

# Long-term recruitment of soft-corals (Octocorallia: Alcyonacea) on artificial substrata at Eilat (Red Sea)

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**ABSTRACT:** Recruitment of soft corals (Octocorallia: Alcyonacea) on concrete plates was studied in the reefs of the Nature Reserve of Eilat at depths of 17 to 29 m over 12 yr. *Xenia macrospiculata* was the pioneering species, appearing on the vast majority of the plates before any other spat. This species remained the most conspicuous inhabitant of the substrata throughout the whole study. Approximately 10 % of the plates were very extensively colonized by *X. macrospiculata*, resembling the percentage of living coverage by the species in the surrounding reef, thus suggesting that during the study *X. macrospiculata* populations reached their maximal potential to capture the newly available substrata. The successive appearance of an additional 11 soft coral species was recorded. The species composition of the recruits and their abundance corresponded with the soft coral community in the natural reef, indicating that the established spat were progeny of the local populations. Soft coral recruits utilized the edges and lower surfaces of the plates most successfully, rather than the exposed upper surfaces. Such preferential settling of alcyonaceans allows the spat to escape from unfavourable conditions and maintains their high survival in the established community.

## INTRODUCTION

Studies on processes and dynamics of reef benthic organisms are concerned mainly with hermatypic corals. A variety of biological and ecological aspects have been examined on their recruitment (Loya 1976, Birke-land et al. 1981, Colgan 1981, Neudecker 1981, Pearson 1981, Wallace & Bull 1981, Coles 1984, Rogers et al. 1984, Sakai & Yamazato 1984, Baggett & Bright 1985, Fitzhardinge 1985, Harriott 1985, Hughes 1985, Sammarco 1985, Wallace 1985). Strikingly, studies dealing with such features among soft corals (Octocorallia: Alcyonacea) are sparse. Most of the current information on their recruitment capabilities is derived from more general reef surveys (Schuhmacher 1974, Bouchon et al. 1981; see Pearson 1981 for further references).

It has been shown that some soft corals are capable of translocation and are therefore able to quickly take over reef substrata (Benayahu & Loya 1981, 1985, La Barre & Coll 1982, Dinesen 1985). However, quantitative data concerning formation of soft coral communities on newly available substrata is practically lacking. Such information is of primary importance to

determine the role played by alcyonaceans in the course of reef colonization and in the reef's space allocation.

In the present study, we followed recruitment of soft corals on artificial substrata in Eilat reefs over a 12 yr period. This is the first long-term quantitative account which deals exclusively with settling patterns of reef alcyonaceans and formation of their assemblages.

## MATERIALS AND METHODS

To study recruitment of soft corals we set out 90 concrete plates, each with a surface of  $50 \times 50$  cm ( $2500 \text{ cm}^2$  on each side) and 4 cm thick. The plates were laid down on the reef of Eilat Nature Reserve, Israel, in August 1973, at depths from 17 to 29 m. This area has a well-developed reef with high diversity of stony corals (Loya 1972) and rich assemblages of soft corals (Benayahu 1982). The plates were set out from the R/V *Arnona* of the Marine Biological Laboratory of Eilat, at a site marked by floats. To avoid sand coverage, SCUBA divers positioned the plates obliquely onto hard natural substrata. Each plate was marked by

a numbered tag, attached to a neighbouring reef projection.

During the first 2.5 yr after exposure of the plates to settlement (August 1973 to February 1976), recruitment was recorded every 3 mo. Thereafter, for the following 5 yr (until Feb 1981), the plates were examined every 2 to 5 mo. The abundance and identity of all species on each plate were recorded using SCUBA equipment. In addition, the orientation of the recruits on the plates was routinely documented, indicating whether attachment took place on the exposed upper surface, or on the edges of each plate. All recruits except for *Xenia macrospiculata* spat were individually marked by piercing wired tags through the colonies. Settlement on the lower side of the plates was documented in February 1980. For this purpose each plate was carefully removed from its position, searched by SCUBA divers for hidden spat, then replaced in its original site and position. An additional survey of the plates was carried

out in August 1985, 12 yr after the initiation of the experiment. Since most of the tags were lost over the years, this final examination only yielded information regarding the total species composition and abundance on the 90 plates.

