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COMPARISON OF SPECIES DIVERSITY AND ECOLOGY
OF REEF-LIVING INVERTEBRATES ON
ALDABRA ATOLL AND AT WATAMU, KENYA

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SYNOPSIS

Extensive quantitative samples of components of the invertebrate fauna (Errant Polychaeta, Decapod and Stomatopod Crustacea, and Echinodermata) associated with intertidal and subtidal reef areas on Aldabra and at Watamu, Kenya are analysed statistically to give estimates of population sizes, species diversity, dominance and distribution. A brief description of the topography and general ecology of the reefs studied is given and the two areas are compared. Techniques for sampling reef fauna are discussed and a method of obtaining quantitative samples of the infauna of hard substrates is described. Results are given for several "habitats" (e.g. channel, subtidal coral platform, intertidal cobble ridge) and for different substrates within the same "habitat" e.g. live coral, dead coral) in order to test the validity of existing "habitat" classifications and to determine which factors may account for species diversity. In a section on the breakdown and colonization of dead coral, the action of boring organisms is considered and also their interaction with subsequent colonizers. It is concluded that, in general, hard substrates support a larger and more varied infauna than soft substrates; that biotic interactions play a very important part in determining species diversity (a measure of the importance is given in the section on colonization of coral) and that reef areas at Watamu support a greater diversity of species than similar "habitats" and substrates on Aldabra.

INTRODUCTION

Much work has been carried out, particularly in recent years, to establish why tropical regions support a greater diversity of species than regions of higher latitude (MacArthur, 1965; Lowe-McConnell,

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1969), but although some of it has been concerned with the theoretical aspects of species diversity in marine tropical communities (Thorson, 1957; Dunbar, 1960; Connell and Orias, 1964) there has been very little practical work (Parker, 1963; Paine, 1966). Several studies of reef environments and reef-living invertebrates have described the major types of "community" or "habitat" (Yonge, 1963a; Scheer, 1967; Taylor, 1968) and a few have attempted to describe the trophic structure (Odum and Odum, 1955). The "biomorphology" of Solomon Island shores is described in great detail by Morton and Challis (1969) and they have proposed a new terminology for the various components. Papers by Sanders (1968) on the marine benthic diversity of soft substrates in tropical and temperate seas and by Kohn (1967, 1968) on the diversity and distribution of *Conus* on reef platforms in the Indo-West Pacific have added a great deal to our knowledge of the subject and to the methods for studying it. Species diversity and the origin of species are interesting in their own right and also for the part they play in an understanding of community organization.

This paper describes our attempts to discover why certain "habitats", areas or substrates will support a high diversity of species, while others have few. We hope to show how the present ecological structure is able to support the number of species which it does, rather than to postulate how such a level has been attained, although the two are ultimately inseparable.

The groups dealt with in this contribution are the errant polychaetes, Decapod and Stomatopod Crustacea and Echinodermata. It has not been possible to include all the data on the detailed distribution of the animals of each phylum and the data on the sedentary polychaetes, Isopoda, Amphipoda, Cirrepedia, Mollusca, Sipunculida, and Pycnogonida have yet to be worked up. Fauna lists and further publications, which will treat the special features and adaptations of the major phyla are in preparation.

A very large proportion of the time was spent in the identification of the collections and the authors are responsible for all the identifications (Brander—Polychaeta; Humphreys—Echinodermata; McLeod—Crustacea).

TOPOGRAPHY, CLIMATE AND PHYSICAL CONDITIONS

General description of Aldabra

Aldabra is an elevated limestone atoll (9°24'S, 46°20'E; Fig. 1) 650 km off the African mainland. It is separated from all land, save

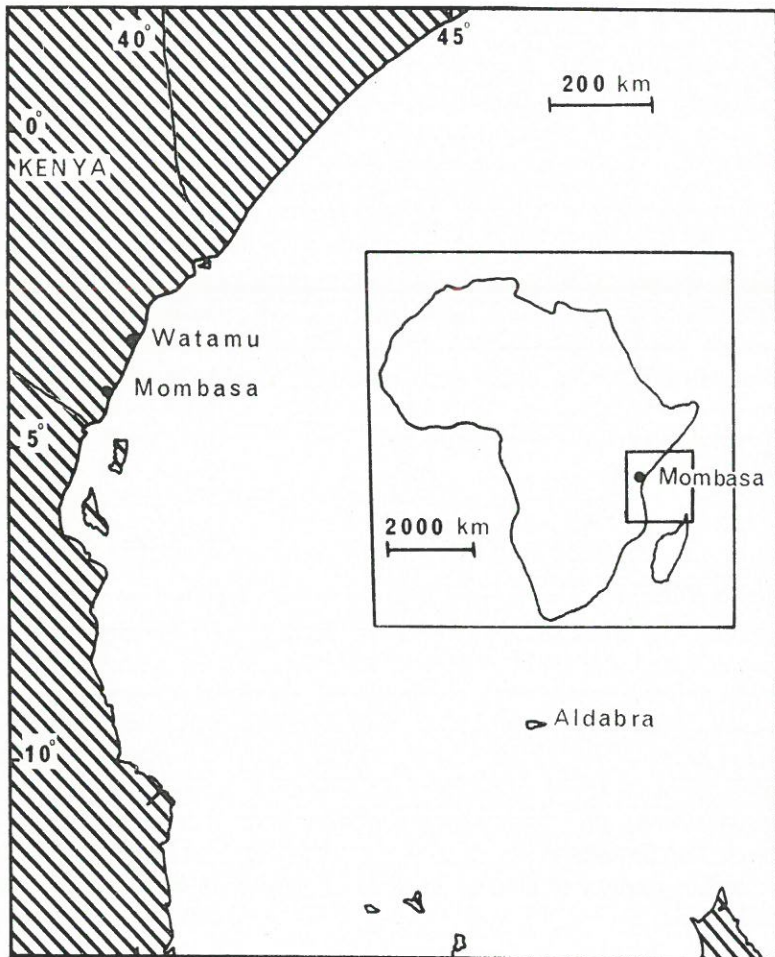


FIG. 1. East African coastline, showing the position of Aldabra in relation to Watamu.

for Cosmoledo and Assumption, by an oceanic basin of between 2 and 3 thousand fathoms.

The morphology of recent and fossil reefs has been reviewed by Stoddart (1969); that of Aldabra by Stoddart *et al.* (1971) and Barnes *et al.* (1970). The raised limestone rises to a general level of around 3 m and reaches a maximum of 10 m. Stoddart (1967) reviews and supplements previous work on the atoll.

The atoll is surrounded by a moderate to extensive reef flat of varying level and the rim is penetrated by a series of shallow and deep

channels. The nature of the shore varies according to the degree of exposure, from high energy in the east and southeast to medium and low energy in the north and west. The characteristics of the Aldabra reefs have been discussed by Barnes *et al.* (1970) and their work suggests that the reef is advancing only to the west.

The seasons on Aldabra are governed by the migration of the subtropical high pressure belt and the intervening equatorial trough. From April to October the S.E. Trade-winds blow strongly, bringing negligible rainfall. During the summer months of November to March the monsoon season brings moderate N.N.W. winds and with them the major rainfall. Farrow (1971) has shown that much of the annual rainfall can fall within a few days and that Aldabra is in the most arid section of the Indian Ocean. His work indicates potential lagoon surface temperatures of 35°C if extreme low water coincides with the middle of the day in summer.

Description of the sampling areas on Aldabra

Passe du Bois

Figure 2 is a map of the Western Channels and Settlement area and the positions of the profiles shown in Figs 3 and 4 are marked.

Passe du Bois is the only one of the Western Channels which deeply dissects the reef platform and as such is comparable with the other major channels of the atoll: Grande Passe, Passe Houareau and Passe Gionnet. It is bounded by low energy cliffs with a deep solution notch, which rise from the *Cymodocea*-covered intertidal flats bordering the channel. The flats drop off very steeply and the sides of the channel are lined with a variety of corals and coral rubble (Fig. 5). The coral cover is fairly low—about 20%—and a notable feature is the presence of a black *Dendrophyllia* sp. This occurs from near the bottom right up to the lower intertidal and is more abundant on the north side.

