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Clonal propagation by the azooxanthellate octocoral *Dendronephthya hemprichi*

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Abstract. The azooxanthellate octocoral *Dendronephthya hemprichi* (Octocorallia, Alcyonacea) is the most abundant benthic organism inhabiting the under-water surfaces of oil jetties at Eilat (Red Sea); however, it is very rare on Eilat's natural reefs. This soft coral exhibits a newly discovered mode of clonal propagation that results in autotomy of small-sized fragments (2–5 mm in length). They possess specialized root-like processes that enable a rapid attachment onto the substrata. An autotomy event is completed within only 2 days; large colonies can bear hundreds of pre-detached fragments. Temporal fluctuations in the percentage of fragment-bearing colonies indicate that autotomy is stimulated by exogenous factors, probably flow-related events. Recruitment of fragments onto PVC plates placed horizontally adjacent to *D. hemprichi* colonies, was immediate and remarkably high. Attached fragments were observed 2 days after placement of plates; after 52 days, densities of more than one recruit per cm^2 were recorded. The negative buoyancy of fragments causes them to land on horizontal surfaces rather than on vertical ones. However, their survivorship on vertical surfaces is much higher. This pattern corresponds with dominance of *D. hemprichi* on vertical substrata at the oil jetties and on natural vertical reefs of the northern Red Sea. Such a mode of clonal propagation provides an efficient mean for genets of *D. hemprichi* to exploit food resources within a zooxanthellate-dominated reef community.

Introduction

The ability to form more than one individual of identical genetic composition is a common feature in the life history of many bottom-dwelling aquatic invertebrates (e.g., Jackson 1977, 1985; Hughes 1989). Such individuals are termed ramets and a genet consists of all ramets that are derived from the same zygote (e.g., Harper 1977; Coates and Jackson 1985; Hughes et al. 1992). Asexual reproduction is the clonal proliferation of individuals by separation of ramets, either at the time of ramet formation or by partial mortality and/or mechanical fragmentation of previously united groups of ramets (Jackson 1985). In most clonal invertebrates the potential number of ramets per genet is unlimited because modular construction generally eliminates surface to volume constraints on overall clonal size (e.g., Jackson 1977). The consequences of producing disjunct modules in terms of spreading the risk of mortality and exploitation of patchily distributed resources have already been discussed in several studies (Cook 1979; McFadden 1986; Hughes and Cancino 1985; Hughes et al. 1992). Clonal organisms are characterized by great morphological flexibility, by the potential to accumulate large biomass, and often by the potential for rapid growth. These characteristics enable the dispersal of clones to opportunistically exploit patches of resources as well as generating large aggregations (Hughes and Cancino 1985). Cloning by somatic division, i.e., budding, fission or fragmentation, occurs among a wide variety of anthozoans, including scleractinian corals (e.g., Highsmith 1982; Harrison and Wallace 1990), zoanthids (Karlson 1988), sea anemones (e.g., Chia 1976), and octocorals (Lasker 1988, 1990). Soft corals (Octocorallia, Alcyonacea) tend to form large monospecific aggregations on coral reefs, composed of numerous colonies, most probably derived by asexual processes (Benayahu and Loya 1977, 1981). Octocorals exhibit a particularly large range of mechanisms of clonal propagation (Lasker 1988). Among the described mechanisms, budding of daughter colonies is found in *Sarcophyton gemmatum* (Verseveldt and Benayahu 1978), fragmentation in *Junceella fragilis* (Walker and Bull 1983), colony fission in *Capnella gaboensis* (Farrant 1987), *Xenia macrospiculata* (Benayahu and Loya 1985), *X. lepida* and *Nephthea cf. cupressiformis*, and the generation of new colonies by stolons in *Efflatounaria sp.* (Lasker 1988; Karlson et al. in press).

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The species examined in this study is the azooxanthellate octocoral *Dendronephthya hemprichi* of the family Nephtheidae, which includes several hundreds of reef-inhabiting species across the Indo-Pacific basin, (see Bayer 1981). *Dendronephthya hemprichi* is abundant on many reefs of the northern Red Sea (Benayahu 1985), where it forms aggregations composed of numerous colonies with a wide array of colors. This species is the most abundant benthic organism inhabiting artificial underwater constructions at Eilat, but is very rare on Eilat's natural reefs. Unlike the vast majority of the coral-reef octocorals, all *Dendronephthya* species are azooxanthellate, i.e., they are not associated with endosymbiotic algae at any stage in their life cycle. However, *D. hemprichi* successfully inhabits reef sites dominated by numerous zooxanthellate species of stony corals, soft corals, zooanthids and sea anemones.

In this work we describe a unique mode of clonal propagation exhibited by *D. hemprichi*, resulting in autotomy of small fragments. The study also examines short- and long-term dynamics of recruited fragments. The consequences and benefits of this mode of propagation for rapid recruitment and space utilization are demonstrated.

Materials and methods

The study was conducted at the oil jetty area, located 4 km south of Eilat (Gulf of Elate, Red Sea) during 1989–1990. The underwater steel jetties were built in the early 1970s and since then have been densely colonized by a diverse benthic community (Goren 1992). *Dendronephthya hemprichi* is the most abundant soft coral at this site (20% cover), growing on the vertical supporting pillars of the jetties and on the surrounding coiled barbed wire.

