to be collected by raking the sand manually. Since it was impractical to sample 400 m^2 in this manner, the sand bar was divided into 4, 10×10 m areas along its length. Twenty-five 1 m^2 quadrats were chosen at random from each of the 4 squares for sampling.

Only 15 species were recorded, 9 of which comprised 99 % of the biomass: *Muraenichthys macropterus* (47.0), *Albunea* sp. (12.2), *Kraemeria samoensis* (11.2), *Capitobranchus* sp. (7.8), *Siphonosoma cumanense* (6.2), *Oliva episcopalis* (5.2), *Terebra maculata* (4.2), *Oliva annulata* (2.6), *Dasybranchus caducus* (2.6).

Most of the species are specially adapted to rapid burrowing through the clean sand. Typical of these animals are the highly polished *Oliva* and *Terebra* spp., the burrowing fishes *Muraenichthys* and *Kraemeria*, and the white anomuran *Albunea*.

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Station 8 was situated approximately 300 m south of station 7 and 50 m from the edge of East Channel. It was slightly less sheltered than station 6, in an area of slack tidal currents, emersed for some 2 h at low water springs.

About five eighths of the clean sandy substratum was covered predominantly by *Thalassia* with a small proportion of *Thalassodendron* and an admixture of *Halimeda*. Areas of *Thalassodendron* appeared to have been cropped down to the main stem, possibly by green turtles or herbivorous surgeon fish seen in the area. There was a poorly developed algal-mat. The area supported a large population of *Axius acanthus* among which were several very large (3 cm diameter) burrows of undetermined origin.

82.6 % of the biomass was rather evenly apportioned among 10 dominant species: *Thalamita chaptali* (15.5), *Menaethius monoceros* (13.2), *Metalia spatagus* (11.9), *Axius acanthus* (10.9), Pagurid (8.5), *Tellinella crucigera* (5.8), *Dasybranchus caducus* (5.6), *Clibanarius* sp. (5.0), *Siphonosoma cumanense* (4.4), *Aonides oxycephala* (1.8).

Station 9 was in the very sheltered backwater immediately behind (east) Middle Camp. Tidal currents were extremely slack and even on low water neaps there were 3–4 cm of standing water with algal-mat just breaking the surface. Only a very sparse stand of *Thalassia* was present but seven eighths of the surface area was covered by a thick mat of *Enteromorpha* sp.

Large numbers of *Cerithium echinatum* were present, some of which were retained for ash free dry mass–shell length regression.

Dominant species (91.2 % of biomass) were: *Dasybranchus caducus* (48.5), *Cerithium echinatum* (11.3), *Siphonosoma vastum* (11.0), *Thalamita integra* (5.5), *Syllis exilis* (5.1), *Holothuria pardalis* (4.1), *Typhlocarcinodes piroculatus* (2.0), *Codakia tigerina* (1.9), *Lumbrinereis latreilli* (1.8).

Apart from *Cerithium echinatum*, molluscs were relatively scarce. The *Enteromorpha* mat supported large numbers of the small polychaete *Syllis exilis* and ophiuroid *Amphipholis squamata*.

Locality: West Island (Ile Picard)

Station 10 was a sand patch surrounded by angiosperm beds and rubble half way out on the reef flat near the westernmost corner of West Island. Here, as elsewhere on the peripheral reef flat, the tidal situation is more normal, with longer emersion on low springs than neaps. Station 10 was emersed for 2–3 h at low springs. It was sheltered from the SE trades but unprotected from the west.

There was no vegetation. The sand was covered with small ripples perpendicular to the beach and there were occasional rocks.

Only 21 species were recorded, 9 of which comprised 97.4 % of the biomass: *Glycera lancadivae* (40.4), *Scolelepis squamata* (23.9), *Clibanarius* sp. (14.4), *Kraemeria samoensis* (5.7), *Nichomache* sp. (3.5), *Dasybranchus caducus* (3.3), *Dardanus deformis* (2.7), *Bulla ampulla* (2.0), *Lepidasthenia elegans* (1.5).

Most of the species present were typical of sandy areas with occasional immigrants from stony areas and angiosperm beds, e.g. *Columbella turturina*, *Vasum turbinellus*, *Gutturnium muricinum*. The specimen of *Conus ebraeus* encountered was probably derived from the well established population on the beach rock at the landward edge of the reef flat.

Station 11 was midway on the reef flat just to the north of Passe Femme (West Channels) in an area of moderate tidal currents. Exposure was similar to station 10 but the substratum remained covered by 1–2 cm of water at low water springs. The substratum was very stony and difficult to sample. About four eighths of the surface area was covered by a sparse stand of *Thalassia*. The holes of *Axius acanthus* were a conspicuous feature.

90.1 % of the biomass was due to the following species: *Axius acanthus* (33.5), *Siphonosoma vastum* (23.3), *Kraussia nitida* (13.1), *Typhlocarcinodes piroculatus* (8.9), *Menaethius monoceros* (6.2), *Clibanarius* sp. (2.0), *Siphonosoma cumanense* (1.6), *Dasybranchus caducus* (1.5).

The rather clean *Thalassia*, devoid of algal-mat, did not support many epibenthic species.

Station 12 was about a quarter of the way out on the reef flat slightly north of Point Passe Femme. Exposure was as for stations 10 and 11. A fairly strong current flowed northwards parallel to the beach due to tidal outflow from the lagoon.

The spongy, muddy substratum was topped by calcareous foraminiferan debris. A luxuriant stand of *Thalassia* covered the entire surface area.

Species accounting for 92.8 % of the biomass were: *Pagurus* sp. (48.6), *Siphonosoma vastum* (17.0), *Thalamita integra* (5.8), *Clibanarius* sp. (5.1), *Liomera monticulosa* (3.9), *Dasybranchus caducus* (3.4), *Phymodius ungulatus* (2.5), *Siphonosoma cumanense* (1.8), *Ophiocoma valenciae* (1.7), *Smaragdia rangiana* (1.5), *Conus arenatus* (1.5).

As with station 11, the clean *Thalassia* did not support a very rich epibenthic fauna.

Locality: Lagoon, Passe Femme (West Channels)

Station 13 was immediately behind Ilot Parc, exposed to SE winds across the lagoon and subject to gentle flood-tide currents sweeping northeastwards from Passe Dubois. The substratum was emersed for about 1 h at low water springs and for about 2 h during the later neaps due to the time lags involved in flushing the lagoon.

About seven eighths of the surface area was covered by *Thalassia* with a fine algal-mat of *Ceramium* sp. The latter tended to accumulate detached *Thalassia* leaves, as occurred at station 6.

The following species accounted for 88.7 % of the biomass: *Thalamita admete* (21.1), *Dasybranchus caducus* (21.0), *Siphonosoma cumanense* (8.6), *Menaethius monoceros* (8.3), *Thalamita chaptali* (8.3), *Axius acanthus* (6.9), *Syllis exilis* (3.4), Pagurid (3.2), *Eurythoe complanata* (2.8), *Iphione muricata* (2.0), *Holothuria pardalis* (1.6), *Lumbrinereis latreilli* (1.5).

Station 14 lay northeast of station 13, towards the centre of Passe Femme. Exposure was similar to station 13 but large waves would be dispersed by the many small islets in the area. The tops of the weed patches were exposed for up to 2 h during later neap tides.

The substratum was completely covered by *Thalassia* among which were patches of *Halimeda*. The well developed algal-mat contained large quantities of *Gracilaria* sp.

Nestled among the basal interstices of the *Thalassia* was an exceedingly dense population of ophiuroids, almost entirely *Ophiocoma valenciae* but also a few *O. dentata* and *O. scolopendrina*.

The well developed algal-mat supported a rich fauna of small gastropods, errant polychaetes and xanthids. Notable among the latter was *Phymodius ungulatus* which was seen scraping *Halimeda* with its spooned chelae.

At this, the most productive station, 92.3 % of the biomass was comprised of the following species: *Ophiocoma valenciae* (40.3), *Phymodius ungulatus* (15.3), *Lophozozymus dodone* (8.3), Pagurid (5.9), *Chlorodiella laevissima* (4.8), *Pilumnus* sp. 1 (4.0), *Lumbrinereis latreilli* (3.5), *Thalamita admete* (2.7), *Dasybranchus caducus* (2.5), *Clibanarius* sp. (1.8), *Dromidiopsis dormia* (1.6), *Thalamita integra* (1.6).

