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Reproduction of *Dendronephthya hemprichi* (Cnidaria: Octocorallia): year-round spawning in an azooxanthellate soft coral

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Abstract Sexual reproduction in the azooxanthellate octocoral *Dendronephthya hemprichi* Klunzinger, 1877 was studied in Eilat (Red Sea) for 2 years beginning March 1989. *D. hemprichi* is a gonochoric broadcasting species. Gonads at all developmental stages were found throughout the year. Small-sized oocytes and sperm sacs, 51 to 100 μm in diameter, are highly abundant, accompanied by numerous smaller primordial gonads. These features result from continuous gametogenesis, and lead to year-round oocyte and sperm maturation and release. Gamete release was observed in the laboratory on all monitoring dates, and most of the female colonies spawned repeatedly for several successive nights. The reproductive features of *D. hemprichi* constitute an exception to the generalization that free-spawning reef-corals have brief and synchronized broadcast-spawning episodes. This species demonstrates early onset of first reproduction, which further increases its reproductive output.

Introduction

There are three modes of sexual reproduction in reef soft corals (Cnidaria: Alcyonacea) – broadcasting of gametes, external surface brooding, and internal brooding of planulae (reviewed by Benayahu et al. 1990). Most of the species studied to date are gonochoric, and hermaphroditic ones are rare. The broadcast spawners, mostly members of the family Alcyoniidae, have one annual spermatogenic cycle while their oogenesis is completed over a longer period and achieved through overlapping oogenic cycles (Yamazato et al. 1981; Alino and Coll 1989; Benayahu et al. 1990). The gametogenic cycle of surface brooders lasts for approximately 1 year, whereas internal brooders have multiple gametogenic cycles every year (Benayahu 1991). Reef soft corals were found to have short, seasonal and synchronized spawning episodes (Alino and Coll 1989; Benayahu et al. 1990), similar to the well-documented short, discrete annual spawning of stony corals (Harrison and Wallace 1990; Richmond and Hunter 1990). On the Great Barrier Reef, Australia, the soft corals spawn during the multispecies mass spawning event (Babcock et al. 1986; Alino and Coll 1989). In contrast, Red Sea soft corals exhibit a temporal reproductive isolation (Benayahu et al. 1990), as do the scleractinian corals of that region (Shlesinger and Loya 1985). Brooding species of both coral groups tend to planulate throughout extended periods, or all year round (Harrison and Wallace 1990; Benayahu 1991).

The azooxanthellate alcyonacean *Dendronephthya hemprichi* of the family Nephtheidae is a phytoplankton feeder, only occurring in habitats exposed to strong water currents (Fabricius et al. 1995a, b). In Eilat (Red Sea), it is the most abundant inhabitant of vertical artificial underwater structures, despite being very rare on adjacent natural reefs (Dahan 1992). The unusual success of this obligatory heterotrophic soft coral within a predominantly zooxanthellate coral community motivated us to examine its life history. Recently, we reported that *D. hemprichi* has a highly specialized mode of clonal propagation, featuring the autotomy of small fragments (Dahan and Benayahu 1997). The present study describes sexual reproduction in *D. hemprichi*, including its oogenic and spermatogenic cycles, reproductive mode, breeding period, and onset of sexual maturity.

Materials and methods

Monthly sampling and gonadal condition in fixed material

The study was conducted at oil jetties, 4 km south of Eilat, Israel, from March 1989 to April 1991. *Dendronephthya hemprichi* Klun-

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zinger, 1877 is highly abundant on the vertical metal support pillars of the jetties and on the surrounding coiled barbed wire. Individual branches, 3 to 5 cm long, were removed once a month from 10 to 25 haphazardly selected colonies >40 cm in length. The samples were routinely fixed in 4% formalin in sea water for 24 h, rinsed in fresh water, and transferred to 70% ethanol. They were later decalcified for 40 min in a solution of formic acid and tri-sodium citrate (Benayahu and Loya 1983). Polyps from three or four different groups (catkins) of each sample were dissected by fine-pointed forceps under a binocular microscope. Wet preparations of their mesenteries were made and examined under a microscope. The sex of each colony was determined and the diameters of 100 haphazardly selected oocytes or sperm sacs (>50 μm) were measured from each colony using a calibrated ocular. In addition, gonad structure was studied by histological sections (for methodology, see Benayahu and Loya 1983). Data are presented as the mean percent frequencies for oocytes and sperm sacs of different size groups.