Numerous colonies were maintained in running sea water at the Marine Biological Laboratory at Eilat for detailed examination of the autotomy process. The fine structure of the fragments was studied by histological sections, following the methodology of Benayahu and Loya (1983). Colonies of *D. hemprichi* (> 20 cm) were monitored monthly in the field during September–December 1990 for the presence of predetached fragments. Surveys were conducted along 6 m line transects on each of four vertical pillars at a depth of 2–8 m. Short- and long-term dynamics of recruited *D. hemprichi* fragments were studied on white PVC plates, measuring 20 × 20 cm by 3 mm thick, placed adjacent to large *D. hemprichi* colonies. The plates were individually tagged and wired to the jetties at depths of 6–15 m. Throughout the study period, recruits appearing on the plates were counted and those > 3 cm in length were measured. Short-term recruitment was examined on 30 plates placed horizontally in September 1990 and monitored 2, 4, 9, 22 and 52 days after placement. Long-term recruitment was studied on 124 plates, which were monitored every 30–40 days for 203 days. Initially, in July 1989, 24 plates were placed horizontally. Later on, in order to examine possible effects of the position and placement date of plates, a set of 5 horizontal and 5 vertical plates were deployed, every 30–40 days, starting in September 1989. The possible contribution of sexual recruitment onto the plates was determined by placement of two additional sets, 20 plates in total, in September and October 1989. They were deployed in areas densely populated by *D. hemprichi*, but with no colonies for a distance of at least 5 m above them. Since the fragments were negatively buoyant (see Results), recruitment onto these 20 plates due to fragmentation was precluded. The deployment dates of new plates in the long-term recruitment study coincided with the monitoring dates of the older ones. In April 1991, all the plates were re-examined for presence of *D. hemprichi* recruits > 3 cm. The ANOVA and paired *t*-tests were conducted after square root transformation.

Results

Features of the fragments

Clonal propagation of *D. hemprichi* is performed by autotomy of fragments, 2–5 mm in length, each composed of several polyps. Autotomy is first observed as a gradual narrowing of the coenenchyme connecting the parent colony and the incipient fragment. Within 20 hours of commencement of the autotomy process, only a thin cord of tissue connects the predetached fragment to the colony (Fig. 1a). At this stage, root-like processes, each approximately 1 mm long, develop at the basal part of the fragment and subsequently the fragment detaches from the colony (Fig. 1b). Laboratory observations indicated that completion of an autotomy process takes only 2 days. After detachment of the fragment, its root-like processes continue to elongate and additional ones may appear. The number of processes per fragment ranges between 2–15, each with a diameter of 200–800 μm. Histological studies indicated that the processes have a central cavity that is continuous with the gastrovascular canals of the fragment. The wall is 7–12 μm in width, composed of an ectoderm rich with nematocysts and separated by a thin mesoglea from the internal ciliated endoderm.

The frequency distribution of detached fragments, in terms of number of polyps per fragment, indicates that most of them are small (Fig. 2). In 84.4% of the fragments ($n = 506$) the number of polyps ranged from only 4 to 12. The fragments were negatively buoyant; their settling velocity, measured in a glass cylinder, was 3.6 ± 0.6 (SD) cm/s ($n = 88$ fragments). Field observations indicated that, while sinking, fragments may drift in water currents to lateral distances of over 60 m away from the parent colony, within several minutes. During this period, if the fragments encountered appropriate solid-substratum, they attach on it.

The fragments rapidly adhere to a variety of artificial and natural substrata (Fig. 1c). Firm attachment is achieved within 5–10 h. During attachment, the fragments rise into an upright position and become vertically oriented on the substratum, anchored by their root-like processes. This position appears to be maintained by hydrostatic pressure within the cavities of the processes. Within 2 weeks of attachment, the root-like processes disappear and the basal part of the small colony remains attached to the substratum.

In a preliminary survey of *D. hemprichi* on the oil jetties at Eilat, predetached fragments were not found on colonies smaller than 5 cm in length. Large colonies (> 20 cm) can bear hundreds of predetached fragments per colony. Figure 3 presents the percentage of colonies (> 20 cm) with predetached fragments as recorded along the four marked transects at the oil jetty on four successive dates of one year. The frequency of fragment-bearing colonies along each of the four transects varied significantly among dates ($R \times C$ test, $df = 3$; $G = 21.34$, $G = 18.63$, $G = 18.4$ and $G = 18.17$ for transects 1–4, respectively, $P < 0.001$ in all cases). No significant heterogeneity existed among transects within each date ($df = 9$, $G = 3.7$, $P > 0.05$).

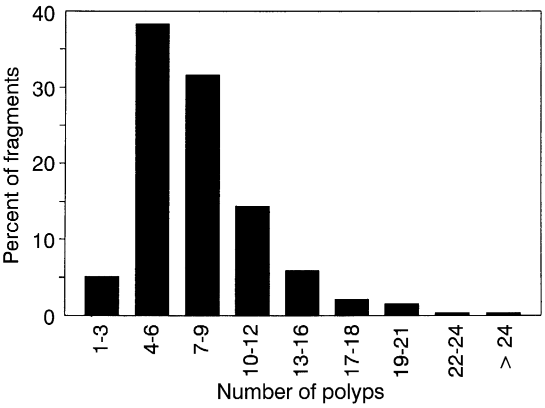


Fig. 2. Frequency distribution of fragments of *Dendronephthya hemprichi* according to number of polyps per fragment ($n = 506$)

Short term recruitment

The most striking result was an immediate recruitment by fragments of *D. hemprichi.* On the second day after placement recruits were found on 26 out of 30 plates, and on the 4th day all plates had been colonized by fragments (Fig. 4). By day 9, most of the plates showed a remarkable increase in density, up to 120 recruits per plate, while on other plates the density sharply declined. The number of recruits per plate differed significantly between days (ANOVA with repeated measures, $F_{3,87} = 28.59$, $P < 0.0001$). The number of recruits increased significantly during the first 3 counts (paired *t*-tests, $df = 29$; between 2nd and 4th day $t = -8.09$, $P < 0.0001$, 4th and 9th day $t = -4.29$, $P < 0.0002$). There was no significant difference between the 9th and the 22nd day ($t = -0.79$, $P < 0.44$). An additional count conducted 52 days after placement showed a further density increase of *D. hemprichi* recruits; the three most crowded plates had 467, 380 and 279 recruits respectively, demonstrating a maximal density of more than one recruit/cm^2. No recruits were found on the lower side of the plates.