## RESULTS

During the first months following the initiation of the study, a low and sparse algal coverage was established on the plates. Among the alcyonaceans, colonies of *Xenia macrospiculata* Gohar were the pioneering recruits. *X. macrospiculata* colonies were already recorded on some plates within the first weeks after initiation of the study. On the vast majority of the plates *X. macrospiculata* appeared before any scleractinian spat (Loya unpubl. data). This species remained the most conspicuous inhabitant on the plates throughout the study. The initial rapid recruitment of *X. macro-*

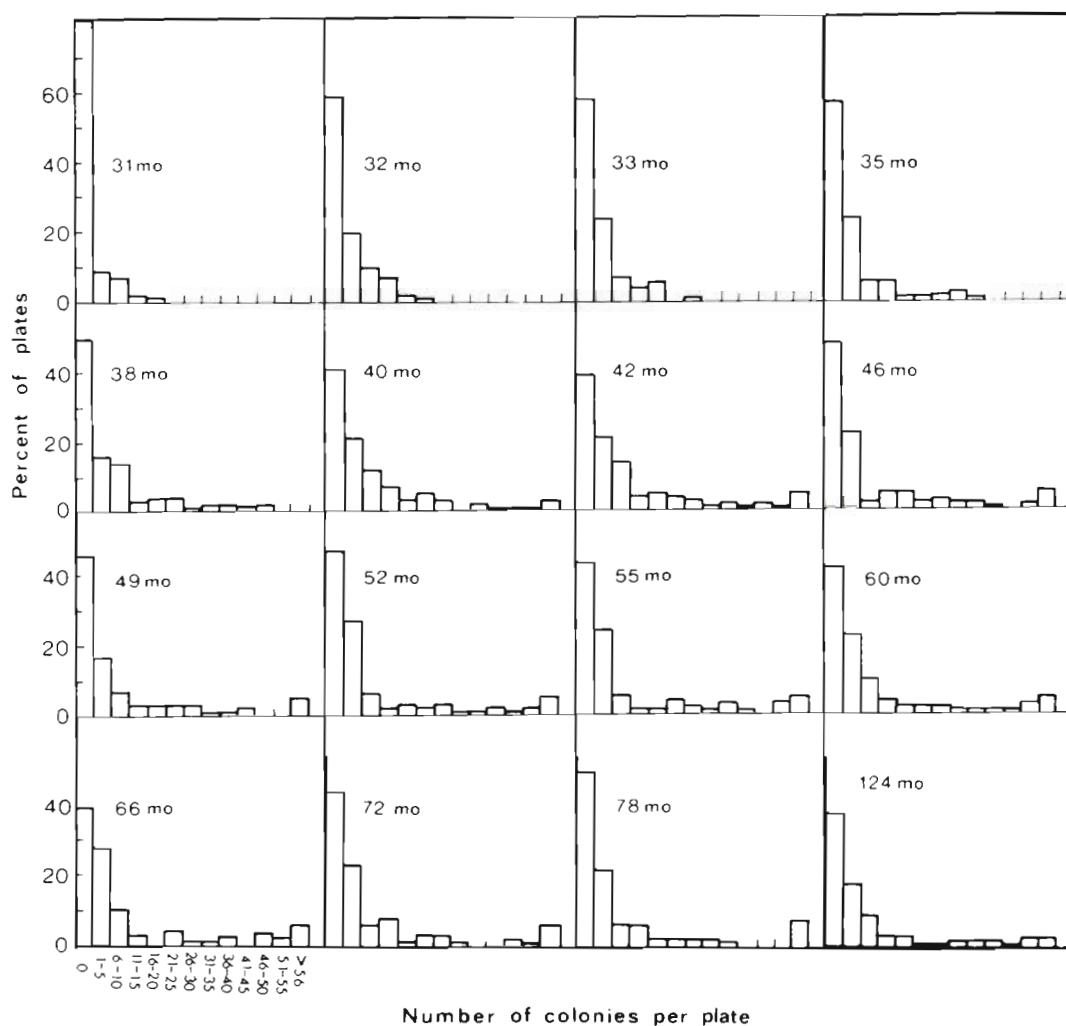


Fig. 1. *Xenia macrospiculata* settlement on 90 concrete plates at Eilat reef. Time from initiation of the experiment is indicated beside each histogram

*spiculata* colonies was a result of translocation from adjacent natural substrates onto the experimental plates (Benayahu & Loya 1985). As time progressed, further translocation took place and asexual colony fission of these recruits gradually increased their density (Benayahu & Loya 1985). Sexual spat of *X. macrospiculata*, which developed from planulae, were also recorded on the experimental surfaces (see below).

