Settlement and recruitment of a soft coral: why is Xenia macrospiculata a successful colonizer?

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SETTLEMENT AND RECRUITMENT OF A SOFT CORAL: WHY IS *XENIA MACROSPICULATA* A SUCCESSFUL COLONIZER?

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ABSTRACT

Rapid recruitment in the Red Sea soft coral, *Xenia macrospiculata* Gohar, 1940, depends largely on both its ability to migrate and its asexual reproduction. Colonization of artificial substrates and experimentally-denuded natural surfaces by this species takes place all year round. The migratory behavior of *X. macrospiculata* was detected as translocation of a wide size range of colonies from densely populated patches towards vacant neighboring spaces. The most intense colonization occurrs in the shallow reef (3–5 m), while in the deep zone (27–30 m) recruitment rate is lower. The migratory nature of *X. macrospiculata* enhances dispersion and enlarges the area of its aggregations. Furthermore, *X. macrospiculata* multiplies asexually by colony fission, facilitating dispersal and colonization capacity of this coral. Fission results in not only an increase of population density but also the regulation of colony size.

Colonization and space dominance exhibited by *X. macrospiculata* are largely due to vegetative processes. These features coupled with high fecundity, prolonged period of planulation and an early onset of reproduction, suggest that among Red Sea soft corals, *X. macrospiculata*, is situated on the "r" end point of an r–K continuum. Nevertheless, this species deviates from a "typical" r-strategist by displaying high competitive ability, which reinforces its success in maintaining high population density.

Flourishing of soft corals (Octocorallia: Alcyonacea) at many Indo-Pacific reef sites and their marked ability to colonize substrates has been noted in several studies (Bayer, 1973; Endean, 1976; Pearson, 1981). Their success in space occupation has been attributed to their ability to overgrow adjacent organisms (Fishelson, 1970; Sheppard, 1979; Benayahu and Loya, 1977; 1981). In addition, the competitive ability of soft corals is enhanced by their toxic and allelopathic features (Bakus, 1981; Coll et al., 1982a; 1982b; Tursch and Tursch, 1982; Sammarco et al., 1983). Recent studies indicated that the alcyonaceans *Xenia macrospiculata* Gohar, 1940 and *Nephthea brassica* Kükenthal, 1904, are capable of translocation and therefore, able to quickly capture reef substrates (Benayahu and Loya, 1981; La Barre and Coll, 1982).

Among the soft corals of the Gulf of Eilat, *X. macrospiculata* is very abundant and forms large beds which monopolize space in numerous localities (Benayahu and Loya, 1981; Mergner and Schuhmacher, 1981). The present study is concerned with the colonization rate of *X. macrospiculata* on artificial substrates in shallow water (3–5 m) and in a deeper reef zone (27–30 m). It also deals with the recruitment of denuded natural surfaces by this alcyonacean. A newly described mode of asexual colony fission among the xeniids is described. This survey points out the significance of the migratory ability and asexual propagation in *X. macrospiculata* in increasing its competitive features and population size. It is concluded that the two vegetative mechanisms serve as major means for rapid colonization and cause the successful dispersion of *X. macrospiculata* on the reef.

MATERIALS AND METHODS

The study was conducted at two reef sites in the northern Gulf of Eilat. The shallow water experiments (3–5 m) were carried out at Muqebla', 12 km south of Eilat. The reef of the Nature Reserve of Eilat

(27–30 m) was selected to carry out the deep water study. Among the xeniids in both reefs, *X. macrospiculata* is the most abundant species (Benayahu and Loya, 1981; Benayahu, 1982).

Settlement plates were made of pieces of PVC measuring 5.0 × 7.5 cm by 1.5 mm thick. Plates were uniformly roughened with coarse sandpaper. Every five plates were linked together, with thin plastic-coated wires, forming chains (Fig. 1a). The distance between two adjacent plates was 5 cm. The two terminal plates of the chain were wired to hard reef projections.

Every 2 months, for a period of 1 year, five series of three chain-plates were placed in the shallow reef of Muqebla' and in the deep reef of the Nature Reserve (Table 1). One chain from each series was anchored within a patch of *X. macrospiculata,* where its living coverage approximated 70–100% of the surface. A second chain was mounted near the margins of such an area, where the PVC plates did not touch the *Xenia* colonies. The third chain was fixed to a substrate lacking any colonies of *Xenia,* and located 1 m from the nearest *Xenia* patch (Table 1). Plates were monitored monthly for the first year and then every few months. The shallow reef plates were exposed for 1,000–1,150 days (33–38 months) and the deep water plates for 900–1,150 days (30–38 months). Each time, the colonies on the plates were counted, and the largest diameter of the uppermost part of the colony was measured. A similar method was applied in order to determine size of other living soft-bodied coelenterates, such as sea anemones (Sebens, 1981). The measurements were made with a caliper with an accuracy of 1 mm.