Long-term recruitment

The density of *D. hemprichi* recruits varied among the horizontal plates and fluctuated with time. The plates were classified according to their maximal number of recruits over the 203 days of deployment into three groups: up to 20, 50 and 200 recruits per plate: low, medium and high density respectively (Fig. 5). Significant differences occurred in the number of recruits per plate at the different dates among all three densities (Fig. 5, ANOVA with repeated measures, $F_{5,115} = 19.25$, $P < 0.0001$). Paired *t*-test analysis ($df = 23$) indicated a significant decrease in

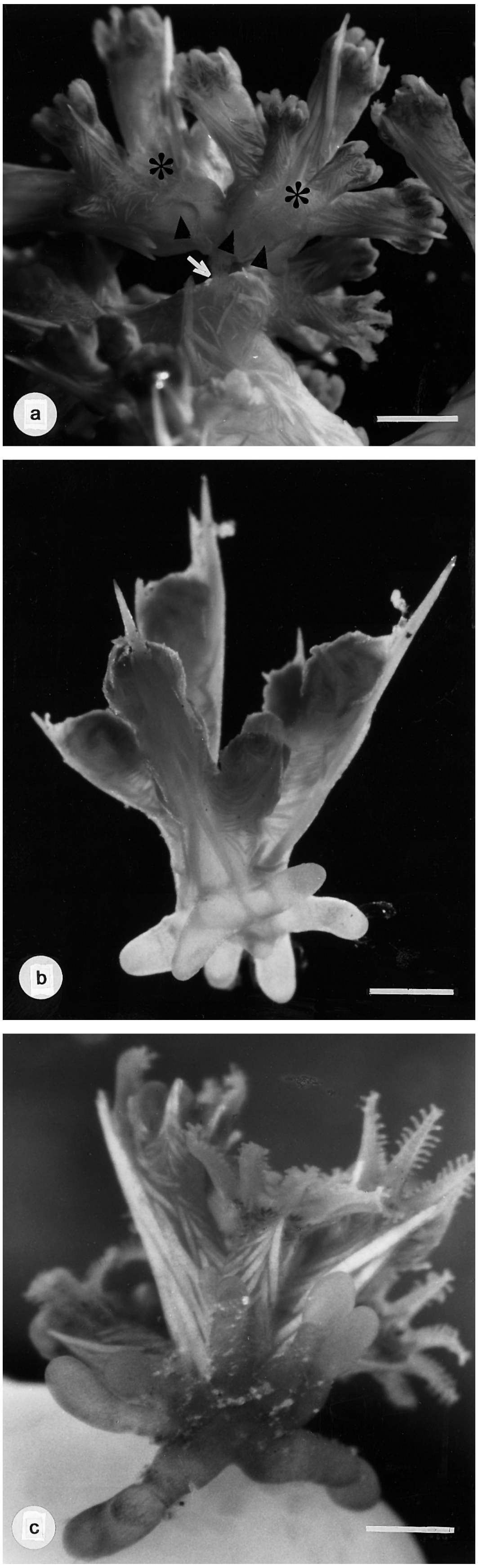


Fig. 1a–c. Autotomy of fragment in *Dendronephthya hemprichi*. **a**. Predetached fragments still connected to the colony (*asterisks*), *arrow* indicates the region of detachment, *arrow heads* indicate initiation of root-like processes; scale bar = 1 mm. **b**. Detached fragment with root-like processes; scale bar = 1 mm. **c**. Fragment attached on a natural calcareous substratum; scale bar = 1 mm

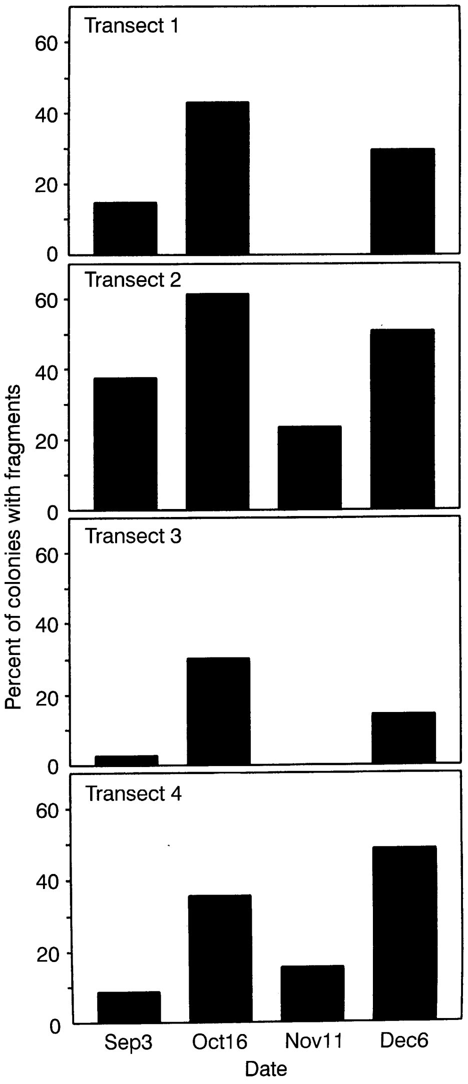


Fig. 3. Percentage of *Dendronephthya hemprichi* colonies with predetached fragments along marked transects on 4 successive dates

