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ECOLOGY OF THE CRINOIDS OF THE NORTHERN RED SEA WITH EMPHASIS ON EPI- AND ENDOZOIC FAUNA ASSOCIATED WITH THEM*

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ABSTRACT

The coral reefs along the Gulf of Aqaba consist of 14 species of crinoids with aggregations of different species in various depths. The most shallow group consists of several species of which the most common are *Lamprometra klunzingeri* and *Heterometra savignii* which occur in the shallow subtidal down to 2.0 to 3.0 metre depth. Other species of this group occur to a depth of 12 to 15 metres and from here another group of species occur which is headed by *Decametra chadwicki* and *Oligometra serripinna*. The deepest crinoids were collected at a depth of 45 metres by SCUBA and the most common ones were found to be *Colobometra arabica* and *Comaster brevicirrus*.

Feeding on micro and nano-plankton, the shallow water population of crinoids showed a typical circadian rhythm, whereas in groups occurring from 10 to 12 metres depth, this behaviour changes to a diurnal one gradually with the decrease in illumination.

Investigating the symbiotic animals living on the crinoids it was found that 27 taxons are involved in this interaction among them: Copepoda (6 species); Mollusca (2 species); Polychaeta (11 species) especially Myzostomida; Ophiurids (1 species); Crustacean decapod (6 species) and fish (*Lepadichthys lineatus*).

All these symbiotic animals were found to form typical food webs and groupings distributed according to the distribution of the host crinoid and depth. The occurrence of typical E. Indo-Pacific and Mediterranean Myzostomids on the same crinoid in the Gulf of Aqaba was found to be of special interest.

INTRODUCTION

OF all the classes of Echinodermata, the crinoids remain the least investigated, although extensive studies of their taxonomy have been published by Clark (1931-47). Papers on their ecology were published by Pott (1915), Clark (1921), Magnus (1963, 1967) and Barraclough (1966). Their feeding behavior was described by Gislen (1924), Magnus (1963, 1964) and Rutman and Fishelson (1969).

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This paper summarizes investigations of the crinoid fauna found along the coral reefs of the northern Red Sea, especially those found in the vicinity of Elat [Gulf of Elat (Aqaba)]. There is some reference also to crinoids collected among the islands of Dahlak Archipelago, Southern Red Sea. Most of the observations were performed by snorkeling and scuba-diving during various times of day and night, a technique described elsewhere (Rutman and Fishelson, 1969). For a different kind of analysis single specimens of crinoids were collected and isolated in plastic bags or glass containers. Some of them were immediately fixed in Ethyl alcohol, 70%; others were kept alive in captivity, for observations of movement, feeding and other activities. The parasitic and commensalic animals occurring on the crinoids were carefully picked out using stereomicroscopes, and their colours, forms and other meristic characters described. This type of research, begun in 1964, is still being pursued, several days every month.

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DESCRIPTION OF THE HABITAT

The coral formations of the northern Red Sea are mostly of the fringing type, occurring on a platform in the shallow water. This is especially prominent in the Gulf of Aqaba, where the reefs are frequently interrupted by wide passages and sandy slopes. Along the northernmost part of the Gulf, these reefs form table-like formations 10 to 30 metres wide, nearly horizontal and very shallow (Pl. I A), or even exposed during low tides (Fishelson, 1968; Loya, 1970). A great number of scleractinians are found on this table, but the most characteristic animal species here are the hydrocoralinians *Millepora dichotoma* and to a lesser extent *M. platyphyla*. Large colonies of these fire-corals occur all along the tables, their most dense and strong growth being found along the seaward fringe of the reefs. It should be mentioned here that these *Millepora* growths (Pl. I B) were found to be utilized extensively by several crinoid species.

Fig. 1. The beach rock surface and fringing coral growth found along the Sinai Peninsula.

The shoreward side of the coral reef table faces a shallow, sediment-rich lagoon, containing sparse groups of dead or living corals. Along the shore line, this lagoon is framed by beach rock of fossil corals or terrestrial rocks, together with gravel. The typical animal communities of the tropical infralittoral are found here - such as the *Tetraclita squamosa* - *Tectarius armatus* community (Fishelson, In press). The outer, sea-facing side of the coral table is 2 to 6 metres high, severely eroded and descending vertically or gradually, sometimes without clear borders, terminating at a depth of 20 to 35 metres. On these levels, Gorgonaria and Antipatharia colonies become the most dominant part of the habitat.

Further south, on the Sinai Peninsula within the Gulf of Aqaba, the lagoon becomes displaced by wide beach rock surfaces (Fig. 1).

THE CRINOIDS INVESTIGATED

The investigated population of comatulid crinoids was found to occur throughout the above-mentioned sub-habitats, from the very shallow subtidal down to a depth of 45 to 80 meters.

