Initial phases in reef development, studied at artificial reef types off Eilat, (Red Sea)*

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ABSTRACT: The initial steps in the formation of a coral reef (as distinct from the enlarging of an already existing reef) have been observed at block moles off Eilat (Red Sea). Within a period of 11 years, thus far four phases can be distinguished: (1) start-phase: rapid and homogeneous colonization by fouling organisms, still indeterminant for the final reef development; (2) preparation-phase: settling of shells, calcareous red algae and foraminiferans not affected by grazing animals which largely consume the initial settlers and subsequently attaching larvae; (3) phase of pioneer frame-building: growth of scleractinians and hydrocorals, settled on the remains of rock-attached shells or on other places inaccessible to grazers; secondary frame-builders (e.g. *Tridacna*) grow in their shelter; (4) phase of frame-binding: dead coral colonies are overgrown by calcareous foraminiferans, algae and bryozoans consolidating the coralline structures by their deposits. Living corals are successively colonized by a specific community (mainly decapods and molluscs); among these, borers are the earliest settlers. Upon death of the coral, there is a complete change in associated organisms forming a less specific but more diverse community.

INTRODUCTION

The term "coral reef" implies a solid, three dimensional structure rising from the seabed towards the surface as well as an assemblage of organisms forming a specific, highly diverse community. Whereas the geologist is concerned with the first aspect, the biologist focuses his attention to the latter one concentrating on living organisms. The ecologist, however, must consider b o t h a s p e c t s realizing the permanent interactions between reef structure and reef organisms: Organisms deposit and transform the reef substance to mould the habitat they utilize.

In recent times there have been very few occasions where the formation of this complex ecosystem has been observed. Where the environment is suitable, living reefs already exist. The flourishing reefs offer superficial impressions, but their complexity defies analytical insight. Grigg & Maragos (1974) had the rare opportunity to trace the development from a barren virgin substrate to a coral reef on submerged lava flows off Hawaii. In the present case, artificial embankments near Eilat (Gulf of

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Aqaba, Red Sea) provide a unique possibility to study step by step the increasing complexity, from the settling of the first invaders onward.

The development of the coral reef ecosystem from the first coral nucleus onward takes decades or centuries. Hence the observations off Eilat covering a total of 11 years represent only the i n i t i a l   s t a g e s in reef formation. The longevity of this community usually masks the dynamics of the developmental processes. On the other hand, this extended process makes it possible to study simultaneously abiotic and biotic parameters, including behaviour and adaptations of colonizing organisms, successional events and the increasing complexity of the total system. Furthermore, it allows us to analyse the forces which preserve or break down the calcareous framework; finally, one may measure the increase in diversity and substance.

OBSERVATION PERIOD, LOCATION AND METHODS

The studies reported began at the end of 1969 and continued until March, 1971; thereafter, sporadic observations were taken until March, 1976. The sites of the observations were the breakwaters of the yacht harbour (YH) and the glassbottomed boat harbour (GBH) at Eilat, as well as parts of the embankment along the coastal road from Eilat to southern Sinai (Fig. 1). At the beginning of my observations, the block moles along the road were just emplaced. The new mole of the GBH was half a year old; the old mole, four years, when the studies began. Details of colonization on pillars of the merchant harbour have been considered elsewhere (Schuhmacher, 1973).

The total length of the harbour moles and the studied part of the road embankment is ca. 450 m. The length of the sea walls and their various exposures to insolation, wind, currents, sedimentation, temperature regimes and sea swell offer excellent opportunities for discerning the interaction of combinations of these factors. The moles, constructed of polygonal granite boulders of between 50 and 120 cm in diameter, slope down to depths of 1 to 7 m (Fig. 2c). They represent a system of holes and projections exposed to abiotic and biotic influences like a natural reef. Further description, especially concerning the environmental details of the moles, can be found in a previous paper (Schuhmacher, 1974).

In addition, asbestos panels of different size and in various configurations (Fig. 2a, b) were set out near the harbour moles and exposed for periods ranging from 1 month to 6 years. Mapping, measurements and collections were done along representative transects by periodic skin- and scuba-diving. The zoological material collected was identified by many specialists whose assistance is sincerely acknowledged. In the laboratory, SEM and various geological techniques were used to elucidate the calcareous infrastructure.