density took place between day 34 and 63 ($t = 3.334$, $P < 0.003$) and between day 63 and 104 ($t = 6.02$, $P < 0.0001$). A significant increase was recorded between day 104 and 132 ($t = -3.44$, $P < 0.003$), between day 132 and 163 ($t = -3.3$, $P < 0.004$), and between day 163 and 203 ($t = -3.84$, $P < 0.0008$). Size measurements conducted on the last count, carried out 203 days after placement, showed only six *D. hemprichi* recruits with lengths of > 3 cm. In an additional survey performed 630 days (21 months) after placement, 141 colonies > 3 cm were measured on 24 plates.

Recruitment rate of *D. hemprichi* fragments depended critically on the orientation of the plates (Fig. 6). Although the sets of horizontal plates were placed on four successive dates (arrows in Fig. 6a–d), no significant differences in number of recruits per plate existed at the last count among the different sets (Kruskal-Wallis test: $F = 0.42$, $df = 3$, $P = 0.743$). Nonetheless, significant differences existed among the number of recruits found at the first count after placement, on each of the four horizontal sets (Kruskal-Wallis test: $F = 0.464$, $df = 3$, $P = 0.016$). Thus, the placement dates influenced the initial number of recruits on the four sets of plates. Except for the first two counts, recruitment on the horizontal plates (Fig. 6a–d) was significantly higher compared to the vertical ones (Fig. 6e–h) (Mann-Whitney tests: at day 163, $F = 23.24$, $df = 1$, $P < 0.0001$ and at day 203, $F = 43.71$, $df = 1$, $P < 0.0001$). The 20 plates placed in areas with no *D. hemprichi* for a distance of at least 5 m above them, were colonized after 7–8 months by far fewer recruits. On these plates, located far from a source of fragments, the highest density recorded per plate was six recruits on the horizontal plates and three among the vertical ones compared to over 100 recruits on some plates close to a source of recruits (Fig. 6a–d).

The higher number of colonies counted on the horizontal plates derived mainly from the high abundance of the smallest group size (Fig. 7). Figure 7 presents the size frequency distribution of *D. hemprichi* colonies, > 3 cm in length, found on the horizontal and vertical plates, 16 months after placement of the last set of plates (see Fig. 6d, h). No significant difference exists between the two size frequency distributions ($X^2 = 6.53$, $df = 4$, $P > 0.05$).

Discussion

Propagation by fragmentation occurs among several groups of modular organisms (e.g., Karlson 1988; Stoner 1989; Lewis 1991; Wulff 1991), usually as a consequence of external physical or biotic factors (Hughes 1989). Among scleractinian corals, disturbances such as storms and boring organisms' activity can induce fragmentation (Highsmith 1982). Later, the surviving fragments can re-attach and regenerate, a process which is a common mode of clonal propagation and dispersal especially among fast-growing branching species (e.g., Tunnicliffe 1981; Woodley et al. 1981; Highsmith 1982; Hughes 1985). Among Octocorallia, fragmentation has been described for several gorgonian species and involves breakage of the axial skeleton (Walker and Bull 1983; Lasker 1984, 1990). This study provides the first evidence for autotomy of numerous small-sized fragments from a single soft-bodied octocoral, such as those of the families Alcyoniidae or Nephtheidae.

The root-like processes developed at the basal part of *D. hemprichi* fragments provide an effective means for immediate attachment to a substratum, including a vertical one. The numerous nematocytes on the ectodermis of the processes may assist in anchoring. The cavities of these processes are continuous with the gastrovascular canals of the fragment, and most probably the hydrostatic pressure within the cavities lifts the fragment to an upright position during attachment. In the gorgonian *Junceella fragilis*, active lifting of fragments has also been reported and attributed to differential regional expansion and contraction of the flexible coenenchyme following holdfast formation (Walker and Bull 1983).

Among soft corals, fission is the most common mode of clonal propagation (Lasker 1988). The time required to complete a fission event is highly variable among species. Fission in *Xenia macrospiculata* is completed within 10–14 days (Benayahu and Loya 1985), in some *Sinularia* species

