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Reproduction in the Red Sea soft coral *Heteroxenia fuscescens*: seasonality and long-term record (1991 to 1997)

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Abstract *Heteroxenia fuscescens* is a common zooxanthellate soft coral on the shallow reefs in the Gulf of Eilat, northern Red Sea. In the Red Sea, during its prolonged planulation, *H. fuscescens* is subjected to a seasonal environmental regime that alternates between stratified warm summer waters and upwelling of low-temperature winter waters. To examine the possible relationship between these seasonal fluctuations and the reproductive characteristics of *H. fuscescens,* we monitored its breeding activity for a 6-year period, including the percentage of colonies releasing planulae, number of planulae released per colony per night (fecundity), planula size and percentage of released deformed planulae. During summer and fall the combined average percentage of planulating colonies of *H. fuscescens* was significantly higher than in winter and spring. In addition, fecundity was greater during the summer than the rest of the year. Planulae released during summer were longer, with almost zero percent deformation. During the rest of the year they were shorter, with a higher percentage of deformation. The current study indicates that although *H. fuscescens* reproduces all year round, the quantity and quality of its reproductive features are subject to seasonal variability. In the Gulf of Eilat seasonal changes in the abiotic features of the water may have an impact on its reproduction. During summer, primary productivity reaches a distinctive maximum up to a depth of about 40 m. The winter upwelling waters introduce nutrients from the depths into the upper 200 m, and especially into the major primary productivity zone, thereby triggering the annual phytoplankton bloom. Because colonies of *H. fuscescens* gain nutritional benefit from uptake of organic material dissolved in the water and by carbon fixation by zooxanthellae, we suggest that the seasonal fluctuations in the species' reproductive traits are related to these fluctuations in nutrient and light levels.

Introduction

In the Red Sea, soft corals (Octocorallia: Alcyonacea) are the second most important faunistic component occupying space on the reefs, comprising more than 180 species (Benayahu 1985, 1990). The family Xeniidae is represented there by five genera, constituting a total of 29 species that form dense coverage over large reef areas below the surf zone (Benayahu 1990). For many years sexual reproduction in octocorals was best known for the temperate species *Alcyonium digitatum* (see Hartnoll 1975). In the last two decades, however, accumulated knowledge of the reproduction of Indo-Pacific species (see references in Benayahu 1991, 1997) has emphasized the plasticity of their sexual characteristics, and three modes of reproduction are known for reef alcyonaceans: broadcast spawning, internal brooding and external surface brooding of planulae. A large variety of species of the family Alcyoniidae are broadcast spawners, although a recent study indicates that members of the Nephtheidae such as *Dendronephthya hemprichi* and *D. sinaiensis* also reproduce in this way (Benayahu 1997; Dahan and Benayahu 1997). Planulation is demonstrated by numerous Xeniidae species such as *Heteroxenia fuscescens*, *Xenia macrospiculata* and *X. umbellata*, as well as the Nephtheidae species *Litophyton arboreum* and *Nephthea* sp. (Benayahu 1991, 1997; Benayahu et al. 1992). External surface brooding has been described for the Red Sea *Parerythropodium fulvum fulvum* and *Clavularia hamara* (Benayahu 1997).

Most of the broadcasting stony corals (Harrison and Wallace 1990) and soft corals (Benayahu 1997) have a brief and highly synchronized reproductive period.

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However, brooders demonstrate prolonged annual breeding activity (Harrison and Wallace 1990; Dahan and Benayahu 1997). In the Gulf of Eilat (Red Sea), most stony and soft corals reproduce during the summer, coinciding with high water temperature (e.g. Shlesinger and Loya 1985; Benayahu 1997). Seasonal variation in seawater temperature has been widely accepted as the most important environmental factor in the timing of reproduction in reef corals (e.g. Shlesinger and Loya 1985; Babcock et al. 1986; Harrison and Wallace 1990; Pearse 1990; Fadlallah 1996; Acosta and Zea 1997; Benayahu 1997). Seasonal variation in reproductive rates of species with prolonged breeding activity was found in the stony coral *Stylophora pistillata* and later in the soft coral *Dendronephthya hemprichi* (Rinkevich and Loya 1979; Dahan 1992; respectively). Year-to-year variability in planulation intensity was found in *S. pistillata* and in the soft coral *Litophyton arboreum* (Rinkevich and Loya 1987; Weil 1990; Ben-David-Zaslow 1994). There is still much to learn about long-term trends and variability in reproduction traits of corals.