Spawning of gametes

Spawning of gametes in the laboratory was monitored, at least once a month, for several successive nights from May 1990 to April 1991 (during early 1991 no sampling was conducted due to the Gulf War). Each day, 10 to 20 branches of different *Dendronephthya hemprichi* colonies were collected, placed in separate, water-filled plastic bags and transferred to the Marine Biology Laboratory at Eilat. The branches were maintained for acclimation in running sea water for 1 h, then transferred to aerated aquaria containing 2.5 liters filtered sea water. The presence of gametes was monitored during both day and night hours. Each morning the eggs were removed and counted, and the water was replaced. Samples of water were taken from aquaria with colonies that did not release eggs, for microscopical examination of possible released sperm. Branches were kept in the laboratory for up to 5 d and then fixed as described above; those that did not spawn were dissected, and their sexual condition was determined. Spawning in the field was detected by covering colonies with plankton nets (200 μm mesh) overnight.

Relationship between colony size and sexual maturity

Onset of sexual maturity of *Dendronephthya hemprich* was examined in a newly established population of known age, which had developed underneath a raft near the oil jetties. The first sampling, comprising colonies of all sizes, was conducted from a population established for 12 months. Complete colonies <10 cm in length were collected and five samples were taken from the larger ones. Another sampling was carried out 5 months later, consisting of the 13 largest colonies. These samples were all fixed and their sexual condition was determined.

Results

Monthly sampling and gonadal condition in fixed material

The soft coral *Dendronephthya hemprichi* is gonochoric; female and male gonads develop along the mesenteries within the polyp cavities. Within the population, oocytes and sperm sacs at all developmental stages were found throughout the entire study period. Primordial gonads appeared in clusters, covered by a common layer of endodermal cells. Gonads <150 μm in diameter were transparent. The oocytes had visible nuclei and nucleoli and were surrounded by a follicular cell layer. The sperm sacs had a light periphery and a darker center. As they became larger, the gonads of both sexes gradually lost their transparency and became opaque.

Clusters of primordial gonads of both sexes were numerous in all sexually mature colonies. Each cluster contained several gonads, but it was not possible to enumerate them. Monthly size–frequency distributions of female and male gonads, >50 μm in diameter, for the period April 1989 to April 1991 are shown (Figs. 1, 2). Each monthly distribution shows the average frequencies of the different size groups in the sampled colonies. The oocytes revealed similar size–frequency distributions throughout the study (Fig. 1). The most abundant were the 51 to 100 μm size group, constituting 50 to 70% of the measured oocytes, while the other size groups were present in low frequencies. The maximal oocyte diameter measured was 500 μm. Sperm sacs, 51 to 100 μm in size, were relatively less abundant and comprised approximately 40% of all those measured (Fig. 2). Sperm sacs >300 μm were rarely observed with the largest measured being 400 μm. Among the 522 sexually mature colonies sampled, 338 were female and 184 male, a sex ratio of 3:2 (females were significantly more abundant than males; χ^2, $p < 0.01$).

Spawning of gametes

Sperm and egg release was observed in the laboratory at night on all dates, from October 1989 to April 1991. Most of the colonies spawned repeatedly for several successive nights; spawning occurred after sunset and continued until 0200 hrs. While spawning, the colonies became inflated and their polyps expanded. The process of egg release was rather slow (5 to 10 min). An emerging egg passed the contracted pharynx, becoming oval in shape and, after release, rapidly gained its spherical shape. The spawned egg often stayed attached to the mouth opening for a few minutes by a short mucus thread. The released eggs lacked a follicular cell layer and were cream-pink in color. They were negatively buoyant and slowly settled to the bottom of the aquarium. The egg size was variable (diam = 260 to 470 μm). Figure 3 presents the percent of female colonies that spawned in the laboratory on the monitoring dates; most nights 70 to 100% of them released eggs. Spawning was also recorded in the field in samples collected with plankton nets placed over *Dendronephthya hemprichi* colonies, but this procedure damaged the colonies and we did not apply it routinely. On all dates (June, August, October 1990 and April 1991) embryos were found developing in the nets during the night.