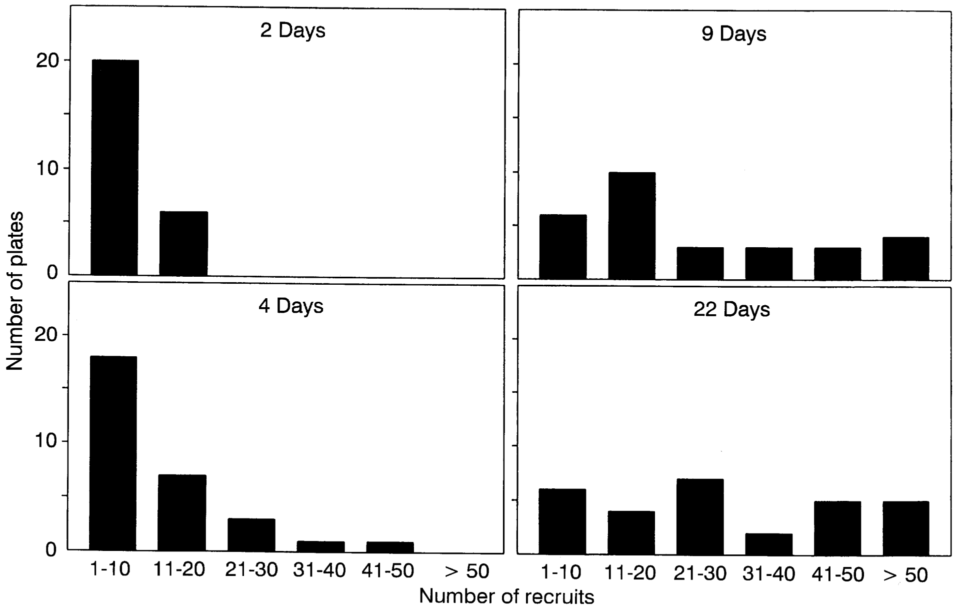
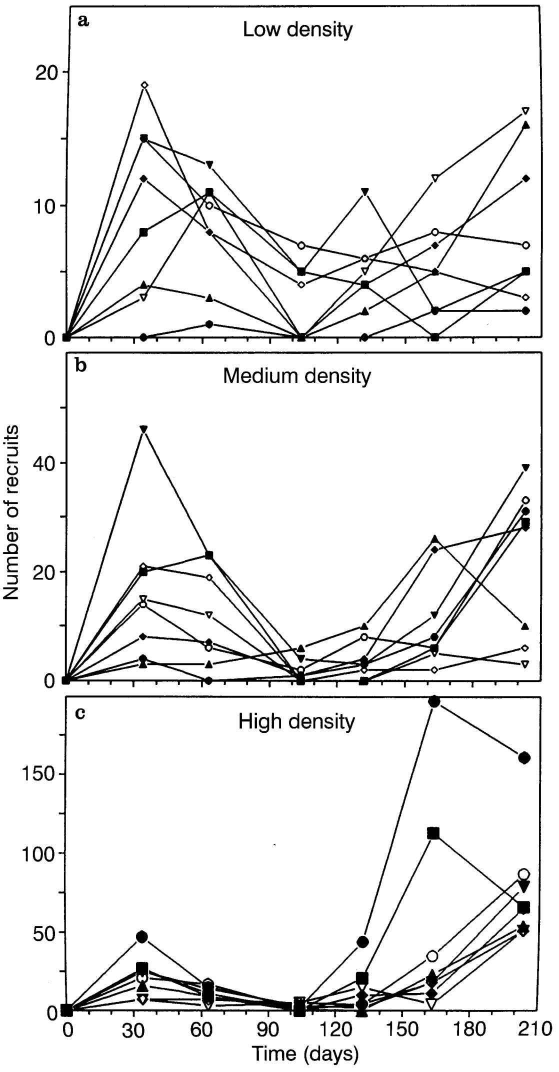


Fig. 4. Short-term recruitment: density of recruits on 30 horizontal plates recorded 2, 4, 9 and 22 days after placement



within 100–155 days (Klainman 1990), and in *Capnella gaboensis* within several years (Farrant 1987). In addition, in *Efflatounaria sp.*, propagation of a new colony by stolons requires periods ranging between 1–2 weeks to 4 months (Dinesen 1985; Karlson et al. in press) In *D. hemprichi* completion of an autotomy event takes only 2 days, and a single colony can simultaneously detach several hundred fragments. Most of the fragments are composed of 4–12 polyps each (Fig. 2), indicating endogenous regulation of the fragment size. Highsmith (1982) proposed that in order to escape size dependent mortality, stony corals have evolved to produce small numbers of large fragments. Previous studies have shown that many soft corals also produce a few, large daughter colonies (Benayahu and Loya 1985; Farrant 1987; Klainman 1990). We propose that the exceptional clonal propagation of *D. hemprichi* into numerous and miniature fragments is highly advantageous for rapid and successful colonization of vertical surfaces, which are the favoured habitat of this species. Larger fragments are too heavy for initial attachment onto vertical surfaces.

The temporal fluctuations in the percentage of fragment-bearing colonies of *D. hemprichi* within the population (Fig. 3) suggest that the autotomy rate is stimulated by exogenous factors. Similarly, asexual reproduction of sea anemones is stimulated by various abiotic factors such as temperature, food availability and current regime (Shick and Hoffmann 1980; Sebens 1980; Lin et al. 1992; Tsuchida and Potts 1994). Our preliminary observations demonstrate that the increased autotomy rate of *D. hemprichi* might be induced by flow related events, a topic that is now under study.

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Fig. 5a–c. Long-term recruitment: temporal changes in number of recruits on 24 horizontal plates, with low, medium and high recruit densities per plate, respectively. Each symbol indicates a plate

