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SUBSTRATUM PREFERENCES AND PLANULAE SETTLING OF TWO RED SEA ALCYONACEANS: *XENIA MACROSPICULATA* Gohar AND *PARERYTHROPODIUM FULVUM FULVUM* (Forskål)

Y. BENAYAHU and Y. LOYA
Department of Zoology, George S. Wise Center for Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel

Abstract: The settling behaviour and substratum preferences of the planulae of the Red Sea soft corals *Xenia macrospiculata* Gohar and *Parerythropodium fulvum fulvum* (Forskål) were examined in the laboratory. The planulae of the two species have a short pelagic phase and they tend to settle immediately upon leaving the parent colonies. Mucous secretion is used by the larvae for crawling and adhering to the substratum. They exhibit an aggregated pattern of settlement. The developing polyps are found in depressions or pits of the substratum. The planulae preferentially settle on rough substrata and avoid smooth surfaces. They search for substrata covered with an organic coating, composed of turf or crustose coralline algae. Such substrata create better conditions for larval settlement and metamorphosis. The planulae of *P. f. fulvum* exhibit a striking preference for upside-down attachment on undersides of the substrata, while *Xenia macrospiculata* utilizes both substratum faces for settlement. Light intensity seems insignificant in determining attachment sites. The findings of the experiments correspond well with the distributional patterns of juveniles of the two species as found in the natural environment. The specific requirements for settling of both species increase their chances of successful development and thus enhance their survival.

Key words: Octocorallia; Red Sea; planulae settling; larval ecology

INTRODUCTION

Studies dealing with settlement and substratum exploitation by marine invertebrates elucidate the problems of site-specificity of settling larvae. Such studies may also explain the spatial distribution of organisms in their environment (Hadfield, 1977). Planulae of many coelenterates are capable of selecting substrata for settlement and thus, their post-metamorphic survival is enhanced (Chia & Bickell, 1977). Extensive studies on the settling of planulae have been conducted on hydrozoans (Müller, 1973a,b: Donaldson, 1974; Hughes, 1977), scyphozoans (Brewer, 1976a,b; Otto, 1977; Cargo, 1979; Neuman, 1979) and on scleractinian corals (Duerden, 1902; Harrigan, 1972; Lewis, 1974; Gerrodette, 1981). Some surveys deal with substratum preferences of gorgonian larvae (Théodor, 1967; Kinzie, 1971; Weinberg, 1979). Among soft corals (Octocorallia : Alcyonacea) the larval ecology and selective settlement of the temperate species *Alcyonium siderium* (Verrill) has been recently examined by Sebens (1983a,b). Although various studies point out the frequent abundance of soft corals in Indo-Pacific reefs (Benayahu & Loya, 1977, 1981; La Barre & Coll, 1982; Tursch & Tursch, 1982;

Dinesen, 1983), the only existing information on their substratum selection is derived from the study of Gohar (1940) on the Red Sea Xeniidae.

The present study deals with substratum selection by two common Red Sea soft corals: *Xenia macrospiculata* Gohar and *Parerythropodium fulvum fulvum* (Forskål). We have studied life history features and the detailed reproductive biology of these species (Benayahu & Loya, 1983, 1984a,b). In the present study laboratory experiments were conducted in order to examine the type of cues involved in settlement of these planulae. We examined their response to organic and inorganic surfaces, together with the effect of substratum position and shade, upon larval attachment. Our results and observations are used to consider the consequences of substratum preferences upon the distributional pattern of each species in the field.

Material and Methods

General experimental conditions and design

The experiments were conducted during the breeding period of the studied species (June–July, 1980) at the Marine Biological Laboratory (M.B.L.) at Eilat, Israel. Planulae of *Xenia macrospiculata* were obtained from colonies reared in the laboratory (Benayahu & Loya, 1984b). Larvae of *Parerythropodium f. fulvum* were removed from brooding colonies at the M.B.L. reef (Benayahu & Loya, 1983). All experiments were set up within 3–4 h after obtaining the larvae. The laboratory was air-conditioned (28–30 °C), and its light regime simulated natural day length. Glass aquaria with 4–6 l of filtered sea water were used and the planulae were released on the water surface of each aquarium. The water temperature was 23-24 °C, corresponding to the ambient sea temperature at this time of the year. Each aquarium was supplied with an airstone located at its centre for uniform aeration. In order to maintain fresh sea water in the experimental tanks, the water was replaced every 4–5 days.