Relationship between colony size and sexual maturity

During the study period, recruitment of *Dendronephthya hemprichi* was observed year round on several artificial substrata at Eilat. The underside of a raft was

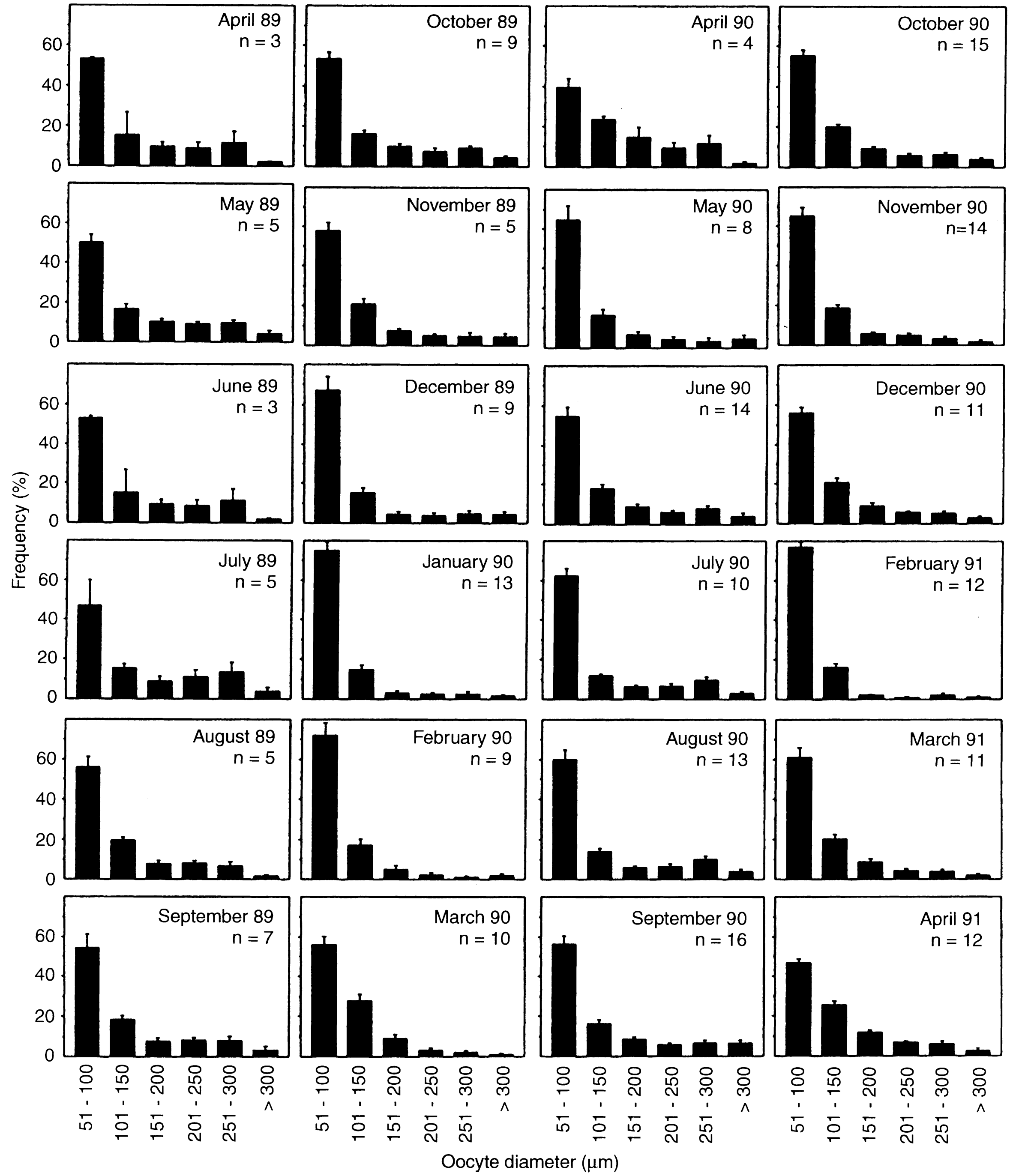

Fig. 1 *Dendronephthya hemprichi.* Monthly size–frequency distributions of oocyte diameters (> 50 μm) during the study period; standard deviations are given for each size group, *n* = number of female colonies examined each month; 100 oocytes were measured per colony