Heteroxenia fuscescens is a common zooxanthellate soft coral on shallow reefs in the Gulf of Eilat, northern Red Sea (Benayahu 1985). The main nutritional source of the coral is from the uptake of dissolved organic material and from carbon fixation by its zooxanthellae, while particulate food is of a lesser importance (Schlichter and Liebezeit 1991). At Eilat *H. fuscescens* displays continuous gametogenesis and planulation throughout the year without lunar synchronization (Benayahu 1991). Upon release, the mature planulae lack zooxanthellae, and the primary polyps acquire the symbiotic algae during early metamorphosis (Benayahu et al. 1989). In the Red Sea *H. fuscescens* is subjected during its prolonged planulation to a seasonal environmental regime that alternates between stratified warm summer water and upwelling of low-temperature winter water (Lindell and Post 1995). The waters of the Gulf of Eilat undergo stronger seasonal fluctuations than those of other subtropical seas. During summer, the water column is stratified, and the surface layers become depleted of nutrients (Reiss and Hottinger 1984; Erez et al. 1991; REEFLUX 1991; Genin et al. 1995). Therefore we suggest that reproductive traits of *H. fuscescens* respond to temporal changes in the environment. In order to examine such possible relationships, we monitored the breeding activity of *H. fuscescens* for a 6-year period, including percentage of colonies releasing planulae, number of planulae released per colony per night (fecundity), planula size and percentage of released deformed planulae.

Materials and methods

Study site

The Gulf of Eilat is a narrow basin, about 2 km deep, 180 km long and 6 to 25 km wide, situated at the northern end of the Red Sea, and separated from it by the Straits of Tiran (see Lindell and Post 1995). This narrow connection between the Gulf and the Red Sea has a major impact on water column mixing efficiencies, and on nutrient dispersion in the Gulf. Water exchange is effected by differences in salinity, and as a result the high salinity water from the Gulf exits through the deeper water layer, while water lower in salinity and nutrients enters from the Red Sea through the upper water layer (Reiss and Hottinger 1984). In the Gulf of Eilat intensive stratification occurs in the summer, reaching its maximum during August, at which time the thermocline is between the surface (27 °C) and 200 m deep (21.7 °C), with almost no mixed layer. In September the surface temperature starts to decrease, and a mixed layer appears. During the next 4 months (October to January) water temperature continues to drop to a minimum of about 21 °C, until the thermocline disappears, and the water column is completely homothermal. In April the thermocline reappears, and stratification builds up again. Vertical mixing during the cold months transports nutrients from the depths and enriches the upper water layers, which are poor in nutrients during the hot summer months (Erez et al. 1991; REEFLUX 1991). Other than this mixing event, there are no additional significant sources of nutrients in the Gulf (Levanon-Spanier et al. 1979).

Sampling

Colonies of *Heteroxenia fuscescens* were sampled randomly from the coral reef (3 to 6 m deep) across from the Marine Biology Laboratory at Eilat over a 6-year period (October 1991 to September 1997). Planulation was monitored monthly in the laboratory for at least three successive nights, using eight fresh colonies each night. The seawater temperature was recorded at 4 m depth at the MBL reef. Sexually mature colonies of approximately the same size were placed in containers with running seawater, at a flow rate of 2 liter min^{-1}. Prior to sunset each colony was transferred to a separate aerated aquarium, and examined the following morning for the presence of planulae (see also Ben-David-Zaslow and Benayahu 1996). For each colony, the released planulae were counted and placed in 500-ml PVC containers filled with filtered (0.2 μm) seawater. For each colony for the last 3 years of the study (1994 to 1997) planulae length was measured under a binocular, and the percentage of deformed individuals with irregular shape (see also Benayahu and Loya 1984) was calculated. Colonies were replaced on the reef after the trial, and no colony was sampled repeatedly.