Fig. 1 presents the relative percentage of plates settled by various densities of *Xenia macrospiculata* throughout the study. Observations after 31 mo indicated rather low *X. macrospiculata* densities. However, Fig. 1 demonstrates the successive increase of *X. macrospiculata* abundance with time coupled with the decreasing number of non-colonized plates. Note that 31 mo after the initiation of the experiment 80 % of the

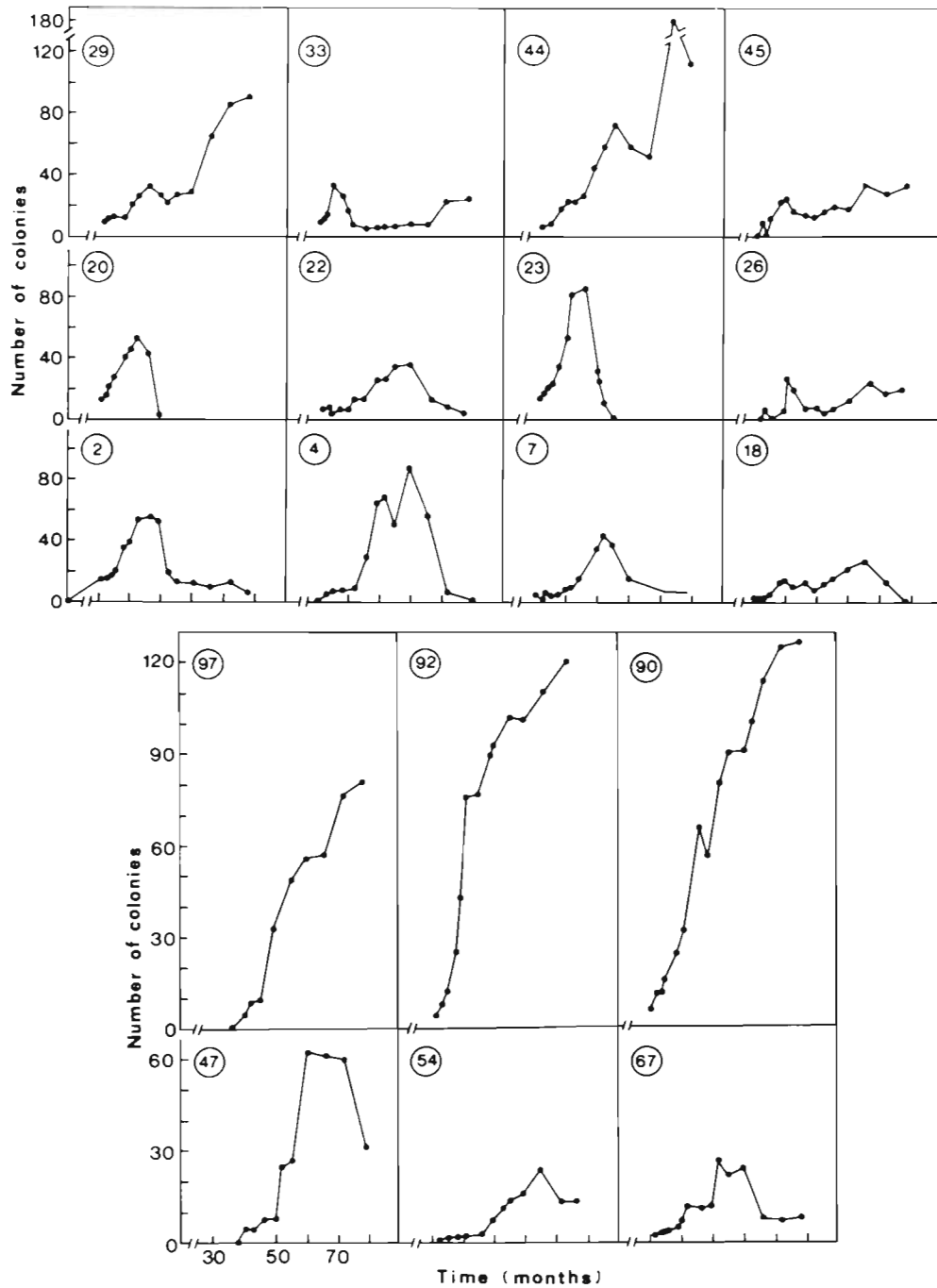


Fig. 2. *Xenia macrospiculata* population dynamics on 18 highly populated plates. Circled numbers represent the tag number of the plate

substrates lack any *X. macrospiculata* spat. The last census, carried out 12 yr after the experimental set up, demonstrated that 40 % of the plates were free of *X. macrospiculata*. Remarkable densities of *X. macrospiculata* were recorded on several substrates (Fig. 1: >56 colonies per plate). These particular plates were monopolized by *X. macrospiculata*, with a 80 to 100 % coverage of their exposed surface area.

Dynamics of recruitment on the 18 most densely populated plates is presented in Fig. 2. High *Xenia macrospiculata* coverage on the upper surface (Fig. 3a) and edges of the plates (Fig. 4a) occurred on plates with more than 100 colonies. On some substrata (e.g. Nos 90, 92, 97) a rapid increase in density was recorded. Density fluctuations of *X. macrospiculata* with time were observed on some other plates (e.g. Nos 26, 33, 45). Another pattern observed was a gradual increase in density, followed by a steep decline (e.g. Nos 18, 20, 23). These patterns are affected by settlement and mortality of the spat and thus represent net recruitment (see 'Discussion').

Recruitment of *Xenia macrospiculata* far exceeded that of any other species (Fig. 3a). Nevertheless, several additional soft coral species settled on the plates. A total number of 69 octocoral colonies (excluding *X.*