colonized within a year of its deployment by ca. 500 recruits, which could only have been derived as a consequence of sexual reproduction (see Dahan and Benayahu 1997). The size–frequency distribution of the *D. hemprichi* population established for 12 months (Fig. 4), consisted of a wide size range of colonies, with a maximum length of 26 cm attained by one colony. The population was sampled 12 and 17 months after deployment of the raft (Fig. 5). Sterile colonies were found over the entire size range. Immature gonads were found in colonies >9 cm in length, and mature gonads in colonies >19 cm in length. After 12 months a single male (the above-mentioned, 26 cm long), had ripe sperm sacs, whereas no ripe oocytes were observed. Five months later, among the 13 largest colonies on the raft (>18 cm in length), three sexually mature females and two males were found.

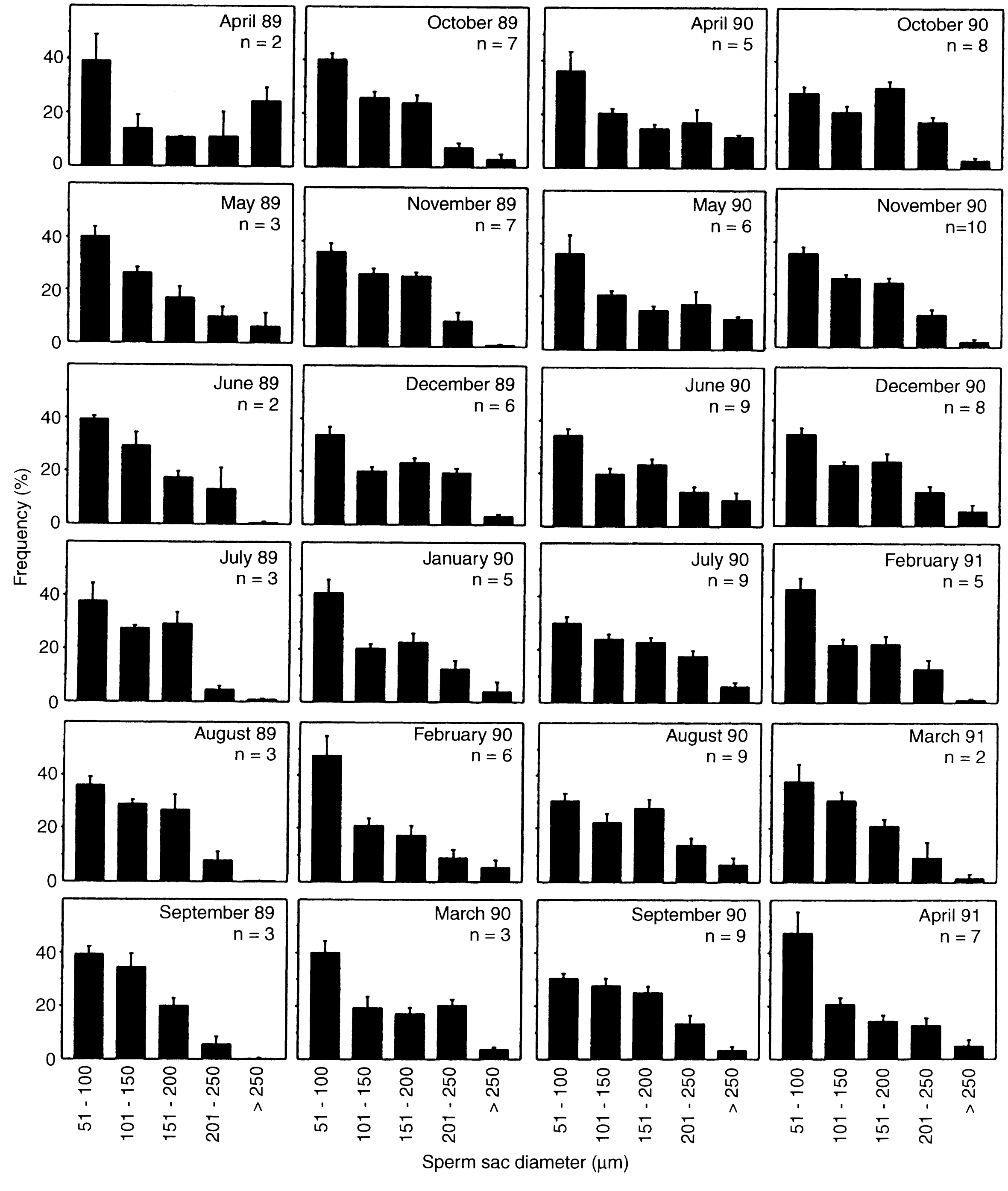

Fig. 2 *Dendronephthya hemprichi.* Monthly average frequencies of sperm-sac size groups (> 50 μm) during the study period. Standard deviations are given for each size group, *n* = number of male colonies examined each month; 100 sperm sacs were measured per colony

Discussion