Station 15 was close inshore, northwest of station 14 and about 500 m further east along the shore from La Gigi on the north side of Passe Femme. The area was very well protected by islets in the lagoon and the substratum was emersed at low water neaps when station 14 remained covered.

The sandy substratum was colonized by a sparse stand of the early successional angiosperm *Syringodium isoetifolium* (Ascher) Dandy. Stones in the area bore the occasional anemone.

The thin leaves of *Syringodium* offered little cover. Many of the species were burrowers in the sandy substratum. The following species represented 96.9 % of the biomass: *Glycera lancadivae* (29.0), *Strombus gibberulus* (21.5), *Codakia tigerina* (15.5), *Syllis exilis* (13.9), *Dasybranchus caducus* (6.4), *Armandia intermedia* (2.5), *Thalamita integra* (2.5), *Dardanus megistos* (2.4), *Clibanarius* sp. (1.7), *Glycera tessellata* (1.5).

Locality: Anse Cèdres

Station 16 was on the mid reef flat at Anse Cèdres which is considerably exposed to the SE trades. The substratum was exposed only at extreme low water springs. It was also very stony and difficult to sample. About four eighths of the surface area was covered by a mixed stand of equal proportions of *Thalassia* and *Thalassodendron*. The leaves were short and abraded while the rhizomes were particularly well developed, no doubt in response to the considerable wave action at this station.

The fauna was moderately rich but the number of epibenthic species was restricted by the absence of an algal-mat.

The following species accounted for 91.8 % of the biomass: *Holothuria pardalis* (40.2), *Axius acanthus* (21.2), *Ophiocoma valenciae* (8.8), *Lophozozymus dodone* (7.5), *Ophiocoma brevipes* (4.1), *Thalamita integra* (3.0), *Dasybranchus caducus* (2.8), *Kraussia nitida* (2.5), *Conus arenatus* (1.7).

Locality: Bras Anse Dubois

The mangrove-surrounded and very sheltered station 17 at the tip of the western arm of Bras Anse Dubois was characterized by a 30 cm deep layer of white, anaerobic mud on top of a firmer bed of mangrove debris. The most conspicuous feature was the many holes of the crab *Macrophthalmus convexus*.

Two species typically found in mangrove muds were the eunicid *Marphysa mossambica* and the gastropod *Terebralia palustris*. Adults of the latter species were superabundant among the mangroves but those out on the bare mud in the sampling area were all juveniles. Dead shells of the juveniles were occupied by the hermit crab *Dardanus deformis*.

Of the 7 species present, 99.5 % of the biomass was accounted for by *Macrophthalmus convexus* (90.2) and *Marphysa mossambica* (9.3).

Locality: Ile Michel

Station 18 was two thirds northwards on the east coast of Ile Michel with slight exposure to the SE trades. The moderate tidal currents were probably the early manifestations of the flow into East Channel. The firm white sand was scarcely rippled and was emersed for more than half the full tidal period.

Signs of life were almost confined to the castings of the ubiquitous capitellid *Dasybranchus caducus* and the numerous holes of *Callianassa* sp.

All the 13 species present were burrowers, of which 9 represented 88.5 % of the biomass: *Callianassa* sp. 1 (36.8), *Dasybranchus caducus* (23.3), *Holothuria pardalis* (8.0), *Glycera tessellata*

(7.2), *Codakia tigerina* (3.8), *Anemone* sp. 1 (3.8), *Armandia intermedia* (2.1), *Lumbrinereis latreilli* (1.8), *Malacoceros indica* (1.7).

Locality: Ile Esprit

Station 19 was slightly west of midway along the south coast of Ile Esprit and thus exposed to the waves generated by the SE trades across several kilometres of the lagoon. The sand was less firm than at station 18, was covered with small ripples and was emersed for more than half the total tidal period, although for shorter periods than station 18.

Seven burrowing species were present of which 4 comprised 98.8 % of the biomass: *Callianassa* sp. 2 (90.7), *Glycera tessellata* (3.4), *Dasybranchus caducus* (2.5), *Scyphoproctus* cf *steinitzi*.

Locality: Anse Polymnie

Station 20 lay in the centre of the sandy beach of Anse Polymnie on the west side of Main Channel. The site was exposed to SE trades across the lagoon and the substratum was emersed on all tides. Patches of sand remained saturated to the surface at low tide and there was a sparse scattering of *Enteromorpha*.

The sand was particularly rich in burrowing gastropods such as *Conus arenatus*, *C. tessulatus*, *Terebra affinis*, *T. casta*, *T. pertusa*, *Nassarius coronatus*, *N. arcularis*, *N. gaudiosus*, *N. albescens*, *Natica marochiensis* and *Atys cylindrica*. The single specimen of *Phasionella aethiopica* had probably been washed in from neighbouring rocks or angiosperms.

Crustacea were only represented by a dense population of *Callianassa* sp. and a few juvenile ghost crabs *Ocypode kuhlii*.

Thirteen species comprised 97.7 % of the biomass: *Callianassa* sp. 2 (32.1), *Eurythoe complanata* (14.5), *Dasybranchus caducus* (10.7), *Siphonosoma cumanense* (7.2), *Glycera tessellata* (6.6), *Malacoceros indica* (5.8), *Scolelepis squamata* (4.3), *Holothuria pardalis* (4.2), *Euclymene mossambica* (3.2), *Armandia intermedia* (3.0), *Conus tessulatus* (2.1), *Pinna muricata* (2.0), *Anemone* sp. 1 (2.0).

Locality: Anse Malabar

Station 21 was on the mid reef flat at Anse Malabar on the open north coast of the atoll. The site was exposed but would not get the direct effects of the SE trades.

The substratum retained about 1 cm of water at low water springs. It was very stony and difficult to sample. The general topography was a reticulated patchwork of stony pools among higher standing platforms. Sampling was confined to these platforms which were five eighths covered by *Thalassia* with a smaller proportion of *Thalassodendron*. Traces of *Halimeda* and of the conspicuous, dark green alga *Udotea* were present.

A moderately rich molluscan fauna was collected but the burrowing animals may have been underestimated due to the difficulty of sampling.

Fourteen species accounted for 9.16 % of the biomass: *Siphonosoma vastum* (25.6), *Ebalia erosa* (10.7), *Ochetostoma* sp. 2 (10.4), *Typhlocarcinodes piroculatus* (9.3), *Codakia tigerina* (5.2), *Ochetostoma erythrogrammon* (5.2), *Glycera tessellata* (4.0), *Ophiocoma valenciae* (3.9), *Ophiocoma brevipes* (3.6), *Thalamita integra* (3.5), *Dromidiopsis dormia* (3.3), *Dasybranchus caducus* (2.9), *Lumbrinereis latreilli* (2.3), *Clypeaster fervens* (1.7).

Locality: Anse Grand Poche

Station 22 was in the centre of Anse Grande Poche on the west side of Main Channel. The site was fairly sheltered from waves generated across the length of the lagoon. The sand was

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rather coarser than at station 20, with very small ripples and traces of *Enteromorpha*. The substratum was emersed for about half the total tidal period during spring tides.

This was the only site where we found the cephalochordate *Assymmetron lucayanum*. The 15 species recorded were typical sand dwellers, 6 of which represented 96.5% of the biomass: *Callianassa* sp. 2 (68.0) *Dasybranchus caducus* (16.1), *Euclymene mossambica* (4.2), *Nassarius albescens* (3.5), *Armandia intermedia* (3.2), *Siphonosoma cumanense* (1.5).

Locality: Anse Mais

Station 23 was about 150 m out onto the reef flat from the sand beach at Anse Mais. The site was sheltered from the SE trades but open to the west and consisted of a sand bar covered with small ripples. The sand was fine, well sorted and appeared to be mobile. The sand bar was emersed from 2–3 h at low water springs. No external signs of life were seen.

In this unstable habitat, only 3 species were recorded: *Glycera lancadivae* (82.8), *Terebra lanceolata* (11.0), *Kraemeria samoensis* (6.2).