At Muqebla' 16 experimental surfaces were selected within patches of *X. macrospiculata.* A metal frame measuring 25 × 25 cm was tossed at random within each patch and the bordered areas were totally scraped free of soft corals and other benthic organisms. The corners of the denuded quadrats were marked by nails and numbered with plastic tags. From August 1977 and during the following 20 months recruitment was examined monthly. Each time the number of colonies was counted and measured.

RESULTS

Settlement on PVC Substrates.—Observations during the first 2–4 weeks after introducing the PVC plates indicated that chains located within the patches of *X. macrospiculata* were colonized very rapidly. Colonies which grew very close to the experimental plates gradually detached from their substrate and within 5–10 days adhered to the adjacent new surfaces (Fig. 1b). The rapid colonization of the PVC plates was due to the active migration by the neighboring corals onto the plates. This colonization took place throughout the study, resulting in massive settlement on the artificial substrates.

Figure 2 presents the total number of colonies of *X. macrospiculata* recorded throughout the experimental period on the chains mounted within the *Xenia* beds in Muqebla' (3–5 m depth). The number of colonies presented for each stage is the total number of corals counted on all five chains (25 plates) introduced to the reef at a certain date (Table 1). It can be seen that during the first period of colonization, the density of colonies increased rapidly in all the series and maximum density was attained within 300 days. Similar colonization patterns were also recorded on substrates anchored within the deep *Xenia* patches (27–30 m depth) in the Nature Reserve (Fig. 3). A comparison of the average density of *Xenia* on the experimental plates between the shallow and deep series is presented in Figure 4. Each value represents the mean number of colonies counted on the plates *within* the *Xenia* beds during similar recruitment periods. It is evident that the shallow water plates exhibited a significantly higher density throughout the study (*t*-test, $P < 0.05$). The shallow plates were so densely covered by colonies of *X. macrospiculata,* that no space was left between the colonies (Fig. 1c).

Size measurements of the colonies at both localities indicated that throughout the study large recruits of *X. macrospiculata* dominated the plates. The size range of the vast majority of the colonies was 6–50 mm. Colonies measuring less than 5 mm were recorded rarely: they constituted only 1–2% of the total count. It should be noted that very few of the *Xenia* recruits were sexual ones.

The experimental plates located near the margins of the xeniid beds were poorly colonized. Table 2 presents the number of *Xenia* corals found on these chains in