The soft coral *Dendronephthya hemprichi* is a gonochoric broadcast spawner, reproducing all year round. Its gonads develop along the mesenteries within the polyp cavities, similar to the two previously studied species, *Capnella gaboensis* (Farrant 1986) and *Litophyton arboreum* (Weil 1990), in the family Nephtheidae. The size–frequency distribution of *D. hemprichi* oocytes was similar throughout the year. Oocytes 51 to 100 μm in diameter were very abundant, as were primordial oocytes (< 50 μm). These gonadal features indicate a continuous proliferation of oocytes with year-round cycles of maturation and release. The relatively high abundance of sperm sacs of 101 to 200 μm may result from their rather rapid development and maturation compared to the slower process of oogenesis. Previous studies on both soft and stony corals indicated a shorter spermatogenic than oogenic cycle (Benayahu et al. 1990; Harrison and Wallace 1990).

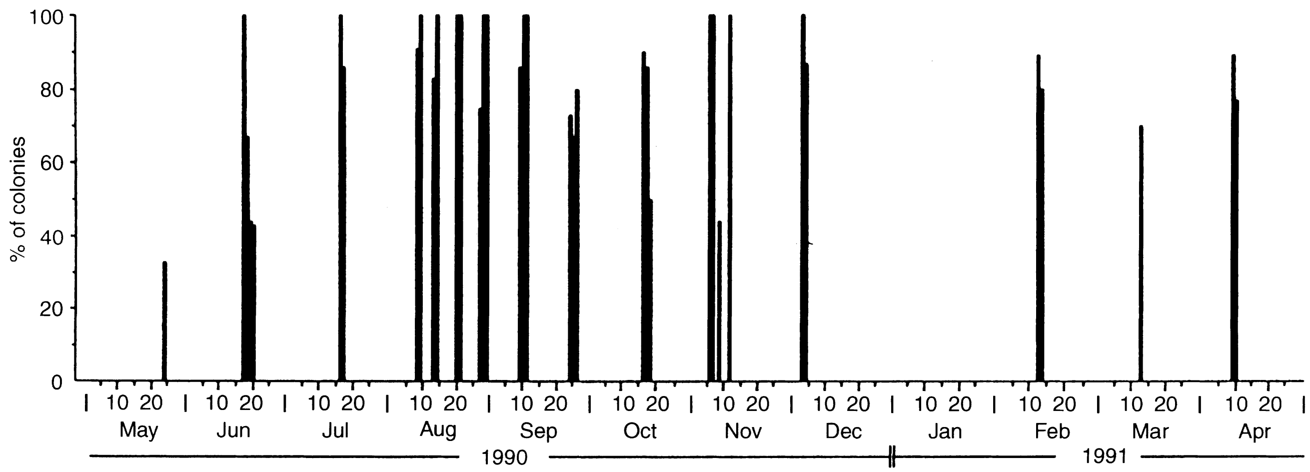

Fig. 3 *Dendronephthya hemprichi.* Percentage of spawning females on the monitoring dates

Premature release of gametes by corals (Szmant-Froelich et al. 1980) and abortion of planulae (Loya and Rinkevich 1980) have been recorded under various stressful conditions (Fadlallah 1983). In the present study, the diurnal pattern of gamete release observed in the laboratory strongly suggests that spawning was not a response to collection or adverse laboratory conditions. The high rate at which fertilized eggs developed into planulae in the laboratory (Dahan and Benayahu in preparation) further supports this suggestion.

