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DISTRIBUTION OF THE MACRO- AND MEIOBENTHIC ASSEMBLAGES IN THE LITTORAL SOFT-BOTTOMS OF THE GULF OF AQABA (JORDAN)

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ABSTRACT

The spatial distribution of macro- and meiobenthic assemblages in organogeneous and terrigeneous sandy bottoms of the Jordanian coast of the Gulf of Aqaba was studied by SCUBA-diving. Transects were sampled along the shore in various types of bays and fringing coral reefs from beaches to the depth of 35 meters. Variations of densities as well as the main taxonomic groups are analysed according to sedimentary environments. In the embayed bottoms, macrobenthic densities show large fluctuations related to the types of biotopes (15,000-450 ind m^{-2}). They are homogeneous in sandy patches situated along the reef slopes. Polychaetes are largely predominant followed by sipunculids and bivalves. Meiobenthic densities vary between 0.3 to $5.4 .10^{6}$ ind m^{-2} showing a decrease according to depth. Nematodes are dominant followed by copepods, nauplii, micropolychaetes, and other taxa like Kinorhynchs, Tardigrades, Gastrotrichs. Variations of macro/meiobenthos ratio are analysed according to ecological data. Comparisons with avaliable data in similar biotopes of the tropical indopacific area are developed.

INTRODUCTION

Soft-bottoms communities in the northern Gulf of Aqaba (Elat) were firstly described by Por and Lerner-Seggev (1966) and Fishelson (1971) following many papers dealing with taxonomic works (review in Fishelson 1971). Recent studies were devoted to : (1) the sandy beach assemblages (Hulings 1975a, b, Wahbeh 1976, D. Dexter 1979-survey, first data in Por 1983, Amoureux 1983) ; (2) the littoral communities of enclosed lagoons along the Sinaï peninsula (Jørgensen 1973, Kristensen 1973, Por & Tsurnamal 1973, Thane 1973a, b, Por 1974, Por & Dor 1975a, b, Por *et al.* 1977) ; (3) the shallow terrigeneous and coral bare sandy biota (Lawrence & Ferber 1971, Clarke 1972, Mergner & Schuhmacher 1974, Holthuis 1975, Ferber 1976, Mastaller 1979, Yaron 1979, Karplus *et al.* 1981, de Vaugelas & Saint-Laurent 1984 ; (4) the *Halophila* meadow epi- and endofauna (Hulings 1979b, Lipkin 1979, Zohary *et al.* 1980, Hulings & Kirkman 1982, Wahbeh 1982); (5) the deep slope infauna from Por's & Fishelson's dredgings (Bratcher & Burch 1967, Bonaduce *et al.* 1976, Schmalbach & Por 1977, Wägele 1981).

In same times, shallow and deep coral assemblages in the Gulf were finely described (Loya 1972, Mergner & Schuhmacher 1974, Fricke & Hottinger 1983, Fricke & Schuhmacher 1983).

In April-May 1981 a joint research survey (Univ. Nice and Univ. Jordan) was carried out upon infralittoral soft-bottom communities of the Aqaba Jordan coast within the framework of the large oceanographical and biological programme supported by the "Mission Océanographique française au Moyen-Orient". This survey included definition of meio- and macrobenthic assemblages according to environmental parameters (sediments, bacterial and diatom densities), as well as evaluation of bottom productivity (Bay 1982, Grelet *et al.* 1983, Grelet 1984, Falconetti & Thomassin to be published).

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ENVIRONMENTAL CONDITIONS

The Gulf of Aqaba represents one of the northern extensions of the Red Sea. It is a narrow and deep trench of the Syrian-African rift system (15-25 km width, depth down to 1,800 m) ; so, the infralittoral bottoms (down to about 100-110 m deep from Fricke & Schuhmacher 1983) are restricted to littoral narrow fringes just more extended in front of some wadi openings, mainly the northern Elat-Aqaba beach.

General climatic and hydrological conditions of the Gulf were reviewed by several authors (for recent paper, see Klinker *et al.* 1976, Paldor & Anati 1979). The main parameters influencing benthic fauna are the high salinity of water (about 41‰) and its high temperature (annual mean = 23°C). According to Mergner & Schuhmacher (1974) and Hulings (1979a), the surface water flows southward on both sides of the Gulf, while the deeper water flows northward along the east coast and southward along the west one. However, even a narrow tidal-range (0.4-0.7 m, max. 1.2 m in spring, Mergner & Mastaller 1980) is recorded, weak tidal currents were observed on reef flats and along the shallow outer reef slopes playing a role in food supplies of communities. In the narrow canyons and also in the bays, returned bottom currents probably occur as sediment distribution analyses point out.

Winds induce local swells but, in comparison with other oceanic environments, the northern Aqaba Gulf represents a weak-wave exposed littoral, more strengthened along beaches at the opened bays.

Nutritive richness of waters along the Jordan coast and the northern Aqaba beach is maybe increased by the possible occurrence of up-wellings, phenomena induced after strong wind periods (Anati 1974, Hulings 1979a). According to the arid climate of the region, the coastal waters do not receive silty terrigeneous inputs, therefore, they are very clear and are classified among the oceanic waters. Phytoplankton characteristics and nutrient levels are those of oligotrophic waters (Sournia 1977). However, as in all other tropical littoral environments, sediments harbour an high microphytobenthic productivity (Sournia 1977, Plante-Cuny 1978). From Pascal (1981), bacterial densities in the Jordan coastal waters vary between 1.11-2.20 .10^6 in surface for non polluted areas and decrease in the Gulf midline. As recorded in the Pacific (Sorokin 1974), these values characterize coastal environments rather than oceanic environments.

The Jordanian coast is, as well as the Sinaï coast, characterized by a succession of bays (at the wadi openings) and of landheads upon which well developed fringing reefs take place (Friedman 1968, Gvirtzman & Buchbinder 1978, Guilcher 1979, Bouchon *et al.* 1982). Therefore, an alternate succession of terrigeneous and organogeneous (coral) sedimentary areas occur along the coasts (Erez & Gill 1977, Gabrié & Montaggioni 1982). As confirmed by our sedimentary data (Fig. 1 & 2, Table1) , the far end of the Gulf is occupied by the largest beach , at the wadi Arava opening. In some large bays, coral patches growth at intermediate depths (10-25 m); they might represent a first stage of the fringing reef building (Bouchon *et al.* 1982) or just to be in connection with local ridges encounter in front of the Pleistocene elevated reefs. The organic matter content of these sediments reach 0.07-0.26% for coral sands, 0.14-0.34% for seagrass sediments and 0.05-0.16% for terrigeneous bare sands (Wahbeh 1976, Hulings & Ismail 1978, de Vaugelas & Naïm 1982).

METHODS

Samples of macro- and meiofauna and sediments for grain-size and biochemical analyses were made in SCUBA-dives, along transects from beach to 35 meters (Fig. 1 & 2, Table 1).

Sediment analyses were done according to Weydert's 1976 methods; carbonate content was evaluated with Bernard's calcimeter. The method for determination of organic carbon content of sediments was that of Walkley & Black (1934) as described by Buchanan & Kain (1971).

Macrobenthos was sampled using an hydropneumatic sucker (Thomassin 1978a, Bussers *et al.* 1983) inside a frame (375 mm i.d.) until 40 cm maximum of depth with a 1.5 mm mesh sieve net. After preservetion in buffered formalin at 10%, macrofauna was sorted by CENTOB, Brest.

Meiobenthos was collected by coring sediment with transparent plexiglass tubes (36 mm i.d.) on the deepest thickness according to the nature of soft-bottoms; then conserved with buffered formalin at 4%. A Rose Bengal solution was used to facilitate sorting. The extraction of meiofauna was carried out by means of successive centrifugations and animals were collected on a 0.04 mm mesh-sieve.

RESULTS

Results obtained all along the Jordan coast of the Gulf of Aqaba concern, firstly the terrigeneous soft-bottoms in bays and canyon and, secondly the mixed and organogeneous sandy patches on coral fringing reefs (Table 2 & 3, Fig. 3, 4 & 5).