As a substratum for planular settlement skeletal fragments of the common Red Sea hermatypic coral *Stylophora pistillata* (Loya & Slobodkin, 1971) were used. Such fragments are utilized for settlement by many soft corals. Living colonies of *S. pistillata* (Esper) were collected, bleached with 10% sodium hypochlorite solution, rinsed with fresh water and dried. The fragments were glued by hypoxy cement onto plastic Petri dishes, 9 cm diameter. Prior to the experiment they were soaked for 2–3 h in filtered sea water and then transferred to the aquaria. The bleached fragments were used to determine the planular response to inorganic surfaces. As organic substrata branches of dead colonies of *Stylophora*, covered with turf algae and crustose coralline algae, collected shortly before the experiment were used. These branches were fastened to Petri dishes by thin plastic coated wires. In order to establish whether the planulae discriminate between shaded and non-shaded sites, they were exposed for settlement on Petri dishes, half the surfaces of which were painted black on both sides. Planular settlement and polyp abundance were recorded on the available surfaces: coral fragments, dish surfaces and aquarium glass. After the attachment of planulae, each dish was carefully removed into a finger bowl with sea water and the polyp count was conducted under a stereoscopic microscope. This procedure was carried out for each experiment during 4-6 wk (see below).

SETTLEMENT OF PLANULAE

An experiment was designed in order to determine the response of planulae to coral fragments with organic coating and to inorganic surfaces. Planulae of *Xenia macrospiculata* were exposed to Petri dishes containing equal proportions of bleached *Stylophora* branches and organic-coated fragments. For this experiment three aquaria were used, each containing four dishes and 200 larvae. The *Parerythropodium f. fulvum* experiment was comprised of three aquaria, each supplied with 250 planulae and four dishes: two containing bleached branches and the other two organic fragments.

To establish whether larval settlement is determined by the position of the substrata, dishes with organic fragments on their upper side and dishes with organic fragments fastened on to their lower side were used. Three rubber corks were glued to each dish providing an elevation of 2 cm above the aquaria bottom. Thus, both sides of the dishes were available for settlement. In such an experimental set-up, most of the fragment surface area was exposed for larval attachment (see p. 254). In the *Xenia* experiment three aquaria, each with 250 planulae and four dishes were used: two of the dishes were with organic substrata directed upwards and the other two downwards. The *Parerythropodium* experiment included five aquaria each with 250 planulae, two dishes with fragments on their lower side, and one on its upper surface.

In order to examine larval response to shade, the dishes with half surfaces painted black, were also elevated in a similar way to that described above. Larval settlement on both their sides was recorded. The *Xenia* experiment consisted of two aquaria, each with four dishes and 200 planulae. The *Parerythropodium* experiment consisted of five aquaria, each with three dishes and 250 larvae.

RESULTS

GENERAL OBSERVATIONS

Planulae of *Xenia macrospiculata* and *Parerythropodium f. fulvum* exhibited rapid settlement after shedding (see also Benayahu & Loya, 1983, 1984b). During the first 2 days after exposing the larvae to the substrata, they might alter their primary attachment sites. Towards the end of the second day all the larvae settled, and started their metamorphosis into polyps. Some planulae were attached to narrow crevices among the coral fragments, whereas many others settled in depressions and pits of the substrata (Fig. 1a,b). Thus, during the first counts conducted in the early stages of the experiments, it was often difficult to detect all the small-sized juveniles. Once they developed into tentaculate polyps, they were easily recognized and counted. Planulae of both *Xenia macrospiculata* and *Parerythropodium f. fulvum* settled in aggregates resulting in clumps of polyps.