RESULTS

A synopsis of the observations from the differently aged reef types yields the following outlines of succession in reef development (Fig. 7). In spring time, two
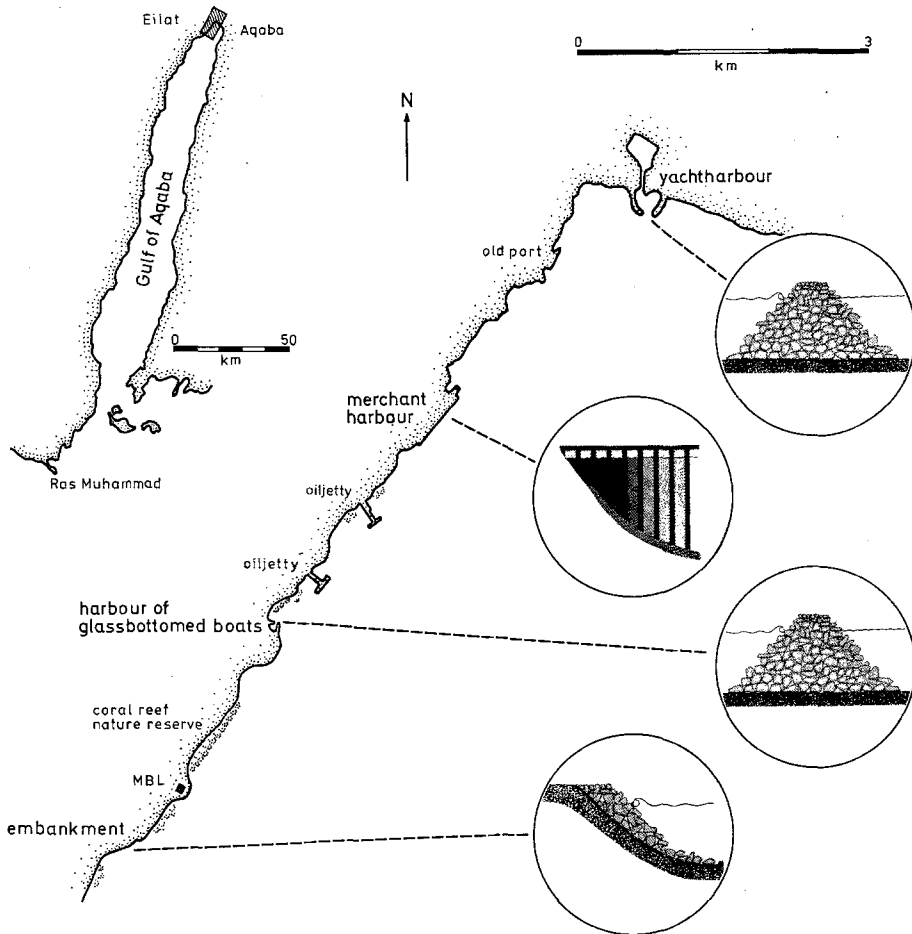
Fig. 1: Location of investigated sites; encircled symbols indicate type of artificial reef struc-
tures (MBL: Marine Biology Laboratory)