Terrigeneous Soft-bottoms in Bays and Canyon

Sedimentary bottoms in bays and canyon entrance result of the very occasional inputs of terrigeneous gravelly and sandy materials by littoral wadi; very fine sediment particles, transported by sand-winds, could be added in those sedimentary environments. So, the carbonate content in those bottoms is low, less than 10%. When the rate increases (in the deepest bottoms colonized by seagrass), it is connected with an input of the calcified epibiotic fauna living on the leafage (values vary between 10 to 18.5%).

The northern beach of the Aqaba Gulf (transect A). The far end of the Gulf of Aqaba is the largest beach of the littoral in front of the Arava wadi opening. This beach extends from Elat to Aqaba, a distance of almost 4 km. The infralittoral sampling stations, distributed from 1 to 25 m deep, were located in the upper levels in bare very fine sands and, down to 5 m deep, in a dense *Halophila stipulacea* meadow. Por & Lerner-Seggev (1966) described in these bottoms their "infralittoral *Lovenia elongata-Mactra olorina* community" (from low tide level to about 3-5 m deep) and the *Halophila* meadows. The first one corresponds to the deeper assemblage of the Fishelson's (1971) "*Hippa picta-Mactra olorina* community" whereas the second one is a part of his "*Halophila stipulacea-Asymetron (lucayanum ?)* community".
Macrofauna. Densities were high ; they varied between 1,500 individuals per square meter (ind m^{-2}) at 10 m deep to 1,100 ind m^{-2} at 25 m depth in the *Halophila* meadow. These densities, are related to a high dominance of polychaetes (54%) and sipunculids (16%) and represent the typical assemblage of this kind of seagrass bed.
Meiofauna. All samples gathered, this transect appeared the richest. A decrease of density was observed down to 5 m deep and the abundance was, at this depth, the highest recorded in this study (5,239 ind 10 cm^{-2}). Nematodes, copepods, nauplius larvae and micropolychaetes constituted the four main groups (dominance from 99 to 100%). Nematodes were the more numerous with a relative abundance varying between 68 to 91%, while micropolychaetes (0.70-3.50%) showed near homogeneous densities all along the transect.

The other embayed bottoms.
A) Transect E : This transect is an example of a typical bay transect ; it is located in the largest bay of the eastern coast of the Gulf ; it is flanked at its opening by two fringing reefs "kp 12" and "Cherif Nasser" and this bay has a well northern prevailing wind exposure.

Down to a gravelly beach (midlittoral zone), the shallowest bottoms (on the top of an upper embankment), consisted of fine to very fine sands colonized by belt-meadows of the seagrasses *Halodule uninervis* (0.5-1 m deep) then *Halophila ovalis* mixed with bare sand banks. Deeper, a dense *Halophila stipulacea* meadow occurs. Between 10 to 15 m deep, the first massive coral heads (*Porites*) occured at the foot of the sandy embankment while, deeper, spurs of coral growths were observed with their surrounding bare sandy bottoms and alternating *Halophila* meadows (with tumuli and funnels, down to 32 m deep). This is the typical physiography of the bottom before the drop-off occuring near 40 m deep.
Main faunistic assemblages in these infralittoral bottoms were those colonizing seagrass beds and their sand banks ("*Halophila* community", and those settling the bare coarse and medium coral sands "*Asymetron (lucayanum?)* community" Fishelson 1971).
Macrofauna. In the shallowest fine sands of the *H. uninervis* + *H. ovalis* belt meadows, large populations of polychaetes, actinians and sipunculids produced a density up to 15,000 ind m^{-2}, forming so a particular facies of the community. Deeper, in the *H. stipulacea* meadow, densities varied between 2,500 and 610 ind m^{-2} at 10 and 26 m depth respectively. Soft-bottoms assemblages along this transect were among the more diversificated. All the main zoological groups were well represented : polychaetes (33%), sipunculids (27%), crustaceans and actinians (15%), gastropods (3%), bivalves (2%) and they comprised 95% of the macrobenthos.

Meiofauna. Although this transect was less rich than the previous one, mean abundance of meiofauna was among the highest values recorded. As for macrofauna, the highest density was observed in the bare sand bank among the *H. uninervis* meadow, at 1 m deep. Down to a water depth of 16 m, densities decreased then, progressively, increased again down to 33 m deep. Copepods, nauplii larvae and, at a lesser degree, nematodes and polychaetes were responsible of this last increase. Nematodes were the dominant group (54-82% of total meiofauna) followed without a depth influence by copepods (10-36%), nauplii (2-9%) and polychaetes (1-8%).

B) Transect F. This southern bay is the most wave-exposed of the Jordan coast, and therefore exhibits a distinctive sedimentological patterns related to local topography. Below a gravelly midlittoral beach, a steep slope of coarse sediments extends down to 15 m deep, where it grades into a very fine sands colonized by a *H. stipulacea* meadows.

Macrofauna. In the gravelly midlittoral beach, density was high (1,720 ind m^{-2}) with a numerical explosion of polychaetes (*Polygordius ?*) (74%), of mole-crabs (*Hippa picta, H. celaeno*)(12%) and of the bivalve *Mesodesma glabratum* (8%). This was the typical assemblage of this upper level as described by Por & Lerner-Seggev (1966), Fishelson (1971) and Hulings (1975a). At a depth of 5 m, in coarse sands of the steep slope, density decreased down to 440 ind m^{-2}, while at its base, in a less mobile biotope the density increased again (1,250 ind m^{-2}). Deeper (25m), in the very fine sands of the *Halophila* meadow, this value was similar to the last one (1,270 ind m^{-2}).

Although polychaetes were predominant in these bottoms, a very low density of sipunculids (6%) appeared in the more stable sediments found at the deepest levels (from 15 m down to 25 m deep).

Meiofauna. Densities, as well as relative abundances of the main taxonomic groups, were reflected by the sedimentological characteristics of the bottoms of transect F, a transect that exibits the lowest densities in this study. Up to 15 m deep, coarse sands were unpropicious for a nematode settlement, particularly at a water depth of 5 meters where they just expressed 31% of total meiofauna; so, the main group consisted of nauplii (34.5%) and adult copepods were well represented with 29.7% of dominance. Deeper, sediments became finer with an increase of silts and allowed the settling of nematodes (74%). Despite this nematode increase, a decrease of meiobenthic densities was observed according to depth.

C) Transect B. This transect is located, in front of the Marine Science Station, at the top of a strait and deep canyon flanked by fringing coral reefs. Samples were taken, firstly in an hydraulic fine sand bank (3 m deep) at the entrance of the Marine Station harbour, secondly in the canyon axis in very fine sands fixed by dense *H. stipulacea* meadow (10-15 m deep), and finally in medium sands colonized by scarce seagrasses (25 m deep).

Macrofauna. Density increased between 3 and 15 m deep from 840 to 2,160 ind m^{-2} then decreased, deeper, down to 600 ind m^{-2} . Community was largely dominated by polychaetes, particularly at a water depth of 15 m in the dense meadow where they reached 61%. Principal zoological groups were well represented (polychaetes : 61% ; sipunculids : 10% ; bivalves and gastropods : 7 and 3% ; actinians : 6%). Sipunculid dominance increased between 10-15 m deep in the seagrass meadow which correlated to a higher silt ratio and, probably, to an increase of the organic matter content.

Meiofauna. The highest density (3,246 to 677 ind 10 cm -2) was observed in shallower *Halophila* meadow while a decrease of total number of meiobenthos was recorded according to depth. Adult copepods and nauplii densities increased in the washed, cleaner sands of the upper levels (3 m deep) as well deeper (25 m deep), because of better oxygenation of sediments

Mixed and Organogeneous Sandy Patches on Coral Fringing Reefs

Two transects were studied on flats and outer slopes of the coral fringing reefs of kp. 8 and kp. 12 (transects C and D). In residual pools of the narrow inner reef flat (named as "reef lagoon" by Mergner & Schuhmacher 1974, "boat channel" by Bouchon 1980, "backreef channel" by Bouchon *et al.* 1982), between 1-2 m deep, the thin sedimentary layer (a thickness of 15-20 cm) is colonized along the littoral by patches of seagrasses (*Halodule uninervis* and *Halophila stipulacea*). These sediments were fine to very fine sands, sometimes little clogged by silts and, according to their low carbonate content (41-67%), they belonged to the "impure carbonate facies". In front of reef flats, from the small cliff base (5 m deep) down to 25 m on the outer reef slopes, medium coral sands have cumulated in pockets between coral growths or patches. Down to a water depth of 25 meters, the topography of the slope changes : large basins filled with fine coral sands (30-35 m long and 3-5 m wide) cut across the coral-covered fore-reef slope.