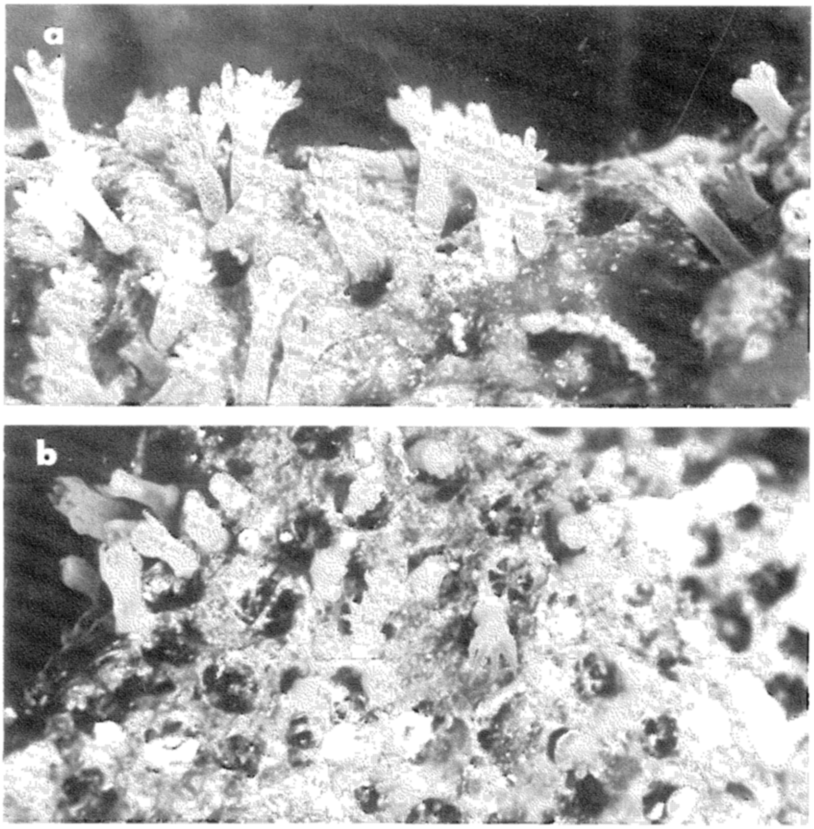

Fig. 1. a, cluster of young polyps of *Xenia macrospiculata* settled on a coral fragment; b, polyps of *Parerythropodium fulvum fulvum* growing on a coral fragment.

Survival of planulae in the different experiments was highly variable. Most of the mortality occurred during the first 48 h. The factors that affected larval survival are complex and may vary in each experiment. Nevertheless, the major causes for mortality are probably due to aeration and mechanical damage caused by water agitation (see also Sebens, 1983b). At a later stage of the experiments (4–6 wk) unicellular organisms sporadically developed and gradually caused the death of some polyps.

RESPONSE OF PLANULAE TO ORGANIC AND INORGANIC SURFACES

Xenia macrospiculata

Immediately after placing the planulae in the aquaria they randomly attached to any available surface. Two days later, however, the vast majority settled on the organic-coated fragments. The first polyp count was conducted on the 7th day after the initiation of the experiment. Table I presents the polyp distribution on the available surfaces

TABLE I

Settlement of *Xenia macrospiculata* in response to organic and inorganic substrata: polyp abundance during the experimental period.

Days	Total polyp number	Percentage of polyps		
		Organic fragments	Bleached fragment	Petri dishes
7	154	91.0	7.1	1.9
10	174	85.0	9.8	5.2
17	202	82.6	11.9	5.4
22	206	83.4	11.2	5.3
34	181	84.0	12.2	3.8
44	176	81.3	11.9	6.8

during 44 days. The results are presented as total polyp count in all aquaria. Note the successive increase of polyp abundance during the first 22 days, followed by partial mortality of the polyps. The results indicate that an extensive settlement took place on the organic fragments, while a much lower percentage of polyps were found on the bleached corals. Few polyps were found on the Petri dishes and no polyp development occurred on the glass surface of the aquaria. During the last count 176 polyps were recorded indicating that 29% of the initial number of planulae survived and developed into polyps.

Parerythropodium f. fulvum

Settlement of planulae was recorded only on coral fragments. Table II presents the total number of polyps recorded in all the aquaria and their abundance on the substrata. The results indicate a successive increase of polyp abundance during the first 2 wk, although a low percentage of the initial 750 planulae reached a polyp stage. A significantly higher settlement occurred on the organic substrata than on the inorganic fragments (χ^2 test, $P < 0.05$). The general decline in the percentage of polyps attached to the organic fragments (Tables I, II) was probably caused by predatory micro-organisms, which accumulated in the vicinity of the algal coverage. The polyps on the bleached surfaces (which are free from any algal coverage) were less subjected to predation and therefore showed a higher survival.

TABLE II

Settlement of *Parerythropodium fulvum fulvum* in response to organic and inorganic substrata: polyp abundance during the experimental period.