The bottom of the channel (Fig. 6) is composed of mobile sand and rubble and supports no live coral, except at the seaward end, where it becomes wider and shallower, before falling again to the sandy fan just beyond the edge of the intertidal boulder ridge. Lagoonwards the channel is soon lost amongst the *Cymodocea* flats and coral growth.

Tidal records and current measurements made during the course of our work in Passe du Bois are fully described in Farrow and Brander (1971). Temperature and salinity records were also kept and between 12th August and 8th September they show a mean temperature of 25.3°C, with a maximum of 28.5°C (at the end of the ebb period) and a minimum of 23.0°C (during the inflowing tide). The mean salinity

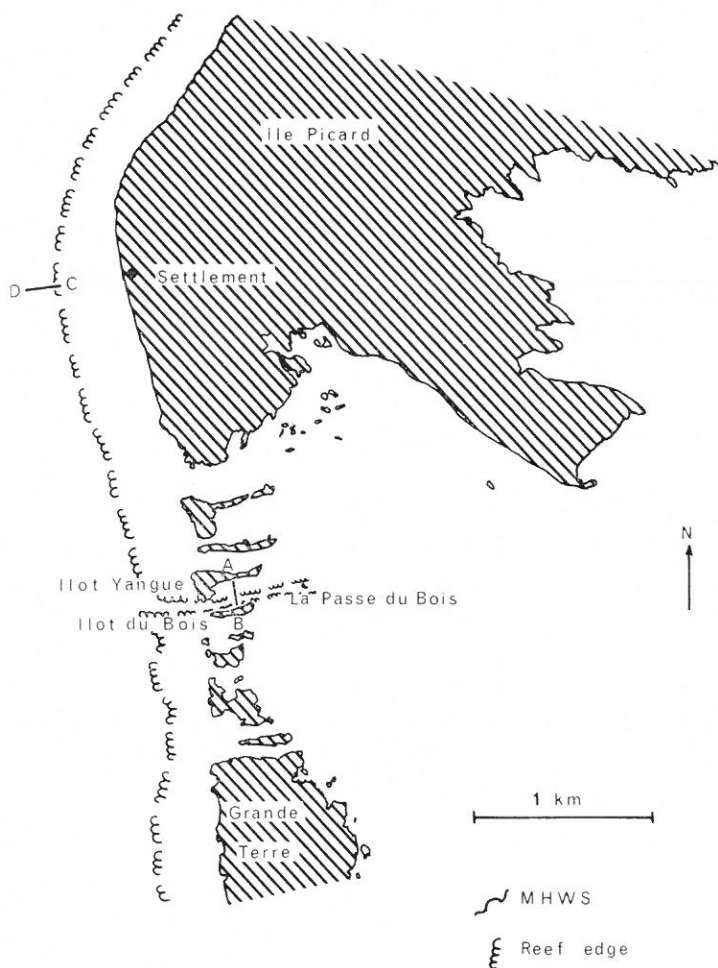


FIG. 2. Western end of Aldabra, showing the position of the transects in Passe du Bois and off Settlement.

for the period was $35.16^{0}/_{00}$ with a maximum of $35.64^{0}/_{00}$ and a minimum of $33.24^{0}/_{00}$. Thirteen out of eighteen readings fell within the range $35-35.5^{0}/_{00}$. Measurements made over a complete tidal cycle and analysis of other records indicate highest salinities at the end of the ebb period and the fluctuation over the cycle is about $1^{0}/_{00}$.

Settlement reef

The beach at Settlement is the only extensive one on the island. It is a steeply shelving low energy beach, due to its leeward position

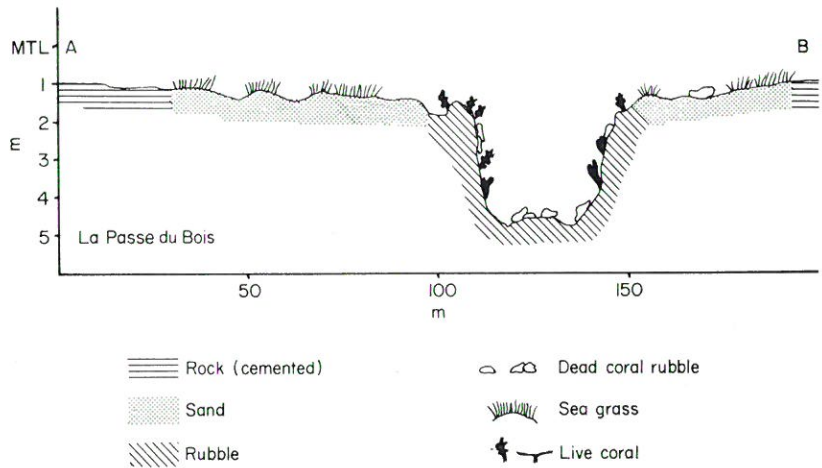


FIG. 3. Profile of the transect across Passe du Bois, Aldabra.

during the dominant S.E. Trades. An inshore rock platform fringes part of the beach, but is only extensive immediately north of the landing. The reef flats are intertidal at Settlement, but slope down into the shallow sublittoral to the south. They are sparsely covered with marine angiosperms, chiefly *Cymodocea* sp., which is progressively eroded and covered by sand to the north during the S.E. Trades. The flats are pitted with erosion hollows up to one meter deep and lined with sand and rubble.

At the seaward limit of the intertidal flats there is a well defined boulder ridge, beyond which a gently shelving rock platform merges into sand patches, *Cymodocea* beds and millepore corals (Fig. 3). Barnes *et al.* (this volume, pp. 87–114) have outlined a zonation scheme for this reef front, based on a photographic transect. Our sampling was carried

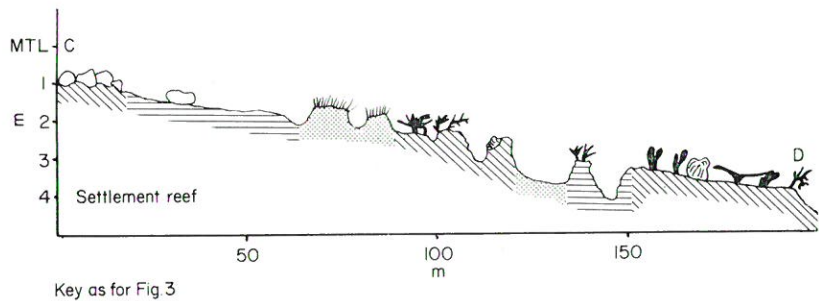


FIG. 4. Profile of the transect off Settlement, Aldabra.

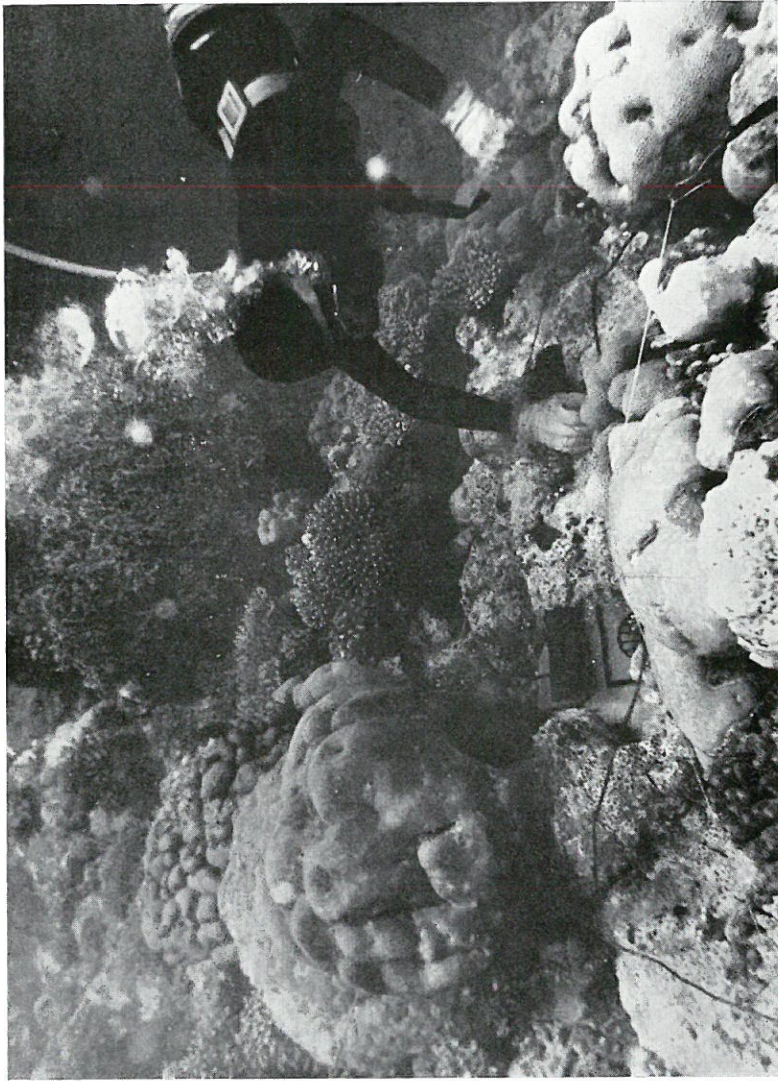


FIG. 5. Side of Passe du Bois, showing a diver sampling a one meter square quadrat.