Two types of faunistic assemblages could be recognized along these two transects : (1) the sparse seagrass meadows (narrow *Halodule* belt and *Halophila* meadows)(Por & Lerner-Seggev 1966, Fishelson 1971, Wahbeh 1982); (2) the clean medium-size coral sands colonized by the "*Asymetron (lucayanum ?)* community" of Fishelson (1971).

Macrofauna. Accepting that reef flat samples were not taken in account, highest densities were recorded at the foot of the reef flat cliff (at 5 m deep) in fine sands (1,200 and 950 ind m^{-2}) while a population decrease was observed in sandy pockets of the outer slope (810 and 560 ind m^{-2}).

Deeper, in sandy depressions, densities seemed to increase in relation to larger surfaces of sediment and its stability (940-770 ind m^{-2}) while they decreased near 35 m deep in finer sands (730 ind m^{-2}).

The macrobenthos here was also mostly composed of polychaetes (64%). Sipunculids were sparce in clean and well oxidized sands while an increase of bivalves (8%) was recorded with an increase of depth down to 25 m deep.

Meiofauna. Densities varied in relation with depth as well as with sediment parameters. The abundance along transect C were lower than those recorded along transect D. For the two transects, densities of total meiofauna decreased from upper levels to mid-outer reef slope (23-25 m deep), but the density somethimes did increase again in the deepest sandy patches (as at 35 m deep, transect D). Nematodes, copepod adults and nauplii larvae were always the main taxonomic components of meiobenthos (91-99%). Kinorhynchs were present only in orgageneous sediments, but lacking silt were never abundant (O.O5-1.9%).

DISCUSSION

General Features of Macrobenthic Densities

Variations according to sedimentary environments. From the sediment analysis, it was pointed out two environmental types of soft-bottoms (compactness and thixotropy of sediments being correlated with their carbonate content: organogeneous and terrigeneous sands, our data corroborating those obtained by Gabrié & Montaggioni (1982) and de Vaugelas & Naïm (1982). To understand the variation of macrobenthic densities according to these both environments, transects were classified following mean-density values (Table 4).

From Table 4, the terrigeneous quartzitic sands, in front of wadi openings, appeared to be colonized by a richer macrobenthos ($1,400 < \partial < 1,200$ ind m^{-2}) than the coral sands of outer fringing reef slopes ($950 < \partial < 800$ ind m^{-2}). Transect B, in terrigeneous sandy bottoms of a narrow canyon flanked by fringing reefs, seems to correspond to a peculiar zone between these two sedimentary environments: a narrower bottom surface, linked with sediment gravity currents, could induced here a macrofaunal decrease .

Variations according to depth. Analyses of macrobenthic densities variation according to depth (Table 2) revelated three features : (1) in bays, where nature of bottoms was more heterogeneous, differences among sampled densities were more pronounced (2,520 down to 190 ind m^{-2}) than in organogeneous sands of outer fringing reef slopes (959-550 ind m^{-2}); (2) density fluctuations were narrowest below a water depth of 15 m. They appear to be independent of sedimentary environment, and related to more stable conditions than those found in shallower wathers; (3) highest densities were recorded at about 15 m deep , mainly in terrigeneous very fine sands colonized by *H. stipulacea* meadows, or in their vicinity.

Variations of faunistical composition. Principal taxonomic groups of macrobenthos were polychaetes (82-37% of dominance), sipunculids (34-2%) and bivalves (11%). However, some remarks concerning other groups could be noted : (1) abundance of burrowing actinians in shallow bare sand banks, covering by *Halodule/Halophila* beds, could represent a facies of the faunistic assemblage ; (2) abundance of the lancelets *Asymetron lucayanum* in some medium sands could characterize some aspect of the assemblage (23-27%, as in transect C at 15 m deep and transect B at 25 m) ; (3) presence of juveniles of a burrower brachyopod, *Lingula sp*., recorded in terrigeneous sands (transect E, 26 and 33 m deep) and in coral sands at the upper reef outer slope (transect C, 5 m deep).

General Features of Meiobenthic Densities

Variations according to sedimentary environments. At the opposite of the macrobenthos distribution, densities of total meiobenthos, nematodes and copepods did not show significant variations according to (biogeneous or terrigeneous) nature of sediments (non-parametric statistical Man-Whitney U test used). The only differences noticed concerned : (1) the exclusive presence of kinorhynchs living in carbonate sands and (2) the high relative abundance of nematodes in very fine sediments, more often terrigeneous. In contrast with terrigeneous sands, a highly significant linear correlation ($r = -0.88$; $n = 9$) could be demonstrated in the organogeneous ones between meiofaunal densities and sediment mean-size, meiofauna increasing in finer sands (see below, relation with depth).

Variations according to depth (Fig. 4). In soft-bottoms of the Jordan coast, meiobenthic densities varied from 263 to 5,329 individuals per 10 cm^{-2}. All along transects, a decrease of density was observed from beaches to a water depth of 25 m. At this depth, density values became more homogeneous reaching near 1,000 ind 10 cm^{-2}.

In the mid-northern part of the Jordan littoral (transects A, B, C), an optimum density was recorded near 5-10 m deep, whereas in the southern part (transects D, E, F) an enrichment occured down to 25 m deep. Schmalbach & Por (1977) in their dredgings along the Gulf midline recorded highest density in shallow (1-5 m) and deep (50-250 m) water and lowest in mid-depths (10-50 m).

To explain this fact, several considerations can be given. The low density values observed between 1-5 m deep in the northern littoral, as also the enrichment recorded in the southern area down to 25 m deep, seem to be induced by particular hydrodynamic conditions in relation to bottom topography. Firstly, the wave action in the upper levels of soft-bottoms (between 0-2 m deep) is more pronounced in the northern littoral (inner area of the Gulf) and could limit the meiofaunal settling. It is promoted deeper (down to 3 m deep) by lower water agitation allowing deposition of finer sediments, and by bottom stabilization induced by the seagrass meadow growth. Secondly, a break in slope, parallel to the Jordan coast, occurs around 20-25 m on the outer reef slopes, and near 40 m deep all along the littoral (Bouchon *et al.* 1982), and corresponds to submerged Pleistocene terraces (Gvirtzman & Buchbinder 1978, Fricke & Schuhmacher 1983). The upper slope break could locally strengthen deep water currents, inducing an increase of the sand mean-size as well as a better oxygenation of sediments which are enriched in organic matter derived from nearby *Halophila* meadows. All these environmental conditions are propitious to the meiofaunal settling, characterized by a development of copepods and nauplius larvae.

The highest densities were recorded at shallow depths (from 1 to 10 m deep) in the vicinity of *H. stipulacea* meadows and in very fine sands, more often terrigeneous, and generally less sorted and less graded. These seagrass beds stabilize the sediments as well as they enrich them in organic matter, directly or indirectly, by trapping particles. This leads to analyse the role of the organic matter content on meiofauna distribution.

Variations according to organic matter content of sediments. Organic matter content of the Jordan littoral sediments was analysed by Wahbeh (1976), Hulings & Ismail (1978), de Vaugelas & Naïm (1982). In our study, we recorded the following values of organic carbon (% of dry weight) : 0.17-0.53 in coral sands, 0.09 in bare terrigeneous sands, and 0.06-0.53 in *H. stipulacea* meadows. These data are in accordance with those of the authors cited above. But, they demonstrated that the total organic matter content shows good correlation (1) with carbonate content : terrigeneous sands showing the lowest values whereas organogeneous ones have the highest, (2) with sediment grain-size: the finest sands show the highest values. These last results do not agree with ours because we could not shown relations between organic matter content and (1) carbonate content and (2) sediment grain-size.