Table 1. Abundance of octocorals other than *Xenia macrospiculata* on the settling plates 12 yr after initiation of the experiment (n = 69)

Species rank	Species	% Abundance
1	<i>Parerythropodium fulvum fulvum</i> (Forskål)	33
2	<i>Paralemnalia thyrsoides</i> (Ehrenberg)	13
3	<i>Sarcophyton glaucum</i> (Quoy & Gaimard)	12
4	<i>Litophyton arboreum</i> (Forskål)	12
5	<i>Heteroxenia fuscescens</i> (Ehrenburg)	9
6	<i>Dendronephthya hartmeyer</i> (Kükenthal)	7
7	<i>Stereonephthya cundabuluensis</i> Verseveldt	6
8	<i>Tubipora musica</i> Linneus	3
9	<i>Anthelia glauca</i> Lamarck	3
10	<i>Nephthea chabrolii</i> Audouin	1
11	<i>Sinularia</i> sp.	1

*macrospiculata* spat) were recorded 12 yr after the initiation of the survey (Table 1). The first 5 ranked species (Table 1) comprised 79 % of the spat. The abundance of the remaining species was rather low. The first recruits of *Parerythropodium fulvum fulvum* appeared during the third year of the study. They exhibited a rapid growth rate, forming colonies with approximately 30 cm<sup>2</sup> surface area within 1 yr. Recruits of *Paralemnalia thyrsoides* settled in a contagious pattern and propagated asexually by colony fission. Small aggregates of *Sarcophyton glaucum* and *Litophyton arboreum* were also established. *Heteroxenia fuscescens* colonies were individually located on some plates (Fig. 3b).

Most of the recruitment took place along the edges of the plates (Table 2; Fig. 3b & 4a). This settlement pattern is noteworthy, since the surface area of the edges is more than 3 times smaller than the available upper-plate surface (see 'Materials and Methods'). Most of the xeniid juveniles (sexual recruits) were recorded on the lower surfaces of the plates (Fig. 4b) and rarely on their edges (Fig. 4c). Hardly any juveniles were found on the upper surfaces. Colonies attached to the lower surface of the plates gradually moved, as they grew in size, to the exposed surfaces of the plates.