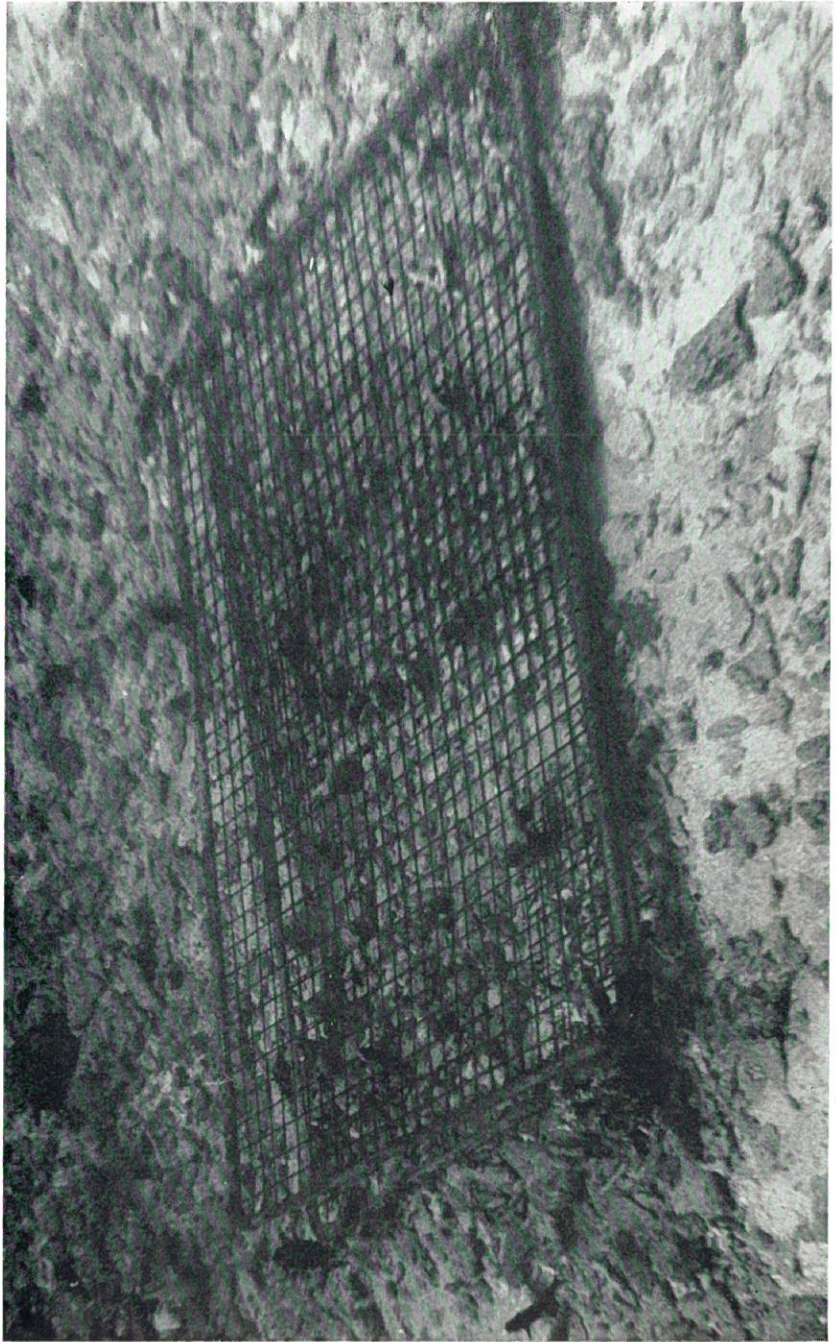


FIG. 6. Wire mesh shark cage on the bottom of Passe du Bois. The mesh has been undercut by the current over a period of two weeks and some small stones have been carried on top of it.

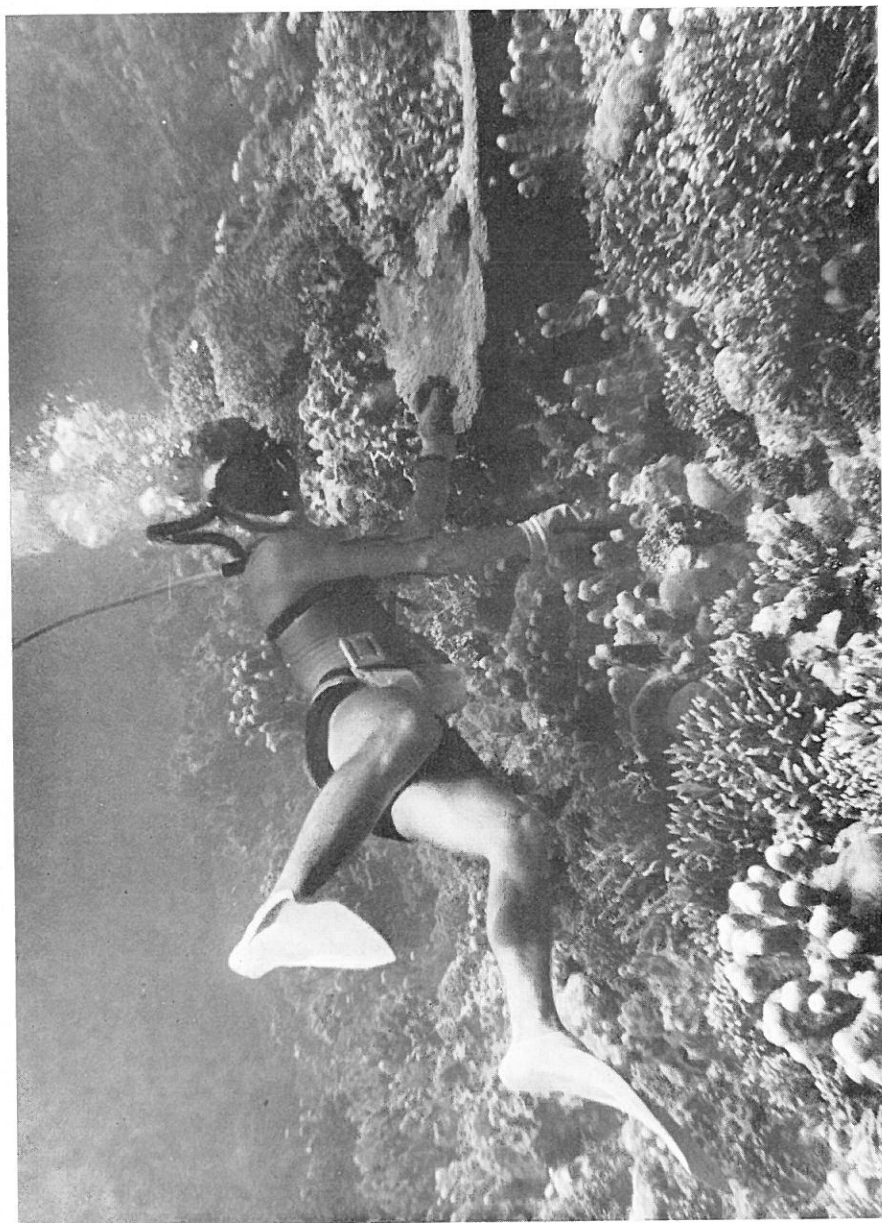


FIG. 7. Profuse coral growth 4 m below MTL in the sampling area off Settlement, Aldabra.

out on the boulder ridge and subtidally on the coral area at a depth of 3–5 m below Mean Tide Level (MTL) (Fig. 4). A narrow sandy channel runs parallel to the boulder ridge about 100 m out from it, and at a depth of 3–4 m below MTL. This divides the coral terrace into an area of predominantly branching acroporan corals on the landward side and an area of mixed, small corals on the seaward side. Most of our sampling was carried out on the latter, where the diversity of corals is very high and the cover of live coral about 50% (Fig. 7). Beyond this terrace there is a shelf break at a depth of 4–5 m below MTL, below which is a belt of predominantly soft corals and below which we were unable to dive.