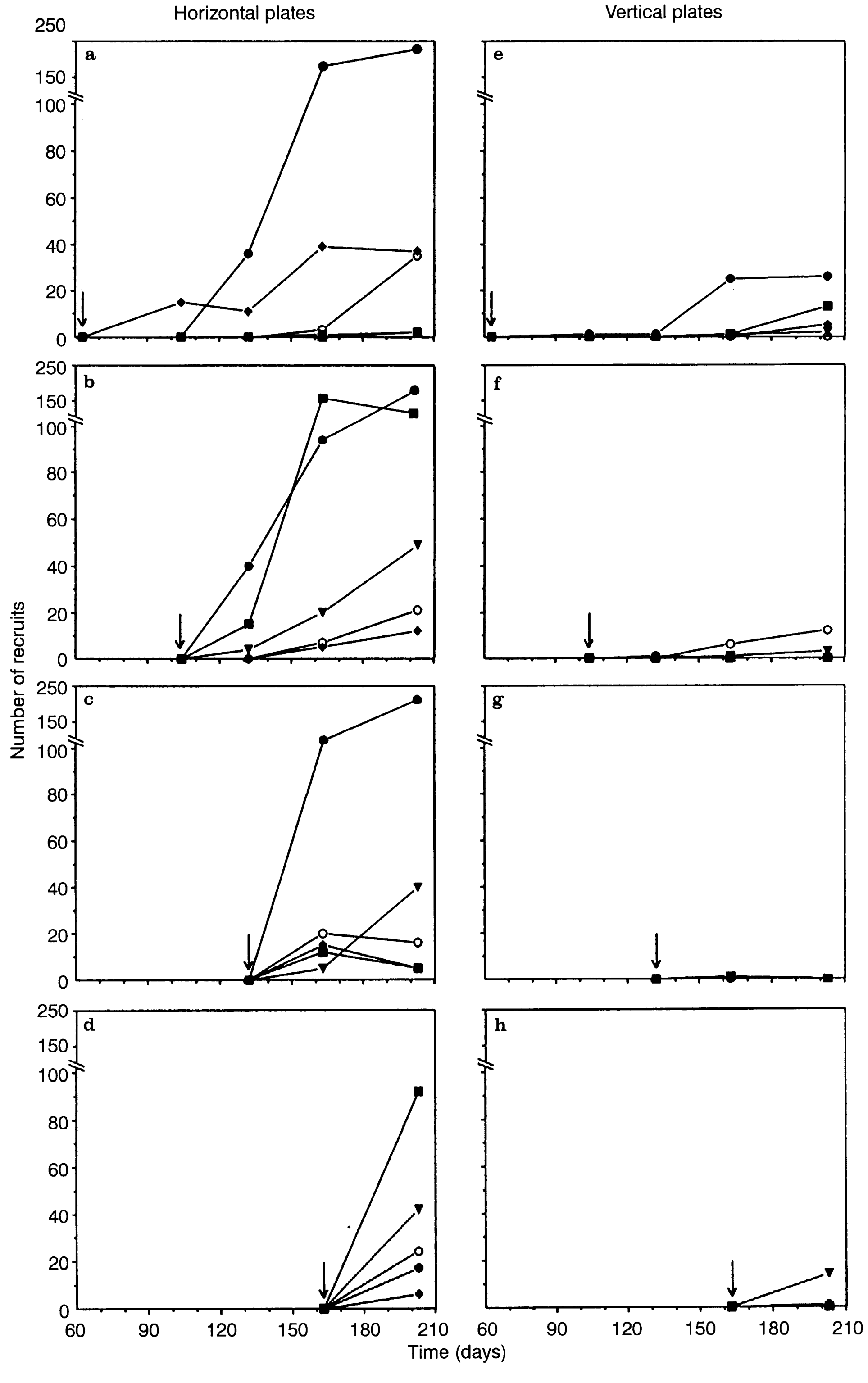

Fig. 6a–h. Long-term recruitment: temporal changes in number of recruits on 4 sets of 5 horizontal and 5 vertical plates (40 plates in total) placed on 4 successive dates: **a–d** recruitment on horizontal plates; **e–h** recruitment on vertical ones. Arrows point the placement day. Each *symbol* indicates a plate

Clonal propagation of *D. hemprichi* caused an immediate and dense recruitment on the upper side of horizontal plates (Fig. 4); within only four days of placement, attached fragments were observed on all these plates. A density of one recruit per cm^2 was recorded on the most crowded plate 52 days after placement. To date, as far as we know, no comparable densities have been obtained within such a short period of time for sexual or asexual recruited octocorals.

The long-term recruitment-plates showed similar temporal fluctuations in the abundance of *D. hemprichi* recruits, regardless their densities (Fig. 5). Thus, the net result of both recruitment and mortality on most of these plates was similar. The high mortality rate of the

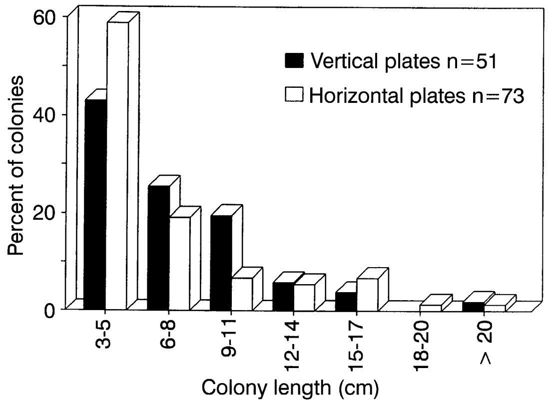

Fig. 7. Size frequency distribution of *Dendronephthya hemprichi* colonies measured on 20 vertical (51 colonies) and 20 horizontal plates (73 colonies) 16 months after placement

fragments is demonstrated by the decrease of approximately 90% in recruit numbers within a period of 70 days (between the first count after 34th day and the 104th day count, Fig. 5). In the course of the 203 days of this survey, only a few colonies exceeded 3 cm in length. Considering the fast growth rate of *D. hemprichi* (Dahan 1992; Fabricius et al. 1995), this result reflects the high mortality rate among recruited fragments and their fast turnover on the plates. However, after 630 days 141 colonies > 3 cm were counted, which may indicate that the recruits' survivorship improved with time as their density increased. A similar pattern was found for juvenile stages of the temperate soft coral *Alcyonium siderium*, which had higher survival and growth rates when they are aggregated near large colonies (Sebens 1991). In the present study, the number of recruits recorded was not directly related to the time elapsed since placement (Fig. 6a–d). Therefore, the number of recorded recruits within a given date presented an instantaneous value derived from rapid and dynamic processes of recruitment and mortality. The differences in recruit numbers among the four sets of plates at the first count (Fig. 6a–d) are most likely derived from temporal variations in autotomy rate within the population of *D. hemprichi*, as already demonstrated (Fig. 3).