Table 2. Distribution of recruits on various surfaces of the experimental plates

Species	Percentage of recruits		
	Edges	Upper sides	Lower sides
<i>Xenia macrospiculata</i>	59	28	13
<i>Parerythropodium fulvum fulvum</i>	84	4	12
Other soft corals	58	16	26

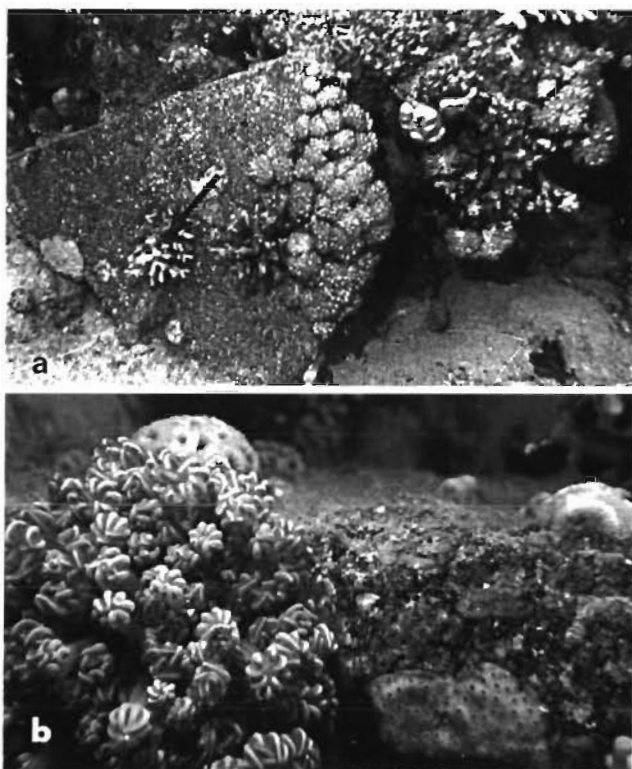


Fig. 3. (a) *Xenia macrospiculata* settlement on an experimental plate. Arrow indicates a living colony of the scleractinian coral *Stylophora pistillata*. (b) *Heteroxenia fuscescens*: mature colony growing on an edge of a plate ( $\times 0.5$ )