The seasons were defined in this study according to the stability of the water column, following Lindell and Post (1995). "Winter" refers to December–March, "spring" to April and May, "summer" to June–September, and "fall" to October and November. We considered an annual cycle to commence in October, when the thermocline starts to break, till September when it is still in evidence. All analyses of temporal changes in reproductive features of *Heteroxenia fuscescens* were performed according to these defined periods. Statistical procedures of the percentage data were carried out after arcsine-transformation to satisfy the conditions of normality and equal variance. In all figures (see "Results"), variation around the means is given as standard deviation (SD).

Results

There was no significant difference among the years in the percentage of colonies releasing planulae (Fig. 1; ANOVA, $p > 0.05$). *Heteroxenia fuscescens* planulated nearly all year round, with the exception of certain months in the winter (Fig. 1a, b, d–f) and/or in the spring (Fig. 1a, f). Over the course of the entire monitoring period, 13.5 ± 9.0 percentage of all sampled colonies reproduced each month ($n = 63$ months). Throughout the 6 years of observations the monthly percentage of planulating colonies corresponded with

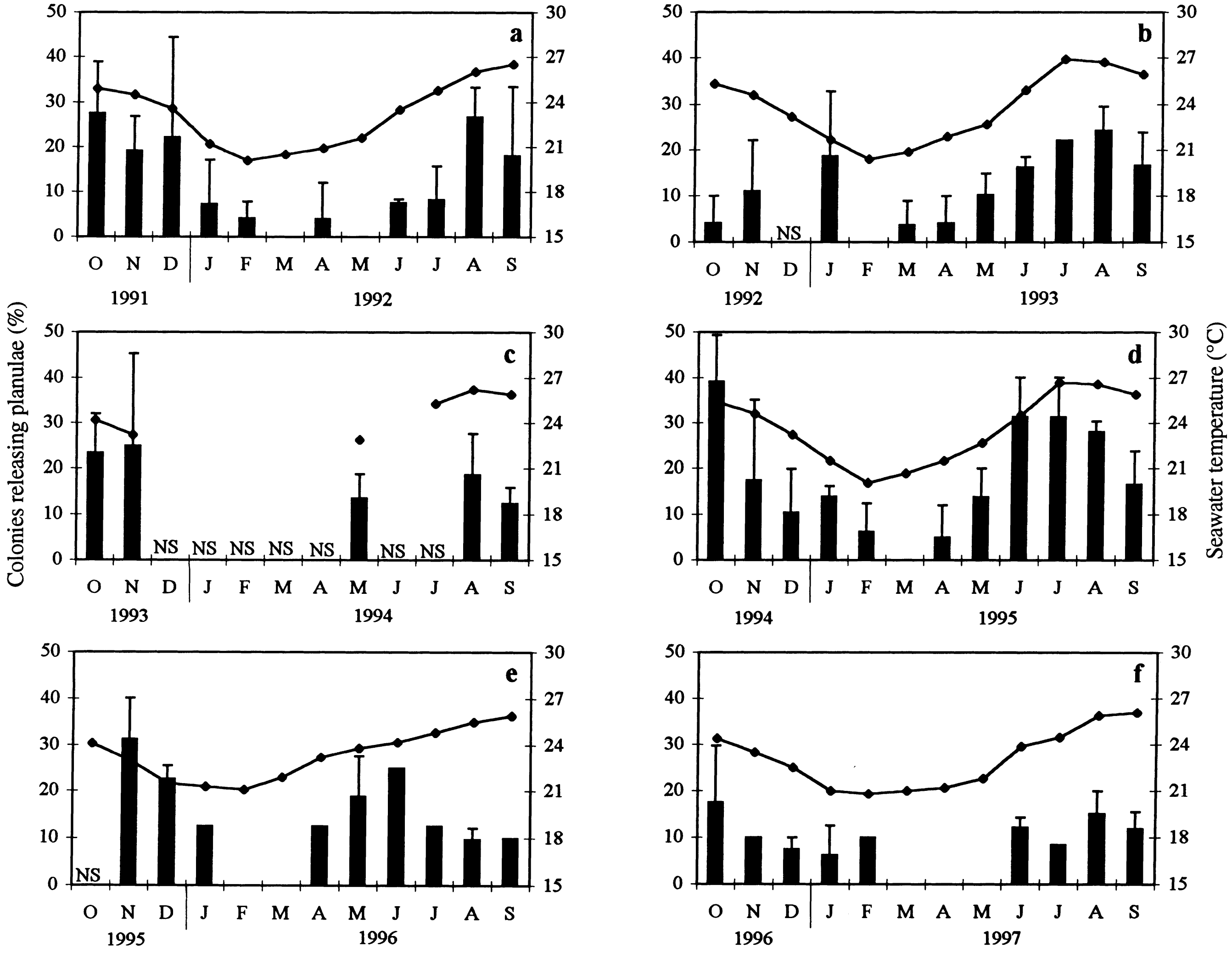

Fig. 1 *Heteroxenia fuscescens*. Average percentage of colonies that reproduced each month over the 6 studied years. Line represents the water temperature curve (*NS* no sampling)

the water temperature curve, i.e., a higher percentage was noted when the temperature was high and vice versa. There was a significant difference between the combined average percentage of colonies releasing planulae in the summer and fall (June to November; 18.5 ± 8.4%, $n = 33$ months), and that of the winter and spring (December to May; 7.6 ± 7.0%, $n = 30$ months; t-test, $p < 0.001$).