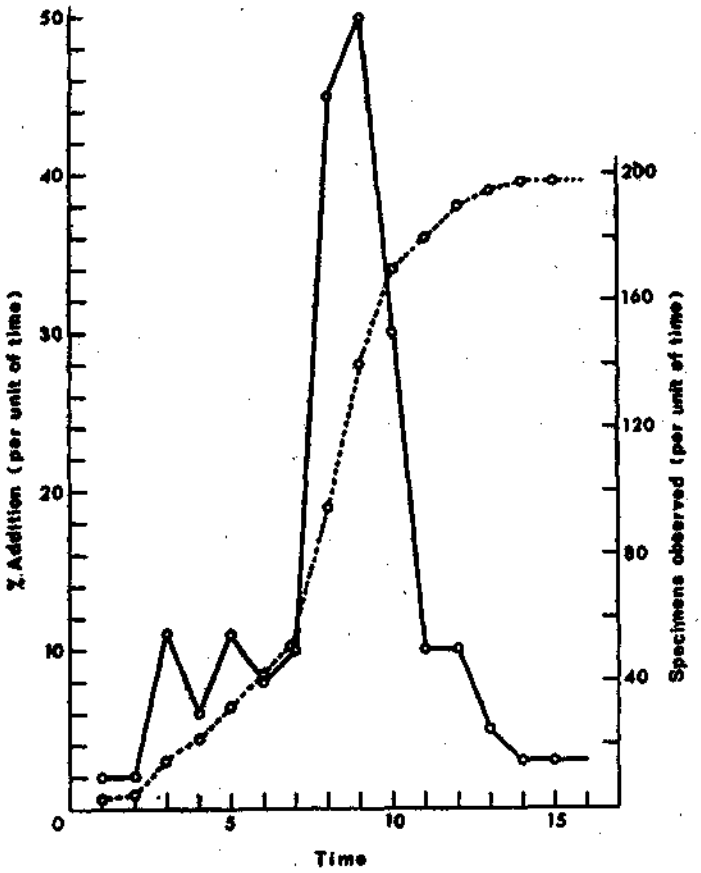

Fig. 2. The emergence of a group of *Lamprometra* (time intervals average 5 minutes).

As mentioned by H. M. Clark (1921), 18 species seem to be found in the Red Sea and adjacent parts of the Indian Ocean. Until 1962 only several of them were known from the Gulf of Aqaba (Clark, 1966). During our investigations their number rose to the following 12 identified species:

Capillaster multiradiatus (L.)
Comissia hartmayeri A. H. Clark
Lamprometra klunzingeri (Hartl.)
Tropiometra carinata (Lark.)
Heterometra savignyi (Müller)
Heterometra atra (A. H. Clark)
Comaster brevicirrus (Bell)
Oligometra serripinna (P. H. Charpenter)
Decametra chadwicki A. H. Clark
Colobometra arabica A. H. Clark
Colobometra sp. n. (?)
Antedon parviflorum (A. H. Clark)

BATHYMETRIC DISTRIBUTION

As the observations showed, the crinoids of the Gulf can be divided according to habitat preference, and depth of distribution. The subtidal group of species consists of *Lamprometra klunzingeri, Capillaster multiradiatus, Comissia hartmayeri* and partly *Heterometra savignyi*. The comatulids belonging here are distributed from the subtidal, and *L. klunzingeri* is sometimes even found in crevices of the low infratidal. This species prefers in general to hide among branches or plates of *Millepora* and is usually not found deeper than 1.5 to 2 metres. On several occasions they form groups of 50 to 75 specimens per sq. m. The estimated number of specimens along a *Millepora* fringe of a 200 m long coral table counted during one night was found to be 12,000. This species, as well as *Capillaster multiradiatus* that occurs together with it, are typical crepuscular animals, very sensitive to the amount of illumination, their activity regulated by the sunset and dawn. The first specimens crawl out of their hiding places half an hour before dark. Supporting themselves on their bending arms, they normally move upwards, taking up positions on the ends of coral branches (Pl. I C). The rate of emergence is slow during the first 10 minutes, then increases rapidly, ending more or less abruptly after 25 to 35 minutes (Table 1 and Fig. 3), when the comatulids form a dense cover over the corals (Pl. I D). Agitated by the local currents, they now spread out their arms and start to feed, collecting planktonic organisms (Gislen, 1924; Magnus, 1963, 1967; Rutman and Fishelson, 1969). This type of activity is sometimes accompanied by spawning (Fishelson, 1969) and continues throughout the night, till 4.30 or 5.30 a. m.; usually one hour before sunrise. At this time, all the exposed comatulids move suddenly down to crevices and cavities, where they disappear within 25 to 35 minutes. There they remain all day with coiled arms and contracted pinnuli.