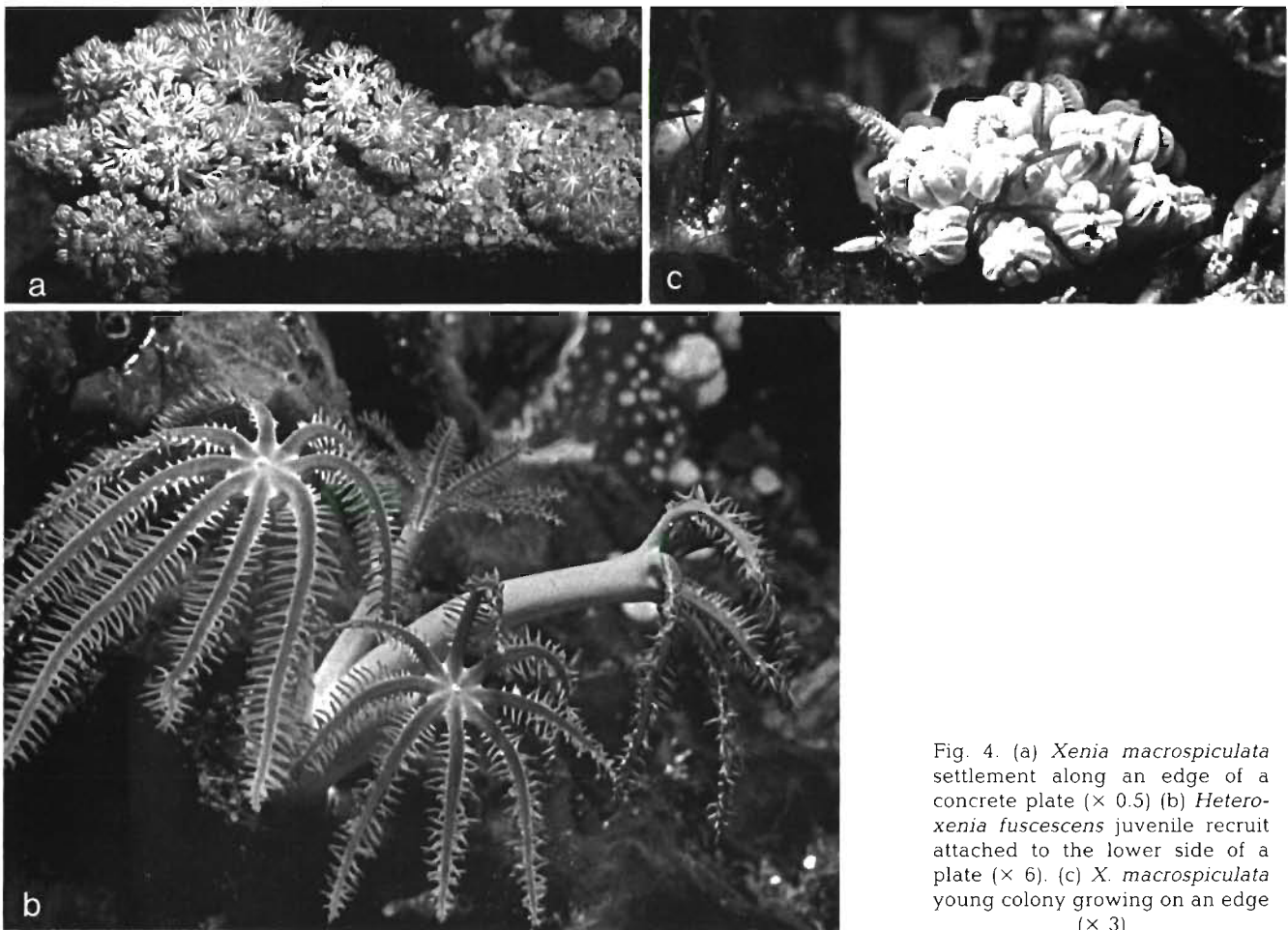


Fig. 4. (a) *Xenia macrospiculata* settlement along an edge of a concrete plate ( $\times 0.5$ ) (b) *Heteroxenia fuscescens* juvenile recruit attached to the lower side of a plate ( $\times 6$ ). (c) *X. macrospiculata* young colony growing on an edge ( $\times 3$ )

Juveniles of *Parerythropodium fulvum fulvum*, composed of a few polyps each, were most commonly attached to the edges. Through further growth, these colonies tended to cover the upper plate area. Upside-down attachment on lower surfaces of the plates was recorded along the whole depth gradient (17 to 29 m).

## DISCUSSION

The present study indicated that colonization of the newly exposed plates led to formation of alcyonacean assemblages predominated by *Xenia macrospiculata*. *X. macrospiculata* colonies were recorded prior to any scleractinian corals, indicating their pioneering colonization capability. Recruitment and space occupation are strongly affected by presence of propagules. Planulae of *X. macrospiculata* are available annually during the breeding season, which is restricted to a certain period of the year (Benayahu 1982, Benayahu & Loya 1984). However, in addition to sexual recruitment, *X. macrospiculata* exhibits rapid space acquisition all

year round, by translocation of colonies and asexual propagation (Benayahu & Loya 1985).

The study area at the reef of the Eilat Nature Reserve has a diverse scleractinian community with a high live cover (Loya 1972) leading to extensive competition for space in this area (Abelson unpubl. data). Therefore, the persistent increase in abundance of *Xenia macrospiculata* on the plates (Fig. 1) emphasizes the vigorous competitive capabilities of this species (Benayahu & Loya 1985). The densities of *X. macrospiculata* observed in the study reveal net recruitment. Factors positively affecting this recruitment include high fecundity, prolonged period of planulation and early onset of reproduction (Benayahu & Loya 1985). These characteristics, together with the afore-mentioned colony fission and translocation, account for the flourishing of *X. macrospiculata* on the plates. Decline of the recruits' density has been caused by occasional translocation of *X. macrospiculata* colonies from the experimental plates to neighbouring natural substrates (Benayahu & Loya 1985). Some mortality due to smothering by sediment, mainly affecting juvenile

recruits, may also occur (Grigg 1977). Neither competitive exclusion by other recruits nor predation destroyed the established spat of *X. macrospiculata*. Variation in recruitment of *X. macrospiculata* on the experimental plates (Fig. 2) may be affected by spatial differences in larval abundance and dispersal. Variable distribution of the recruits may reflect a differential survivorship among the plates, most probably caused by grazing or sedimentation as suggested by Fitzhardinge (1985) for scleractinian corals. Wallace (1985) found that differences in recruitment of stony corals is a result of small-scale location effects. The recruitment patterns obtained in this study (Fig. 1 & 2) supply additional evidence for this effect in processes involved in reef colonization.