Sea temperature records kept from the beginning of October to the end of November showed an increase over that period, from an average of 25.2°C for the first half of October to just over 26°C for November. One also found a thermocline, particularly at low tide on calm days, with temperatures in the surface layer 0.6–1.0°C higher than on the bottom. No current speeds of over one knot were recorded during this period and observations while diving and from R.V. "Manihine" using a Carruthers totalizing current meter showed a prevailing northerly or northeasterly drift, with occasional changes to southerly. Surge has a much stronger influence on the coral area and made diving impossible on several occasions. It is likely to be even more important during the N.W. monsoon.

General description of the Watamu area

The Watamu Marine National Park is situated on the coast of Kenya (40°00'E, 3°20'S; Fig. 1) 22.5 km S.S.W. of Malindi and 960 km N.W. of Aldabra.

The past and present reefs of the East African coast have been studied at points ranging from the Sudan to Moçambique (Table I) and the Malindi area in particular by Thompson (1956). The coastal plain of Kenya is generally below 33 m and is 11 km wide in the Watamu area. The coast here is backed by a wide band of raised fossil reef and coral breccia, which shows little dolomitization. It is overlain by sands and sandstone and gypsum belts around Mida Creek and Kibirijini Point. Thompson further recognizes several marine transgressions and coastal terraces which are summarized in Table II.

The coast is fringed by a reef platform up to 1.75 km wide and patch reef development occurs immediately southeast of Malindi. Resistant coquinas form a series of champignon islets on the reef flats around Watamu. At Kibirijini and Watamu headlands these are joined to the shore by sands, forming tomboles.

TABLE I

Previous workers on the reefs of the east coast of Africa

S. Africa:	Boshoff, 1958
Tanzania:	Cox, 1927 Crossland, 1902, 1903 Ortmann, 1892 Talbot, 1965 Werth, 1901
Kenya:	Caswell, 1953, 1956 Crossland, 1903 Lawson, 1969 McKinnon Wood, 1930 Thompson, 1956
Sudan:	Berry, Whiteman and Bell, 1966 Crossland, 1907 Veeh and Giegengack, 1970

There is little continental shelf and consequently the water is deep fairly close offshore, although not as close in as around Aldabra. Thompson recognizes submarine terraces at -8 m and -35 m.

The weather on the Kenya coast is governed by the same seasonal factors as at Aldabra. During the S.E. Trades from April to October the winds blow strongly with great constancy and bring the main rainfall, which reaches a maximum in May. The "short rains" occur during the calmer N.E. monsoon from November to March. As with Aldabra the rainfall can be torrential and much of a month's rainfall can occur within a few days. Comparative meteorological data for Malindi and Aldabra are given in Table III.

Neither Aldabra nor Watamu come under the influence of a major drainage system. The nature of the terrain on Aldabra mitigates against any large scale run-off across the reef flats. The catchment area of Mida Creek is very restricted and the sands inland lead to slow percolation drainage rather than rapid surface run-off (Thompson, 1956). Hence the main rainfall effects in both areas can be expected when monsoonal rainfall coincides with extreme low water. At such times considerable damage to exposed corals can be expected (Taylor, 1968).

Turtle Bay (Fig. 8) is bounded in the north by a raised limestone platform with characteristic medium energy cliffs and adjacent reef flats. To the south the bay ends with the channel of Mida Creek. The

TABLE II

Recent earth movements and events in the Malindi area

Period	Local representatives	Earth movements and events	Pluvials etc.
Recent	Wind blown sands Marine sands	Sea level as at present day. Silting up of Mida Creek etc.	
	Upper	<p>Silting up of Mida Creek starts. Sea level rises to present day. Terrace cut. Sea-level drops to about -25' O.D. Coquinas accumulate. Sea level rises to about +25' O.D.</p>	Post-pluvial Gamblian
		<p>Wind blown sands accumulate on coastal plain.</p>	3rd Inter-pluvial
Pleistocene	Middle	<p>Wind blown sands start to accumulate. Sea level drops. Platform cut about -130' O.D. Coquinas accumulate as off-shore bars. Wind blown sands accumulate as dunes. Lagoonal sands accumulate. Corals grow. Sea level rises to about +120' O.D.</p>	2nd Inter-pluvial
	Lower	<p>Marine platform cut on which corals grow. Marine recession. Marine recession.</p>	Kamasian Kageran
Pliocene	Lower	Uplift.	
Miocene	Lower	Marine invasion.	
Cretaceous		Uplift.	
Jurassic	Upper	Fluctuations in sea level.	
Triassic	Upper Lower	Karoo Uplift. Uplift.	

From Thompson, 1956.

TABLE III

Meteorological data for Aldabra (Settlement) and Malindi (22.5 km N.E. of Turtle Bay)

	Aldabra	Malindi
Rainfall mean	670 mm	1020 mm
Rainy days	112	105
Max. annual rainfall	1192 mm	
Min. annual rainfall	349 mm	
Mean humidity 0800	No data	80 %
1400	See Farrow, 1971	72 %
Temperature		
extreme max.	36.3°C	36.2°C
min.	19.5°C	15.6°C
Mean summer max.	32°C	30°C
Mean winter min.	22°C	22.8°C
Annual mean temp. fluctuations	4°C	
Mean diurnal temp. fluctuations	6.5°C	
Extreme diurnal range	11°C	
Mean wind speed (Beaufort Scale)	2.9	
Month max. rain	Variable	May
Mean rainy days		
March, Nov., Dec.	See Farrow, 1971	3
Jan., Feb.		1
May		19
Wind constancy April to October	91.8	

Sources: Aldabra—Farrow, 1971.
Malindi—Meteorological Office.

predominantly sandy beach is backed by low stabilized dunes overlying raised reef limestone, which occasionally outcrops on the beach. During the S.E. Trades the beach is exposed to the full force of the waves at high spring tides. Jones (1970) has shown, by particle size analysis, that the beach is increasingly sheltered to the north of Turtle Rock.

The beach and cliffs drop to a rock platform about one meter above datum. This platform occurs at a uniform level throughout the park and is characteristic of many parts of the coast to the north and south. A remnant of it forms the roof of the Big Three Caves in the middle of Mida Channel.

The most widespread bottom community in Turtle Bay is that dominated by beds of marine angiosperms, particularly *Cymodocea ciliata*. The flora of the coast has been described by Graham (1929),

Isaac (1967, 1968) and that of Turtle Bay in particular by Kay (1970). The grass beds extend from 0.5 m below MTL to 5 m below and those in shallow water are extensively eroded during the S.E. monsoon. To the south the grass beds are increasingly broken by sand channels and coral growth, ending in the mobile sands and coral areas of Mida Creek.

To seaward a poorly developed rocky ridge diverges slightly from the coast, to which it is attached by the peninsula at the northern end of the park. At its northern end it emerges on low spring tides, but to the south it gradually shelves down and is broken by surge channels up to 1.5 m deep. There are several lines of sunken reefs running parallel to the coast beyond this "inner reef".

The physical features, conditions and the principal animal and plant communities of the park are described in some detail in the Preliminary Report of the 1969 Bangor Watamu Expedition (Jones, 1970).

Description of the sampling areas at Watamu

Most of our rock samples from Turtle Bay were taken in the region of the coral heads (Figs 8, 9) at a depth of about 5 m below MTL. The coral here is mainly in the form of massive heads of *Porites*, with a fair diversity of other species and a cover of about 50% live coral. The heads border a deep sandy channel running parallel to the beach, but there are no currents along it. A few of the samples came from an area of dense coral growth near the Big Three Caves in Mida Creek, from an area which may in many ways be compared with the sides of Passe du Bois. Currents of up to four knots run through the channel, but the cover of hard and soft corals is high, even on the floor of the channel.