TABLE 1. *Number of specimens of* Lamprometra klunzingeri *observed emerging along a line of 10 metres of the reef fringe (Elat)*

Time (p. m.)	No. of specimens	Average spec. / m	% of population (n = 198)
17:55	2	0.2	1.01
18:02	4	0.4	2.02
18:10	15	1.5	7.55
18:14	21	2.1	10.6
18:16	32	3.2	16.1
18:18	40	4.0	20.2
18:20	50	5.0	25.2
18:25	95	9.5	47.8
18:30	140	14.0	70.7
18:35	170	17.0	86.4
18:40	180	18.0	90.9
18:45	190	19.0	95.8
18:50	195	19.5	98.4
18:55	198	19.8	100.0
19:00	198	19.8	100.0

The same type of photosensitivity is also demonstrated by *Heterometra savignyi* but only by that part of the population that occurs in shallow waters 3 to 6 m deep. As described by Magnus (1963) and observed by us this species prefers gravel bottoms. In the vicinity of Elat, the population of *H. savignyi* is intermixed on the upper level with that of *Capillaster*, whereas downwards they descend to 10 to 12 m. Along the southern Red Sea they are dredged from depths of 45 to 60 m. The rhythmus of activity is quite pronounced in shallow water, resembling that of *Lamprometra*. From a depth of 5 to 6 m, this behaviour becomes less and less

observable, the specimens are observed to be active before sunset and also during the morning hours. In deeper water the population of *Heterometra* is active all day long. In captivity as well, the shallow-water specimens of *Heterometra* run into holes and crevices, whereas those brought from deeper water remain inert, sitting on one place. Such specimens react to strong illumination by coiling in their arms, a posture taken by the other two species within the day rest-crevices.

These three large and many-armed comatulids are accompanied on several occasions by the small *Comissia artmayeri* usually found in great numbers in crevices along the eroded seaward side of the coral tables, 1 to 2 m below the water surface. *Comissia* behaves in an entirely different manner from that of the three previous species; they are never found exposed. Remaining attached by their short, strong cirri, they stretch out their short arms from their crevices and thus they catch their food. Taken out, the specimens of *Comissia* are clumsy, very limited climbers with their stiff arms, and are usually washed away by waves.

This same region seems to be inhabited also by *Antedon parviflorum* (?), of which only single specimens were found. An intermediate group of comatulids, that include, together with *H. savignyi* the species *H. atra* and *Tropiometra carinata*, seems to be a transitional one between the shallow water forms and those found in deeper water, occurring from depths of 5 to 20 m. Both *H. atra* and *Tropiometra carinata* are found on rocky-coral bottoms, the first exposed, whereas the second usually hides with only its arms visible. In captivity both of them exhibit only very slight signs of direct reactions to changes in illumination. On the deeper levels of their distribution these species are accompanied by *Colobometra arabica*. The first specimens of *Comaster brevicirrus* are also found here.

These two forms initiate the region of delicate ten-armed comatulids usually attached in hundreds to the branched arms of *Gorgonaria* and *Antipatharia* growing here (Pl. II B). The commonest here are *Decametra chadwicki* and *Oligometra serripinna*, dominating from a depth of 25 m down to 45 m, the deepest region investigated. Along the upper level of their distribution they are usually accompanied by *Colobometra arabica* and *Comaster brevicirrus*. At depths of more than 30 metres only the dominant species are found, with their sharp, hook-like cirri hanging on *Athipatrus*. On one occassion (according to a diver), 200 specimens hanging on a single bush-like colony were observed on the same place for several months. In captivity these species are also very stationary, remaining for weeks on the same attachment, stretching only their arms during feeding.

EPIZOIC AND ENDOZOIC ANIMALS ASSOCIATED WITH CRINOIDS

During collection of the various crinoid species for ecological investigations, special attention was paid to collect also the population of organisms found on their arms and central bodies. Separating single crinoid specimens, it was also possible to establish the frequency and number of these associated animals. Among these animals were Crustacea (Copepoda, Macroura, Brachyura, Anomura), Polychaeta (Errantia, Myzostomida), Mollusca (Gastropoda) and one fish (Gobiesocidae).

Crustacea: Copepoda occur almost on all specimens of crinoids, crawling or being attached by anterior hooks to their arms, pinnuli or central body. Several species were found in populations of 350-400 specimens on a single crinoid (Pl. II C, Fig. 3). Thus, they seem to form the bottom level of a food chain that includes predator

species involved in this association. Almost all of them were new species, described by J. Stock (1966 a, 1966 b, 1967). The most abundant of them are *Pseudoanthessius major* and *P. minor*, that were found mostly on *Lamprometra klunzingeri* and *Heterometra savignyi*. According to Stock (1967) *P. minor* seems to be a sibling species of *P. major* and develops on *Lamprometra klunzingeri*. Only afterwards is this same comatulid also invaded by *P. major*. On this same crinoid species the copepods *Collorchus uncinatus* Stock and *Kelleria gradata* are found. An additional *Lichomolgus fishelsoni* Stock (1967) was found on *Oligometra serripinna*.