Significant differences (one-way ANOVA, $p < 0.001$) were recognized among the average number of planulae released per colony on a given night in the different seasons (Fig. 2). During the summer a colony may release several hundred planulae per night; however, during the rest of the year some colonies may release a much lower number. The number of planulae released per colony per night was 690 ± 498 in the summer ($n = 22$ months), whereas in the fall, winter and spring it was only 166 ± 138 ($n = 11$ months), 151 ± 216 ($n = 19$ months) and 208 ± 267 ($n = 11$ months), respectively. Significant differences (one-way ANOVA, $p < 0.05$) were found among the average number of planulae released per colony per night over the different studied years. In the first year this average was 475 ± 616 ($n = 12$ months), in the second 577 ± 413 ($n = 11$ months), in the third 598 ± 478 ($n = 5$ months), in the fourth 330 ± 298 ($n = 12$ months), in the fifth 85 ± 108 ($n = 11$ months) and in the sixth 185 ± 154 ($n = 12$ months). A least-significance-difference (LSD) test identified significant differences between the first 4 years (Fig. 2a–d), compared to the last 2 (Fig. 2e, f; $p < 0.05$). Even in the summer of the last 2 years this average reached no more than 194 ± 78 planulae per colony per night ($n = 8$ months).

There was no significant difference in planula length and in the percentage of deformed planulae during the last 3 years of the study, October 1994 to September 1997 (one-way ANOVA, $p > 0.05$). However, significant seasonal differences in planula length (Fig. 3) and percentage of deformed planulae (Fig. 4) were obtained between the summer and the other seasons during this period (LSD-test, $p < 0.05$). Summer released planulae were 3.6 ± 0.4 mm in length ($n = 12$ months), with only 0.9 ± 1.4% deformed. During the rest of the year