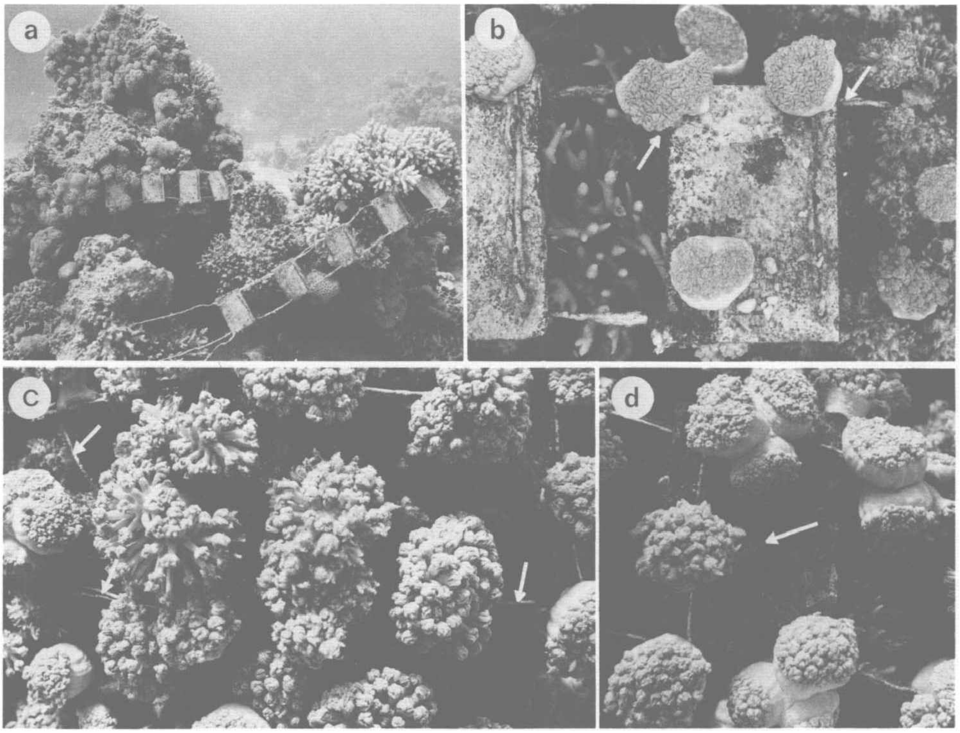

Figure 1. Settlement of *Xenia macrospiculata* on PVC plates: a, chains attached to the reef of Muqebla'; b, first recruits on a plate, arrows indicate the newly settled colonies along its margins; c, dense coverage on the plates, arrows indicate the wires; d, branched colonies on a plate, arrow indicates the plate surface.

the last field record. Recruitment was sparse except for the high colony abundance found on series A_1–A_5. In addition, four colonies of *Parerythropodium fulvum fulvum* (Forskål, 1775) settled on these chains. This is the only other coral that settled on any of the PVC plates throughout the whole study. It should be noted that only a sparse coverage of turf algae developed on the plates located 1 m from the beds.

Recruitment onto Denuded Natural Substrates.—Xeniids were the first recruits to settle on the cleared substrates. Figure 5 demonstrates the dynamics of coloni-

Table 1. Experimental plate series: Dates of placement and identification marks. Each series consisted of 3 chains of 5 linked plates (15 plates per series; 75 plates per date)

Muqebla' (3–5 m)		Nature Reserve (27–30 m)	
Date	Marks of plate series	Date	Marks of plate series
19 Oct 76	A_1–A_5	18 Dec 76	G_1–G_5
13 Dec 76	B_1–B_5	22 Feb 77	H_1–H_5
27 Feb 77	C_1–C_5	19 Apr 77	I_1–I_5
19 Apr 77	D_1–D_5	13 June 77	J_1–J_5
6 June 77	E_1–E_5	8 Aug 77	K_1–K_5
22 Aug 77	F_1–F_5	12 Oct 77	L_1–L_5