Locality: Grand Cavalier

Station 24 was situated 50 m out from the shore on the extensive sand flats between Iles Moustique and Grand Cavalier. Large areas of sand were emersed for about 4 h on spring tides, resulting in quite strong currents on the ebb and flow.

The fine, silty-sand supported large populations of the capitellids *Dasybranchus caducus*, *Scyphoproctus* cf *steinitzi*, the opheliids *Armandia intermedia*, *A. longicaudata*, and the burrowing prawn *Callianassa* sp. These extensive invertebrate populations were the food of large flocks of wintering palaearctic waders.

Five of the 9 recorded species accounted for 98.6% of the biomass: *Callianassa* sp. 2 (69.9), *Dasybranchus caducus* (17.7), *Glycera tessellata* (4.4), *Armandia intermedia* (3.3), *Nassarius albescens* (3.3).

5. Analysis and discussion of results

(*a*) *Ordination of stations*

Ordination is a technique, of which there are several alternative methods differing in details of calculation, for revealing the major components of variation in sets of data (Hughes & Thomas 1971). The original data, in our case species–station occurrences, are transformed such that the entities being compared are given coordinates on new axes, the latter representing components of variation in the original data. The first axis represents the largest component of variation, or strongest trend, in the data, successive axes representing lesser components. A non-centring, eigenvector method of ordination (Hill 1973*a*) was used with presence–absence data to give a simultaneous ordination of stations and species.

We found that, even though the data did not contain information about ecological gradients, the ordination led to groupings consistent with our direct observations and provided a clear, visual summary of the various categories of stations.

All the useful information is contained in the first two axes. Figure 2 shows that the first axis orders the stations according to their species richness. It gives high coordinates to species-rich angiosperm dominated stations and low coordinates to poorer sandy stations. It will be seen that stations 5, 12, 17, 23 have unexpected coordinates. Station 5 was a mosaic of sand patches and

Thalassia stands. Its fauna was strongly associated with angiosperm communities but also contained a large number of sand dwellers.

Station 12 was a pure stand of *Thalassia* free of epiphytic algae. It had a relatively low species richness but those species present were also associated with stations 1, 3, 14 which have the highest coordinates on axis I.

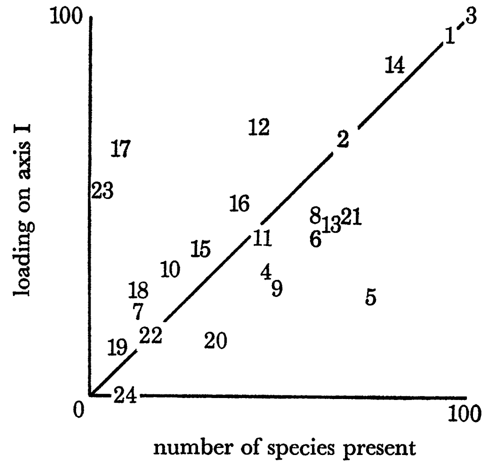

Figure 2. Loadings of stations on the first ordination axis plotted against the number of species recorded at each station. Entries on the graph are station identification numbers.

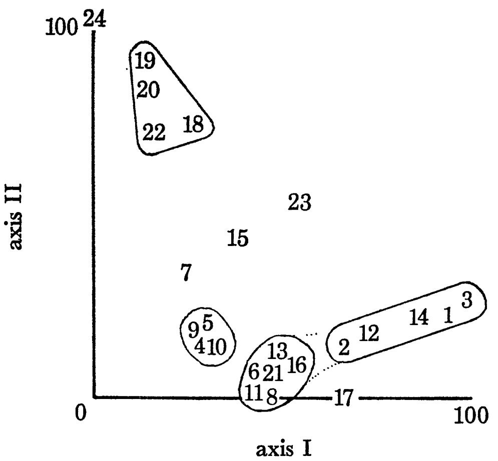

Figure 3. Ordination of stations. Loadings of stations on the second ordination axis are plotted against their loadings on the first ordination axis. Entries on the graph are station identification numbers.

Station 17 was quite different from any other station. The few species living there were adapted to anaerobic mud peripheral to mangroves. All except *Lumbrinereis tetraura* are given intermediate coordinates on axis I since they were neither associated with the fauna of species-rich angiosperm beds nor with the fauna of species-poor sandy stations. *L. tetraura* has a low coordinate because it was also found at sandy stations.

Station 23 was a patch of sand on the leeward, peripheral reef flat, containing only 3 species. *Kraemeria samoensis* has a low coordinate on axis I, while *Glycera lancadivae* has a moderately high coordinate, being more associated with angiosperm communities.

The second axis gives high coordinates to the stations on sand flats which were emersed for long periods at low tide. All other stations are given intermediate to low coordinates.

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An ordination of stations on axes I and II clearly displays the different categories of habitat surveyed (figure 3). Starting with the top left hand corner of the ordination diagram, station 24 is distinct as part of very extensive sandy-mud flats.

Stations 18, 19, 20, 22 were a group of sand beaches which were emersed for long periods at low tide.

Station 7 was a well sorted sand bar in an area of strong tidal currents.

Station 15 lay among a stand of *Syringodium* whose sparse foliage did not support as many species as *Thalassia* or *Thalassodendron*.

Station 23 was a mobile sand bar on the leeward, peripheral reef flat with only 3 species, one typical of other sandy areas and one found also in angiosperm beds.

Stations 4, 5, 9, 10 contained patches of sand among stands of *Thalassia* in areas with very slack tidal currents. Station 10 did not actually contain *Thalassia* but stands existed in the vicinity. This group of stations was characterized by a mixed fauna with elements typical of both angiosperm beds and sandy areas.

Stations 6, 8, 11, 13, 16, 21 form a group allied to the group 1, 2, 3, 12, 14. The latter group consists of stations on angiosperm beds which were very species rich, with a higher proportion of localized epifauna among the foliage and algal-mat. The former group consists of stations also on angiosperm beds but with a more ubiquitous epifauna, less rich in species.

Station 17 consisted of anaerobic mud peripheral to mangroves. There were few species and these were adapted to life on or within the soft, oozy substratum.

(*b*) *Equitability of the fauna*

The term equitability was proposed by Lloyd & Ghelardi (1964) to denote the evenness of the distribution of relative abundance of species. This concept has since been combined with species richness under the name 'diversity', of which several indices have been devised (Hurlbert 1971) and which have been shown by Hill (1973*b*) to form a continuum between sensitivity to species richness and to dominance. The relation $1/\Sigma p_i^2$ (see MacArthur 1972) measures diversity predominantly influenced (inversely) by dominance and, since for a set of n equally abundant species $1/\Sigma p_i^2 = n$, the relation $1/n\Sigma p_i^2$ can be used as a useful index of equitability.

In order to account for different sized organisms, we have utilized biomass rather than numerical abundance as a measure of relative abundance.

When equitability is plotted against the number of species recorded for each station (figure 4), two effects become clear.

(1) There is a negative trend in the data. This is because at all stations less than 10 species accounted for at least 75% of the total biomass. An increase in the number of species recorded, therefore, increases the relative dominance of the common species so that equitability decreases.

Conversely, stations with only a few species present (e.g. 7, 18, 23) tend to have high equi-stabilities merely because they lacked many rare species. One or two species would need exceedingly high relative abundances to lower the equitability.

(2) In general, each station had one or two species much more dominant than the rest. Where this dominance was extremely high the equitability is depressed below the general trend (e.g. 5, 6, 9, 12, 22). Conversely, where the dominance of the first to second most abundant species was less marked the equitability rises above the general trend (e.g. 8).

The number of species with relative abundances of at least 0.015 ranged only from 3 to 14.

Usually, about half the total biomass was represented by only 2 species. A similar situation was recorded by Moore (1972) for inshore soft substrata in Florida.

The sets of species forming significant parts of the biomass differed between stations. Predictably, the sets of species from angiosperm beds with algal-mat were composed mainly of small epibenthic species, whereas the sets from stations with less plant cover contained more burrowing species until, in completely sandy areas, the sets were almost entirely of infauna. Even sets from the most similar stations differed in the order of dominance of the species and in some of the species included.