SAMPLING METHODS

The transect and quadrat method

The initial approach was to follow the kind of "habitat" classification widely used in work on coral reefs (Kohn 1967, 1968; Taylor, 1968) and attempts were made to obtain quantitative samples of the invertebrate fauna of intertidal and subtidal "habitats" in Passe du Bois, using a transect and quadrat method. A chain was laid across the channel floor and quarter meter square quadrats were sampled at regular intervals of 4 m or 8 m.

The method followed was for two divers to dig up the substrate to a depth of about 10 cm and put it in large polythene bags underwater. The volume of substrate obtained from each quadrat varied a great deal, depending on whether the frame encompassed coral heads or a

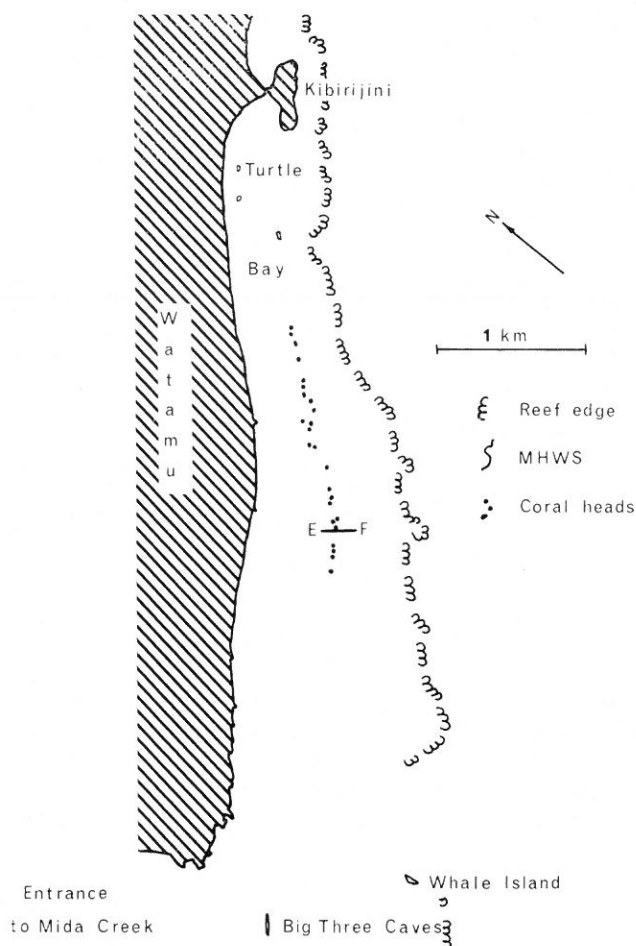


FIG. 8. Watamu Marine Park, Kenya, showing the position of the transect.

flat bottom (Fig. 5). Shovels, hammers, crowbars and a suction pump were used to complete the sampling. The samples were roughly subdivided into sand-and-gravel, coral rock (dead) and live coral. The average volume of material extracted from each quadrat was 18.8 l, made up of 7.0 l of coral rock, 3.7 l of gravel, 7.6 l of sand and 0.5 l of live coral. Figure 10 shows the percentage of each fraction in the samples from the three "habitats". The animals were extracted by breaking up the rocks into small pieces with a hammer and chisel and sorting by hand. In some cases the samples were so large that they had to be subdivided.

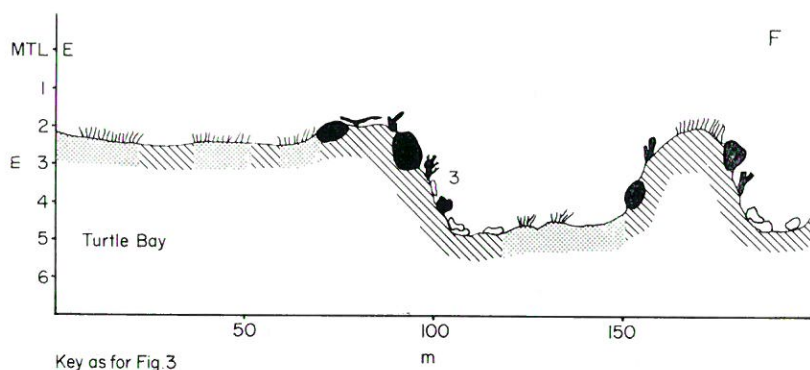


FIG. 9. Profile of the transect in Watamu Marine Park.

It rapidly became apparent that, although this method is suitable for sampling the larger elements of the fauna, particularly molluscs and echinoderms, it would not work with the small and infaunal elements. There are two reasons for this. In the first place the small animals are not sampled efficiently, since the volume of material to be examined is too large and the substrate composition too mixed. This point is illustrated in Table IV, which compares the numbers extracted per litre of coral rock by this method (Method 1) and by the method subsequently adopted (Method 2). Since the latter method has been shown to be only 58% efficient for polychaetes and only 81% efficient for Crustacea, it follows that extraction efficiency by the quadrat method is of the order of 5% efficient for polychaetes and 25% for Crustacea. The second, more important, difficulty encountered with the quadrat method is one of "within-sample heterogeneity". As may be seen from Fig. 10 the

TABLE IV

Numbers of animals per litre extracted from coral rock and sand in Passe du Bois. (1, by the quadrat method; 2, by the rock method) \pm twice the standard error

	Errant Polychaetes	Decapod + Stomatopod Crustacea	Echinoderms
Method 1 Gravel/sand	0.5 \pm 1.58	3.0 \pm 2.50	0.4
Coral rock	3.5 \pm 0.87	1.6 \pm 3.97	0.71
Method 2 Coral rock	35.1 \pm	5.26 \pm 2.35	1.7

composition of the substrate within any quadrat from a particular "habitat" may vary considerably and it was found that the numbers of animals and the species composition of the different fractions within the same quadrat showed even greater variations. Table IV shows that the number of polychaetes per litre in the sand fraction was well below the number found in coral rock. A reasonable analogy might be to sample the animals of mixed woodland and heath with a large quadrat. It might give good results for deer, but would be impossible for counts of small arthropods. This is partly a question of choosing the right size of sample for a particular job, but it also raises the question of how widely applicable the existing kinds of "habitat" classification are in such a heterogeneous area. The infauna of a rock from a subtidal coral area may show greater faunistic affinities to nearby beachrock than to the sand on which it rests. In this context Hiatt's assertion (Hiatt, 1953) that the transect method is the only method by which a quantitative analysis can be made and that "any other means of collecting data will fall short of the critical analyses made possible by the transect method" must be denied.

A further difficulty encountered with all sampling methods is that of quantifying the data, as this can either be per unit of area or per unit of volume. It is common practice to give population densities in units of area, particularly in productivity studies, since this is the only basis on which incident light can be measured, but for infauna in an area of three dimensional complexity such as a coral reef this measure is unsuitable. Quantifying by volume is not ideal either, since the

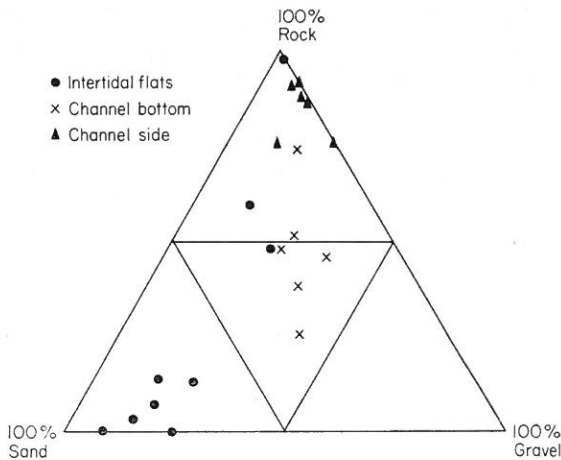


FIG. 10. Triangular diagram of substrate composition in Passe du Bois.

number of animals tends to decrease towards the centre of the rock. Correlations of numbers of animals with volume and area were calculated, but gave no conclusive results, because the numbers were too small. Our approach has been to give numbers per unit of volume, but we also made notes on the nature of each sample, including its surface area and on this basis we have been able to show that for certain groups, particularly Crustacea, numbers are related to surface area.