weeks after their establishment, the solid substrata were covered by thin veils of long
filamentous algae *(Enteromorpha clathrata elongata)*. During summer and autumn,
however, slimy layers of diatoms *(Melosira* spp.) occupied the recently emplaced rocks
(Fig. 3a). They vanished after 2 to 3 months. After 4 to 6 weeks barnacles *(Tetraclita
squamosa rufotincta)* settled in the surf exposed area. Whereas various calcareous
tubeworms (e.g. *Filograna implexa)* and bryozoans already settled on the colonization
plates exposed to open water, these animals were rare among the first invaders on
the block moles. Several *Spirorbis* species belonged to the pioneers on the boulders.
After 3 months, short filamentous green, brown and red algae began to carpet the
substratum trapping fine silt and detritus and thus providing a pasture for grazing
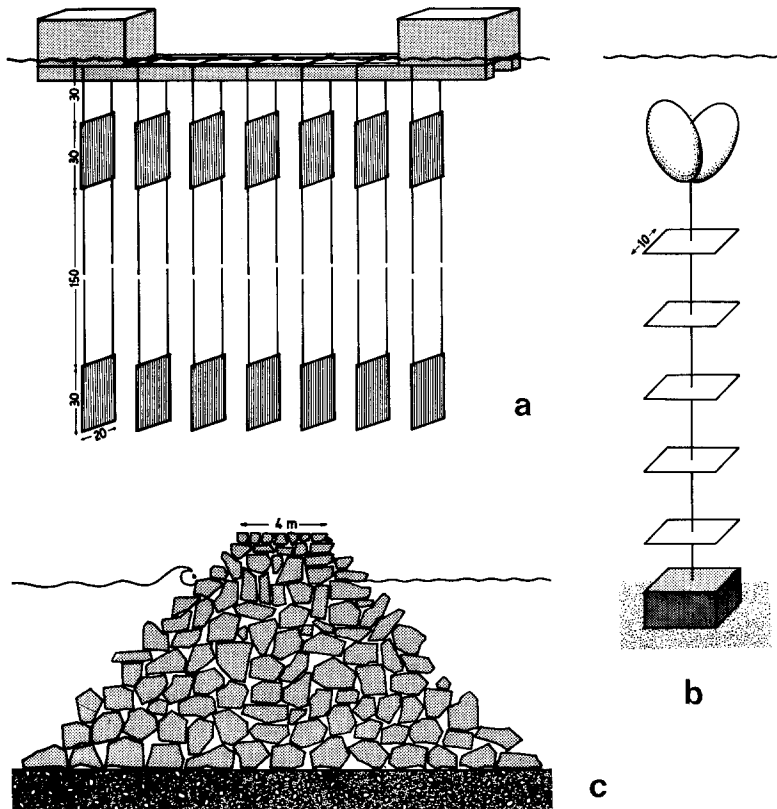animals such as prosobranchs, sea urchins, and sea cucumbers.

Fig. 2: Types of colonization-substrata used: *a* pairs of vertical asbestos plates hanging below a raft at 30 or 210 cm below surface (dimensions of set and plates in accordance with OECD standard 1966, measures in cm); *b* set of horizontal plates kept afloat by buoys; *c* diagrammatic cross-section through a harbour mole of big boulders

After half a year, the shells of vermetids *(Serpulorbis inopertus)*, various oysters *(Hyotissa hyotis, Lopha folium, Saccostrea cucullata)*, at least two *Chama* species and *Spondylus gaederopus* had attached to the granite boulders (Fig. 3b). Most of these shells had a life span of only one or few years; thereafter, the remaining halves attached to the rock provided a preferred substratum for corals. Foraminiferans and some calcareous algae (e.g. *Fosliella* sp.) formed coin-sized layers, conspicuous after half a year following the establishment of the moles. The calcareous alga *Porolithon* sp. was restricted solely to surf-exposed areas.

The hydrocorals *Millepora exaesa, M. dichotoma* and stony corals *(Stylophora pistillata, Pocillopora danae, Cyphastrea microphthalma, Favia favus, F. laxa, Porites* sp.) were first noticed one year after boulder establishment. They exhibited preference · to limestone substratum, including pieces of coral flagstone (which were among the mole boulders), the afore-mentioned half shells (Fig. 3d), or the calcareous layers deposited by algae or foraminiferans (Fig. 3e). Eighty % of the corals settled on

ridges, in small crevices (Fig. 3c) or on the vertical sides of the boulders. Besides some local influence of heavy sedimentation, the grazing sea urchins (the day-active *Tripneustes gratilla* and the night-active *Diadema setosum*) were found to limit the corals from most of the horizontal or gently sloped planes of the rocks (Schuhmacher, 1974).

Individual coral colonies harbour a s p e c i f i c m i c r o - c o m m u n i t y . The following common species made their first appearance: Coral crabs (*Trapezia cymodoce* and – less common – *T. ferruginea, T. guttata, T. rufopunctata* and *Tetralia glaberrima*) were found in 2-year or older *Stylophora* colonies. These crabs were young and had a carapax width of ca. 5 mm. Juveniles of the coral shrimps *Alpheus sublucanus* and *Harpiliopsis depressus* occurred in 1- to 2-year old *Stylophora* or *Pocillopora* colonies which were at least double branched.