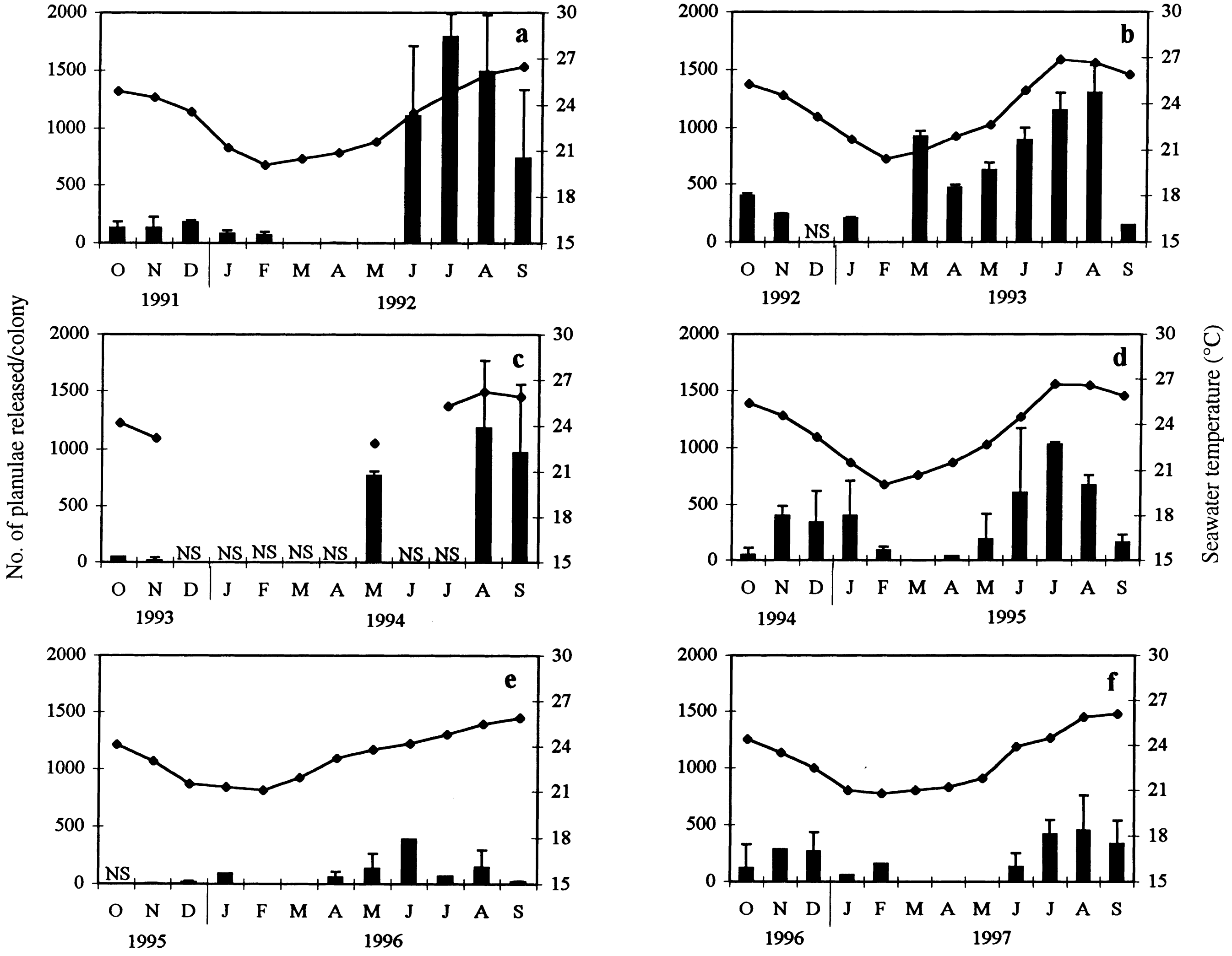

Fig. 2 *Heteroxenia fuscescens*. Average number of planulae released per colony per night each month over the 6 studied years. Line represents the water temperature curve (*NS* no sampling)

they were shorter (fall: 3 ± 0.6 mm, $n = 5$ months; winter: 2.4 ± 0.5 mm, $n = 8$ months; spring: 2.9 ± 0.4 mm, $n = 4$ months) with a higher percentage of deformation (fall: 2.1 ± 1.85, $n = 5$ months; winter: 17.2 ± 10.3, $n = 8$ months; spring: 10.6 ± 9.3, $n = 3$ months).