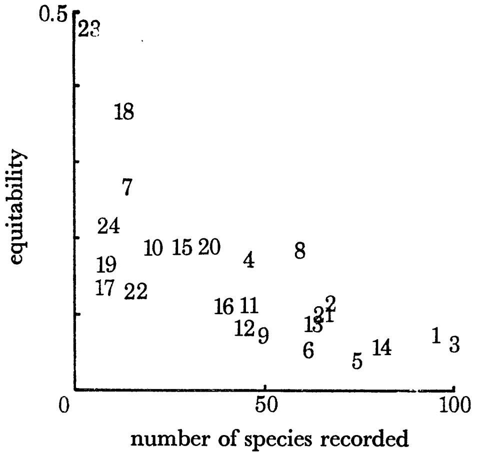

FIGURE 4. The equitability index, $1/n\Sigma p_i^2$, plotted against the total number of species recorded at each station. p_i is the proportion (biomass) of the ith species and n is the number of species used in the index. Entries on the graph are station identification numbers.

It is evident, however, that the number of species contributing significantly to the biomass did not increase much with the total biomass or species richness. The constant representation of over 75 % of the biomass by less than 10 species, of over 50 % by one or two species and the unpredictable specific identity or ranking of the dominant species are all phenomena superficially similar to the characteristics of decaying log communities studied by Fager (1968). He presented evidence that the relative abundance structure of the ephemeral rotting log communities was determined by the probabilities of invasion together with the abilities of species to increase after invasion and that there was no necessary order of invasion.

Fager suggests that there are many species which can fulfil the same function in the community and that any specific case is a result of its particular history of invasion and subsequent growth of the colonizing populations.

Our results are not directly comparable with Fager's because our relative abundances are based on biomass. However, many of the dominant species in terms of biomass were also dominant regarding density, although this positive correlation broke down for the rarer species.

We may tentatively suggest, therefore, that the unpredictable specific identity or ranking of dominant species, especially among the patches of angiosperm and mobile sand bars, is a function of dispersal history and reproductive potential. This implies that these communities are not in long-term equilibrium or structured by subtle biological interactions which have evolved over many generations but that they are formed, destroyed and reformed by environmental forces such as erosion or deposition by tidal currents coupled with colonization from surrounding areas.

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Taking all 24 stations together, the regression of total animal biomass on species richness is not significant ($b = 0.55$, $P > 0.9$). Excluding the atypical stations 3 (*Halimeda*), 14 (ophiuroid aggregation), and 15 (early successional *Syringodium* bed), the group of stations with plant cover has a significantly larger mean biomass than the group of sandy stations ($t_{19} = 7.1$, $P < 0.001$). Since this increased biomass was apportioned largely among the few dominant species, it was probably due to a greater primary production rather than to the increased topographical complexity.

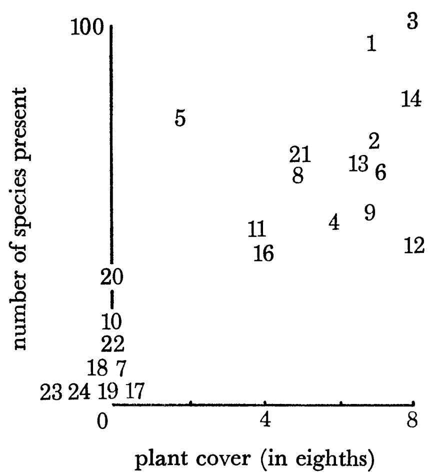

FIGURE 5. The number of species recorded at each station plotted against the area of substratum covered by plants (angiosperm, *Halimeda*, algal-mat). Entries on the graph are station identification numbers.

The converse seems to be true of species richness. Among the stations containing plants, an otherwise strong association of species richness with plant cover (figure 5) is offset by species-rich station 5, which was a heterogeneous mosaic of angiosperm among sand, and by species-poor station 12 containing *Thalassia* free of epiphytes and algal-mat. High species richness occurred whenever there was extensive algal-mat. Thus, comparing stations 1, 2, 6, 8, 9, 13, 14 (algal-mat) with 4, 5, 11, 12, 16, 21 (no algal-mat), $t_{12} = 2.5$, $0.05 > P > 0.02$.

We thought that sediment heterogeneity might also promote species richness (table 1, figure 6), but a multiple regression of species richness on angiosperm cover and sediment heterogeneity (variance of particle size distribution) for all stations revealed a highly significant partial regression coefficient for the former but not for the latter. The redundancy of sediment heterogeneity was confirmed by a significant correlation with angiosperm cover ($r = 0.55$, $P < 0.01$).

(*c*) *Species associations*

Apart from the obvious associations of burrowing species with sandy substrata and of a variety of epibenthic species with plant cover, our survey revealed no definite recurrent groups of species corresponding to particular habitats. This is because our samples were too small to cope with the high species richness and with the low densities of each species relative to the size of quadrat used.

Since our samples do not describe entire communities it is difficult to make faunistic comparisons with data from elsewhere in the Indo-West Pacific. Thus we find that many of our species have also been recorded from the sandy substrata on the reef flats of Tuléar, Madagascar

TABLE 1. SIZE FREQUENCY DISTRIBUTION OF SEDIMENTS

(The variance of the particle size distribution is included as a measure of sediment heterogeneity (degree of sorting). Columns 3–7 are the % abundances of each particle size category.)

station	variance	gravel > 2·812 mm	coarse sand > 0·599 mm	medium sand > 0·152 mm	fine sand > 0·076 mm	silt
1	1.57	0.9	19.7	64.2	13.8	1.4
2	3.15	6.9	27.0	40.6	24.0	1.5
3	3.04	4.2	42.3	35.9	14.7	2.9
4	1.58	0.6	6.6	24.2	65.2	3.4
5	1.88	0.2	8.7	35.3	51.1	4.7
6	2.98	1.7	13.8	33.9	42.1	8.5
7	0.44	0	15.5	84.2	0.2	0.1
8	1.43	1.1	6.3	45.9	45.3	1.4
9	1.37	0.2	4.5	20.8	69.4	5.1
10	0.29	0	0.7	46.9	52.4	0
11	3.71	9.2	20.2	43.7	24.8	2.1
12	2.00	1.7	22.9	60.5	12.0	2.9
13	2.00	0.9	14.5	51.1	30.9	2.6
14	4.60	7.1	14.9	16.6	47.3	14.1
15	1.88	4.2	26.0	58.3	11.1	0.4
16	2.64	6.4	8.3	52.5	32.4	0.4
17	1.50	0	4.1	8.8	52.5	34.5
18	0.96	0	1.1	16.0	76.1	6.8
19	0.91	0	0.4	38.4	60.8	0.4
20	1.38	0	6.0	52.9	39.9	1.2
21	4.27	10.5	14.7	42.6	27.4	4.8
22	3.62	3.4	46.3	13.5	36.5	0.3
23	0.15	0	0.2	93.2	6.6	0
24	0.29	0	0.2	6.4	92.8	0.6

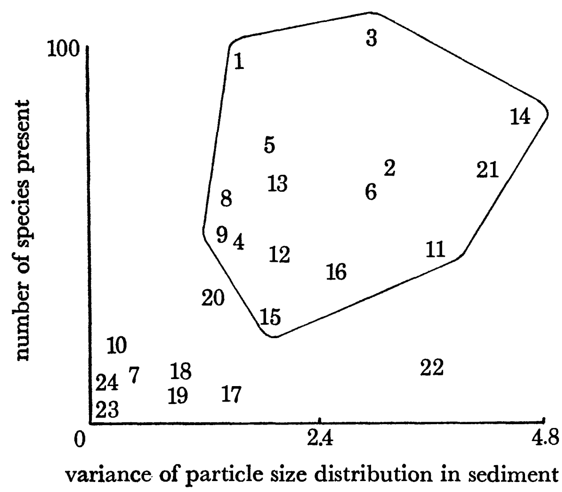

FIGURE 6. The number of species recorded at each station plotted against the degree of sorting (variance of the particle size distribution) of the sediments. Entries of the graph are station identification numbers.