Dendronephthya hemprichi demonstrates continuous breeding activity throughout the year. In both soft and stony corals, spawning is more commonly seasonal and usually restricted to one or a few nights each year. Mass spawning occurs synchronously throughout each population (Benayahu et al. 1990; Harrison and Wallace 1990), and usually takes place during periods of rising or maximum sea temperature. An absence of reproductive seasonality and synchrony of gamete release is known from low latitudes, and has been correlated with a decrease in the annual temperature range nearer the equator (Oliver et al. 1988; Glynn et al. 1991). In Eilat, where reefs are at their northern limit of distribution, the reproductive activity of broadcasting stony and soft corals coincides with the warm summer season (Shlesinger and Loya 1985; Benayahu et al. 1990). The reproductive features of *D. hemprichi* found in this study are thus an exception to the generalization that brief, synchronized, seasonal broadcasting episodes are usual in high latitude coral reefs (Babcock et al. 1994).

Nutritional control of gametogenesis has been noted among a wide variety of invertebrates (Giese and Kanatani 1987), but this topic has seldom been examined for corals. In the cold water soft coral *Alcyonium digitatum* a direct relationship was found between its

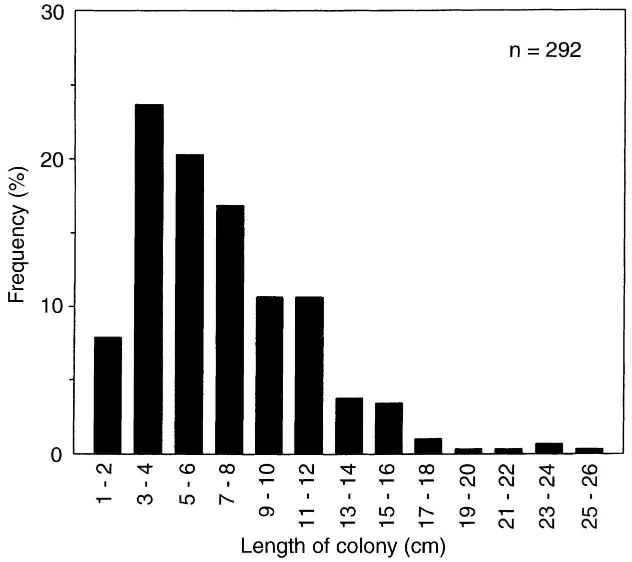

Fig. 4 *Dendronephthya hemprichi.* Size–frequency distribution of colonies in a population established for 12 months

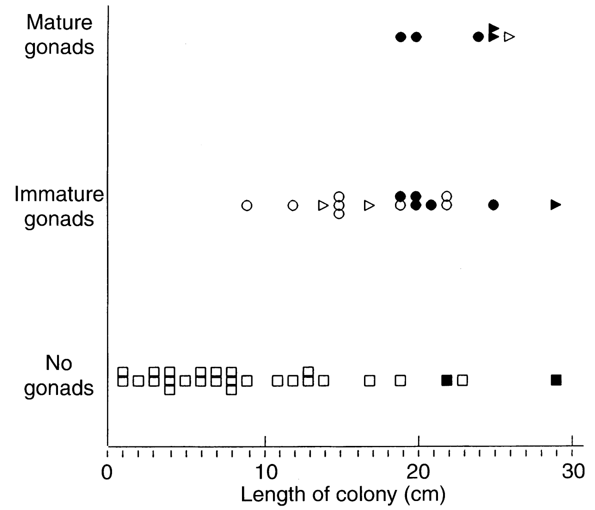

Fig. 5 *Dendronephthya hemprichi.* Onset of gonad development in relation to colony size (*open symbols* represent observations 12 months after the population was established; *filled symbols* 17-month observations; *squares* no gonads; *circles* females; *triangles* males)