As well as in terrigeneous or in organogeneous soft-bottoms, densities of meiofauna were relatively well fitted to fluctuations of the organic carbon content.

Nevertheless, an enrichment of organic matter from seagrass meadows in well oxygenated sediments seems to be a factor favoring the meiobenthic settling; particularly in shallow depths where the availability of a high energy for primary producers induces a higher production of organic matter, secondly recycled by bacterial processes; food sources are well diversified for the meiobenthos. This could explain the highest densities (more than 2,000 ind 10 cm^{-2}) recorded in the shallowest bottoms (up to 10 m deep).

Variations of faunistical composition (Table 3, Fig. 5). In all samples, nematodes were largely dominant in the meiobenthic assemblages (32-91%). Examination of all transects (transect F being excluded according to its singularity) showed highest proportion of nematodes at intermediate depths (5-15 m deep) in terrigeneous bottoms of bays whereas, in reefal organogeneous sands, the phenomenon was inverted. The wave action (between 0 to 2 m deep) and the deep currents (near 20-25 m deep) creating a bottom instability could induce a decrease of the relative abundance of nematodes at these depths (Fig. 5). Copepods represented the second group (5-36%) and nauplii the third (2-35%). Most of the copepods were Harpacticoids (excepted some epibenthic species) and probably most of the nauplius larvae belong to them. Micropolychaetes were the last group recorded in all samples. Their study lacks in precision so, it is difficult to know the proportion of worms belonging to the true meiofauna or to the temporary meiobenthos (juveniles of macrobenthic species). Other groups, as gastrotriches, kinorhynchs, oligochaetes, tardigrades, acarians, ostracods, tanaids and isopods, were poorly represented. Kinorhynchs were only sampled in organogeneous sands while tardigrades showed a larger sedimentological distribution.

Analysis of Macro-Meiobenthic Relationships

The difference in the soft-bottom infauna of the two sedimentary environments (terrigeneous and organogeneous) appeared mainly in density fluctuations of macrobenthic assemblages, as demonstrated above. However, when density variations of macrofauna and meiofauna were analysed (Fig. 6), it was pointed out : (1) inverse fluctuations in terrigeneous bottoms (particularly clear along transect B, in the Marine Station canyon at kp. 8, and between 5-15 m deep along transect F) ;(2) similar profilesin biogenic bottoms, between 15-23 m deep on outer reef slopes (transects C, D).

Variations of macro/meiobenthic ratio (Table 5, Fig. 6) showed a large range; with values of 1/271 (transect C, 25 m deep) and 1/17,100 (transect B, 10 m deep). This ratio generally increased at the vicinity or in the *H. stipulacea* meadows (mean : 1/1,237) where high densities were recorded for the both great benthic groups, but mainly for macrobenthos. In bare sandy bottoms, terrigeneous and organogeneous environments could be distinguished. In the first one, the mean value of the ratio was low (1/5,437) mainly because of low abundance of macrofauna and high density of meiobenthos (at 10 m deep, transect B, density of macrofauna was exceptionally low and the one of meiofauna high, so the ratio was equal to 1/17,000 ; if this station was excluded, mean ratio was 1/2,521). In the second one, the mean value of the ratio is higher (1/1,889) with a lower variability: 18% whereas in terrigeneous samples it was 54% (variability = ratio between standard-deviation and mean value of the macro/meibenthos ratio, expressed in %).

For a general point of view, gathering all the stations, the both sedimentological environments could be recognized. In terrigeneous sediments, values of the macro/meiofauna ratio were lower (mean value = 1/2,668) and less homogeneous (variability = 43%) than in biodetrital ones (mean = 1/1,889 ; variability = 18%). The relative homogeneity of this ratio in organogeneous biota seems to be connected with macrofauna density.

If macrobenthos/meiobenthos density ratio is usually used (McIntyre 1969, Thomassin *et al.* 1976, 1982, for example), its analysis is critical. So, another method was attempted. For each sediment grain-size classe, the wrapping surface of stations was drawned according to densities and depth (Fig. 7). From this graph it appeared that (1) the very fine sand assemblages showed large range of densities according to depth but more important for meiofauna, abundances of which decreasing to 24 m deep whereas this fact was less accurate for macrofauna that had a wider wrapping surface; (2) in fine sands, population fluctuations were particularly narrow, near closed in the shallow bottoms (0-5 m deep) then densities increased for both great benthic groups and, near 33-35 m deep, the variations were rather inverse; (3) in medium sands, mainly biogeneous, density variations were also low, but with some opposition between macro- and meiobenthos: macrofauna reached 550-950 ind m^{-2} at all depths whereas meiofauna decreased from 5 to 25 m deep, reaching its lowest densities.

Comparisons with other Tropical Indopacific Littoral Communities

The benthic communities colonizing the infralittoral shallow soft-bottoms of the Gulf of Aqaba belong to four biocenosis, as defined(Thomassin 1978b, 1983) for the indopacific littoral assemblages, as follows: (1) the "Biocenosis of the well sorted fine sands" colonizes the shallow bare sandy bottoms of the wave-exposed beaches. It corresponds to the true *"Lovenia elongata-olorina* c ommunity" defined by Por & Lerner-Seggev (1966). The *Hippa picta-Mactra olorina* community" (Fishelson 1971) gathers two assemblages : the former biocenosis and the intertidal midlittoral sand assemblage ; the last one is not a biocenosis but a permanent group (Bigot & Picard 1984) and it is equivalent to the " *Hippa* community" (Por & Lerner-Seggev 1966) or the " *Hippa - Mesodesma* community" (Hulings 1975a); (2) the "Biocenosis of the sheltered muddy sediments", in its less sediment clogging aspects with the epifloral facies (seagrass beds), is represented in the Gulf of Aqaba by the *Halophila stipulacea* and *Halodule uninervis* meadows (the scarce *Halophila ovalis* beds are associated with the more clogged medium clean sands colonized by the third biocenosis, see below; the *Thalassodendron ciliatum* and *Syringodium isoetifolium* beds are more developed along the southern coast of Sinaï and in the Red Sea, see (Crossland 1938, Fishelson 1971, Lipkin 1975, 1977). The *H. uninervis* meadows are not well developed all along the Jordan coast and they are located in bays or fringing reef residual pools as very shallow belts. At the opposite, the *H. stipulacea* meadows colonize most of the bottoms in bays (down to 50-60 m deep) with a high productivity (Hulings 1979b, Lipkin 1979). General macrofauna of these beds is described *pro parte* by Fishelson (1971) in his *Halophila stipulacea - Asymetron (lucayanum ?)* community ". However, a large part of fauna of his *"Ptychodera flava - Radianthus koseirensis* community" belongs to this biocenosis; (3) the "Biocenosis of the coarse and medium sands under bottom stream effects" colonizes the clean organogeneous sediments mainly on fringing reefs (outer flats and outer slopes) and also the sandy patches around coral heads growing in the middle of some bays. This last biocenosis overlaps the " *Asymetron (lucayanum ?)* community " (Fishelson 1971). It is well distributed in coastal environments at the vicinity of coral reefs so, in the "coralline algal shelly strait bottoms" (for recent Red Sea data, see Mastaller 1979, Bertz & Otte 1980).

But, to be unbiased, comparisons of benthic populations densities must utilize data coming from samples taken using similar methods (sampling, sorting and counting, evaluation of environmental parameters, see Methods). Therefore, for a quantitative point of view, available data for tropical indopacific littoral communities are few in the literature.

Macrofauna. According to above, only the following works can be used for quantitative comparisons : from Tulear, Madagascar (Pichon-Mireille 1965, Reys & Reys 1966, Le Fur 1972 re-analysed in Thomassin 1978b); from Soudan, Shab Baraja reef (Betz & Otte 1980); from Australia Great Barrier Reef, Lizard I. (Jones 1984); from French Polynesia (Thomassin *et al.* 1982). In coral sands colonized by the " *Asymetron lucayanum* community ", macrobenthic densities recorded at Aqaba on outer reef slopes (560-1,200 ind m^{-2}) were similar to those of equivalent sedimentary biota in another areas (Table 6). Richest populations were always observed in bottoms submitted to currents carrying detrital organic matter from seaward biotopes increasing the suspensivorous and filter feeders. High densities recorded in Shab Baraja coral reef sediments could be explain by the 0.5 mm sieve-mesh size used (42,480-30,599 ind m^{-2} in enclosed lagoon ; 12,125-5,981ind m^{-2} in outer reef slope).