(Thomassin 1969) or from the sand banks and angiosperm beds of Inhaca Island, Moçambique (Macnae & Kalk 1962), but that our samples contain different combinations of species. In most cases, no significance can be attached to these differences since they are due, at least in part, to the fact that we only obtained subsets of the whole communities. However, the following comparisons are worthy of note:

Our mobile sand bars (stations 7, 23) are clearly analogous to the '*Astropecten* associations' described from bare sand banks at Inhaca Island (Macnae & Kalk 1962) and from similar 'dunes hydrauliques' at Tuléar (Thomassin 1969). Sand bars such as stations 7, 23 are unstable, shifting habitats which may have to be recolonized from surrounding sandy substrata as they become destroyed and reformed. It is surprising that the small burrowing fish *Kraemeria samoensis* appeared regularly in our impoverished samples of well sorted sand but was not recorded by Macnae & Kalk (1962) or by Thomassin (1969). On the other hand, we did not record *Aseraggodes filiger* M. Neber which Thomassin (1969) regarded as an ecological equivalent of *Ammodytes* spp. from temperate regions.

Our samples among *Thalassia* and *Thalassodendron* revealed a richer, but otherwise similar, fauna to that described from the same angiosperms at Inhaca Island (Macnae & Kalk 1962). Typical species, common to both regions are:

Thalamita admete	*Cypraea tigris*
T. integra	*C. carneola*
T. danae	*Pleurobranchus peroni*
T. prymna	*Pinctada margaritifera*
Menaithius monoceros	*Ophiocoma scolopendrina*
Dromidiopsis dormia	*O. valenciae*
Dardanus deformis	*Tripneustes gratilla*
D. megistos	*Eucidaris metularia*

Many other genera common to the two areas are represented by different, but morphologically similar species in the records, some of which could even be synonyms or sub-species.

(*d*) *Biomass and productivity*

Primary producers (*table* 2)

Peripheral mangrove mud (station 17), mobile sand bars (stations 7, 23) and sand flats (stations 10, 18, 19, 20, 22, 24) were devoid of macrophytes except for occasional strands of *Enteromorpha* at some stations.

Station 3 was a pure stand of *Halimeda* with 100 % cover and appeared to be a successional stage lying over an extinct angiosperm bed. The total plant biomass of this station, 7512 kcal m^{-2}, was exceeded by two stations only.

All other stations with macrophytes were characterized by angiosperms. Station 15 was a *Syringodium* bed subjected to longer periods of emersion than *Thalassia* or *Thalassodendron*. The *Syringodium* biomass, 96 kcal m^{-2}, was considerably less than that of most other angiosperm beds.

Stands of angiosperms differed in the ratio of *Thalassia* to *Thalassodendron*, the ratio of rhizomes to leaves and in the quantity of associated algae.

Only stations 1, 6, 8, 16, 21 contained *Thalassodendron*, which is a plant less tolerant of emersion than *Thalassia*. The mixed stands of *Thalassodendron* and *Thalassia* did not present a significantly greater biomass than pure stands of *Thalassia*.

The ratio of rhizomes to leaves ranged from 4.7 to 3.0 for all relevant stations except 2, 8, 16, 21. The high value of 9.5 for station 2 may have been due to strong tidal currents stimulating the growth of rhizomes. At station 8, the foliage was heavily grazed down, thus accounting for the rhizome/leaf ratio of 12.0. Values of 9.0 and 10.1 for stations 16 and 21 respectively were due to a marked development of the rhizomes. This was apparent at the time of sampling, the

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Table 2. Biomass (kcal m^{-2}) of plants at each station

(Original observations measured as ash free dry mass were converted to kilocalories using the values of 4.770 kcal per ash free g for angiosperms and 4.669 for algae (Cummins & Wuycheck 1971).)

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Halimeda	1863	—	7512	—	—	—	—	84	—	—	—	—	—	1620	—	—	—	—	—	—	—	—	—	—
algal-mat	1625	5285	—	—	—	—	—	—	1233	—	—	—	61	93	—	—	—	—	—	—	—	—	—	—
angiosperms																								
foliage	639	271	—	758	43	706	—	196	24	—	281	620	391	668	24	296	—	—	—	—	248	—	—	—
rhizomes	2981	2576	—	2280	105	1407	—	2347	81	—	1130	1860	1173	2003	72	2662	—	—	—	—	2495	—	—	—
total	3620	2847	—	3038	148	2113	—	2543	105	—	1411	2480	1564	2671	96	2958	—	—	—	—	2743	—	—	—
grand total	7108	8132	7512	3038	148	2113	0	2627	1338	0	1411	2480	1625	4384	96	2958	0	0	0	0	2743	0	0	0
rhizomes: foliage	4.7	9.5	—	3.0	2.4	2.0	—	12.0	3.4	—	4.0	3.0	3.0	3.0	3.0	9.0	—	—	—	—	10.1	—	—	—
plant cover	$\frac{7}{8}$	$\frac{7}{8}$	$\frac{8}{8}$	$\frac{6}{8}$	$\frac{2}{8}$	$\frac{7}{8}$	0	$\frac{5}{8}$	$\frac{7}{8}$	0	$\frac{4}{8}$	$\frac{8}{8}$	$\frac{7}{8}$	$\frac{8}{8}$	—	$\frac{4}{8}$	0	0	0	0	$\frac{5}{8}$	0	0	0

thickened, extensive rhizomes being a probable phenotypic response to the mechanical effect of severe wave action. The angiosperm biomass of these exposed stations on the peripheral reef flat was not significantly different from that of other stations on the leeward peripheral reef flat or within the lagoon.

Angiosperms on the peripheral reef flat were virtually free of epiphytes or other associated algae. In contrast, the lagoon angiosperm beds often supported large quantities of algae, especially on the platforms bordering east and west channels where multispecific algal-mats grew on top of the angiosperms (stations 1, 2, 13, 14) and in areas of slack tidal currents (station 9) where filamentous algae such as *Enteromorpha* became more important.

The multispecific algal-mat may equal or exceed the biomass of the underlying angiosperms, the ratio of the former to the latter being 1.0, 1.9 and 1.6 for stations 1, 2 and 14 respectively. Quantities of algae in other lagoon angiosperm beds (stations 4, 5, 6, 8, 13, 15) were relatively small.

Unfortunately, we could not find sufficient data in the literature to justify an estimation of primary productivity from these biomass figures. The average angiosperm biomass (excluding *Syringodium* at station 15) of 2172 kcal per m² is quite close to an estimate of 1962 kcal per m² for *Thalassia testudinum* Köning growing subtidally in Florida. This estimate is based on the figure of 601 g per m² given by Moore *et al.* (1968) and a value of 3.264 kcal per g for Zosteracea (Cummins & Wuycheck 1971).

The large biomass of angiosperms at suitable sites on the peripheral reef flat and on the platforms bordering the channels within the lagoon suggest that *Thalassia* and *Thalassodendron* may be important sources of primary production. Certainly they provide food for the green turtle, *Chelonia mydas* L., but the proportions of angiosperm primary production passing along the grazing and detritus food chains remains unknown. However, the topographical diversity provided by angiosperms and especially by associated algal-mat, enables a large array of epifaunal species from several trophic levels to co-exist. Furthermore, Patriquin (1972) has revealed the importance of *Thalassia* as a nitrogen fixer in an environment otherwise depauperate in useful forms of this nutrient.

Angiosperm beds on platforms around the channels occupy only a very small proportion of the lagoon floor. The importance of angiosperm primary production within the whole lagoon ecosystem will depend on the extent of transport of detritus and movement of animals feeding within the angiosperm communities to the rest of the lagoon.

Secondary producers

Table 3 presents the biomass (kcal m^{-2}) of the major taxa and their contribution to the total biomass at each station.

Sufficient data have accumulated in the literature for productivity–biomass (P/B) ratios to be used for the estimation of productivity from biomass to an order of magnitude (Mann 1969; Waters 1969). Mathias (quoted by Mann 1969) gives two regression equations for predicting productivity from biomass for animals with life cycles less than or equal to 1 year and greater than 1 year respectively. However, since we have little information on the life spans of the animals in our survey, we have chosen a very gross approximation by using the P/B ratios given by Moore (1972) for the dominant infauna of muddy sand communities in Florida. The mean of these P/B ratios is 1.76 and this was used to convert station biomass into productivity (table 3).

Table 3. Biomass (kcal m^{-2}) of major taxa at each station

(Italicized entries are percentages of the total biomass at each station. The bottom row gives the productivity at each station kcal m^{-2} a^{-1}.)