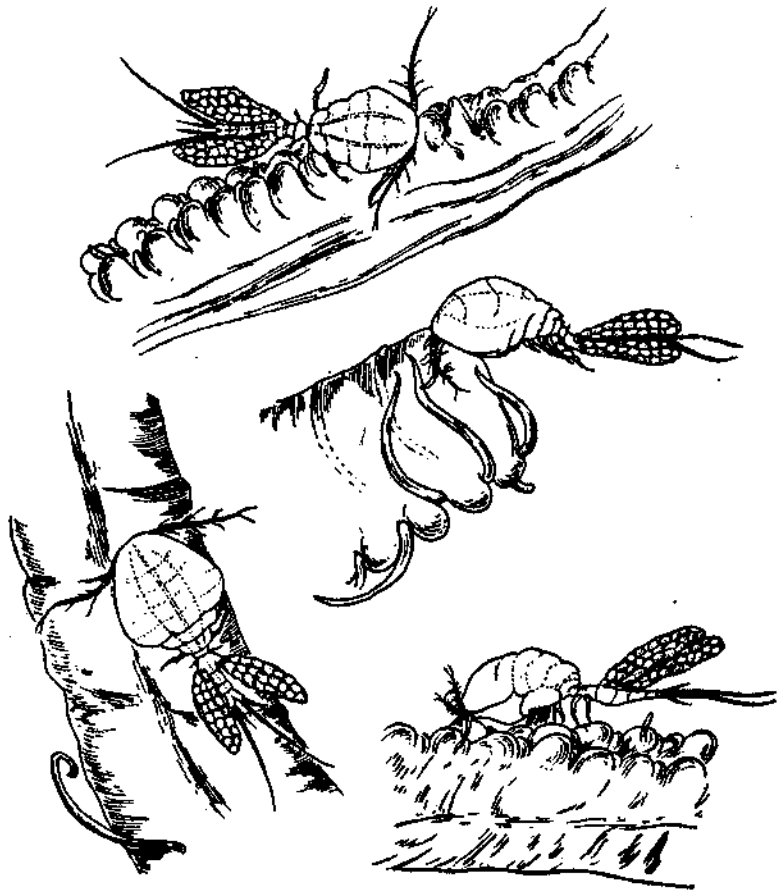

Fig. 3. Various positions taken by the parasitic copepods on their host.

A worm-like endoparasitic species of copepods, *Enterognathus lateripes* Stock, was found on the deeper-living crinoids, *Oligometra serripinna* and *Decametra chadwicki*, as well as on *H. savignyi* from a depth of 15 m. It is worthwhile to mention that the only other known species of the genus *Enterognathus* occurs near England and in the Mediterranean Sea (Stock, 1966).

Observations in captivity showed that the dense populations of copepods are eaten by other crustaceans, polychaetes and a fish species associated with the same crinoid hosts.

Decapoda Macrura forms were represented on our comatulids by three species belonging to Palaemonidae: one of them *Pontoniopsis comanthi* Borradaile, is well known from different parts of the Indo-Pacific, occurring on several types of echinoderms. On our crinoids it is most common on *Lamprometra* and the shallow *Heterometra*. Usually *Pontoniopsis* hides among the pinnuli of the host, occurring rarely on their arms (Fig. 5 a). The other two shrimps from the same hosts are *Preiclimenes tenuis* Bruce (Fig. 4 a) and *Periclimeneus djiboutensis* Bruce, both of them described for the first time. These three shrimp species are perfectly cryptic in their behavior and coloration and live usually in groups of 2 to 5 specimens on a common host. Of all of them, *P. tenuis* has the widest bathymetric distribution,

Fig. 4. a. *Periclimenes tenuis* and b. *Ceratocarcinus spinosus* (female).

occurring from the shallow water *Heterometra* till the deeper living *Decametra*. All of them were observed in captivity to walk along the hosts' arms and feed on the attached copepods as well as on the mucous secretions.

The brachyuran crab, *Ceratocarcinus spinosus* Miers., is common in pairs on *Lamprometra* and the shallow water *Heterometra*. Hiding among the pinnuli

of the coiled arms or on the calyces, they blend perfectly with the background, due to their cryptic structure and pattern (Fig. 4 b). The anomuran genus *Galathea* was found to be represented by two species: one very common - *Galathea elegans* Adam and White, well-known from crinoids also from other regions of the Indo-Pacific (Southwell, 1909; Potts, 1915; Jones and Sankarankutty, 1960; Lewinsohn, 1968). In the region of Elat *G. elegans* occurs on the shallow water crinoids (Fishelson, 1966) usually hiding between the cirri and base of the arms (Pl. II D). They seem to feed on the mucous secretion of the host and on passing detritus particles. The second species, *G. genkai* Miyake and Baba, with a much paler colouration than the first one, occurs at deeper levels, mostly on *Decametra* and *Oligometra* (Fig. 5 b).

The bristle-worms Myzostomida are entirely adapted to live on crinoids (Graff, 1875), and they dominate also on our comatulids, being represented by 10 species of which several were found to be new to science. Among them there are 6 freely living species and 4 endoparasitic ones, forming galls on the pinnuli or pouches on the calyx of the host.