Days	Total polyp number	Percentage of polyps	
		Organic fragments	Bleached fragments
4	20	100	0
11	22	95.5	4.5
15	69	89.9	10.1
40	58	75.9	24.1

RESPONSE OF PLANULAE TO POSITION OF ORGANIC SURFACES

Xenia macrospiculata

The immediate response of the planulae was to aggregate on the organic-coated fragments found on the upper side of the dishes. Gradually, some larvae crawled and settled on the organic substrata located on the lower side of the dishes. The first polyp count was carried out on the 13th day after the initiation of the experiment. Table III

TABLE III

Settlement of *Xenia macrospiculata* in response to position of organic substrata: polyp abundance and survival during the experiment.

Days	Number of polyps		Per cent survival
	Coral fragments	Petri dishes	
13	168	1	22.5
19	159	1	21.3
29	158	1	21.2

presents the total number of polyps found on the coral fragments throughout the experiment: note that only a single planula settled on a Petri dish and no settlement took place on the aquaria walls. Although high larval mortality occurred during the first period, a stable survival of polyps was recorded during the remaining days. Table IV presents polyp abundance on fragments attached to the lower and upper dish surfaces on the 29th day. No significant difference exists between the two groups of recruits (Wilcoxon's signed rank test, $P > 0.01$). Examination of the attachment position of the polyps towards the substrata indicated that all polyps that settled on the upper fragments had their bases facing the aquarium bottom (right side-up). Among the recruits located on the lower fragments, 88% of the polyps settled with their bases facing the water

TABLE IV

Settlement of *Xenia macrospiculata* in response to position of organic substrata: polyp abundance recorded on the 29th day on the lower and upper sides of Petri dishes.

Number of polyps on organic coral fragments	
Lower side	Upper side
18	16
0	9
18	24
16	19
6	8
10	14

surface and their tentacles directed towards the aquarium bottom (upside-down). Only 12% of the polyps found on the lower fragments were orientated "right side-up".

Parerythropodium f. fulvum

Upon introduction into the aquaria, the planulae descended to the upper surface of the substrata. A day later strikingly all planulae accumulated along the margins of the Petri dishes and then crawled to the undersides. The first polyp count was made on the 10th day of the experiment (Table V). The results indicate that settlement occurred on

TABLE V

Settlement of *Parerythropodium fulvum fulvum* in response to position of organic substrata: polyp abundance recorded on the 10th day of the experiment.

	Polyps on organic substrata		
	Upper side	Lower side	
Aquarium	Dish a	Dish b	Dish c
A	22	11	7
B	82	44	59
C	18	28	26
D	63	24	10
E	140	7	35

organic fragments on both sides of the plates. No polyps were found on the plastic surfaces of the Petri dishes or on the aquaria glass. On the 24th day the attachment position of the polyps towards the substrata was examined (Table VI). All the polyps observed on fragments fastened to the upper sides of the dishes were orientated upside-down. Among the polyps settled on fragments attached to the lower sides of the dishes, a significantly higher number were orientated upside-down (Wilcoxon's signed rank test, $P < 0.05$). High variability was detected in the number of surviving polyps due to differential development of unicellular organisms in the different aquaria. It should be noted that in this experiment not a single polyp of *P. f. fulvum* attached right side-up on the upper fragments. All recruits settled on the underside surfaces, either upside-down or right side-up.

TABLE VI

Settlement of *Parerythropodium fulvum fulvum* in response to the position of the substrata: polyp abundance, position of attachment toward the substrata and percentage of the initial number of planulae on 24th day; numbers indicate polyps with their bases directed towards the upper side of the surface (upside-down); numbers in parentheses indicate polyps with their bases directed towards the lower side of the surface (right side-up).

	Polyps on organic substrata			Percentage of
Aquarium	Upper side	Lower side	Lower side	initial number of planulae
A	26	11 (4)	9 (4)	22
B	58	19 (14)	57 (11)	64
C	19	14 (10)	30 (14)	35
D	71	42 (4)	10 (9)	54
E	160	7 (3)	28 (8)	82

RESPONSE OF PLANULAE TO SHADE

Xenia macrospiculata

This experiment ran for six weeks. A marked delay in planulae settlement was recorded, probably due to lack of organic surfaces (see p. 258). Polyp count performed on he 42nd day of the experiment is presented in Table VII. No significant difference

TABLE VII

Settlement of *Xenia macrospiculata* in response to shade: polyp abundance on 42nd day on the upper and lower sides of dishes with half surfaces painted black.