The rock sampling method

The method of sampling subsequently adopted was to pick rocks or pieces of coral of approximately one litre volume (Fig. 7) and to extract the animals by smashing the rock into small pieces, leaving the pieces in a flat gravel tray containing 5 l of seawater and 20 ml of 4% formalin overnight and hand sorting the following day. Fifteen samples were minutely re-sorted to test the efficiency of the method and it was found to be about 37.5% efficient for sipunculids, 58% efficient for polychaetes, 81% efficient for Crustacea, 93% for molluscs and 100% for echinoderms. Only animals which could be seen with the naked eye were dealt with. The efficiency of this method is much higher than the quadrat method for small animals and sampling and processing are much easier. We found that two people could take 6 replicate samples from a particular area or of a species of coral and process them in one day. Working with a quarter meter quadrat only one sample was possible, the extraction efficiency was low and replication of the samples was unsatisfactory. The problem of quantifying remains, but the variability in the volume and surface area of each sample is greatly reduced, which makes estimation of population densities far more accurate. The disadvantages of the method are that sampling is more subjective, because one is selecting rocks or heads of about the right size and one is only sampling a part of the "habitat". The method provides an index of the numbers of species and their abundance, rather than an absolute value. It is interesting to note that a similar method has been found useful in studying the ecology of the fauna of stones in a South African river (Chutter, 1968).

The echinoderms, errant polychaetes and decapod and stomatopod Crustacea have been identified to species and work is continuing on the remaining groups of these phyla, plus the sipunculids and molluscs. It is not possible to give full details of the distribution of animals within each phylum in this contribution, but fauna lists and detailed analyses are in preparation. Tables V-VII give the number of samples, animals and species for each area or type of coral sampled.

TABLE V

Sample sizes and numbers of errant polychaetes, decapod and stomatopod Crustacea and echinoderms
(nos per litre \pm twice the standard error)

	No. of rocks	Total volume	<i>Polychaeta</i> Nos per litre	<i>Crustacea</i> Nos per litre	<i>Echinodermata</i> Nos per litre
ALDABRA					
Intertidal:					
Boulder ridge	14	14.9	7.45 \pm 5.25	7.25 \pm 2.39	0
Subtidal:					
Coral area	17	13.0	30.23 \pm 6.04	4.77 \pm 2.23	0.4
PdB side	12	11.9	28.51 \pm 7.00	7.39 \pm 3.25	1.7
PdB bottom	10	7.9	28.73 \pm 11.0	2.04 \pm 1.38	0
WATAMU					
Subtidal:					
Coral area	14	17.4	9.49 \pm 4.62	5.92 \pm 2.93	

TABLE VI

Comparison of numbers of species per 100 (or per 50) individuals as calculated by the rarefaction method

	No. of animals	Polychaeta		Species per 100	No. of animals	Crustacea		Species per 50	Echinodermata		
		No. of species	Species per 100			No. of species	No. of animals		No. of animals	No. of species	
ALDABRA											
Intertidal:											
Boulder ridge	120	13	12.3	108	18	14.3	0	0	0	0	
Subtidal:											
Coral area	393	33	20.9	62	17	15.3	5	3	3	3	
PdB side	336	37	25.9	88	26	22.1	20	10	10	10	
PdB bottom	227	19	15.4	16	7		0	0	0	0	
WATAMU											
Subtidal:											
Coral area	219	50	38.0	106	30	22.3					

TABLE VII

Sample sizes and numbers of errant polychaetes, decapod and stomatopod Crustacea and echinoderms in coral samples from the Settlement coral area (nos per litre \pm twice the standard error)

Rock	No. of rocks	Total volume	Polychaeta Nos per litre	Crustacea Nos per litre	Echinodermata Nos per litre
Coral area	17	13.0	30.23 \pm 6.04	4.77 \pm 2.21	0
Coral					
<i>Pocillopora</i>	6	4.5	4.44 \pm 3.19	28.40 \pm 11.28	0.9
<i>Stylophora</i>	6	7.4	11.80 \pm 6.25	24.04 \pm 10.94	1.8
<i>Porites</i>	6	3.6	5.00 \pm 3.42	3.63 \pm 1.94	1.1
<i>Millepora</i>	6	2.7	9.26 \pm 9.63	12.39 \pm 9.10	1.5
<i>Acropora A</i>	6	8.6	0.58 \pm 0.57	0.61 \pm 0.64	0.2
<i>Acropora B</i>	6	5.0	0.60 \pm 0.83	54.81 \pm 10.86	0.4
<i>Leptoria</i>	6	11.9	2.02 \pm 1.89	1.92 \pm 1.72	0

In order to permit direct comparison of species diversity between samples of different sizes, we have used the rarefaction method described by Sanders (1968) in his comparative study of within-habitat diversity of temperate and tropical marine benthic communities. Each group of samples is used to generate a line representing the number of species which would be found in a sample containing any particular number of animals (Figs 11, 12). Since the method depends on the shape of the species abundance curve, rather than the absolute number of specimens per sample, it is independent of sample size, however when the sample is very small, it is not worth applying the method and we have only given total numbers of animals and numbers of species. It is only possible to extrapolate for numbers smaller than the size of the sample by the rarefaction method. Even with our larger samples it has not been possible to give confidence limits for the curves and while we regard the general form and separation of the curves as significant we have not attempted to interpret the detail.

Sanders compares the rarefaction methodology with other commonly used measures of diversity. He finds good agreement with the Shannon-Wiener information function.

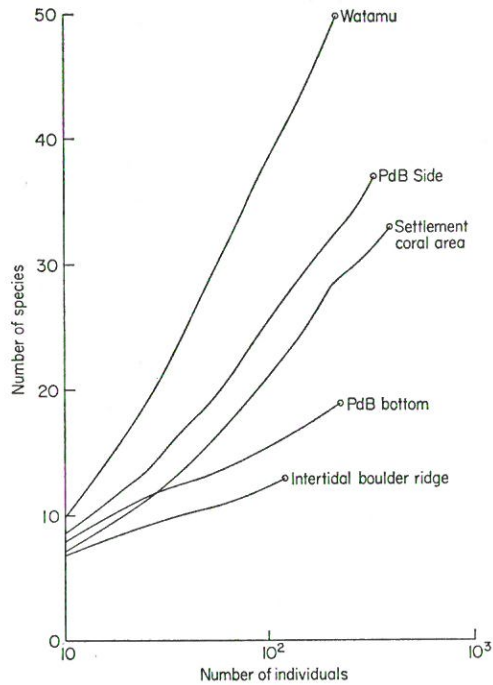


FIG. 11. Rarefaction curves for errant polychaetes.

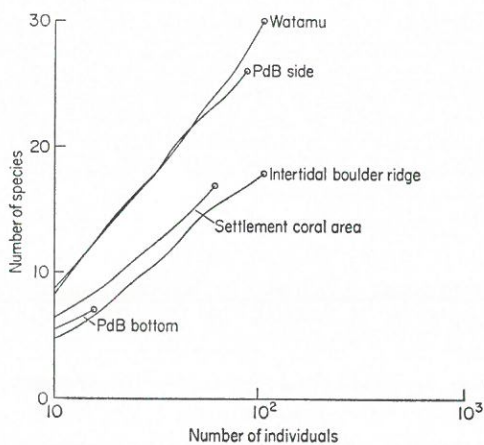


FIG. 12. Rarefaction curves for Decapod and Stomatopod Crustacea.

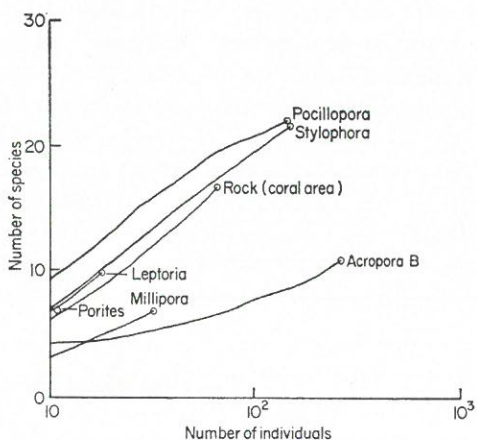


FIG. 13. Rarefaction curves for Decapod and Stomatopod Crustacea on live corals.