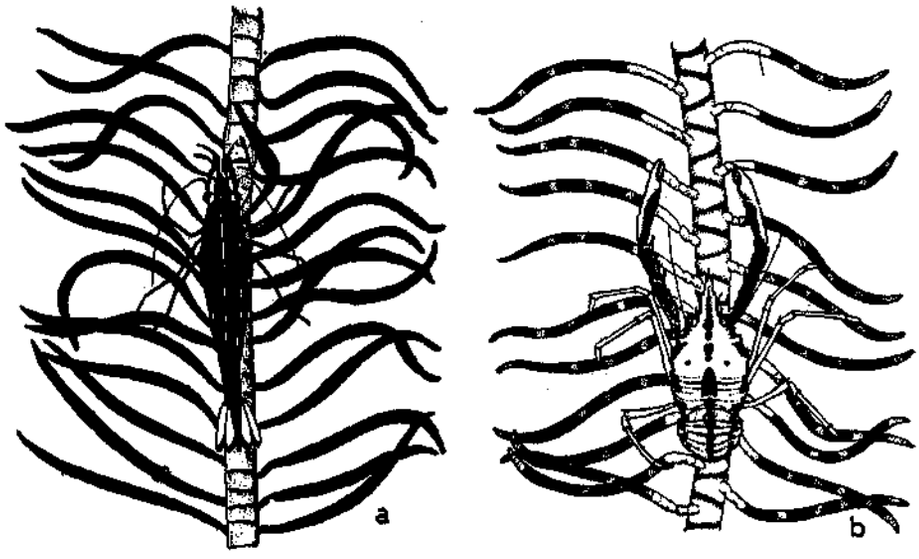

Fig. 5. a. *Ponthiopsis comanthi* and b. *Galathea genkai*.

The species freely living usually have a long, protractile proboscis. They feed on the plankton that passes along the cilliated grooves of the host's arms and is collected there. This group consists of species occurring on several crinoid species from the very shallow water till the maximal depth investigated.

The most common was found to be *Myzostomum crosslandi* Boulenger (Fig. 6 a) usually attached to the dorsal part of the host's arms, its colouring and pattern imitating those of the crinoid. They were found on *Lamprometra, Heterometra* (2 sp.) and *Decametra*. The highest number (65 specimens) was counted on a single *Lamprometra*. Other species were typical for shallow water, as *M. quadrilobatum* (Fig. 7 a) a highly vagile form, crawling on *Lamprometra*, and *M. hexalobatum* on *Capillaster*.