Recruitment on the horizontal plates was much higher compared to vertical ones (Fig. 5). The rapid settling velocity of the detached fragments, 3.6 ± 0.6 (SD) cm/s, enhances the likelihood of their descending on horizontal surfaces. Fragments cannot attach upside-down and therefore, did not appear on the lower side of the horizontal plates. The relatively small difference in the number of colonies > 3 cm between the horizontal and vertical plates, indicates higher survivorship on vertical surfaces. This pattern also corresponds with the dominance of *D. hemprichi* on vertical substrata at the oil jetties of Eilat, as well as on natural reefs of the northern Red Sea (Benayahu 1985). High survival of recruited stony corals on vertical substrata has been attributed to a low growth rate of turf algae coupled with a low rate of sediment accumulation on these surfaces (Birkeland 1977). Differential survival of *D. hemprichi* recruits may be attributed to grazing activity by sea urchins, which occurs predominantly on horizontal surfaces (Dahan 1992). In addition, it is reasonable to assume that in an obligatory heterotrophic soft coral, such as *D. hemprichi*, survivorship of recruited fragments is critically dependent on the current regime, which in turn, determines food availability for the recruits (Fabricius et al. 1995), and may facilitate their success on exposed vertical surfaces rather than on horizontal ones.

Dendronephthya hemprichi is an all-year-round broadcaster (Dahan and Benayahu, in preparation). However, in the current study the recruits were all considered to be derived from fragments, although sexual recruitment is also likely to occur. This conclusion is based on the following evidence: (a) primary polyps were never observed on the plates; (b) post metamorphic development of the sexual recruits is too slow to cause the immediate recruitment shown in Fig. 4; (c) no recruits appeared on the lower plate-surfaces, although planulae of *D. hemprichi* are capable of settling on both sides of the plates; and, (d) the plates placed away from source of asexual propagules were hardly colonized. Asexual propagation in clonal organisms is a means for increasing numbers of genetically identical and physically independent units or ramets (Coates and Jackson 1985). This process may reduce the probability of genotype death (Cook 1979; Highsmith 1982) and may also stimulate the genet growth rate (Stoner 1989). A continual fission of the cold-water soft coral *Alcyonium sp.* is a growth strategy for maximization of its nutrient uptake (McFadden 1986), and may function similarly in *D. hemprichi*. The reduction of energy allocated for sexual reproduction in small-size ramets may favor an increased growth rate of the genet (Sebens 1979; Stoner 1989). Fragments of *D. hemprichi* exhibit a remarkably rapid growth rate (Dahan 1992; Fabricius et al. 1995). Thus, the rapid growth rate of *D. hemprichi* fragments (Fig. 5) probably more than compensates for their high mortality rate, as has already been proposed by Karlson (1988) for *Zoanthus sociatus*.

Dendronephthya hemprichi is the most abundant azooxanthellate soft coral in the reef communities of the Red Sea (Benayahu 1985), where its abundance also far exceeds many zooxanthellate species. This soft coral is a phytoplankton feeder (Fabricius et al. 1995), and highly abundant in habitats exposed to strong water currents, which are essential for its nutritional demands. The rapid clonal propagation by autotomy in *D. hemprichi* may be an efficient means by which a genet may exploit the required food resource in a suitable habitat. The species' onset of sexual reproduction is size-dependent and occurs at an early age (Dahan 1992). Consequently, the mode of clonal propagation exhibited by *D. hemprichi* enhances the fecundity of its genets and promotes population growth. It is likely that the unique autotomy mechanism of *D. hemprichi* allows this azooxanthellate soft coral to thrive within a zooxanthellate dominated reef-community.

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References

Bayer FM (1981) Status and knowledge of octocorals of world seas. In: Seminarios de Biologia Marinha, Academia Brasileira de Ciencias, Rio de Janeiro, pp 3–102

Benayahu Y (1985) Faunistic composition and patterns in the distribution of soft corals (Octocorallia, Alcyonacea) along the coral reefs of Sinai peninsula. Proc 5th Int Coral Reef Congr 6 : 255–260

Benayahu Y, Loya Y (1977) Space partitioning by stony corals, soft corals and benthic algae on the coral reefs of the northern Gulf of Eilat (Red Sea). Helgöland Wiss Meeresunt 30 : 365–382

Benayahu Y, Loya Y (1981) Competition for space among coral reef sessile organisms at Eilat, Red Sea. Bull Mar Sci 31 : 514–522

Benayahu Y, Loya Y (1983) Surface brooding in the Red Sea soft coral *Parerythropodium fulvum fulvum* (Forskäl, 1775). Biol Bull 165 : 353–369

Benayahu Y, Loya Y (1985) Settlement and recruitment of a soft coral: why is *Xenia macrospiculata* a successful colonizer? Bull Mar Sci 36 : 177–188

Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc 3rd Int Coral Reef Symp, Miami 1 : 15–21

Coates AG, Jackson JBC (1985) Morphological themes in the evolution of clonal and aclonal marine invertebrates. In: Jackson JBC, Buss LW, Cook RE (eds) Population biology and evolution of clonal organisms. Yale University Press, New Haven, pp 67–106

Chia F-S (1976) Sea anemone reproduction: patterns and adaptive radiations. In: Mackie GO (ed) Coelenterate Ecology and Behaviour. Plenum Press, New-York, pp 261–270

Cook RE (1979) Asexual reproduction: a further consideration. Am Nat 113 : 769–772

Dahan M (1992) Clonal propagation and sexual reproduction of the alcyonacean *Dendronephthya hemprichi*. MSc Thesis, Tel-Aviv University (Hebrew; English summary)

Dinesen ZD (1985) Aspects of the life history of a stolon-bearing species of *Efflatounaria* (Octocorallia: Xeniidae). Proc 5th Int Coral Reef Congr 6 : 89–94

Fabricius KE, Genin A, Benayahu Y (1995) Flow-dependent herbivory and growth in zooxanthellae-free soft corals. Limnol. Oceanogr. 40 : 1290–1301.