*	1	2	3	4	5	6	7	8	9	10	11	12
gastropods	2.88	3.38	4.35	14.25	6.24	11.45	0.44	1.97	4.04	0.20	1.87	2.16
	4.5	*6.9*	*1.2*	*11.0*	*9.7*	*7.7*	*12.8*	*4.0*	*14.3*	*4.0*	*2.8*	*3.7*
bivalves	0.70	3.22	5.49	5.89	3.78	1.50	0	2.97	0.89	0	0.03	0.61
	1.1	*6.6*	*1.5*	*4.5*	*5.9*	*1.0*	—	*6.1*	*3.2*	—	—	*1.0*
polychaetes	7.63	7.06	247.31	5.56	4.7	6.23	0.35	5.28	15.62	3.54	2.11	2.62
	11.9	*14.5*	*66.7*	*4.3*	*7.3*	*4.2*	*10.2*	*10.8*	*55.5*	*70.9*	*3.2*	*4.5*
asteroidea	0.04	0	0.33	0	0	0	0	0.15	0	0	0	0
	0.1	—	*0.1*	—	—	—	—	*0.3*	—	—	—	—
ophiuroidea	1.47	1.14	25.47	0.02	0	0.27	0	0.66	0.04	0	0.01	1.63
	2.3	*2.3*	*6.9*	—	—	*0.2*	—	*1.4*	*0.1*	—	—	*2.8*
echinoidea	3.28	0	10.03	0	0	0.10	0	6.31	0	0	0	0.03
	5.1	—	*2.7*	—	—	*0.1*	—	*13.0*	—	—	—	*0.1*
holothuridea	0.13	0	0	34.43	38.38	0	0	0	1.36	0	0	0
	0.2	—	—	*26.6*	*59.6*	—	—	—	*4.8*	—	—	—
sipuncula	0.02	0.60	0.58	3.10	4.35	5.33	0.19	1.99	3.34	0	15.23	9.84
	—	*1.2*	*0.2*	*2.4*	*6.8*	*3.6*	*5.5*	*4.1*	*11.9*	—	*22.9*	*16.9*
crustacea	47.77	33.16	75.31	66.36	6.88	123.55	0.43	28.74	2.87	0.94	47.20	41.06
	74.7	*65.1*	*20.3*	*51.2*	*10.7*	*83.2*	*12.5*	*59.0*	*10.2*	*18.8*	*71.0*	*70.7*
pisces	0	0.15	1.77	0	0.07	0	2.02	0.62	0	0.31	0	0.15
	—	*0.3*	*0.5*	—	*0.1*	—	*58.9*	*1.3*	—	*6.2*	—	*0.3*
total	63.92	48.71	370.64	129.61	64.40	148.43	3.43	48.69	28.16	4.99	66.45	55.10
productivity	112	86	652	228	113	261	6	86	50	9	117	102

	13	14	15	16	17	18	19	20	21	22	23	24
gastropods	2.82	0.57	0.90	1.44	0.05	0.03	0.03	0.91	1.16	0.54	0.15	0.99
	4.5	*0.1*	*24.9*	*2.7*	*0.2*	*0.2*	*0.5*	*3.3*	*1.8*	*4.1*	*12.5*	*3.6*
bivalves	0	0.61	0.62	0	0	0.61	0	0.78	4.31	0	0	0.05
	—	*0.1*	*17.2*	—	—	*4.1*	—	*2.8*	*6.7*	—	—	*0.2*
polychaetes	10.78	51.69	1.83	1.72	1.88	6.80	0.50	13.29	6.71	3.07	0.97	6.66
	17.3	*7.6*	*50.7*	*3.3*	*8.3*	*46.2*	*7.8*	*47.7*	*10.5*	*23.3*	*80.8*	*24.0*
asteroidea	0	0.01	0	0	0	0	0	0	0	0	0	0
	—	—	—	—	—	—	—	—	—	—	—	—
phiuroidea	0.55	293	—	7.08	0	0	0	0	7.4	0	0	0
	0.9	*43.1*	—	*13.4*	—	—	—	—	*11.5*	—	—	—
chinoidea	0.72	0.42	0	0.03	0	0	0	0	2.20	0	0	0
	1.2	*0.1*	—	*0.1*	—	—	—	—	*3.4*	—	—	—
olothuridea	1.36	0.31	0	23.20	0	1.36	0	1.36	0	0	0	0
	2.2	—	—	*43.9*	—	*9.2*	—	*4.9*	—	—	—	—
ipuncula	5.94	6.12	—	0.38	0	0	0	1.90	17.94	0.28	0	0
	9.5	*0.9*	—	*0.7*	—	—	—	*6.8*	*28.0*	*2.1*	—	—
rustacea	40.21	326.27	0.26	18.96	26.83	5.91	5.90	9.62	24.35	9.27	0	20.07
	64.5	*48.0*	*7.2*	*35.9*	*91.5*	*40.2*	*91.8*	*34.5*	*38.0*	*70.4*	—	*72.3*
isces	0	0.31	0	0	0	0	0	0	0	0	0.08	0
	—	—	—	—	—	—	—	—	—	—	*6.7*	—
otal	62.38	679.31	3.61	52.81	22.76	14.71	6.43	27.86	64.07	13.16	1.20	27.77
roductivity	110	1196	6	93	40	26	11	49	113	23	2	49

* The original data, measured as ash free dry mass, were converted to kilocalories by using the following values (kcal per ash free rom Cummins & Wuycheck (1971): mollusca 5.492, polychaeta, 4.700, echinoderms 5.821 (mean for macroconsumers), crustac .369, fish 5.296.

Mobile sand bars (stations 7, 23) were the most impoverished, with a mean productivity of 4 kcal m^{-2} a^{-1}. The early successional *Syringodium* bed (station 15) also had a low productivity of 6 kcal m^{-2} a^{-1}.

More stable sandy areas (stations 10, 18, 19, 20, 22, 24) were more productive with a mean of 28 kcal m^{-2} a^{-1}. The most productive of these stations (station 24; 49 kcal m^{-2} a^{-1} occurred on the extensive sand flats between Iles Moustique and Grand Cavalier which supported large flocks of wintering palearctic waders.

Station 14 was unique with a dense population of *Ophiocoma valenciae* which boosted the total productivity to 1196 kcal m^{-2} a^{-1}. The productivity of *O. valenciae* alone amounted to 482 kcal m^{-2} a^{-1}. *Ophiocoma valenciae* is similar in size to the temperate species *Ophiothrix fragilis* (Abildgaard) which it resembles also by holding some of its arms erect in the water to intercept suspended food particles. *Ophiothrix fragilis* tends to form dense aggregations to which Warner (1971) attributes the advantages of increased stability in strong tidal currents, rapid gamete fertilization, slowing of water currents through the forest of arms, thus increasing settlement of food particles, and communication of escape responses to predators throughout the aggregation.

Although *Ophiocoma valenciae* occurred in several other stations, an aggregation was encountered only at station 14 and may have been a response to strong tidal currents through Passe Femme. The dense population of *Ophiocoma valenciae* (416 m^{-2}) did not reduce the species richness or productivity of the remaining fauna. Similarly, the dense aggregations of *Ophiothrix fragilis*, reaching 1330 m^{-2}, did not adversely affect the underlying benthos (Warner 1971).

The high biomass of *Halimeda* at station 3 was associated with commensurately high secondary productivity of 652 kcal m^{-2} a^{-1}.

Crustacea were the largest components of the biomass at most stations. Xanthid crabs predominated in angiosperm beds, especially among algal-mat while *Callianassa* spp. dominated some of the sand communities. Small errant polychaetes were also important among well developed algal-mat. Other taxa were much less important with the following exceptions. The burrowing holothurian *Chiridota violacea* dominated the sand patches at station 5, burrowing fish dominated the mobile sand at station 7, burrowing polychaetes dominated the sandy habitats of stations 9, 10 and 15, ophiuroids were important due to the aggregation of *Ophiocoma valenciae* at station 14.