		Dark half		Transparent half	
Aquarium	Dish number	Upper side	Lower side	Upper side	Lower side
A	1	3	3	1	13
	2	1	5	0	3
	3	2	4	1	3
	4	1	4	0	3
B	1	2	3	2	2
	2	2	12	2	3
	3	2	9	1	3
	4	0	12	3	3

exists between the number of polyps attached upside-down, on the lower dark surfaces and on the lower transparent dishes. Significantly more polyps were, however, counted on the lower dark surfaces than on the upper dark surfaces, and similarly more on the lower transparent sides than on the upper transparent sides. No significant difference exists between the polyp abundance on the upper dark and transparent dishes. No planulae settled on the aquaria glass. All comparisons were statistically tested by Wilcoxon's signed rank test ($P = 0.01$). The results point out that 26% and 30% of the initial number of planulae survived in aquarium A and B, respectively.

Parerythropodium f. fulvum

Most of the planulae introduced into the aquaria accumulated upside-down on the lower side of the dishes. No attachment took place on the glass. Table VIII presents the polyp abundance on the various dishes 24 days after the initiation of the experiment. A similar statistical analysis was applied here as in the previous experiment (Table VII). Note that negligible attachment took place on the upper sides of the Petri dishes. Significantly more polyps settled on the lower dark dishes than on their upper part. Significantly more polyps were attached to the lower transparent surfaces than on the

TABLE VIII

Settlement of *Parerythropodium fulvum fulvum* in response to shade: polyp abundance on 24th day on the upper and lower sides of dishes with half surfaces painted black.

		Type of substratum			
		Dark half		Transparent half	
Aquarium	Dish number	Upper side	Lower side	Upper side	Lower side
A	1	0	18	2	14
	2	4	6	3	13
	3	0	7	0	11
B	1	0	9	0	14
	2	0	15	0	35
	3	0	20	0	9
C	1	0	10	0	6
	2	0	16	0	8
	3	1	10	0	25
D	1	1	11	0	14
	2	3	24	0	23
	3	0	9	0	8
E	1	0	26	0	27
	2	0	7	0	18
	3	0	21	0	16

upper transparent sides. No significant difference, however, exists between the number of polyps which settled upside-down on the lower dark and on the lower transparent surfaces. This experiment indicates that 6.1–9.2% of the initial number of planulae survived in the various aquaria.

DISCUSSION

The findings of the present study suggest that the planulae of *Xenia macrospiculata* and *Parerythropodium f. fulvum* possess distinct settling preferences. These larvae are devoid of an exploiting pelagic phase and upon leaving the parent colony they immediately descend to the bottom (Benayahu & Loya, 1983, 1984b). Their dispersal is determined prior to the final attachment, while the larvae search for a suitable substratum. The planulae of the two species secrete mucus which is employed both for their temporary attachment and permanent settlement. Hughes (1977) pointed out that mucus secretion by the hydroid planulae *Nemertesia antennina* supports dispersal by water currents. Larvae of *Xenia macrospiculata* and *Parerythropodium f. fulvum*, however, utilize mucus only for crawling and attachment (Benayahu, 1982). The possible significance of the mucus during planular clump-formation was noted by Williams (1976). Similarly, we have observed settlement of planulae in aggregations, collectively embedded in mucus.

Several studies point out that substratum roughness and its texture are among the major cues determining the final site of larval attachment (Théodor, 1967; Lewis, 1974; Brewer, 1976a). The present work indicates that only a negligible percentage of planulae settled on the available smooth surfaces (Petri dishes or aquaria glass) whereas, most of the planulae attached to rough coral fragments either organic or inorganic. Similar settling preferences of the two studied species were observed in the field, where juveniles were always located on coarse substrata (Benayahu, 1982).

Planulae of *Xenia macrospiculata* and *Parerythropodium f. fulvum* preferentially settled on surfaces covered with organic coating (Tables I, II). This is a common feature found among other coral species (Gohar, 1940; Harrigan, 1972; Harriot, 1983; Sebens, 1983a,b). Müller (1973a,b) noted that metamorphosis of planulae is induced by the presence of an organic film. In addition, the larvae are capable of displaying searching activity until they are presented with a specific chemical cue, which triggers their fixation and metamorphosis (Müller *et al.*, 1976). Planulae of *Xenia macrospiculata* and *Parerythropodium f. fulvum*, which were kept in filtered sea water without any substrata, did not settle, failed to metamorphose and finally died (Benayahu, 1982). We therefore conclude that both rough surfaces and organic coating are crucial for inducing settlement and metamorphosis of these species.