A conspicuous coral commensal is the gall-forming crab *Hapalocarcinus marsupialis*. The females induce *Stylophora, Pocillopora* and *Seriatopora* colonies to branch abnormally and to form a pocket- or basket-like gall around the crab (Potts, 1915). The earliest symptoms were recorded at colonies 4 to 5 years old. There is evidence that the final formation of the gall is completed within half a year. The related crab *Cryptochirus coralliodytes* penetrated spherically growing corals as *Platygyra lamellina* or *Favia* spp. both at least 2 to 3 years old. It takes approximately the same time for the tubeworm *Spirobranchus giganteus* to become established on a coral. The snail *Quoyula madreporarum*, a parasite, feeds directly upon tissue of the corals *Pocillopora* or *Stylophora*. They were found on corals 4 to 5 years old.

B o r i n g o r g a n i s m s invaded corals very early; 11 individuals of *Lithophaga* sp. of 3 to 5 mm length were found in a 5 mm thick and 18 months old *Montipora* crust (Loya already found the shells in *Stylophora* colonies less than 1 year old, personal communication). Branches of *Stylophora* colonies, 3 years old, were regularly infested by *Lithophaga cumingiana* and *L. hanleyana* which especially weakened the forkings of the skeleton. Boring sponges, however, were found only after the colonies attained an age of 4 years. In order for *Cliona* and related sponges to invade living corals, the coralline tissue must be partially damaged. Such damage typically occurs around the openings of the *Lithophaga* burrows.