In no case were gastropods or bivalves the dominant taxa above the species level. This is in sharp contrast to the subtidal muddy sands of Florida studied by Moore (1972) where bivalves and occasionally gastropods were very important components of biomass. In other respects the Aldabra and Florida benthos were quite similar. By using a conversion factor of 4.229 kcal per g dry mass for aquatic macroconsumers (Cummins & Wuycheck 1971) the Florida subtidal muddy sands had a secondary productivity of about 32 kcal m^{-2} a^{-1} which is close to our values of 40 and 28 kcal m^{-2} a^{-1} for peripheral mangrove mud and sand flats respectively. Intertidal flats supporting the angiosperms *Thalassia testudinum* and *Syringodium filiforme* Kuntzing at low spring tide level and *Diplanthera wrightii* (Anderson) up to mid tide level were studied by Moore *et al.* (1968). Conversion of their biomass figures gives a mean productivity of 167 kcal m^{-2} a^{-1} with areas of up to about 600 kcal m^{-2} a^{-1}. These figures are very similar to the Aldabra plant dominated communities which had an overall mean of 265 kcal m^{-2} a^{-1} and a maximum of 652 kcal m^{-2} a^{-1}. Moreover, the 10 most abundant species comprised about 88% of the biomass in the Florida subtidal muddy sands and the 5 most abundant species comprised 95%

of the biomass on the intertidal flats. A similar confinement of the biomass to between 3 and 14 species occurred throughout the Aldabra stations.

A further comparison can be made between the Aldabra benthos from sandy stations and the benthos from shallow bays in the northwest Mediterranean. Massé (1972) gives biomass figures for the coast of Provence which we have converted to productivity assuming a calorific value of 4.229 kcal per g dry mass (Cummins & Wuycheck 1971) and a P/B ratio of 1.76 from Moore (1972). The benthos living in fine well sorted sand in clear water has an estimated productivity of 37 kcal m^{-2} a^{-1} which is of the same order of magnitude as the mean, 28 kcal m^{-2}, for Aldabra sand communities.

Aldabra intertidal muds and sandy flats seem to have productivities of the same order of magnitude as shallow, subtidal sediments elsewhere in the tropics or subtropics. Aldabra angiosperm beds have secondary productivities which are similar to an example from Florida and which are an order of magnitude greater than those of neighbouring sand or mud flats.

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F. W. E. Rowe of the Polytechnic, London, confirmed our identifications of holothurians while Dr J. H. Wickstead of the Marine Biological Association, U.K., identified the cephalochordate.

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Appendix. Faunal species list

Coelenterata
- Anthozoa
  - anemone 1, 2, 3
  - burrowing anemone
  - *Fungia* sp.

Platyhelminthes
- Turbellaria
  - polyclad 1, 2, 3, 4, 5, 6, 7, 8, 9

Nemertinea
  - nemertine 1, 2, 3, 4, 5, 6

Sipuncula
  - *Sipunculus robustus* Keferstein
  - *Siphonosoma* (*Hesperosiphon*) *vastum* (Selenka & Bülow)
  - *S.* (*Damosiphon*) *cumanense cumanense* (Keferstein)
  - *S.* (*Damosiphon*) *cumanense koreae* Sâto
  - *Phascolosoma nigrescens* Keferstein
  - *P. granulatum* Leukart
  - *Golfingia longirostris* E. Wesenberg-Lund
  - *Golfingia* sp. 1, sp. 2

Echiura
  - *Ochetostoma erythrogrammon* (Leukart & Rüppell)
  - *Ochetostoma* sp. 1, sp. 2

Polychaeta
- Aphroditidae
  - *Iphione muricata* (Savigny)
  - *Alentia australis* (Monro)
  - *Harmothoe* (*Lagisca*) *waahli* (Kinberg)
  - *Lepidonotus* (*Thormora*) *jukesi* (Baird)
  - *Lepidasthenia elegans* (Grube)
  - *L. minikoensis* Potts
  - *L. maculata* Potts
  - *Pholoe* sp.
  - *Psammolyce* cf *petersi* Kinberg
  - *Thalenessa oculata* (Peters)
  - *Sthenelais boa* (Johnston)
- Palmyridae
  - *Bhawania cryptocephala* Gravier
- Amphinomidae
  - *Pseudeurythoe microcephala* Fauvel
  - *Eurythoe complanata* (Pallas)
  - *Notopygos variabilis* Potts
  - *Pherecardia striata* (Kinberg)
- Phyllodocidae
  - *Phyllodoce madeirensis* Langerhans
  - *Phyllodoce* sp.
- Hesionidae
  - *Hesione splendida* Savigny
  - *Kefersteinia* sp.
  - *Leocrates chinensis* Kinberg
  - *Gyptis* sp.
- Syllidae
  - *Pharyngeovalvata* sp.
  - *Syllis* (*Typosyllis*) cf *exilis* Gravier
  - *S.* (*T.*) *cirropunctata* Michel
  - *S.* (*T.*) *prolifera* Krohn
  - *S.* (*T.*) *variegata* Grube
  - *S.* (*T.*) *hyalina* Grube
  - *Opisthosyllis laevis* Day
  - *Trypanosyllis zebra* (Grube)
- Nereidae
  - *Platynereis insolita* Gravier
  - *Nereis* (*Neanthes*) *caudata* Delle Chiaje
  - *Ceratonereis mirabilis* Kinberg
- Glyceridae
  - *Glycera papillosa* Grube
  - *G. lancadivae* Schmarda

Glyceridae—*cont.*
G. tesselata Grube
G. rouxi Audouin & Milne-Edwards
Eunicidae
Eunice (*Palolo*) *siciliensis* Grube
E. australis Quatrefages
E. afra afra Peters
Marphysa mossambica (Peters)
Lumbrinereis latreilli Audouin & Milne-Edwards
L. tetraura (Schmarda)
Arabella iricolor caerulea (Schmarda)
Drilonereis sp.
Spionidae
Malacoceros indica (Fauvel)
Aonides oxycephala (Sars)
Aonides sp.
Laonice cirrata (Sars)
Scolelepis squamata (Müller)
Prionospio pinnata Ehlers
Cirratulidae
Cirratulus africanus Gravier
Trochochaetidae
Poecilochaetus serpens Allen
Opheliidae
Armandia longicaudata (Caullery)
A. intermedia Fauvel
Ophelina acuminata Oersted
Polyophthalmus pictus (Dujardin)
Tachytrypane sp.
Capitellidae
Notomastus aberans Day
Leiochrides africanus Augener
Dasybranchus caducus (Grube)
Capitobranchus sp.
Scyphoproctus cf *steinitzi* (Day)
Maldanidae
Nichomache sp.
Euclymene mossambica (Day)
Praxillella sp.
Terebellidae
Trichobranchus cf *glacialis* Malmgren
Terebellides stroemi Sars
Loimia medusa (Savigny)

Crustacea
Brachyura
Acanthonychinae
Menaethius monoceros (Latreille)
Maiidae
Simocarcinus simplex var. pyramidatus Laurie
Leucosiidae
Ebalia erosa (Milne-Edwards)
Calappidae
Calappa hepatica (L.)
Dromiidae
Dromidiopsis dormia (L.)
Atelecyclidae
Kraussia nitida Stimpson
K. rugulosa (Krauss)
Ocypodidae
Ocypode kuhlii de Haan
Macrophthalmus convexus Stimpson
Portunidae
Portunus granulatus Milne-Edwards
P. cf *hastatoides* Fabricius
Thalamita admete Herbst
T. chaptali Audouin & Savigny
T. demani Nobile
T. integra Dana
T. prymna (Herbst)
Xanthidae
Actaea cavipes Dana
A. hirsutissima (Rüppell)
Actumnus cf *globulus* (Fabricius)
Chlorodiella laevissima Dana
Chlorodopsis granulata (Stimpson)
C. cf *negrocrinita* (Stimpson)
Cycoxanthops sp.
Etisus electra (Herbst)
Hypocolpus diverticulatus (Strahl)
H. cf *sculptus* Nobile
Leptodius sp.
Liomera monticulosa (Milne-Edwards)
L. tristis (Dana)
Lophozozymus dodone (Herbst)
Lybia leptochelis (Zehntner)
L. tessellata (Latreille)
Phymodius ungulatus (Milne-Edwards)