Substratum position and light intensity determine the site of settlement and development of some octocoral larvae (Weinberg, 1979; Sebens, 1983a, b). Planulae of the soft coral *Alcyonium siderium* settle on exposed vertical substrata and fail to metamorphose in the dark (Sebens, 1983a, b). Our results clearly indicate that attachment on undersides of surfaces (lower sides of the experimental substrata) is a remarkable settling feature of *Xenia macrospiculata* and *Parerythropodium f. fulvum* (Tables IV, VI, VII, VIII). It should be noted that this characteristic is much more pronounced among polyps of the latter than in the former. This is the first experimental evidence demonstrating such settlement among octocorals. Field surveys indicate that juveniles of some hermatypic corals exhibit such attachment (Birkeland *et al.*, 1981; Neudecker, 1981; Wallace & Bull, 1981). These studies claim that as depth increased, successful recruitment is shifted from lower to upper surfaces, a process which depends on light intensity. Our results indicate that light does not necessarily determine the settlement sites (Tables VII, VIII). This conclusion is also reinforced by field experiments (Benayahu & Loya, in prep.), indicating that cryptic larval behaviour and attachment of *Xenia macrospiculata* and *Parerythropodium f. fulvum* on overhanging substrata are found along a wide depth gradient (1–40 m).

Settlement on undersides of surfaces may decrease juvenile mortality, due to abiotic factors, such as low tides, wave surge or siltation (see also Cargo, 1979). In addition, these sites are subjected less to grazing or nibbling than exposed reef areas and, therefore, a higher polyp survival is maintained. Some crustose coralline algae are appropriate sites for the settlement of *Alcyonium siderium* (Sebens, 1983a,b). This type of substratum is the major living component on overhanging substrata in Eilat, covering 80-90% of these surfaces. We further suggest that planulae are "better off" in attaching to underside surfaces than to exposed areas, where competition for space is lower. With the size increase of juveniles, colonies of *Parerythropodium f. fulvum* and *Xenia macrospiculata* orientate themselves towards exposed sites (Benayahu & Loya, in prep.).

Previous studies (Brewer, 1976a,b) demonstrated upside-down orientation of scyphozoan planulae as a possible consequence of levels of carbon dioxide. Our study indicates that upside-down polyp development on undersides of substrata is characteristic of the two alcyonaceans studied. This peculiar settlement is dominant in *Parerythropodium f. fulvum* (Tables VI, VIII) while juveniles of *Xenia macrospiculata* settled also right side up on both sides of the substrata (see p. 254 and Table VII). These differences between the two species agree well with field observations demonstrating that young polyps of the former are found only attached upside-down on overhanging substrata, while juveniles of the latter also utilize exposed surfaces (Benayahu, 1982). We therefore conclude that *X. macrospiculata* is able to utilize a wider range of habitats than *Parerythropodium f. fulvum*. This feature enables spatial segregation between the two species and hence limited space is efficiently utilized by both soft corals.

The findings reported here indicate that larvae of these two species are selective in their settling preferences. Their short pelagic phase, immediate attachment and rapid metamorphosis into the polyp stage (Benayahu & Loya, 1983, 1984b), play a major rôle in determining their distributional patterns. These features require searching capabilities for a substratum, which finally cause settlement on favourable surfaces. Such substratum selection may increase the likelihood for successful colony development and higher survival.

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REFERENCES

BENAYAHU, Y., 1982. Population dynamics of soft corals (Octocorallia, Alcyonacea) at the coral reefs of the Gulf of Eilat. Ph.D. thesis, Tel Aviv University, Israel, 212 pp. (in Hebrew, with English summary).

BENAYAHU, Y. & Y. LOYA, 1977. Space partitioning by stony corals, soft corals and benthic algae on the coral reefs of the northern Gulf of Eilat (Red Sea). *Helgol. Wiss. Meeresunters.*, Vol. 30, pp. 362–382.