Fig. 3: Aspects of community development on artificial reef types: *a* start phase – slimy diatom layers (*Melosira* sp.) on recently established boulders (road embankment); *b* preparation phase – *Serpulorbis inopertus* and numerous *Chama* specimens (GBH); *c* phase of pioneer frame building – *Stylophora pistillata* individuals 1 and 2 years old in a rock crevice; each square measures 10 × 10 cm (GBH); *d* phase of pioneer frame building – *Stylophora* colonies (6 to 7 years old attached to old *Chama* shells; frame measures 50 × 50 cm (GBH); *e* phase of pioneer frame building – section of an overgrown granite piece: encrusting foraminiferans developed of fissure in several layers (between arrows), later, they were completely covered by a colony of *Leptastrea purpurea* (YH); *f* phase of secondary frame building – colony of *Stylophora pistillata* with two individuals of *Tridacna maxima* on the edge of a boulder (GBH); *g* phase of framework binding – colony of *Pocillopora danae* which, after a life span of 6 years, has been encrusted mainly by foraminiferans and calcareous algae during an additional 2 years, the scale bar represents 3 cm (YH); *h* phase of framework binding – the left specimen represents a mazerated branch of *Pocillopora danae* compared with (right) a typical branch from the colony in *g* coated by foraminiferans; note increment of calcareous matter by subsequent encrustations
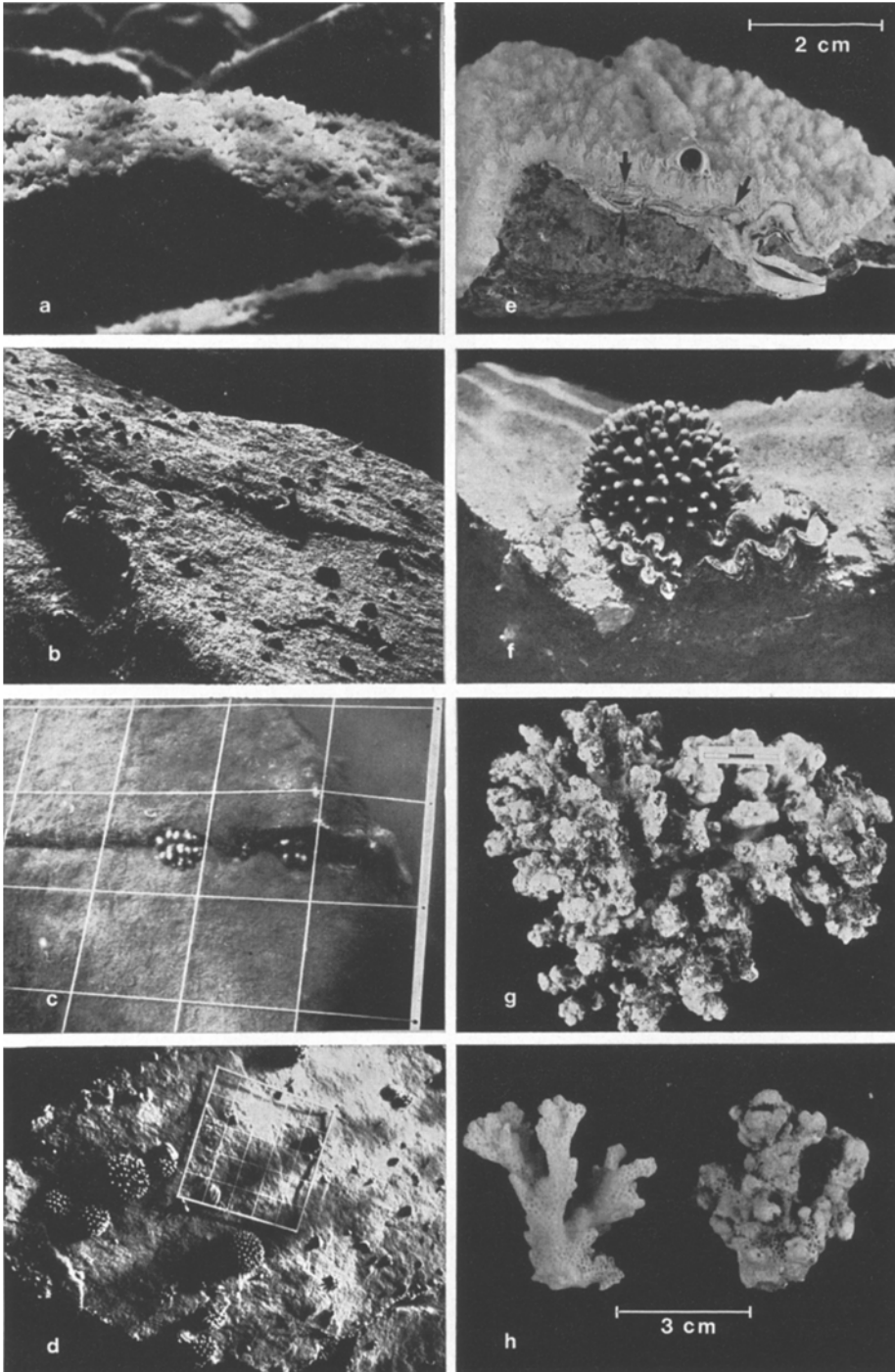
The community around a pioneer coral colony continues to evolve by g r o u p - i n g of additional scleractinian corals, shells, ascidians and other sessile organisms in close neighbourhood. For example, the dominant part of *Tridacna* individuals on the moles is found closely fixed to corals (Fig. 3f, 4).
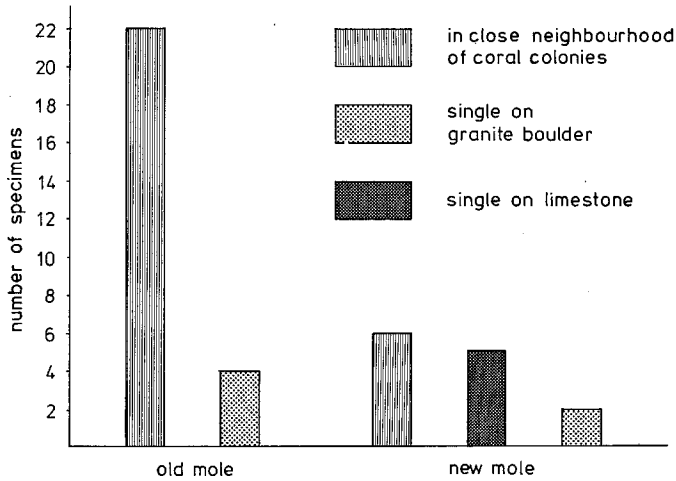

Fig. 4: Occurrence of *Tridacna* on the moles of the GBH (new mole contains two boulders of rugged coral limestone being much more attractive to reef benthos than granite boulders)
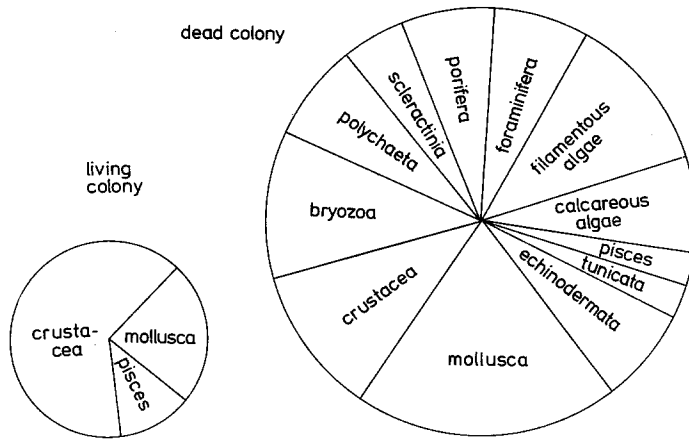