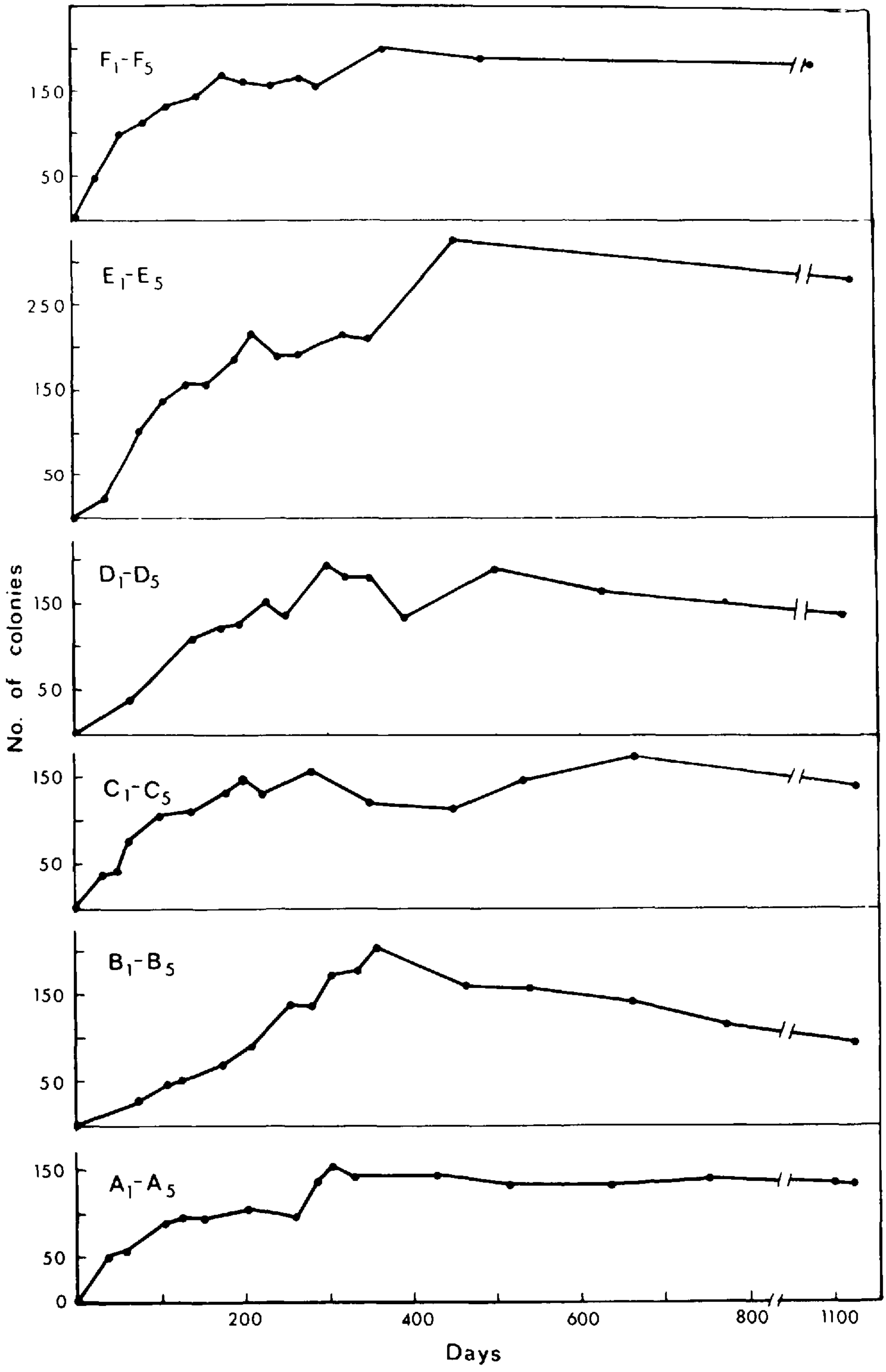

Figure 2. Changes in density of *Xenia macrospiculata* recruited onto PVC plates placed within *Xenia* beds on the reef of Muqebla' (3-5 m).

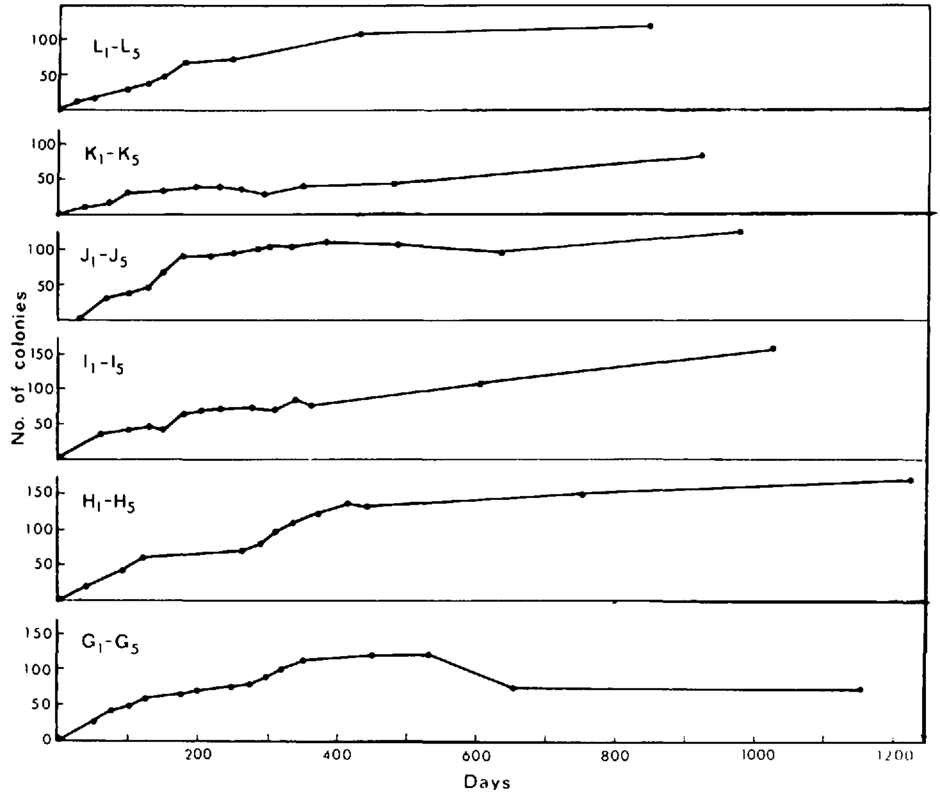

Figure 3. Density of *Xenia macrospiculata* on PVC plates attached within *Xenia* beds in the reef of Eilat Nature Reserve (27–30 m).