Approximately 10% of the plates were extensively colonized by *Xenia macrospiculata* (Fig. 1 & 2), a value which closely resembles the percentage living coverage of *X. macrospiculata* on the surrounding reef (Benayahu 1982). We therefore suggest that during the 12 yr of study, *X. macrospiculata* reached its maximal potential in utilizing the plates. We propose that during this long period an equilibrium was established between the *X. macrospiculata* spat on the experimental plates and on natural reef substrata.

The natural soft coral community in the study area is composed mainly of *Xenia macrospiculata* along with some other species such as *Parerythropodium fulvum fulvum*, *Paralemnalia thyrsoidea*, *Sarcophyton glaucum* and *Litophyton arboreum* (Benayahu 1982). Alcyonacean species composition and abundance on the plates (Table 1) resemble the community features of the neighbouring natural reef. This similarity strongly suggests that most of the recruits were progeny of the local populations. The planktonic phase of planulae of *X. macrospiculata* and *P. f. fulvum* is less than 2 d (Benayahu & Loya 1984). Additional evidence indicates that such a short pelagic phase is widespread also among other alcyonaceans (Benayahu 1982, Benayahu unpubl.). Such a dispersal pattern of planulae enhances patchy distribution of species and localizes the potential for recruitment to particular reef areas. In a space-limited environment this may be beneficial, even for corals with low fecundity, since the larvae are already in an appropriate habitat type (Sebens 1983). In addition, the close resemblance between recruitment (Table 1) and soft coral abundance on the natural reef suggest that post-recruitment events (Harriott 1985) play only a minor role in determining alcyonacean abundance. This does not exclude the possibility of the future appearance of some rare species on the plates. However, these additional species will not cause any dramatic changes in the characteristics of the established soft coral assemblages (see also Hughes 1985).

The massive recruitment on the edges of the plates

(Table 2; Fig. 3b & 4a) indicates a remarkable settling preference. This settling preference was related by Foster (1975) to water flow patterns. Turbulent eddies result from flow separation associated with water movement over edges. Low water speed in these eddies may enhance larval settlement and higher survival of adults (Foster 1975).

Settlement of soft corals on the lower-side of the plates (Table 2; Fig. 4b) fits well with previous laboratory studies, indicating that planulae of *Xenia macrospiculata* and *Parerythropodium fulvum fulvum* are endowed with upside-down settling behaviour (Benayahu & Loya 1984). Higher rate of recruitment of planula larvae on undersurfaces or on vertical substrates, rather than on exposed horizontal areas, has been pointed out in many studies (Birkeland 1977, Bak & Engel 1979, Birkeland et al. 1981, Neudecker 1981, Wallace & Bull 1981, Sebens 1983). Such patterns are interpreted as a response to light intensity, algal turf development, grazing pressure and sediment accumulation (Rogers et al. 1984). A consensus emerges from the literature that with increased depth (lower light intensities), orientation of recruits shifts from vertical to mostly upper horizontal positions. Planulae of *X. macrospiculata* and *P. f. fulvum* exhibit a remarkable upside-down settlement even in shallow reefs (Benayahu & Loya 1984). In view of these results and the findings of the current study (Table 2), we propose that soft coral juveniles most successfully utilize overhanging substrates or their edges rather than exposed upper horizontal areas.

Previous studies dealing with recovery of reefs and their recolonization by alcyonaceans demonstrated some of the soft coral capabilities of colonizing various substrata (Pearson 1981). Colonization of space is eventually determined by life-history strategies of the species, coupled with various abiotic determinants. Further long-term surveys dealing with such issues will elucidate the role undertaken by reef soft corals and the particular factors governing their successful recruitment.

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