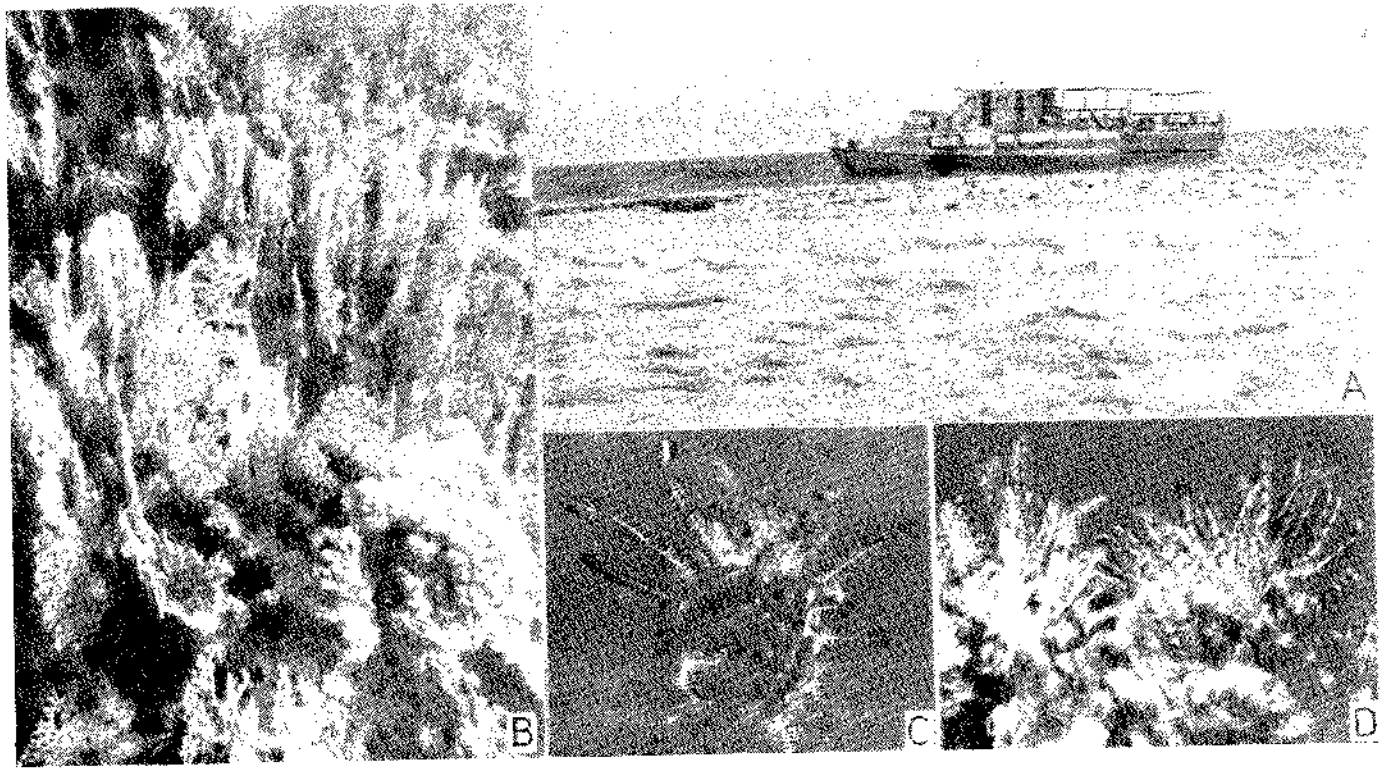

Plate I A. The table reef at Eilat during extreme lowtide. The inner portion of water is over the lagoon; B. *Millepora dichotoma* growths along the seaward portion of the coral reef; C. An emerging *Lampromera klunzingeri* taking up a position on top of a coral; and D. A cover formed by crinoids over the living coral colonies.

Plate II A. *Lepadichthys lineatus* on an arm of *Heterometra*; B. A group of *Decametra* and *Oligometra* on a part of *Antipatharia* colony (Photo in aquarium); C. A photo of copepods (white dots) on coiled arms of a crinoid (*Heterometra*); and D. *Galathea elegans* on *Lamprometra*.

On deeper living comatulids *Myzostomum costatum* (Lenc.) inhabits *Heterometra savignyi*, and *M. bockii* Jägersteen was found on *H. atra* and *Decametra chadwicki* of 15 to 45 m depth. *M. brevilobatum* Jägersteen, the most common in the edep zone, occurs on *Decametra, Colobometra* and *Oligometra.*

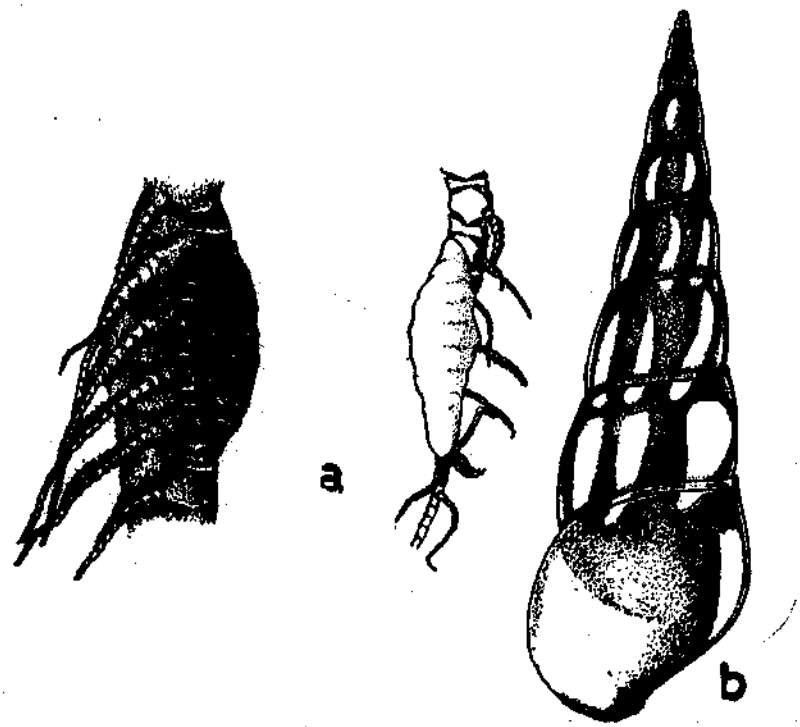

Fig. 6. a. *Myzostomum crosslandi*–pale and pigmented specimens and b. *Melanella* sp.

The endoparasitic group of myzostomids lives in pouches beside the stomach of in galls formed by them along the arms or pinnuli of the hosts. The species belonging to this group are: *Notopharyngoides (Myzostomum) ijimani* Hora and Okada, from *Capillaster*, heretofore known from crinoids of Japanese waters; *Cystomyzostomum cysticolum* (Graff) from *Capillaster*, and *Decametra*; *Eumyzostomum* (*Myzostomum*) *cirricaudatum* sp. n. and an unidentified *Cystomyzostomum* (sp. n?).

The number of specimens of each of the species that occurs on a single host varies from case to case. Mostly there are not more than 5 to 10 parasities on one crinoid. Only on one occasion were 35 specimens of *Eumyzostomum cirricaudatum* collected from a single *Heterometra savignyi.*

An additional brittle-worm, this time an aphroditid, *Scelisetosus longicirrus* Schmarda, was found to be the most polyspecific commensal, occurring on most of the comatulids and more or less at all depths. Specimens of this quickly moving animal occur solitarily and feed on copepods, small myzostomid worms and mucous particles. All the specimens on the various hosts have a colouration pattern well adapted to the variability in colouration of the crinoids (Fig. 8).