zation and changes of abundance of these colonies on each of the 16 quadrats. Although the abundance of the corals varied at the different sites, all the quadrats exhibited an immediate and rapid density increase. After 600 days, the highest recruitment was recorded in quadrats 3 and 10, where 73 and 87 colonies were found respectively (Fig. 5). The number of colonies within a given quadrat fluctuated, but a consistent density increase was recorded. During the first 3–4 months small recruits of *Heteroxenia fuscescens* (Ehrenberg, 1834) dominated the cleared substrates (Fig. 6). These juveniles were composed of 1–4 polyps each and had a diameter of less than 5 mm. Figure 6 also demonstrates that after the fifth month, there was a consistent increase in the relative abundance of large colonies of *X. macrospiculata* and simultaneously a decrease in the number of the *Heteroxenia* colonies. These *Xenia* colonies gradually moved from their densely populated patches into the newly available sites and displaced the former colonizers. In addition, the *X. macrospiculata* recruits reproduced asexually (see below) and thus their density was considerably increased. Few other alcyonaceans were recorded on the cleared areas: three colonies of *Anthelia glauca* Lamarck, 1816, a colony of *Heteroxenia fuscescens* and a young colony of *Parerythropodium fulvum fulvum*. No stony corals settled on the denuded surfaces during the 20 months of the study.

Colony Fission.—Field observations indicated that branched individuals of *X. macrospiculata* (Fig. 1d) reproduce asexually by colony fission. We noted that

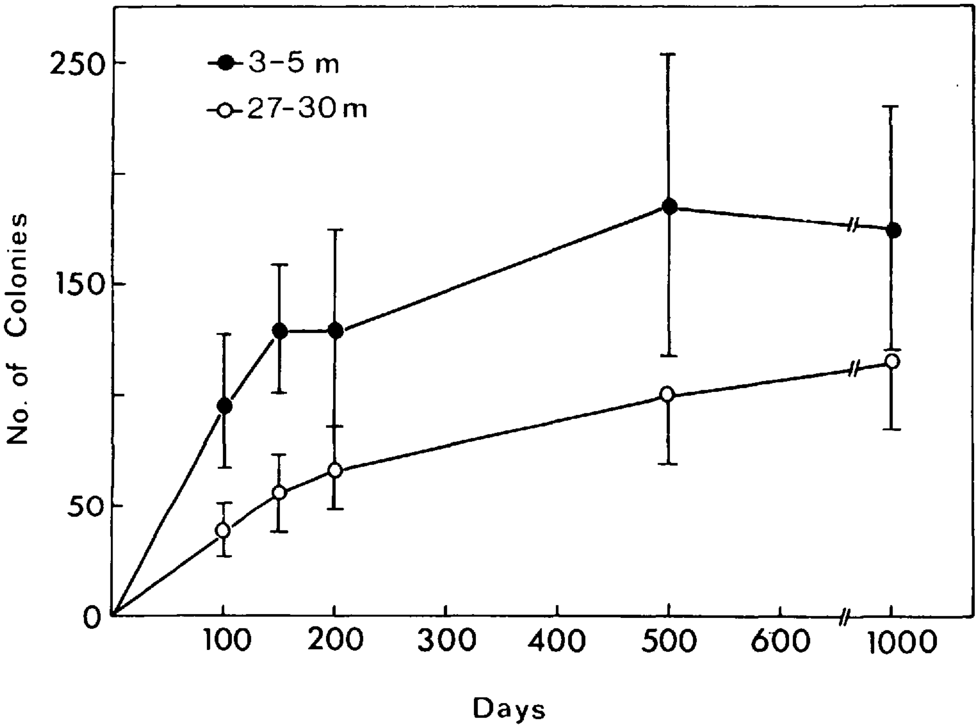

Figure 4. Comparison between the density of *Xenia macrospiculata* on PVC plates within *Xenia* beds at various times throughout the study period.

this process occurred both on the experimental PVC plates and on the natural reef substrate. The process involves gradual splitting away of a branch from the rest of the colony (Fig. 7a, b) and attachment to an adjacent substrate. This process usually takes 10–14 days, resulting in an independent colony located a few cm from its parent (Fig. 7c). This is the first evidence for such a mode of asexual propagation among the Xeniidae.

DISCUSSION

Corals are considered as sedentary organisms whose dispersal is mainly achieved by a free planular stage. Nevertheless, a few scleractinians have adopted a free living existence and have incorporated detachment into their life history (High-

Table 2. Number of colonies of *Xenia macrospiculata* counted on plates placed near the margins of *Xenia* patches during the last observation period

Muqebla' (3–5 m)		Nature Reserve (27–30 m)	
Plate series	Number colonies	Plate series	Number colonies
A_1–A_5	62	G_1–G_5	18
B_1–B_5	2	H_1–H_5	15
C_1–C_5	10	I_1–I_5	8
D_1–D_5	21	J_1–J_5	3
E_1–E_5	3	K_1–K_5	0
F_1–F_5	2	L_1–L_5	0