BENAYAHU, Y. & Y. LOYA, 1981. Competition for space among coral-reef sessile organisms at Eilat, Red Sea. *Bull. Mar. Sci.*, Vol. 31, pp. 514–522.

BENAYAHU, Y. & Y. LOYA, 1983. Surface brooding in the Red Sea soft coral *Parerythropodium fulvum fulvum* (Forskål, 1775). *Biol. Bull. (Woods Hole, Mass.)*, Vol. 165, pp. 353–369.

BENAYAHU, Y. & Y. LOYA, 1984a. Life history studies on the Red Sea soft coral *Xenia macrospiculata* Gohar, 1940. I. Annual dynamics of gonadal development. *Biol. Bull. (Woods Hole, Mass.)*, Vol. 166, pp. 32–43.

BENAYAHU, Y. & Y. LOYA, 1984b. Life history studies on the Red Sea soft coral *Xenia macrospiculata* Gohar, 1940. II. Planulae shedding and post larval development. *Biol. Bull. (Woods Hole, Mass.)*, Vol. 166, pp. 44–53.

BIRKELAND, C., D. ROWLEY & R.H. RANDALL, 1981. Coral recruitment patterns at Guam. In, *Proc. 4th Int. Coral Reef Symp.*, edited by E.D. Gomez *et al.*, *Marine Sciences Center, Univ. of the Philippines*, Vol. 2, pp. 339–344.

BREWER, R.H., 1976a. Larval settling behavior in *Cyanea capillata* (Cnidaria: Scyphozoa). *Biol. Bull. (Woods Hole, Mass.)*, Vol. 150, pp. 183–199.

BREWER, R.H., 1976b. Some microenvironmental influence on attachment behavior of the planula of *Cyanea capillata* (Cnidaria: Scyphozoa). In, *Coelenterate ecology and behavior*, edited by G.O. Mackie, Plenum Press, New York, pp. 347–356.

CARGO, D.G., 1979. Observations on the settling behavior of planular larvae of *Chrysaora quinquecirrha*. *Int. J. Invert. Reprod.*, Vol. 1, pp. 279–287.

CHIA, F.S. & L.R. BICKELL, 1977. Mechanisms of larval attachment and the induction of settlement and metamorphosis in coelenterates: a review. In, *Settlement and metamorphosis of marine invertebrate larvae*, edited by F.S. Chia & M.E. Rice, Elsevier/North-Holland Inc., New York, pp. 1–12.

DINESEN, F.D., 1983. Patterns in the distribution of soft corals across the central Great Barrier Reef. *Coral Reefs*, Vol. 1, pp. 229–236.

DONALDSON, S., 1974. Larval settlement of a symbiotic hydroid: specificity and nematocyst responses in planulae of *Proboscidactyla flavicirrata*. *Biol. Bull (Woods Hole, Mass.)*, Vol. 147, pp. 573–585.

DUERDEN, J.E., 1902. Aggregated colonies in madreporarian corals. *Am. Nat.*, Vol. 36, pp. 461–471.

GERRODETTE, T., 1981. Dispersal of the solitary coral *Balanophyllia elegans* by demersal planula larvae. *Ecology*, Vol. 62, pp. 611–619.

GOHAR, H.A.F., 1940. The development of some Xeniidae (Alcyonaria). *Publ. Mar. Biol. Stn. Ghardaqa, Red Sea*, Vol. 3, pp. 27–79.

HADFIELD, M.G., 1977. Metamorphosis in marine molluscan larvae: An analysis of stimulus response. In, *Settlement and metamorphosis of marine invertebrate larvae*, edited by F.S. Chia & M.E. Rice, Elsevier/North-Holland Inc., New York, pp. 165–175.

HARRIGAN, J., 1972. The planula and larva of *Pocillopora damicornis*: lunar periodicity of swarming and substratum selection behavior. Ph.D. thesis, University of Hawaii, 213 pp.

HARRIOT, V.J., 1983. Reproductive seasonality, settlement and post-settlement mortality of *Pocillopora damicornis* (Linnaeus), at Lizard Island, Great Barrier Reef. *Coral Reefs*, Vol. 2, pp. 151–157.

HUGHES, R.G., 1977. Aspects of the biology and life-history of *Nemertesia antennina* (L.) (Hydrozoa: Plumulariidae). *J. Mar. Biol. Assoc. U.K.*, Vol. 57, pp. 641–657.