Discussion

Seasonality in coral reproduction has been well documented (Babcock et al. 1986; Aliño and Coll 1989; Harrison and Wallace 1990; Benayahu 1991, 1997). Variability in planulation intensity of reef dwelling anthozoans within their reproductive season has been recorded in some species, such as *Stylophora pistillata* (Rinkevich and Loya 1979), *Pocillopora damicornis* (Ward 1992) and *Xenia macrospiculata* (Benayahu and Loya 1984). However, there are only a few long-term studies which have monitored year-to-year variation in coral reproduction (Rinkevich and Loya 1987; Weil 1990; Ben-David-Zaslow 1994). The present study is the first to report variability in reproductive features of a soft coral both among seasons and successive years. During summer and fall the percentage of planulating colonies of *Heteroxenia fuscescens* was significantly higher than in winter and spring (Fig. 1). In addition, fecundity was greater during the summer than during the rest of the year (Fig. 2). In the summer the planulae were longer (Fig. 3) and few of them displayed deformity (Fig. 4). In a previous study we demonstrated a longer competence period for *H. fuscescens* planulae during summer (49 d) compared to winter (34 d). Almost all summer planulae were competent to metamorphose, while in the winter only 52% settled and metamorphosed (Ben-David-Zaslow and Benayahu 1996).

In the Gulf of Eilat the vast majority of soft and stony corals reproduce during the summer (Shlesinger and Loya 1985; Benayahu 1997). *Stylophora pistillata* demonstrates a prolonged annual planulation period of 6 to 9 months, while *Heteroxenia fuscescens* and

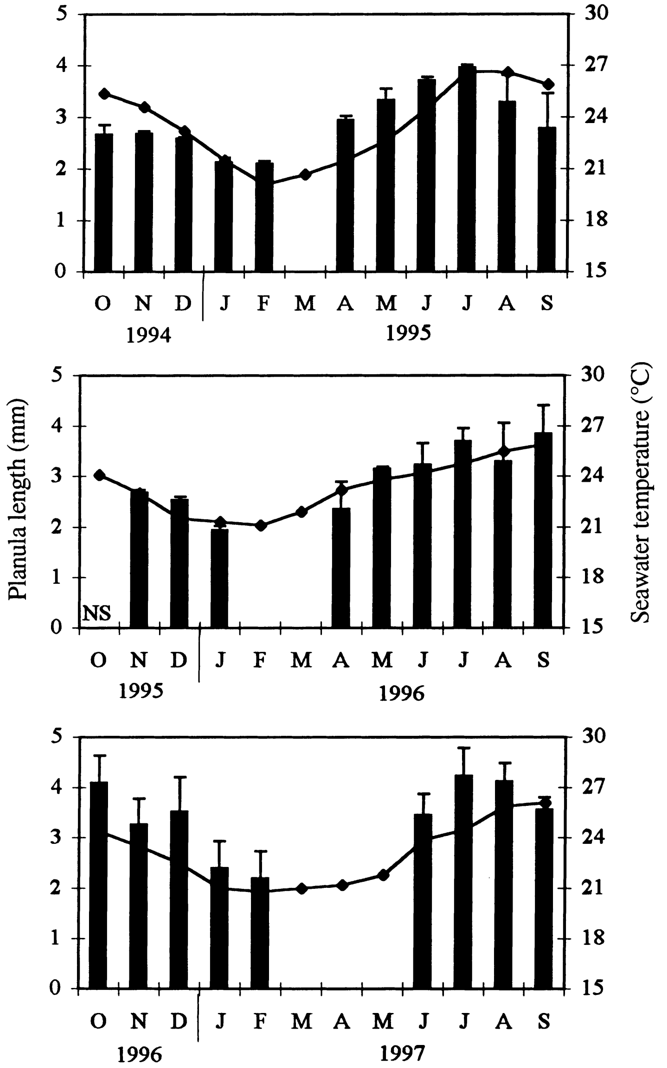

Fig. 3 *Heteroxenia fuscescens*. Average length of planulae released each month over the 3 studied years. Line represents the water temperature curve (*NS* no sampling)