Fig. 5: Comparison between a community on a live colony of *Pocillopora danae* and a dead one of approximately the same size (both ca. 6 years old); the differently-sized circles represent a total of 8 or 42 macroscopic species

There is a considerable mortality of young coral colonies: Thirty % of the age group 5 to 7 years died, thus providing a substratum for successive settlers. Younger corals exhibited an even higher mortality, but their remains were generally
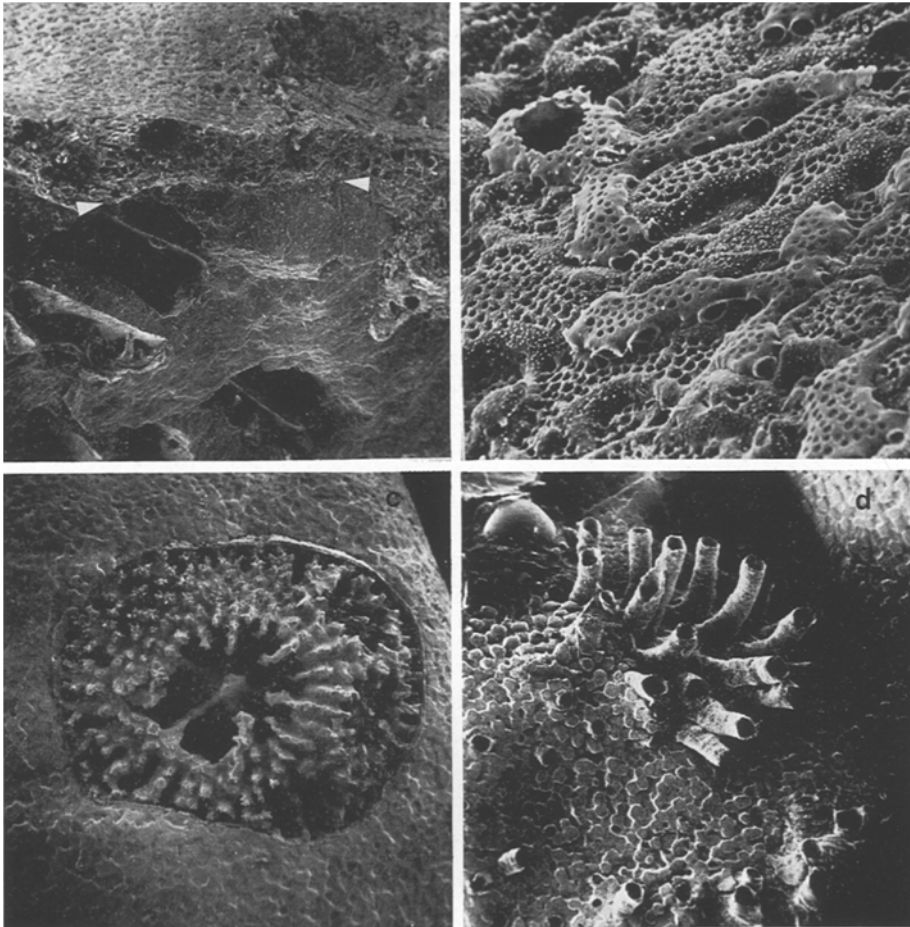
Fig. 6: Aspects of frame binding by subsequent encrustations of foraminiferans on a dead
Pocillopora skeleton (SEM photographs): *a* vertical section showing a 200 μm thick layer of
acervulinid foraminiferans on the coral skeleton (arrows point at the border), 33 x; *b* surface
of a *Acervulina inhaerens* layer (Acervulinidae) partially overgrown by *Planorbulinoides retina-
culata* (?) (Cibicididae), 190 x; *c* young *Pocillopora* colony, 1 to 2 weeks after planula settling,
competing for space with encrusting foraminiferans, 30 x; *d* colony of calcareous bryozoans
overgrown by acervulinid or planorbulinid foraminiferans, 19 x

not big enough to provide a suitable substratum. Foraminiferans and algae were the
principal organisms encrusting the skeletons within a few months. Their layers attained
a thickness of 2 mm within 2 years. A lot of other sessile and motile species colonized
the dead skeletons. In Figure 5, the community associated with a living colony of
Pocillopora danae is compared to the community on an equally sized skeleton. Eight
species are associated with the living coral, 42 species with its dead counterpart.