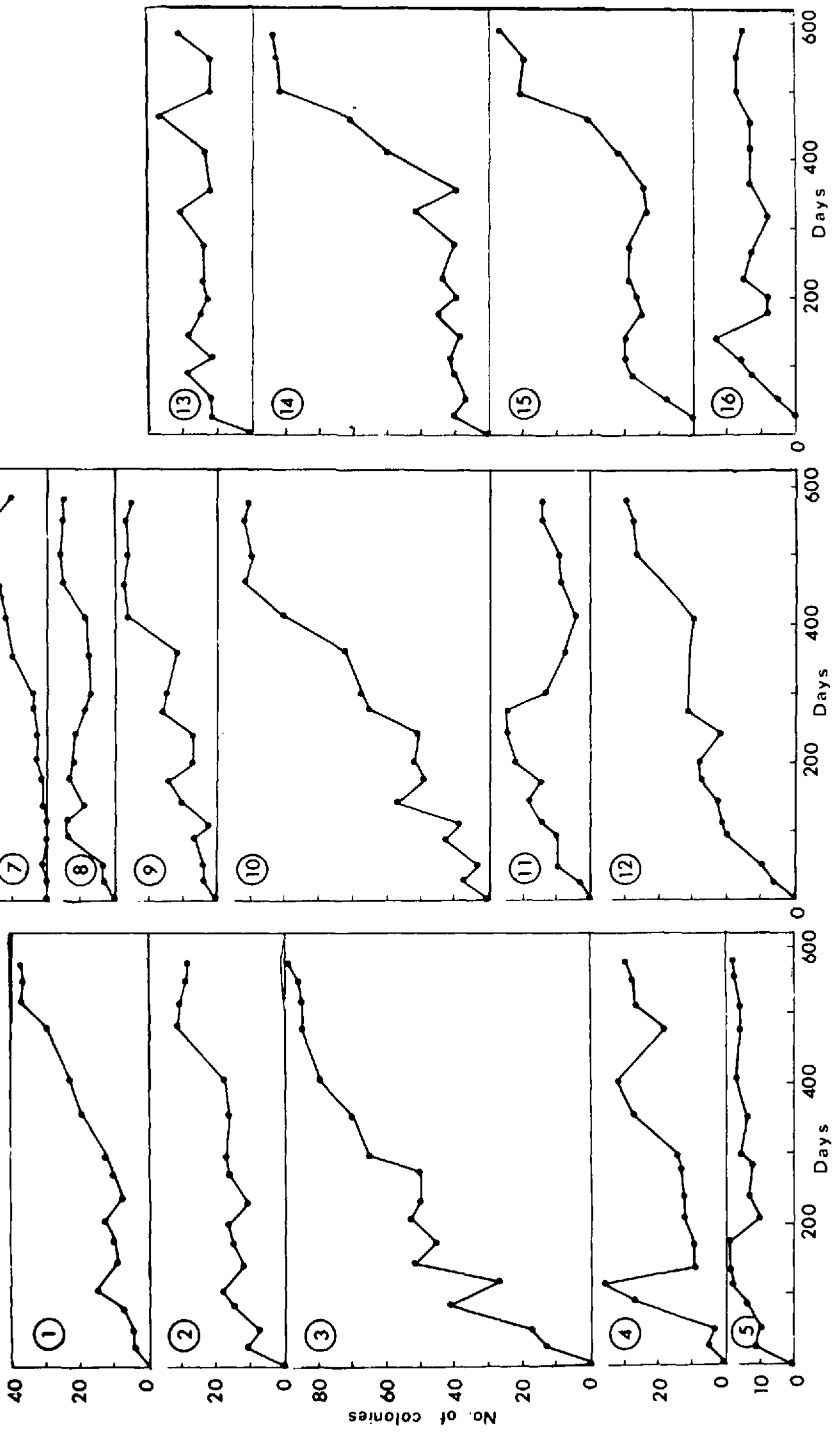

Figure 5. Abundance of xeniid colonies on 16 experimentally-denuded natural substrates.

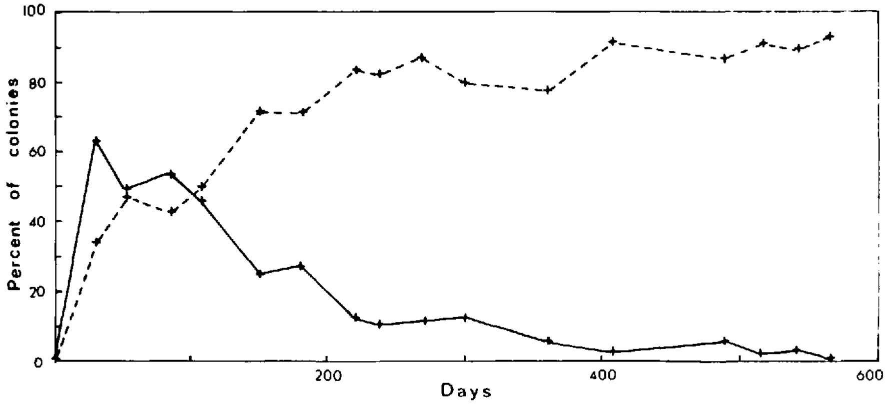

Figure 6. Changes in abundance of *Heteroxenia fuscescens* (solid line) and *Xenia macrospiculata* (dashed line) during recruitment on experimentally denuded substrates.