Crustacea—*cont.*
Brachyura—*cont.*
Pilumnus cf *scabriusculus* Adams & White
Pilumnus sp. 1, sp. 2
Xanthias sp.
Typhlocarcinodes piroculatus (Rathbun)
Typhlocarcinus sp.
Anomura
Albunidae
Albunea sp.
Paguridae
Calcinus herbstii de Man
Clibanarius cf *cruentatus* Milne-Edwards
C. merguiensis de Man
Clibanarius sp.
Dardanus deformis Milne-Edwards
D. cf *evopsis* Dana
D. megistos (Herbst)
Pagurus sp.
Pagurid
Trizopagurus strigatus (Herbst)
Thalassinidea
Axiidae
Axius (*Neaxius*) *acanthus* Milne-Edwards
Callianassidae
Callianassa (*Callichiurus*) *longiventris borradailei* de Man
Callianassa (*Callichiurus*) sp. 1
Callianassa (*Cheramus*) sp. 2
Caridea
Processidae
Processa austroafricana Barnard
P. japonica (de Haan)
Alpheidae
Alpheus bicostatus de Man
A. frontalis Milne-Edwards
A. parvirostris Dana
A. rapax Fabricius
Alpheus sp.
Athanas cf *djiboutiensis* Coutière
Automate cf *gardineri* Coutière
Synalpheus sp.
Pontonidae
Conchodytes tridacnae Peters
Hippolytidae sp.
Palaemonella sp.
Penaeidae
Penaeus sp.
Stomatopoda
Gonodactylus sp. 1, sp. 2
Pseudosquilla ciliata (Fabricius)
Austrosquilla littoralis Michel & Manning
Alima hyalina Leach
A. cf *hieroglyphica* Kemp
Lysiosquillid sp.
Gastropoda
Prosobranchia
Trochus erythraensis (Brocchi)
Stomatia splendidula A. Adams
Turbo chryostoma L.
T. spinosus Gmelin
Leptothyra candida Pease
Phasianella aethiopica Phillipi
Smaragdia rangiana (Recluz)
Heliacus variegatus (Gmelin)
Philippia radiata (Röding)
Modulus tectum (Gmelin)
Terebralia palustris (L.)
Cerithium echinatum Lamarck
C. morum Lamarck
C. piperitum Sowerby
C. rostratum Sowerby
C. nesioticum Pilsbry & Vanatta
C. janthinum Gould
Pyramidella maculosa Lamarck
P. terebellum (Maller)
Strombus gibberulus (L.)
S. mutabilis Swainson
S. dentatus (L.)
S. decorus (Röding)
Lambis crocata Link
Polynices mammilla (L.)
Natica marochiensis (Gmelin)
N. simiae (Deshayes)
N. robillardi Sowerby
Trivia oryza Lamarck
Cypraea annulus L.
C. carneola (L.)

Gastropoda—*cont.*

Prosobranchia

C. helvola L.
C. lynx L.
C. moneta L.
C. tigris L.
Cymatium nicobaricum (Röding)
C. piliare (L.)
Bursa rhodostoma (Sowerby)
Morula uva (Röding)
Drupa ochrostoma (Blainville)
Nassa francolina (Bruguière)
Pyrene cf *dautzenbergi* Hervier
Pyrene sp.
Columbella turturina Lamarck
C. varians Sowerby
Mitrella cf *blanda* (Sowerby)
Marginella sp.
Engina cf *fusiformis* Pease
Nassarius albescens (Dunker)
N. arcularis (L.)
N. coronatus (Bruguière)
N. gaudiosus Hinds
Pleuroploca trapezium (L.)
Peristernia nassatula (Lamarck)
Vasum turbinellus (L.)
Oliva episcopalis Lamarck
O. annulata Gmelin
Mitra mitra (L.)
Mitromorpha stephani Melvill & Standen
Strigatella litterata (Lamarck)
Xenuroturris cingulifera (Lamarck)
Conus arenatus L.
C. betulinus L.
C. coronatus Gmelin
C. ebraeus L.
C. litteratus L.
C. lividus Hwass
C. tessulatus Born
C. virgo L.
C. quercinus Lightfoot
C. litoglyphus Hwass
C. augur Solander
Terebra affinis Gray
T. dimidiata (L.)
T. pertusa Born
T. subulata (L.)
T. casta (Hinds)
T. undulata Gray
T. lanceolata (L.)
T. maculata (L.)
T. guttata (Röding)
Tonna perdix (L.)
Cypraecassis rufa (L.)
Casmaria erinaceus L.
Liotina crenata Kiener
Leptothyra candida Pease
Pusia consanguinea (Reeve)
Imbricaria punctata Swainson
I. filum (Wood)
Philbertia tincta (Reeve)
Hydrobia sp.
Distorsio anus (L.)
Hipponix conicus Schumacher

Opisthobranchia

Bulla ampulla (L.)
Atys cylindricus (Helbling)
Acteon solidula (L.)
Acteocina sp.
Limulatys sp.
Scaphanderid
Phanerophthalmus luteus (Quoy & Gaimard)
Pleurobranchus peroni Cuvier
Asteronotus caespitosus (van Hasselt)

Cephalopoda

Octopus cyaneus Gray

Bivalvia

Anadara antiquata L.
Pinctada margaritifera (L.)
Pinna muricata L.
Chlamys cuneolus (Reeve)
Lima natans Dufo
Ctena divergens (Philippi)
C. fibula (Reeve)
Codakia punctata (L.)
C. tigerina (L.)
Erycina sp. 1, sp. 2
Fragum fragum (L.)
Gafrarium pectinatum (L.)

Bivalia–*cont.*
Pitar cf *obliquata* (Hanley)
Atactodea glabratum Gmelin
Galleomma ambigua Deshayes
Antigona reticulata L.
Jactellina clathrata (Deshayes)
Scissulina dispar (Conrad)
Quidnipagus palatam Iredale
Tellinella crucigera (Lamarck)
T. staurella (Lamarck)
Lasaea rubra Montagu

Echinodermata
Asteroidea
Astropecten phragmorus Fisher
Linckia laevigata (L.)
Tamaria lithosura H. L. Clark
Asterina burtoni Gray

Ophiuroidea
Amphioplus (*Lymanella*) *hastatus* (Ljungman)
Amphipholis squamata (D. Chiaje)
Ophiactis savignyi Müller & Troschel
Macrophiothrix longipeda (Lamarck)
Ophiothrix trilineata Lütken
Ophiocoma brevipes Peters
O. dentata Müller & Troschel
O. scolopendrina (Lamarck)
O. valenciae Müller & Troschel
O. wendti Koehler
Ophiocomella sexradia (Duncan)
Ophionereis dubia (Müller & Troschel)
O. porrecta Lyman
Ophiolepis cincta Müller & Troschel

Echinoidea
'Regularia'
Eucidaris metularia (Lamarck)
Diadema setosum (Leske)
Toxopneustes pileolus (Lamarck)
Tripneustes gratilla (L.)
Echinometra mathaei (de Blainville)

'Irregularia'
Clypeaster fervens Koehler
C. reticulatus (L.)
Fibularia volva L. Agassiz
Echinolampas ovata (Leske)
Maretia planulata (Lamarck)
Schizaster lacunosus (L.)
Brissus latecarinatus (Leske)
Metalia dicrana H. L. Clark
M. spatagus (L.)

Holothuroidea
Actinopyga echinites (Jaeger)
Holothuria (*Cystipus*) *rigida* (Selenka)
H. (*Lessonothuria*) *pardalis* Selenka
H. (*Mertensiothuria*) *leucospilota* Brandt
H. (*Microthele*) *nobilis* (Selenka)
H. (*Theelothuria*) *maculosa* Pearson
Orbythyone megapodia H. L. Clark
Synapta maculata (Chamisso & Eysenhardt)
Chiridota violacea (J. Müller)

Hemichordata
Enteropneusta sp.

Cephalochordata
Asymmetron lucayanum Andrews

Pisces

Moray eels
Lycodontis sp.
Post larval muraenid

Worm eels
Muraenichthys macropterus Bleeker
Myrophis uropterus (Temminck & Schlegel)
Moringua microchir Bleeker

Burrowing fish
Kraemeria samoensis Steindachner

Pipe fish
Ichthyocampus belcheri Duncker

Others
Gunnellichthys pleurotaenia Bleeker
Scorpaenidae juvenile Percomorph