Death of the coral induces a complete change in the composition of associated
organisms. While the coral is alive, the community is mainly recruited from specifically

adapted crustaceans and molluscs; after its death, the associated community is comprised of a much more diverse assemblage of organisms exhibiting less specialized adaptations (Fig. 5). Following death of the coral tissue, the calcareous matter continues to increase, however, not by contributions of coral polyps but by other lime secreting organisms (Figs 3h, 6). On a *Pocillopora* example, 2 years after tissue death, the layers formed by calcareous algae, foraminiferans and bryozoans represented four % of the total weight and also four % of the volume of the specimen (Table 1). Exposure to light and water movement influences the development of these subsequent coatings: the upper sides of the colony, directed to the open water, were covered with layers up to 2 mm thick, whereas the sides facing the substratum were barely coated. Massive corals, which exhibit less surface area than branching forms of comparable age, were not coated to the same extent, probably, since they do not extend into the water to the same degree as branching forms (Table 1).

Table 1

Calcareous substance, colonization-space and community represented by live and dead colonies of *Pocillopora danae* and *Favia laxa* (6 or 5 years old)

Species	Growthform	Dimensions height (cm)	width (cm)	Area covered by the colony (cm²)	Weight (g)	Volume (cm³)
Pocillopora danae	branched	14	16 × 22	14	510	270
Favia laxa	spherical	4,5	8 × 8,5	51	157	133

Species	Surface (cm²)	Colony portion made of secondary encrustations weight (g)	volume (cm³)	Number of species settling on the colony 2 years after death	Number of species settling on a comparable living colony
Pocillopora danae	480	18	10	42	8
Favia laxa	100	1	0,5	12	4

Artificial reefs have been studied in regard to their attractiveness for fishes (e.g. Randall, 1963). The investigations at the embankments of Eilat concerned both the increase in fish population synchronously with the development of the benthic community. Beginning with a few species, more than 70 fish species became regular visitors or residents at the GBH. An analysis of the fish community or its fluctuations is in preparation.

DISCUSSION

For 200 years, man-made structures on the seabed have served as "artificial reefs" improving the coastal-fishery output (Ino, 1974). The reef examples dealt with in this paper create a semantic problem. Most of those structures used in fish management do
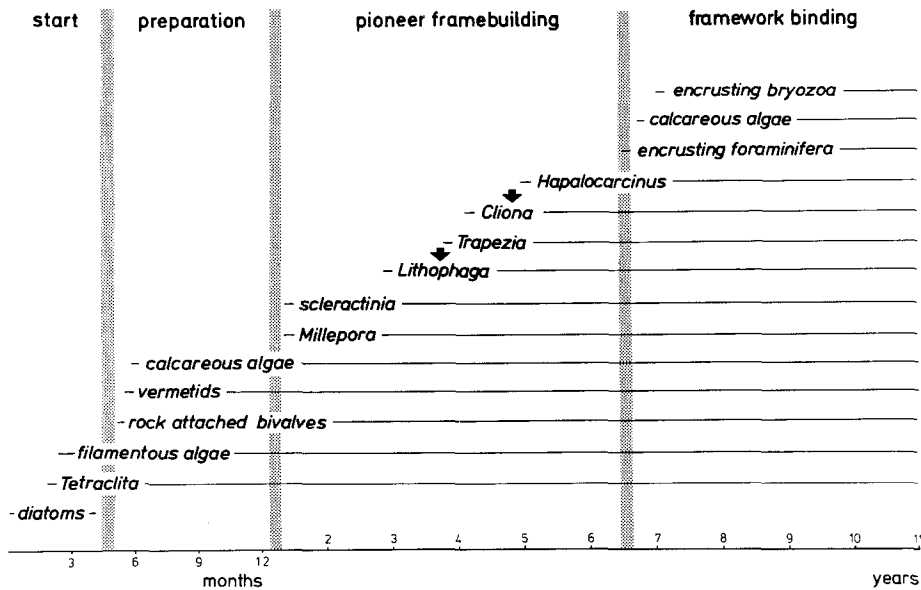
Fig. 7: Successive colonization of artificial reef types thus far classified in four phases of reef
development; the arrows point at coral and reef destructing agents