In dense *Halophila stipulacea* meadows, densities varied more at Aqaba (1,130-2,520 ind m^{-2})than in the Tulear barrier reef complex (1,127-1,733 ind m^{-2}). The highest density was observed in the shallowest *Halodule* belts of Aqaba and, at Nosyve I. (Tulear region), in a near closed environment, it was also recorded a macrofauna increase(4,547 ind m^{-2}).

Meiofauna. Quantitatively, only the de Vaugelas's study (French Polynesia, 1980) can be well utilized (same methods used) for comparisons of infralittoral data in the indopacific area.

In shallower bottoms, meiobenthic densities recorded at Moorea I. and at Aqaba were similar (1,000 to 5,830 ind 10 cm^{-2} at 0.3 m deep in a lagoon of the Tiahura reef complex into the 0-2 cm surface layer against 1,972 to 3,265 ind 10 cm^{-2} at 1-5 m deep in the Aqaba reefs into the 0-5 cm surface layer). In deeper bottoms, at 25-35 m deep, meiofauna of the Gulf of Aqaba was poorer than in lagoonal bottoms of Vairao reef complex, Tahiti I. (at Aqaba, densities varied between 1,555 and 1,936 ind 10 cm^{-2} in embayed bottoms against 5,498 ind 10 cm^{-2} in muddy fine sands under more terrigeneous clay inputs at Tahiti). In Polynesia, meiobenthic densities decreased from coarse to fine sediments and the opposite occured at Aqaba, these facts being correlated with different physiographical environmental conditions.

Available data of meiobenthic densities from tropical Indopacific seagrass beds (belonging as epifloral facies of the "Biocenosis of sheltered muddy sediments" as defined by Thomassin in 1978b and Vasquez-Montoya 1979) refered to reef flat seagrass beds (*Cymodocea-Halodule*) in SW New Caledonia (Thomassin pers. comm.) where densities seemed to be of the same order of magnitude than those recorded at Aqaba (3,703 ind 10 cm^{-2} and 2,147 ind 10 cm^{-2} in New Caledonia against 677-3,732 ind 10 cm^{-2} and 571-2,831 ind 10 cm^{-2} at Aqaba for total meiofauna and nematodes, respectively). Other densities, recorded in muddy bottoms (near mangrove belt) of the Sinaï coast, fluctuated between 130-249 ind 10 cm^{-2} and 138-822 ind 10 cm^{-2} (Thane 1973a, b) showing that these peculiar biotopes were less rich than the *Halophila* meadows. Though thier study of the Florida Keys sediments, Decho *et al.* (1985) showed a significantly lower total meiofauna density in seagrass area than in adjacent barren sand area as at Aqaba; according to Evans (1983) and Hooks *et al.* (1976), these authors suggest that for macrofauna abundances of smaller predators are controlled by larger predators in open areas and, therefore, the seagrass bed serves as a refuge from predation for macrofauna. Consenquently, by a presence of a greater number of potential predators of meiofauna, predation pressures on meiobenthos could be higher in seagrass sediments than in adjacent bare sands. However, the vicinity of seagrass beds would represent a potential source of organic carbon which could be utilized, directly or not (bacterial processes, diversification of food sources), by the meiofauna, so in these biotopes densities are high.

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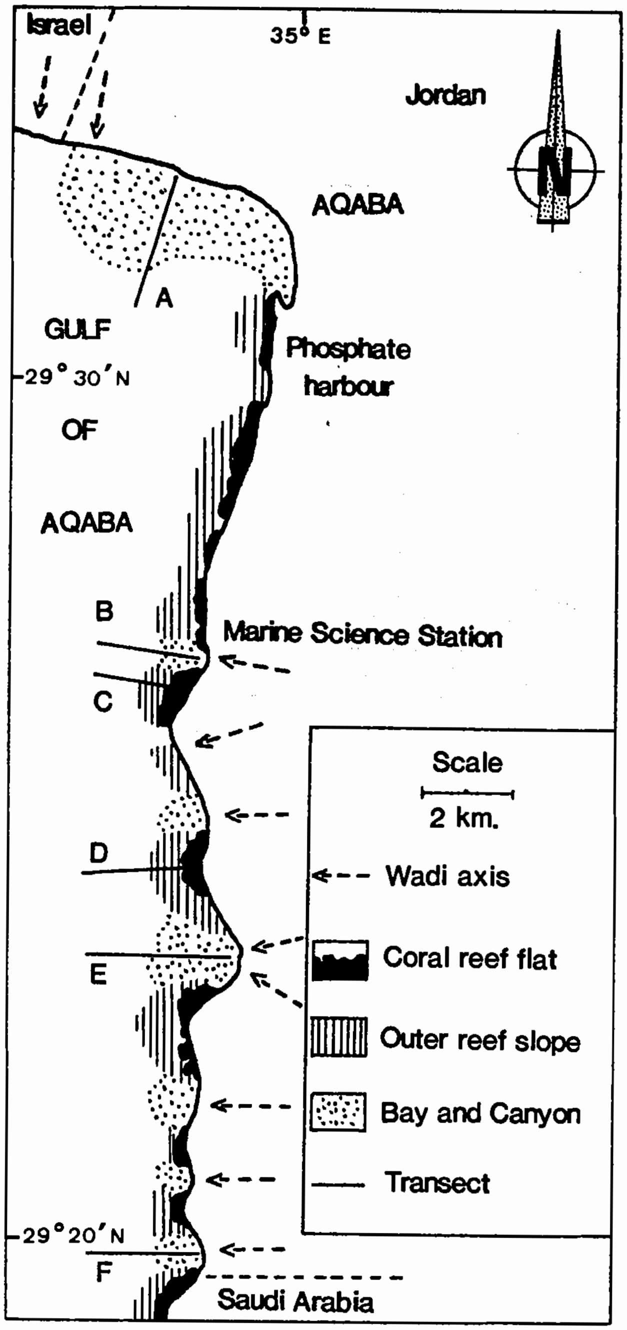

Fig. 1. North-eastern coast of the Gulf of Aqaba with location of the sampling transects (map from Gabrié & Montaggioni, 1982).