RESULTS

Comparison of species diversity on Aldabra and at Watamu

Preliminary surveys of the subtidal grass beds and coral areas at Watamu showed us that, as expected, the diversity of species is greater there than on Aldabra. This increased diversity was most apparent for the echinoderms, particularly asteroids and echinoids, but rock sampling revealed that the diversity of polychaetes and Crustacea was also higher, although only marginally so for the latter (Figs 11, 12).

The fact that the small units of sampling which we were using showed this difference is of particular interest when considering the hypotheses to account for the differences in diversity. Although it is impossible to select samples which are in every way similar from the two areas, our method does allow a high degree of confidence in the comparability of the samples.

The rock samples from Watamu may be most closely compared with those from the coral area at Settlement, Aldabra, which they resembled in type of rock, depth at which found, nature of the surrounding "habitat" and, as described in the "Introduction", physical environment.

There are two hypothetical patterns to account for a greater diversity of species in one region than another. In the first, each small component of one region has x times as many species as each equivalent area of the other. In the second, equivalent areas have equal numbers of species, but there is a greater variety of components in the former region. Our data supports the first hypothesis, although there may also be a greater number of different "habitats" on the East African coast than on Aldabra.

Kohn (1967) discusses similar data for the genus *Conus* in relation to "species diversity gradients" in the Indo-West Pacific from the Indonesian "faunistic centre" (Ekman, 1953) or "centre of dispersal" (Ladd, 1960). Until we can use our methods to obtain data from many more localities, our own views on the question must remain speculative. The diversity of the reef-living invertebrates which we have studied is higher on the mainland than on Aldabra and this is a "within-habitat" difference.

*Comparison of the species diversity of intertidal and
subtidal rocks*

The intertidal samples, taken from the boulder ridge on the edge of the intertidal flats at Settlement, Aldabra, show the lowest diversity of any group of samples. There is however a difference between the polychaetes and the Crustacea in this respect, as the former show a far lower diversity in the intertidal than on adjacent subtidal areas, while for the latter the difference is small (Figs 11, 12). Most of the polychaetes live within the rock and one finds much larger aggregations of one species in the intertidal than in subtidal rocks. The Crustacea tend to be more mobile and scavenging and the dense mat of small green algae, mussels, detritus and sand found on the surface of intertidal rocks provides a suitable habitat. The Isopoda and Amphipoda are particularly numerous, but are difficult to sample accurately.

Topographically, the boulder ridge is very similar in appearance to the subtidal coral area and apart from surface cover, rocks from the two areas are identical. Thus topographic diversity cannot be responsible *per se* for differences in species diversity.

It seems likely that the intertidal ridge represents a community of the type which Sanders (1968) describes as "physically controlled", in which the physical conditions fluctuate widely and the animals are exposed to severe physiological stress, while the subtidal rocks come from a "biologically accommodated" community, which is a more stable, complex and buffered assemblage, characterized by a large number of stenotopic species. This is borne out by the presence of a few abundant and highly aggregated species in the samples from the boulder ridge and the more equable, but spotty distribution of subtidal species.

Table VIII gives the indices of species overlap for the chief sampling areas, using R_o (Horn, 1966). The intertidal polychaete samples resemble the samples from the bottom of Passe du Bois most closely. A possible explanation for this may be that both have lost the fraction of the fauna normally found on the surface of the rock; in the case of the intertidal sample due to wave action and extreme physiological stress and in the channel sample due to current action and abrasion.

The origin of the rocks on the intertidal boulder ridge may be of importance in determining the type of fauna they support. Those examined appeared to be of the same origin as the coral rocks and rubble of the subtidal coral areas. In many cases it was possible to determine the species of coral of the rock and the intertidal and subtidal rocks came from the same species. An experiment to find out how much movement rocks on the boulder ridge undergo showed that little movement took place during the two and a half months of the experiment. This period included some very rough weather and there was considerable movement of nearby sand banks, but none of the experimental rocks had moved more than 7 m.

Comparison of the species diversity of subtidal rocks from the Settlement coral area, Passe du Bois side and Passe du Bois bottom

Of the three subtidal areas sampled on Aldabra the coral and rubble sides of Passe du Bois showed the highest diversity and the bottom of the channel the lowest, with the coral area off Settlement intermediate. The sides of Passe du Bois have a much lower coral cover than the Settlement coral area and there is more loose coral and rubble. Physical conditions in the Passe are described in the "Introduction" and in Farrow and Brander (1971). The high species diversity here may be

TABLE VIII

Indices of species overlap for the chief sampling areas, using R_o (Horn, 1966)

Polychaeta				
	Passe du Bois side	Passe du Bois bottom	Settlement coral area	Settlement intertidal
Passe du Bois bottom	0.8974	—	—	—
Settlement coral area	0.8607	0.8791	—	—
Settlement intertidal	0.4962	0.6778	0.6179	—
Watamu	0.5508	0.5249	0.5234	0.4781
Crustacea				
	Passe du Bois side	Passe du Bois bottom	Settlement coral area	Settlement intertidal
Passe du Bois bottom	0.0428	—	—	—
Settlement coral area	0.5574	0.2509	—	—
Settlement intertidal	0.2003	0.0691	0.2128	—
Watamu	0.3868	0.2536	0.3060	0.1469
Total overlap = 1 Zero overlap = 0				

due to components of the lagoonal fauna being present as well as the oceanic species. There is some evidence for this among the polychaetes, particularly Amphinomidae, but until the lagoon samples are worked up fully, the extent of the lagoonal contribution cannot be assessed quantitatively.

The contrast between the samples from the sides of Passe du Bois and the bottom is particularly striking, since they are in physical respects almost identical. The one important exception is current speed. Detailed measurements of the flow of water through the channel, using fluorescein (described in Farrow and Brander, 1971) have shown that flow along the sides of the channel and among the coral heads is extremely turbulent and the current speed is greatly reduced. Rocks

on the bottom of the channel tend to be smaller and flat and are frequently covered with sand and moved by the current (Fig. 6). They often lack a surface cover of calcareous or filamentous algae and the surfaces are smooth and scoured. The numbers of surface living animals, particularly Crustacea, are correspondingly reduced.

Comparison of the species diversity of the fauna of subtidal rocks from the Settlement coral area and seven species of live coral from the same area

Tables VII, IX give the numbers of animals per litre and the numbers of species per 25 individuals and Fig. 13 gives the rarefaction curves for the Decapod and Stomatopod Crustacea for the corals and the "dead" rock samples from the same area. The coral species are:

Pocillopora eydouxi, a branching species, which forms small heads;

Stylophora mordax, similar to the latter;

Porites nigrescens, a grey branching species;

Millepora platyphylla, forming large upright plates, with numerous barnacles (*Pyrgoma* sp.) on them;

Acropora palifera (= *Acropora A*), a massive species, forming fingers 5-10 cm wide;

Acropora tubicinaria, (= *Acropora B*) a highly branching species forming extensive heads;

Leptoria sp., a "meandrine" brain coral.

The numbers of polychaetes to be found in the live corals is extremely low and those present were generally found near the base of the coral, where it becomes difficult to separate "live" from "dead" coral. A notable exception to this is a large species of serpulid, which is fairly common on many live corals, particularly *Acropora palifera*. The numbers of Crustacea on live corals varies a great deal and there are often more of them than on the coral rock. The high numbers appear to be correlated with the degree of branching, or surface area of the coral and the brain coral and massive *Acropora* support very low numbers.

The rarefaction curves for the Crustacea show that the species diversity varies a great deal between the different species of live coral. *Pocillopora* and *Stylophora* have extremely high diversities and also show a high degree of species overlap (Table X). *Millepora* and *Acropora tubicinaria* show a much lower diversity of Crustacea and are in effect dominated by two or three abundant species. However, they show a very low degree of overlap. The reasons for these similarities are not at present known, but may become apparent in a closer examination of the species involved. There may be physiological and morphological adaptations to living on live coral.