not conform to the term "reef" in the proper sense, since they typically do not extend
to the surface layers of the sea. On the other hand, it is well known that a situation
in shallow water is prerequisite for coral reef development (e.g. Schuhmacher, 1976).
Hence the present embankments can much more be regarded as "artificial reefs" than
other artificial habitats such as the mentioned constructions used in fish management.

Geologists (Ginsburg & Lowenstam, 1958; Schroeder & Zankl, 1974) distinguish
four mechanisms which must interact for the formation of a reef structure: frame-
building and -binding, cementation of pores, and filling by sediments. In established
reefs these processes operate simultaneously and continuously. The observation of a
developing reef community reveals how the processes become sequentially effective
being integrated in an even more extensive succession of the whole community (Fig. 7).

Before any framework is established certain preliminary events seem to determine
the distribution pattern of future frame builders. Usually, a virgin (unpopulated)
substratum is at first colonized homogeneously by fouling organisms. This s t a r t -
p h a s e , not yet immediately affecting the final reef development, is followed by
a   p r e p a r a t i o n - p h a s e ,   during which grazing animals consume the new
growths of first settlers. Early settled barnacles, shells and calcareous red algae are
not grazed because of their resistent tests. These tests provide a foothold for subse-
quently settling larvae, resulting in disjunct distribution patterns. Examination of the
base of coral colonies showed that, in most cases, these were attached to other cal-
careous material and not directly to the granite of the boulders or the asbestos test
panels. The relative importance in site choice of chemotaxis versus rugotaxis remains
to be determined.

The scleractinian *Stylophora pistillata* was abundant among the pioneer frame builders being an opportunistic species (Loya, 1976). In addition, my observations indicate that *Pocillopora* and certain massive corals exhibit the same strategy. Stony corals and hydrocorals continue to produce a disjunct pattern which becomes the p i o n e e r   f r a m e w o r k of the reef. The framework attracts additional reef benthos in the new shelter evolving into numerous proto-reef communities. Among these assemblages certain organisms, for example *Tridacna*, continue the frame-building processes as s e c o n d a r y   f r a m e   b u i l d e r s.

The usually high mortality rate among young scleractinians (Connell, 1973) provides enormous additional colonization sites. A *Pocillopora* colony which died after 6 years of growth occupied a base area of $14 \, cm^2$ and had a skeleton surface of $480 \, cm^2$ available for settlement (Table 1). A dead coral colony harbours an abundant variety of species, resulting in a higher species diversity compared with the few specialized organisms adapted to life in and on living coral tissue. This fact explains the high species diversity in "dead reef parts" (Mergner & Schuhmacher, 1974).

As contrasted to frame-building discussed above, the encrusting forms, especially homotrematid and acervulinid foraminiferans, contribute most substantially to the strengthening layers covering the coral frame. Their activities characterize the p h a s e o f   f r a m e - b i n d i n g. The role of the encrusting foraminiferans is emphasized, whereas bryozoans, which are considered as important frame binders (Cuffey, 1972; Soule & Soule, 1974), are more scarce, and restricted to areas with minimal water circulation. Calcareous algae, especially *Porolithon* sp., are mainly restricted to surf-exposed regions.

The two remaining mechanisms essential for reef formation, cementation and sedimentation, become effective later in reef development, when more coralline material is accumulated than presently available at the artificial reefs. Thus Friedman et al. (1974) showed that the degree of cementation is not yet considerable before some cm below the surface of an already established coral reef. The process of space-filling by sediments requires amounts of loose material not yet produced, too, at the investigated sites.

Borers are among the pioneers successfully colonizing the living coralline tissue. Before the surface of the coral provides proper shelter for epibionts, several *Litho-phaga* species may penetrate into the live skeleton (Gohar & Soliman, 1963). They, in turn, enable boring sponges (*Cliona* spp.) to invade – even though normally they do not infest living corals. Hence, bio-erosion and -corrosion (Schneider, 1973) limit coral reef formation from its very beginning.

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