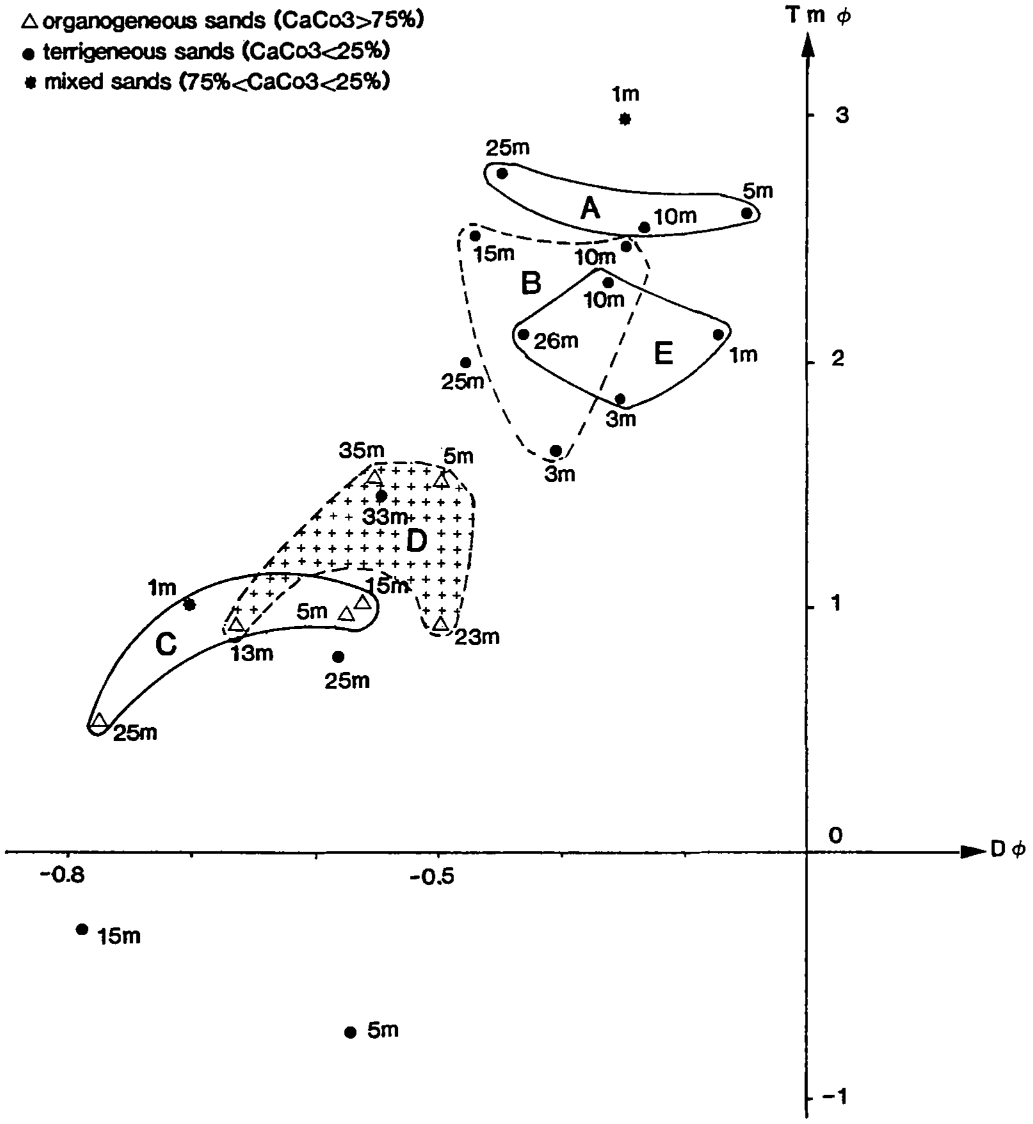

Fig. 2. Sedimentary stocks according to mean-size (Tmø) and sorting index (Dø) (phi scale).

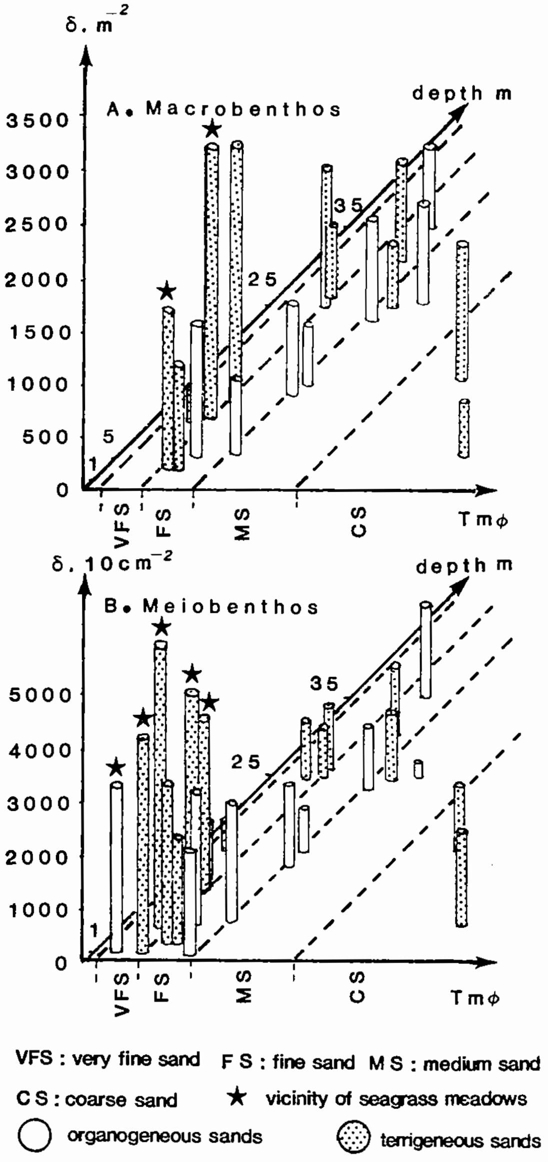

Fig. 3. Variations of macrobenthic (A) and miobenthic (B) densities according to depth and sediment mean-size (Tmø).

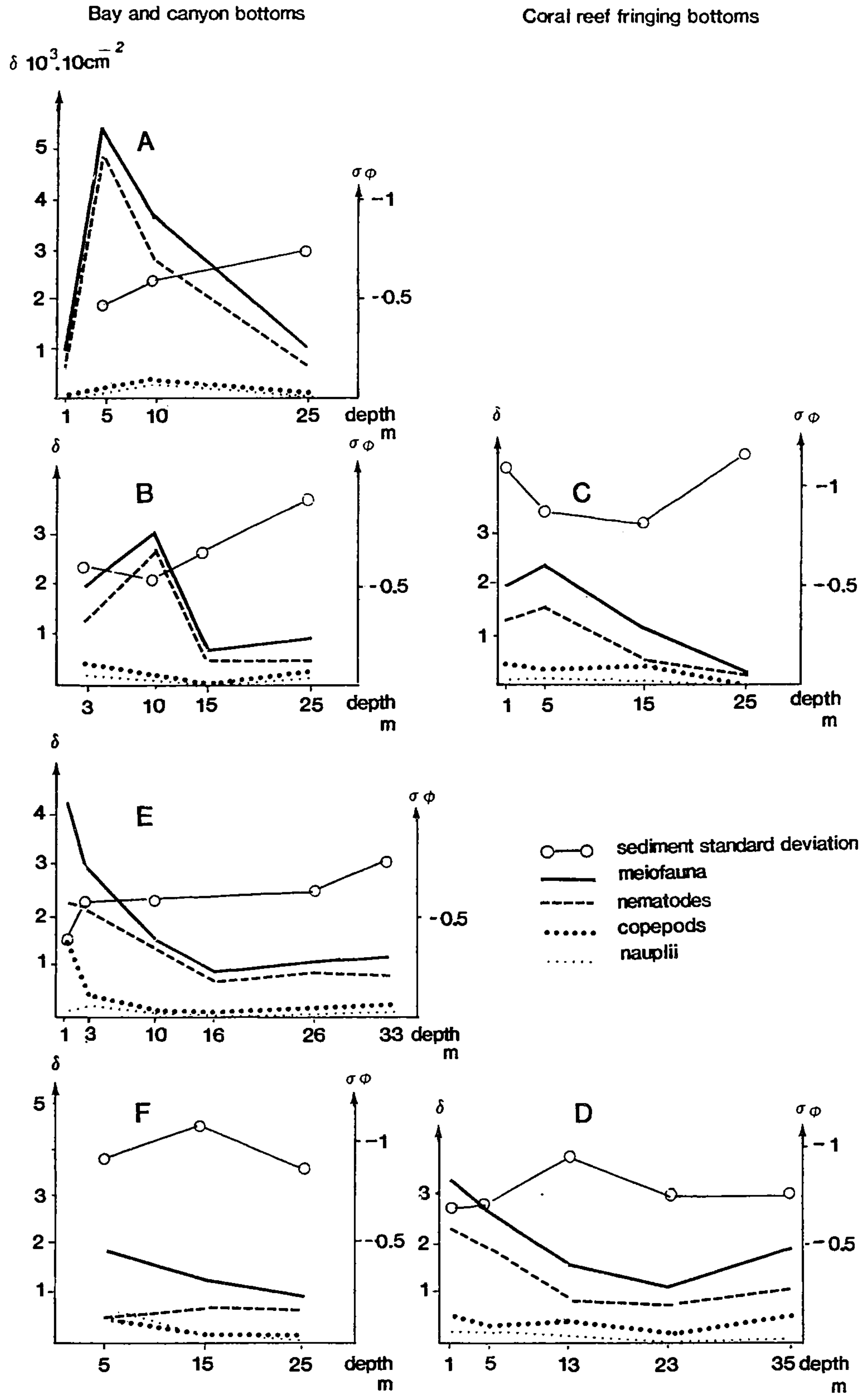

Fig. 4. Variations of meiobenthic densities according to depth and sediment standard deviation (ø).