smith, 1980; Fisk, 1983). Active movement seems to be widespread among some alcyonacean corals (Benayahu and Loya, 1981; La Barre and Coll, 1982). The migratory behavior of *X. macrospiculata* enables the colonies to alter their location throughout their life in a manner which resembles some sea anemones (Robson, 1976; Dunn, 1977). Sebens (1981) pointed out that recruitment of cleared areas by the actinian *Anthopleura xanthogrammica* is due to juvenile migration. The present study indicates that a wide size range of *Xenia* colonies are able to migrate and hence capture space. Presence of vacant space near these colonies stimulates them to gradually detach from their previous place and to simultaneously adhere to adjacent substrates (Benayahu and Loya, 1981). Substrate colonization by *X. macrospiculata* is mainly achieved through active movement (Figs. 2, 3, 5) with colonization occurring faster in the shallow reef than in the deeper one (Fig. 4). This result fits well with a previous report indicating markedly high abundance of *X. macrospiculata* in shallow reefs and its gradual decrease along a depth gradient (Benayahu and Loya, 1981).

The initial appearance of juveniles of *H. fuscescens* on the denuded surfaces (Fig. 6) is most likely due to planular settlement and development. Later the invasion of large colonies of *X. macrospiculata* competitively excluded the young *H. fuscescens* recruits from the experimental surfaces. Destruction of the tiny polyps of *H. fuscescens* was probably due to the poor illumination occurring among the larger *Xenia* invaders. These colonies also eliminated potential space for further development and growth of *Heteroxenia.* To the best of our knowledge this is the first record of such competitive interactions among soft corals.

In the studied reef sites, the *Xenia* beds are composed of numerous colonies in high densities. It was found that a surface area of 25 × 25 cm at Muqebla' (3–5 m), within such a bed contains 57.3 ± 20.4 colonies, whereas at the Eilat Nature Reserve (27–30 m) the average density is 24.6 ± 9.3 colonies per 625 cm^2 (Benayahu, 1982). Asexual propagation coupled with aggregation of newly settled planulae near the parent colonies (Benayahu and Loya, 1984a) cause additional colonization and density increase within the clumps. Hence, space becomes a limiting resource within the beds of *X. macrospiculata,* and the active movement of the colonies towards the vacant peripheries regulates their density. Our observations indicate that the movement of *X. macrospiculata* can take place all year around (Figs. 2, 3), while its annual sexual reproductive period lasts only 4–5 months