Parasitic molluscs were found on *Capillaster multiradiatus* and on *Heterometra savignyi*. These are two new species of the family *Melanellidae*— one of the genus *Melanella* (Fig. 6 b) and one of the genus *Mucronella* (Fig. 7 b). The latter parasitic form, identified by Ivanov (In press) as *M. capillastericola*, is characterised by its dwarf males. They spawn also on the host and produce very pronounced bendings and other deformations on its arms. In most cases observed, the settlement of *M. capillastericola* on any place of the host's arm causes a pronounced degeneration on the hind, distal part of it.

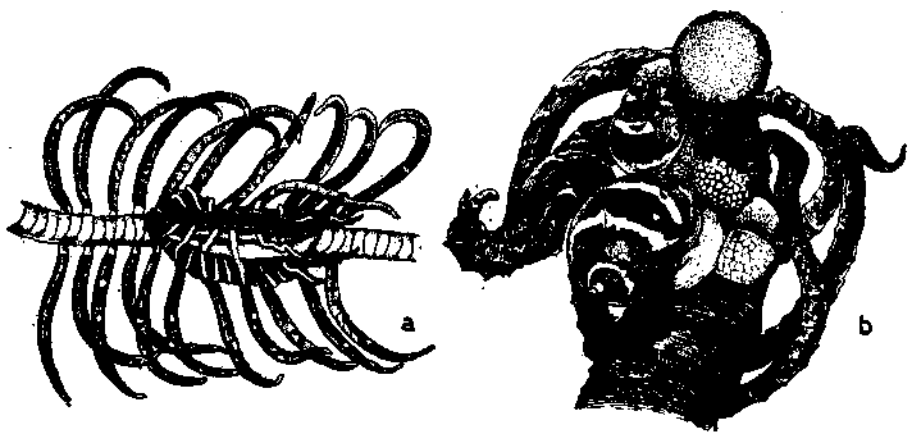

Fig. 7. a. *Myzostomum quadrilobatum* - the quickly crawling species and b. a group of *Mucronella capillastericola* and their spawn on an arm of *Capillaster*.

The fish that was found associated with *L. klunzingeri* and *H. savignyi* belongs to the clingfishes and was described by Briggs (1966) as a new species, *Lepadichthys lineatus*. These clingfishes were found only on crinoids, clinging with their sucking discs to the arms of their host animals (Pl. II A). They are predators, feeding on the pinnuli of their hosts as well as on worms and copepods living there. After observations in captivity it became clear that, being a predator, this fish also cleans its host of other epizoic animals.

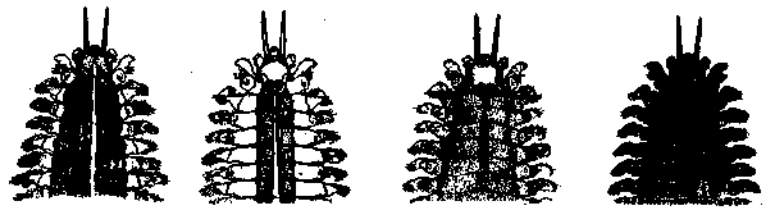

Fig. 8. Anterior parts of *Scelisetosus longicirrus* [from different coloured hosts (without dorsal scales)].

An additional animal species that was found on the deep-sea crinoids at Elat was a brittle-star, *Ophiotrix* (*Acanthophiotrix*) *purpurea* (von Martens). This commensal was found especially abundant on *Heterometra savignyi* dredged from depths of 40 to 60 m of the Dahlak Archipelago. Within the Gulf of Elat it was found also on *Tropiometra carinata*.

DISCUSSION

One of the most striking characters of the shallow-water crinoid fauna along the coral reef of the northern Red Sea is its richness in species and density of population. This is in contradiction with the assumption of H. L. Clark (1921) that the comatulid fauna of coral reefs is the "upper fringe" of a more extensive fauna, existing in deeper waters. In the population of crinoids of the northern Red Sea, 10 species have a highly stenobathic distribution, occurring above the 25 m isobathe, whereas only two species continue downward, reaching depths of 40 to 45 m. It

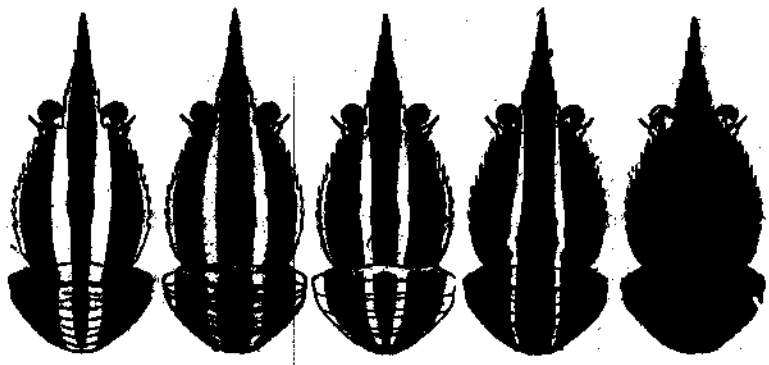

Fig. 9. The polymorphis of the dorsum in *Galathea elegans* from different hosts.