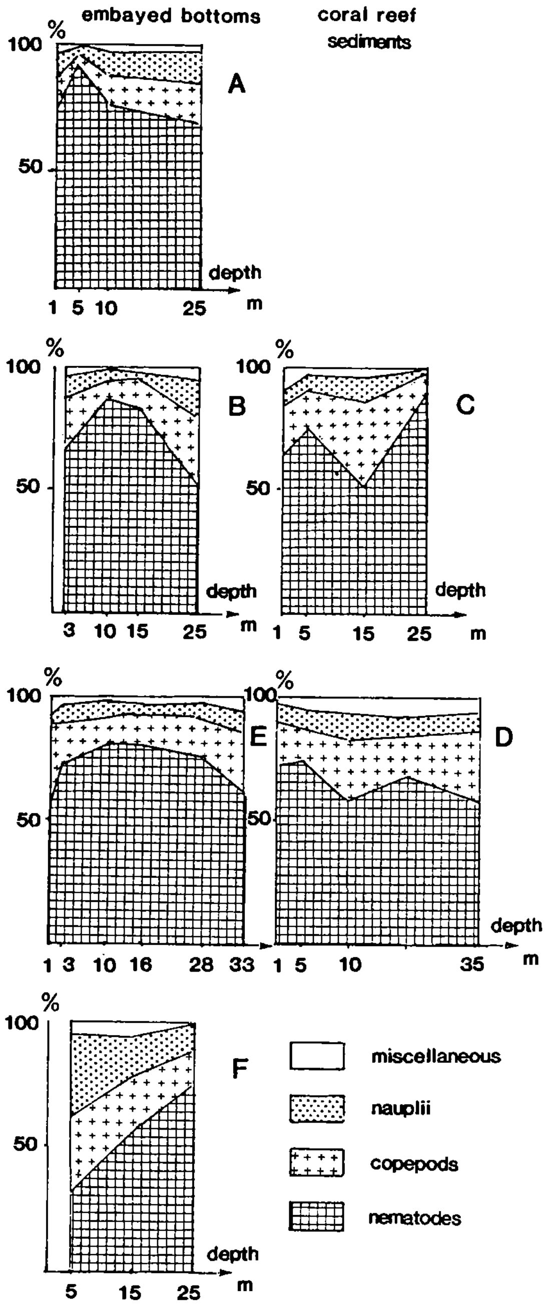

Fig. 5. Fluctuations of major meiobenthic groups along the various transects according to depth.

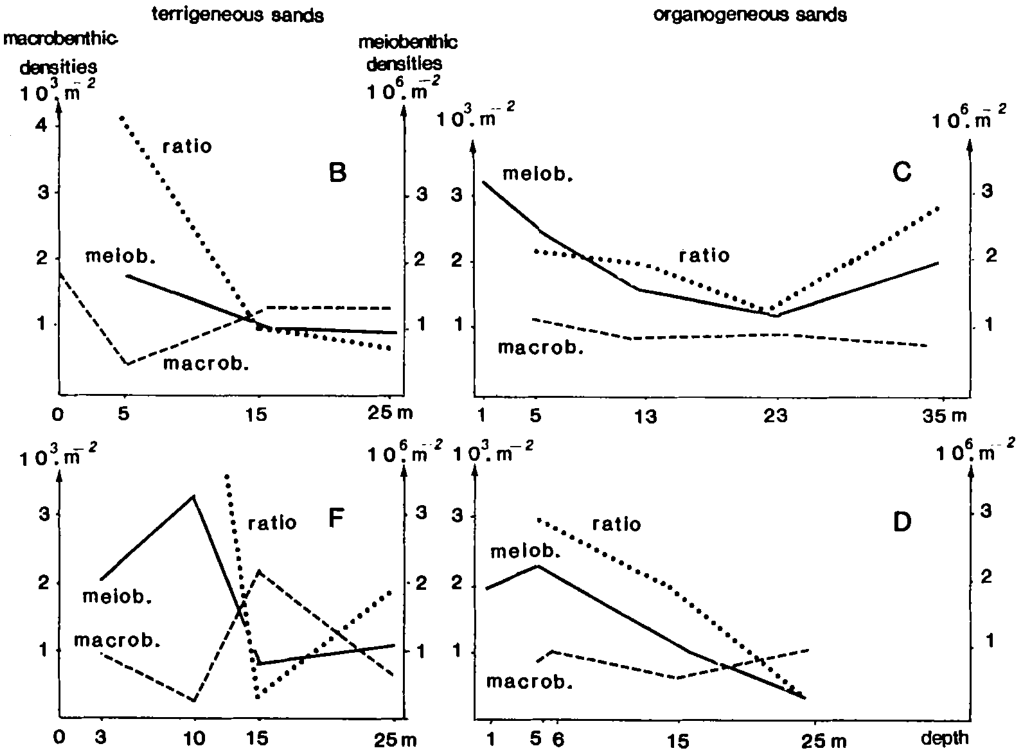

Fig. 6. Macro- and meiobenthic relations along selected transects, according to depth in terrigeneous and organogeneous sands .

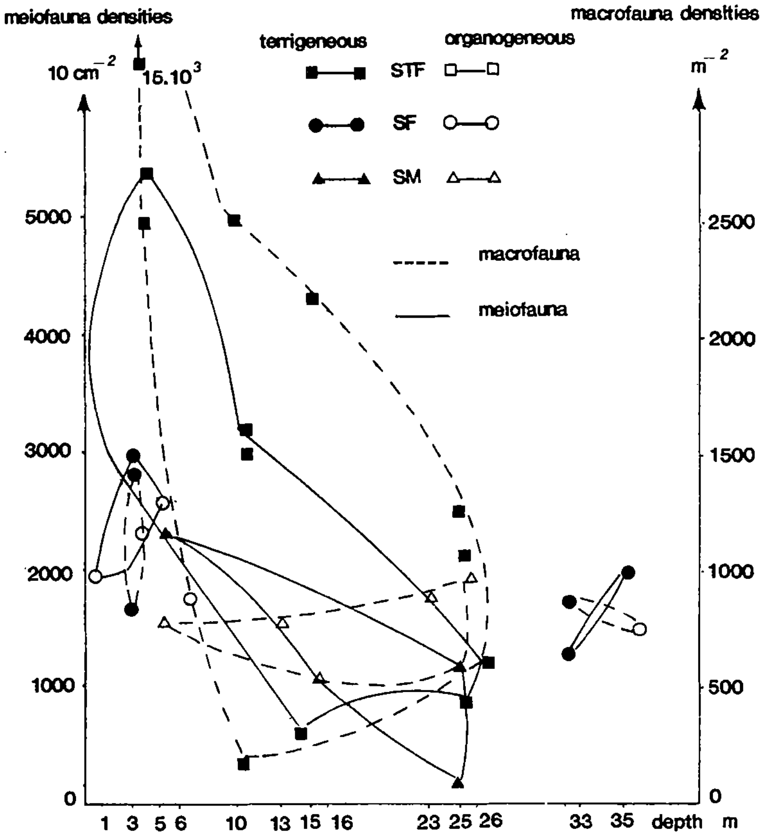

Fig. 7. Density fluctuations of macro- and meiobenthos according to sedimentary stocks. (STF = very fine sands; SF = fine sands; SM = medium sands).

Table 1. Sediment data along sampling transects, Aqaba Jordan coast, April-May 1981. (CS = coarse sands;
MS = Medium sands; FS = fine sands; VFS = very fine sands; organic carbon content in % of dry weight).