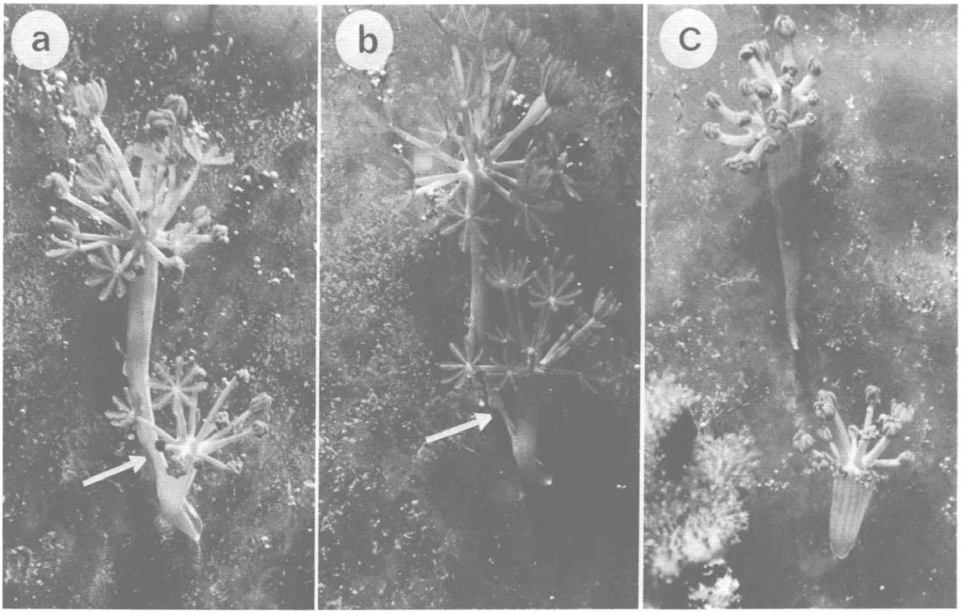

Figure 7. Developmental stages in the asexual reproduction of *Xenia macrospiculata*: a, the connection between two branches of a colony becomes thinner (see arrow); b, an advanced stage of the fission, arrow indicates the thin coenenchymal tissue between the two branches; c, completion of the coral fission resulting in two separate colonies.

(Benayahu and Loya, 1984b; c). The migratory ability of this species allows continuous space occupation. This might explain its dominance on many reef areas.

Most of the studies of soft coral colonization have followed devastation by some catastrophic events (Endean, 1976; Pearson, 1981). Along the Red Sea coast, beds of *X. macrospiculata* are found below 2 m (Benayahu and Loya, 1981) and hence, are not exposed to potentially harmful low tides. However, during seldom southern winter storms, *Xenia* colonies at a depth of 2–8 m may become detached from their substrate. They then spread out on the reef bottom and within a few days may reattach to new hard surfaces. A similar passive dispersal and secondary colonization is exhibited by *Palythoa vestitus* (Cook, 1976) and *Porites lutea* (Highsmith, 1980). We suggest that the ability to resettle increases colony survival and serves as an additional means of dispersal.

The ecological role of asexual reproduction and its significance has been widely reviewed (Williams, 1975; Grassle and Shick, 1979; Charlesworth, 1980). Asexual reproduction is widespread among many coral reef organisms (Grassle, 1973). Asexual reproduction by fragmentation among octocorals, particularly Alcyonacea, is common, but few details of the process are known (Walker and Bull, 1983). Vegetative propagation by runner-like branches was recorded for several nephtheids (Tursch and Tursch, 1982) and for the xeniid *Efflatounaria* (Dinesen, *in* Walker and Bull, 1983). Gohar (1940) described several modes of vegetative propagation exhibited by xeniids, but no mention was made of the mechanism of colony fission, which is described here (Fig. 7). Among soft-bodied anthozoans asexual reproduction has been thoroughly studied in sea anemones (Chia, 1976; Minasian and Mariscal, 1979; Schick et al., 1979). Similarly to sea anemones, the phenomenon of colony fission in *X. macrospiculata* enables it to exhibit features such as: (1) rapid population growth (Minasian, 1976); (2) formation of large aggregations (Francis, 1979); (3) a remarkable ability to colonize vacant space (Shick, 1976; Sebens, 1982) and (4) control of body-size (Sebens, 1980), which can lead into the shifting of the size structure of a *Xenia* population towards smaller colonies (Benayahu and Loya, 1984b). Hence, not all of the small colonies of *X. macrospiculata* are necessarily young. It should be noted that vegetative propagation of colonial organisms complicates the relationship between colony size and its age (Hughes and Jackson, 1980). Further studies are required in order to detect possible seasonality of asexual division of xeniids, the rate of this process, and the nature of cues which regulate it.

Life history characteristics of *X. macrospiculata* include small body size, early onset of reproduction, high fecundity and prolonged planulation period (Benayahu and Loya, 1984b; c). The present study indicates that this species is endowed with the capacity to rapidly exploit space all year round, along a wide depth gradient. All these features suggest that among the Red Sea soft corals *X. macrospiculata* is situated on the "r" end point of an r–K continuum (Pianka, 1970). Nevertheless, *X. macrospiculata* deviates from a "typical" r strategist by exhibiting a distinctive competitive ability leading to space monopolization.

Dominance is regarded by Maguire and Porter (1977) as the best competitive strategy in mature communities that remain undisturbed. Local space dominance is achieved by *X. macrospiculata* in reef zones that are usually devoid of severe environmental disturbances. Although soft corals do not perform extracoelentric digestion when touching other organisms (Sheppard, 1979; Sammarco et al., 1983; Benayahu and Loya, pers. obs.), *X. macrospiculata* is capable of settling on and overgrowing stony corals. Thus, it is able to successfully out-compete them (Benayahu and Loya, 1981). Due to massive colonization achieved mainly by immigration and asexual reproduction, this coral is able to exclude juveniles of other alcyonaceans (Fig. 6). Owing to their toxicity (Coll et al., 1982b), mortality due to predation is negligible in xeniids. Asexual propagation of *X. macrospiculata* renders an individual colony virtually "immortal."

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