is striking that none of the numerous dredgings performed at depths of 150 to 600 m have brought up crinoids. Only one species, *Heterometra savignyi*, was collected at a depth of more than 60 m. This is in contradistinction to other parts of the Indo-Pacific basin, where most of the comatulids are collected in fairly deep water. Perhaps in the closed basin of the Gulf of Elat we are dealing with a tendency to "shallowness" in the benthic fauna, a phenomenon that is observed not quantitatively, but qualitatively also in other groups of benthic invertebrates. It seems that this phenomenon is one cause for the high diversification of the crinoid fauna.

Along the coral reefs, between depths of 1 m to 25 m, a population of 12 crinoid species is found, a phenomenon not noted in any other locality. But not only is the species diversity high, the density per square metre of surface seems to be the highest observed. The highest number of specimens of comatulids from other regions mentioned was 65 per sq. m (Marr, 1963), and this was at a depth of 650 m. In our shallow population 40 to 65 specimens per sq. m seems to be an average number in several localities.

Barraclough (1966) mentioned that no benthic community has been defined in terms of a crinoid component. It seems that in future definitions of the bathymetric zones in the northern Red Sea, the comatulids should be defined as one of the important components participating in the increase of species diversity, as well as in consumption of large amounts of planktonic food. From this last viewpoint, they are able to compete with the basic carnivorous coral population.

The adaptability of the comatulids to this habitat is strongly emphasized by the circadian rhythm of the shallow water population and the decline of this rhythmicity, till its general absence, at the deeper levels. This behaviour, of course, influences the feeding behaviour of the various species: the group of *Lamprometra, Capillaster*

and partly *Heterometra savignyi* of shallow waters feeds only at night (Rutman and Fishelson, 1969), being hidden during the day in dark crevices and holes. The deeper living species feed practically round the clock, remaining more or less active continuously, exposed to the diffuse light of the surroundings. This different behaviour influences the activity of the whole animal ensemble associated with these crinoids.

One of the most characteristic features of this diverse group of 27 animal species occurring on our crinoids is their polychromism, adapted to the polychromism of their hosts (Fig. 8 and 9). In addition, the crinoids serve as environment and medium, enriching the general habitat of the reef. Some of these epi-or endozoans are widely distributed in the Indo-Pacific, as for example *Scelisetosus longicirrus, Myzostomum ijimani* and *Galathea elegens*. Other species, such as *M. crosslandi, M. hexalobatum* are endemic for the Red Sea, having analogous forms in the eastern Indo-Pacific. According to Vagin (personal communication) the splintering off in speciation of myzostomids in the Red Sea seems to be connected with the more. numerous fauna of crinoids found there.

As for the distribution of the crinoid inhabiting species, of the 27 species found 11 occur only on one species of crinoids; 8 on two; 6 on three; 2 on four, and only one occurs on 10 different hosts (*Scelisetosus longicirrus*). Four species of commensals, mostly connected with *Lamprometra* and *Capillaster*, are found only in the most shallow waters; 17 species are found till a depth of 10 m and other 17 species continue down to the maximum depth investigated. The richest fauna of inhabitors (18 species) was found on the population of *Heterometra savignyi*. This may be connected with the wide distribution of this host along the red sea as well as its penetration from the very shallow water down to the depths.

The interrelations among the different epi-crinoid forms occurring on the same host animal, seem to occur on two levels; the food level and the space competition level. As for predator–prey interaction, the majority of crinoids inhabited by their symbiotic clingfish are devoid of epizoic polychaets (Fishelson, 1966). Frequently these fishes were observed to prey on *Scelisetosus* and myzostomids, in addition to feeding on the rich copepod fauna. These copeopods, hanging on the crinoids' arms, serve also as food for the palaemonid shrimps and the errant polychaets. The myzostomids utilize the host: the free moving ones by catching the plankton from their cilliated food-transporting grooves, the parasitic ones by utilizing the tissue and body fluids of their host. The gastropods are also parasitic forms, found with their probosci penetrating deep into the crinoids' bodies. Concerning competition, it was observed (Fishelson, 1966) that clingfishes are not found on hosts inhabited by *Galathea elegans*. This seems to be because both of these species try to hide within the space between the arm base and cirri of the host. *Ceratocarcinus*, on the other hand, may be found together with the palaemonids as well as galatheids, not interfering with them, but sitting on the central calyx of the host or on the oral basis of the arms.

In conclusion, it seems that the large population of commensalic copepods serves as a primary food source for the carnivorous members of the society that feed also on secretions and particles accumulating on the host's arms and body.

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