SAMPLING TRANSECT	DEPTH (m)	MEAN SIZE Tmφ		KRUMBEIN sorting Dφ	FALK & WARD standard deviation σφ	SILT and CLAY (%)	$CaCO_3$ (%)	ORGANIC CARBON (%)
A	5	VFS	2.60	-0.24	-0.47	2	7.2	0.28
	10	VFS	2.55	-0.36	-0.59	5	11.3	0.13
	25	VFS	2.76	-0.46	-0.74	16	18.5	0.27
B	3	FS	1.62	-0.41	-0.59	0	5.9	-
	10	VFS	2.40	-0.35	-0.54	1	9.0	-
	15	VFS	2.51	-0.47	-0.68	8	10.5	0.09
	25	MS	0.80	-0.58	-0.94	0	6.6	0.21
C	1	FS	1.07	-0.71	-0.08	3	66.8	0.48
	5	MS	0.94	-0.57	-0.87	1	85.6	0.26
	15	MS	0.97	-0.56	-0.82	0	73.8	0.17
	25	MS	0.53	-0.76	-1.16	3	80.2	0.18
D	1	VFS	2.98	-0.35	-0.68	9	41.0	0.53
	5	FS	1.51	-0.50	-0.70	1	75.4	0.38
	13	MS	0.94	-0.66	-0.95	3	82.8	0.21
	23	MS	0.91	-0.49	-0.76	0	83.1	0.26
	35	FS	1.47	-0.55	-0.77	1	84.4	0.39
E	1	VFS	2.14	-0.27	-0.38	0	8.4	0.31
	3	FS	1.82	-0.36	-0.57	2	8.1	0.19
	10	VFS	2.36	-0.37	-0.57	2	9.2	0.06
	26	VFS	2.15	-0.43	-0.62	1	13.3	0.09
	33	FS	1.40	-0.54	-0.78	1	11.2	-
F	5	CS	-0.70	-0.57	-0.91	0	-	-
	15	CS	-0.34	-0.77	-1.09	11	6.3	0.48
	25	VFS	2.06	-0.48	-0.87	16	12.3	0.31

Table 2. Densities of macrofauna (ind m^{-2}) along the sampling transects, Aqaba Jordan coast.

	EMBAYED AND CANYON BOTTOMS		FRINGING REEF	CORAL BOTTOMS	EMBAYED BOTTOMS	
Depth (m)	Transect A	Transect B	Transect C	Transect D	Transect E	Transect F
0						1,720
1					15,060	
3		840			1,490	
5			780	1,200		400
6			950			
10	1,510	190			2,520	
13				810		
15		2,160	560			1,250
23				940		
25	1,130	600	970			1,270
26					610	
33					850	
35				730		
means	1,320	948	815	920	4,106	1,170

Table 3. Density (ind 10 cm^{-2}) and percentage of meiobenthic groups along the sampling transects.

SAMPLING TRANSECT	DEPTH (m)	NEMATODES	COPEPODS	NAUPLII	MICRO-POLYCHAETES	KINORYNCHS	TARDIGRADS	MISCELLANEOUS (GASTROSTRICHS OLIGOCHAETES ACARIANS OSTRACODS TANAIDS)	TOTAL MEIOFAUNA
A	1	677 73.43	111 12.04	100 10.85	32 3.47		1 0.11	1 0.11	922 100%
	5	4,837 90.80	259 4.90	187 3.50	35 0.70		4 0.07	7 0.13	5,329 100%
	10	2,839 76.10	414 11.40	363 9.70	51 1.40		9 0.24	58 1.55	3,734 100%
	25	724 68.20	172 16.20	138 13	22 2.10		2 0.18	5 0.47	1,063 100%
B	3	1,340 66.40	426 21.20	181 9.00	61 3.00		1 0.04	4 0.19	2,013 100%
	10	2,840 87.49	215 6.60	171 5.30	18 0.60		2 0.06		3,246 100%
	15	571 84.34	76 11.23	13 1.92	12 1.77		4 0.59	1 0.15	677 100%
	25	586 53.10	291 26.40	163 14.80	53 4.80		4 0.36	8 0.72	1,105 100%
C	1	1,275 64.70	394 20.00	124 6.30	136 6.90	1 0.05	36 1.82	5 0.25	1,971 100%
	5	1,742 75.80	384 15.10	152 6.60	41 1.80	1 0.04	14 0.60	2 0.08	2,300 100%
	15	565 51.50	388 35.30	107 9.70	31 2.80	1 0.09	3 0.27	4 0.36	1,099 100%
	25	233 88.60	24 9.10	4 1.50	2 0.80				263 100%
D	1	2,371 72.60	579 17.73	233 6.83	70 2.14		15 0.46	8 0.24	3,266 100%
	5	1,950 74.40	339 12.90	207 7.90	64 2.44	43 1.64	8 0.30	11 0.41	2,622 100%
	13	928 57.80	409 25.50	167 10.40	74 4.60		30 1.86	3 0.18	1,611 100%
	23	791 68.50	195 16.90	85 7.40	69 6.00	5 0.43	5 0.43	4 0.34	1,154 100%
	35	1,139 58.80	570 29.40	124 6.40	91 4.70	1 0.05	14 0.72	2 0.10	1,941 100%
E	1	2,223 53.50	1,525 36.00	104 3.50	337 8.00		49 1.17	1 0.02	4,239 100%
	3	2,156 72.70	509 17.20	189 6.40	69 2.30		33 1.11	9 0.30	2,965 100%
	10	1,273 82.00	149 9.60	111 7.20	13 0.80		7 0.45		1,553 100%
	16	733 81.00	112 12.36	36 3.97	23 2.54		1 0.11	1 0.11	906 100%
	26	922 75.80	192 15.80	74 6.10	17 1.40		10 0.82	1 0.08	1,216 100%
	33	850 62.27	324 23.74	116 8.50	67 4.91		6 0.44	2 0.15	1,365 100%
F	5	577 32.00	535 29.67	621 34.44	25 1.39		28 1.55	17 0.94	1,803 100%
	15	691 55.60	252 20.30	204 16.40	35 2.80		56 4.50	9 0.72	1,247 100%
	25	682 73.57	130 14.02	101 10.90	8 0.86		2 0.22	4 0.43	927 100%

Table 4. Macrobenthic mean densities along sampling transects according to carbonate content of sediments
(kp. = kilometric point).

Transect	Locality	Mean density (ind.m^{-2})	Sediment carbonate content (%)	Mean (%)	Standard-deviation
E	kp. 14 bay	1,370	8.4-13.3	1.00	2.58
A	Aqaba beach	1,320	7.2-18.5	12.3	5.75
F	kp. 21 bay	1,170	6.3-12.3	9.3	3.15
B	kp. 8 canyon	948	5.9-10.5	8.0	2.13
D	kp.12 coral reef	920	73.8-85.6	79.9	5.91
C	kp. 8 coral reef	815	75.4-84.4	81.4	4.08

Table 5. Variations of the macro- meiobenthos ratio in the littoral sediments of the Jordan coast of the Gulf of Aqaba.

Transects	F	E	B	A	D	C
Depth (m)						
1		★1/281				
3		△1/1,989	●1/2,395			
5	●1/4,091				●1/2,183	●1/2,946
10		△1/616	●1/17,100	△1/2,472		
13					●1/1,983	
15	★1/995		△1/313			●1/1,961
23					●1/1,229	
25	△1/729		★1/1,840	△1/938		●1/271
26		●1/1,993				
33		●1/1,606				
35					●1/2,652	
means	1/1,938	1/1,297	1/5,412	1/1,705	1/2,012	1/1,726
means	1/2,668				1/1,889	

△seagrass beds ; ★seagrass bed vicinity ; ●bare sands

Table 6. Macrobenthic densities in the Indopacific "Biocenose of coarse and medium sands under bottoms currents" (= "*Asymetron lucayanum* community").

LOCATION	DENSITY (ind.m^{-2})
Tulear, Madagascar (Thomassin, 1978b)	
Barrier reef :	
outer reef slopes, fine and medium sands of the grooves or sandy basins Urothoe serrulidactylus assemblage	696
reef flats	480
enclosed lagoon slopes	833-2,720
Lagoonal reef :	
microatoll reef flat	7,980
Mayotte Island (Gout, pers. comm.)	
Barrier reef flats pools	2,739
Noumea, New Caledonia (Thomassin, pers. comm.)	
Barrier reef inner slope	6,081
Lagoonal bottom	1,166
Moorea Island, Polynesia (Thomassin et al., 1982)	
Deeper outer reef slope	636
Barrier reef flat	496-1,824
Fringing reef flat	2,242
Aqaba (our data)	
Fringing reef outer reef slopes, transect C	780 - 970
transect D	810 -1,200