Farrant PA (1987) Population dynamics of the temperate Australian soft coral *Capnella gaboensis*. Mar Biol 96 : 401–407

Goren R (1992) Benthic communities on artificial substrata at Eilat (Red Sea). MSc Thesis, Tel-Aviv University (Hebrew; English summary)

Harper JL (1977) Population biology of plants. Academic Press, London

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z (ed) Coral Reefs. Elesvier, Amsterdam, pp 133–207

Highsmith RC (1982) Reproduction by fragmentation in corals. Mar Ecol Prog Ser 7 : 207–226

Hughes RN (1989) A functional biology of clonal animals. Chapman and Hall, New York

Hughes RN, Cancino JM (1985) An ecological overview of cloning in metazoa. In: Jackson JBC, Buss LW, Cook RE (eds) Population biology and evolution of clonal organisms. Yale Univ Press, New Haven, pp 153–186

Hughes TP (1985) Life histories and population dynamics of early successional corals. Proc 5th Int Coral Reef Congr 4 : 101–105

Hughes TP, Ayre D, Connell JH (1992) The evolutionary ecology of corals. Trends Ecol Evol 7 : 292–295

Jackson JBC (1977) Competition on marine hard substrata: the adaptive significance of solitary and colonial strategies. Am Nat 111 : 742–767

Jackson JBC (1985) Distribution and ecology of clonal and aclonal invertebrates. In: Jackson JBC, Buss LW, Cook RE (eds) Population biology and evolution of clonal organisms. Yale University Press, New Haven, pp 297–347

Karlson RH (1988) Size-dependent growth in two zoanthid species: a contrast in clonal strategies. Ecol 69(4) : 1219–1232

Karlson RH, Hughes TP, Karlson SR (1996) Density-dependent dynamics of soft coral aggregations: the significance of clonal growth and form. Ecology (in press)

Klainman M (1990) Comparative life history features of the *Sinularia* species (Octocorallia: Alcyonacea) at Eilat. MSc thesis, Tel-Aviv University (Hebrew; English summary)

Lasker HR (1984) Asexual reproduction, fragmentation, and skeletal morphology of a plexaurid gorgonian. Mar Ecol Prog Ser 19 : 261–268

Lasker HR (1988) The incidence and rate of vegetative propagation among coral reef alcyonarians. Proc 6th Int Coral Reef Symp 2 : 763–768

Lasker HR (1990) Clonal propagation and population dynamics of a gorgonian coral. Ecol 71(4) : 1578–1589

Lewis JB (1991) Testing the coral fragment size-dependent survivorship hypothesis for the calcareous hydrozoan *Millepora complanata*. Mar Ecol Prog Ser 70 : 101–104

Lin J, Chen C-P, Chen I-M (1992) Sexual and asexual reproduction of *Anthopleura dixoniana* (Anthozoa: Actiniaria): periodicity and regulation. Mar Biol 112 : 91–98

McFadden CS (1986) Colony fission increases particle capture rates of a soft coral: advantages of being a small colony. J Exp Mar Biol Ecol 103 : 1–20

Sebens KP (1979) The energetics of asexual reproduction and colony formation in benthic marine invertebrates. Am Zool 19 : 683–697

Sebens KP (1980) The regulation of asexual reproduction and indeterminate body size in the sea anemone *Anthopleura elegantissima* (Brandt). Biol Bull 158 : 370–382

Sebens KP (1991) Habitat structure and community dynamics in marine benthic systems. In: Bell SS, McCoy ED, Mushinsky HR (eds) Habitat structure: the physical arrangement of objects in space. Chapman and Hall, London, pp 211–234

Shick MJ, Hoffmann RJ (1980) Effects of the trophic and physical environments on asexual reproduction and body size in the sea anemone *Metridium senile*. In: Tardent P, Tardent R (eds) Developmental and Cellular Biology of Coelenterates. North-Holland Biomedical Press, pp 211–216

Stoner DS (1989) Fragmentation: A mechanism for the stimulation of genet growth rates in an ecrusting colonial ascidian. Bull Mar Sci 45(2) : 277–287

Tsuchida CB, Potts DC (1994) The effects of illumination, food and symbionts on growth of the sea anemone *Anthopleura elegantissima* (Brandt, 1835). II. Clonal growth. J Exp Mar Biol Ecol 183 : 243–258

Tunnicliffe V (1981) Breakage and propagation of the stony coral *Acropora cervicornis*. Proc Nat Acad Sci 78 : 2427–2431

Verseveldt J, Benayahu Y (1978) Description of one old and five new species of Alcyonacea (Coelenterata: Octocorallia) from the Red Sea. Zool Meded, Leiden 53(6) : 57–74

Walker TA, Bull GD (1983) A newly discovered method of reproduction in gorgonian coral. Mar Ecol Prog Ser 12 : 137–143

Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koehl MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. Science 214 : 749–755

Wulff JL (1991) Asexual fragmentation, genotype success, and population dynamics of erect branching sponges. J Exp Mar Biol Ecol 149 : 227–247