TABLE IX

Comparison of numbers of species per 25 individuals as calculated by the rarefaction method

	Polychaeta			Crustacea			Echinodermata		
	No. of animals	No. of species	Species per 25	No. of animals	No. of species	Species per 25	No. of animals	No. of species	
ROCK									
Settlement coral area	393	33	11.2	62	17	10.5	5	3	
CORAL									
<i>Pocillopora</i>	20	12	12	146	22	14.68	4	4	
<i>Stylophora</i>	72	18	12.17	159	22	11.92	11	4	
<i>Porites</i>	18	6	—	11	7	—	4	2	
<i>Millepora</i>	25	11	11	32	7	5.91	4	3	
<i>Acropora A</i>	5	5	—	6	5	—	2	2	
<i>Acropora B</i>	3	3	—	271	11	5.01	2	1	
<i>Leptoria</i>	24	12	12	18	10	—	0	0	

TABLE X

Indices of species overlap for some of the corals sampled, using R_o
(Horn, 1966)

Polychaeta				
	<i>Pocillopora eydouxi</i>	<i>Stylophora mordax</i>	<i>Millepora platyphylla</i>	<i>Leptoria</i> sp.
<i>Stylophora mordax</i>	0.6012	—	—	—
<i>Millepora platyphylla</i>	0.6773	0.7719	—	—
<i>Leptoria</i> sp.	0.6664	0.6742	0.6475	—
Settlement coral area	0.9422	0.6141	0.7809	0.7744
Crustacea				
	<i>Pocillopora eydouxi</i>	<i>Stylophora mordax</i>	<i>Millepora platyphylla</i>	<i>Acropora tubicinaria</i>
<i>Stylophora mordax</i>	0.8008	—	—	—
<i>Millepora platyphylla</i>	0.1122	0.1204	—	—
<i>Acropora tubicinaria</i>	0.0587	0.0571	0.0880	—
Settlement coral area	0.0642	0.0775	0.5482	0.0225
Total overlap = 1 Zero overlap = 0				

The degree of overlap between the samples from live coral and from coral rock is very low. This suggests that, unlike the polychaetes, there is a change in the crustacean species composition when the coral dies.

Other animals found in the live coral include various boring sponges, Sipunculida and various boring bivalves, including *Lithophaga* sp. They all bore into the rock and make cavities, which are then occupied by other species. Most of the original colonizers of live coral are relatively large species, compared with the small polychaete and crustacean species which then move in. The breakdown is offset by the growth of a layer of calcareous algae, or even other encrusting corals, but these also produce "microhabitats" for other species to colonize.

An interesting contrast to the rich infauna of coral rock was provided by three rocks from Mida Creek, two composed of granite and one of

sandstone. These had the usual profusion of species on the surface, but no boring species at all.

*The relationship between the fauna of coral rock and the
"habitat" as a whole*

We have largely ignored the problem of relating our findings for coral rocks to the "habitat" as a whole, in the present paper. This can be partly justified because in the "habitats" investigated, coral rock made up at least 50% of the substrate. However in order to give some idea of population sizes per unit of area and per unit of volume for the whole "habitat" and to estimate the numbers of the larger animals—particularly molluscs and echinoderms, for which the rock method is inadequate—we have carried out a variety of quadrat counts and searches, the results of which will be published separately.

The validity and usefulness of trying to calculate population densities and diversities of small invertebrates for large scale "habitats" such as "smooth intertidal limestone platforms" and "subtidal coral reef platforms" is in any case doubtful. "Habitat" classifications based on characteristic organisms must also be treated with caution when trying to apply them to organisms for which they were not originally intended. As Stoddart (1969) puts it: "The description of zones by characteristic organisms fails to aid in reef comparisons, because of the wide variations in species composition and colony density within them."

DISCUSSION AND SUGGESTIONS FOR FURTHER WORK

In this study of differences in species diversity between coral rock samples (i.e. "within-habitat" samples) from different areas we have made three main comparisons (i) we have compared rocks from widely separate geographical areas, (ii) rocks from areas of differing physical conditions and (iii) live and dead coral, which may be described as rocks at different stages in an ecological succession. Although it is possible to establish differences in species diversity and abundance between samples, one may only guess at the reasons for such differences, since none of the factors held to be responsible was open to manipulation under controlled conditions.

The differences in diversity between Aldabra and Watamu are probably due largely to historical processes and to differing rates of colonization and extinction in the two areas. Beyond recording that such differences exist there is little we can add.

Differences due to physical factors may be open to experiment, such as moving rocks from the side of Passe du Bois to the channel floor and studying changes in the fauna. Our results indicate that species diversity is higher in areas where physical conditions are stable and not liable to great fluctuations. It has often been claimed (Sanders, 1968; MacArthur, 1969) that where conditions are stable marginal ways of life become possible and highly specialized forms of mutualism, symbiosis and "biotic interaction" evolve. This argument runs the risk of becoming circular, but if one looks at the present ecological structure and at the progressive breakdown of live coral by invertebrates, it does seem that "biotic interactions" play an important part in the structure. Whether the present-day ecological succession mirrors the evolution of such marginal ways of life is a different matter. We do not propose an extension of Haeckel's Biogenetic Law.

There have been a number of accounts of rock-boring organisms and of the breakdown of coral (Otter, 1931; Bertram, 1936; Yonge, 1963b; Neumann, 1966), but as far as we are aware no one has studied this from the point of view of an ecological succession, although Morton and Challis (1969) do give some details. The works of Thorson (1955, 1964, 1966) have dealt with many aspects of the establishment of marine benthic communities, principally on soft substrates. A paper by Kensler and Crisp (1965) describes the crevice fauna in temperate waters and the establishment of colonies in artificial crevices. We carried out two experiments to investigate the colonization of coral rock and building blocks and interesting results were obtained within a very short space of time.

Comparisons between the coral rock community and similar temperate communities have not been possible as we know of no study similar to this one from temperate waters with which to make comparisons. Laminarian holdfasts might provide a similar biotope. A study of the "community organization" of coral rock, including productivity measurements to show the trophic structure of the community would make direct comparison between the trophic levels and between this and other communities possible. As Dickman (1968) has pointed out, an index of diversity sensitive to changes in the relative abundance of all trophic levels can be obtained by using relative productivity rather than numerical abundance as a measure.

SUMMARY

The position, topography, general structure and physical environment of reef areas on Aldabra and at Watamu, Kenya are compared. A method of obtaining reasonably accurate estimates of

components of the infaunal invertebrate populations of coral rock and live coral is described and compared with a transect and quadrat method. It is shown that for Polychaeta and Crustacea the extraction efficiency of the former method is much higher and where the substrate is heterogeneous it provides a more consistent index of species diversity.

Species diversities of errant polychaetes, Decapod and Stomatopod Crustacea and Echinodermata are determined for subtidal samples of coral rock from Watamu, Kenya and Aldabra, plus one intertidal sample from Aldabra and seven species of live coral from subtidal coral areas on Aldabra.

The highest diversities, as calculated by the rarefaction method, of both Crustacea and Polychaeta were found in the sample from Watamu and it is concluded that this falls in with the general pattern of higher species diversity on mainlands than on isolated islands. Of the subtidal samples from Aldabra, those from the side of Passe du Bois showed the highest diversities and this may be because both oceanic and lagoonal fauna are present here. The adjacent channel floor showed the lowest diversity, which is ascribed to the unstable, current swept nature of the substrate. The sample from the intertidal boulder ridge at Settlement showed the lowest diversity for both polychaetes and crustacea, but a few of the species present were abundant. This falls into the pattern of a "physically controlled" habitat, in which conditions of physiological stress determine the level of diversity.

The live coral samples gave mixed results, which will ultimately have to be interpreted for individual species. They show that there is an ecological succession as the coral is penetrated by various boring organisms, which in turn create "microhabitats" for further colonizers. Some organisms tend to break down the coral rock (sponges, bivalves, sipunculids), while others form encrusting layers which build it up (calcareous algae, other corals). As this process continues the diversity and numbers of polychaetes increases, but for the Crustacea the situation is complicated by the presence of large numbers of surface living species, which may either feed on the live coral or have some sort of symbiotic relationship with it. As the coral dies off many of these species disappear and are replaced by others. Thus the overall diversity of the Crustacea may not change, although the species composition will. Such biotic interactions play an extremely important part in determining the faunistic composition and diversity of this kind of community.

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DISCUSSION

- GIBBS (The Marine Laboratory, Plymouth): J. Stanley Gardiner considered that the polychaetes constituted the prime and most effective agents in the destruction of coralline rocks. From his work on Aldabra, would Mr. Brander agree with this opinion?
- BRANDER: No. Our impression was that sponges and molluscs are the most important agents of coral erosion, particularly in dead coral. Polychaetes are less important, and echinoderms even less.