gonad development and the seasonal abundance of plankton (Hartnoll 1975). In the field, the temperate stony coral *Astrangia danae* demonstrates seasonal spawning, while colonies maintained in the laboratory and fed regularly spawned year round (Szmant-Froelich et al. 1980). Since the soft coral *Dendronephthya hemprichi*, is azooxanthellate, and thus does not photosynthetically fix carbon, it is likely that oocyte maturation is controlled by availability of food. Recently, it has been found that this soft coral feeds almost exclusively on phytoplankton (Fabricius et al. 1995a, b), a food source previously unknown for cnidarians. We suggest that the two relatively persistent phytoplankton blooms each year at Eilat (Genin et al. 1995) supply the metabolic demands for gametogenesis in *D. hemprichi*, thus permitting the year-round gamete release.

Complex interactions among age, size, physiological, and environmental conditions determine the onset of first reproduction among clonal invertebrates (Harvell and Grosberg 1988). Corals exhibit a minimal size below which no colonies develop gonads. This has been attributed to the initial need to allocate energy towards growth, in order to escape size-dependent mortality (Kojis and Quinn 1985; Karlson 1986). Only colonies >9 cm in length were found bearing gonads in *Dendronephthya hemprichi*, but colonies with a wide size range above this length were also sterile. These findings agree with previous studies on stony corals, in which gametogenesis occurs only among a small proportion of colonies at their minimal size of first reproduction (Rinkevich and Loya 1979; Babcock 1984; Kojis and Quinn 1985). *D. hemprichi* colonies reach sexual maturity relatively quickly, <12 months for males and <17 months for females (Fig. 5), compared to other tropical broadcasting soft and stony corals, which have a first reproduction at an age of several years (Benayahu and Loya 1986; Harrison and Wallace 1990). In this respect, it is interesting to note that both azooxanthellate and ahermatypic broadcasting stony corals are apparently more precocious than symbiotic and hermatypic ones (Harrison and Wallace 1990).

The most common mechanism by which freely spawning marine invertebrates ensure fertilization success and reduce gamete wastage is by synchronized spawning (Campbell 1974). This can be induced in one sex by the opposite sex (Szmant-Froelich et al. 1980; Tranter et al. 1982; Miller 1989) or cued by environmental factors, such as moon phase, temperature, photoperiod, etc. (Giese and Kanatani 1987). Lunar rhythms are commonly observed in spawning of stony and soft corals (Alino and Coll 1989; Benayahu et al. 1990; Harrison and Wallace 1990). The final synchronization and timing of spawning were found to be controlled by daily light and dark cycles (Harrison and Wallace 1990). In *Dendronephthya hemprichi*, both sexes released gametes in the absence of colonies of the opposite sex, a finding that suggests that induced spawning does not occur in this species. Our results also indicate that spawning of *D. hemprichi* is cued by cyclic diurnal patterns, although it is not yet clear if this is the sole factor involved.

Colonies of *Dendronephthya hemprichi* inhabit sites exposed to strong water currents. Polyp contraction occurs predominantly at flows of <3 and >25 cm s^{-1}, and expansion in the intermediate flow velocities (Fabricius et al. 1995b). Our work indicates that in *D. hemprichi*, gamete release occurs only in the expanded state; hence, flow regime may be an additional factor affecting the spawning schedule. Fertilization success is known to decrease with increasing water flow due to rapid dilution of sperm (Pennington 1985; Yund 1990; Levitan et al. 1991, 1993). Fertilization rate is enhanced by high population densities (references in Lasker et al. 1996), which in *D. hemprichi* is in part a result of rapid clonal propagation (Dahan and Benayahu 1997). The relatively slow emergence of spawned eggs through the mouth, and their attachment to the mouth by a mucus thread, may be adaptive in that the egg is retained temporarily in the vicinity of other colonies, some of which are male. It is proposed, therefore, that spawning behaviour of this soft coral is adapted to relatively high-flow environments.

Features such as rapid somatic growth (Fabricius 1995b), clonal propagation (Dahan and Benayahu 1997), year-round spawning, and early age of reproduction (present study) play an important role in the life history of *Dendronephthya hemprichi*. The gamete release observed in *D. hemprichi* colonies at Eilat suggests year-round, nightly reproduction so that planulae are always available for settlement in favorable habitats.

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