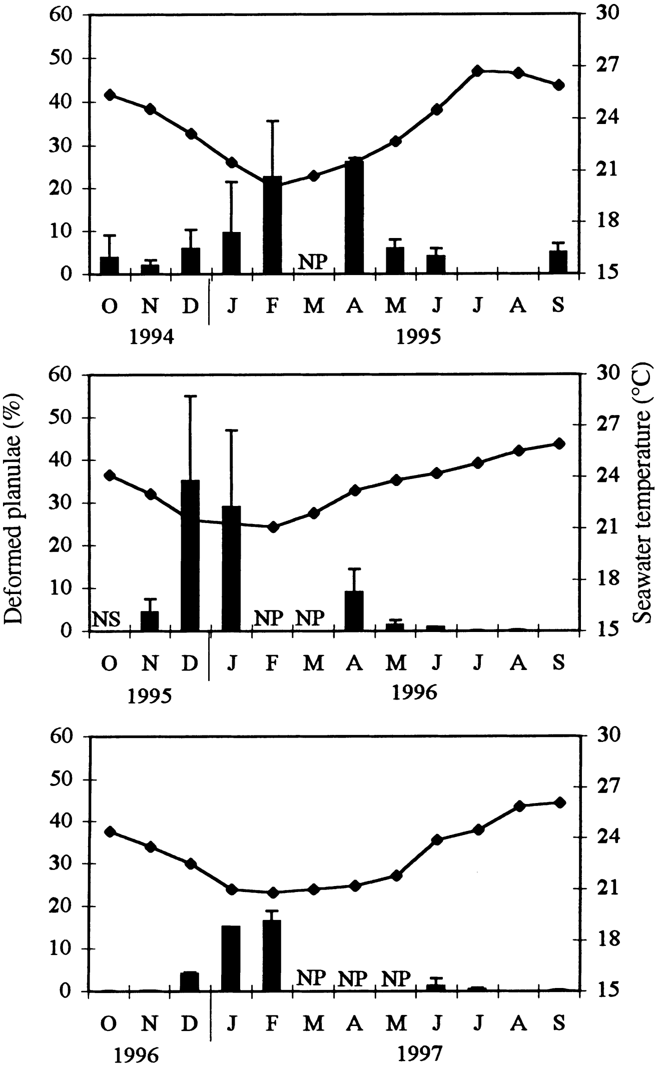

Fig. 4 *Heteroxenia fuscescens*. Average percentage of deformed planulae released per colony per night each month over the 3 studied years. Line represents the water temperature curve (*NS* no sampling; *NP* no planulae)

Dendronephthya hemprichi (Rinkevich and Loya 1987; Benayahu 1991; Dahan and Benayahu 1997; respectively) show year round reproductive activity. Fecundity in *D. hemprichi* was significantly higher during the summer than in the winter (Dahan 1992). The current study indicates that although *H. fuscescens* reproduces all year round, the quantity and quality of this species' reproductive features show seasonal variability.

Many recent studies have suggested that water temperature is not the only, or direct factor, affecting reproduction in marine invertebrates (Hartnoll 1975; Harrold and Pearse 1980; Szmant-Froelich and Pilson 1984; McClintock and Watts 1990; Vernon et al. 1993; Fan and Dai 1995; Fautin 1995; Fadlallah 1996; Knowlton et al. 1997). Fan and Dai (1995) suggested that sea temperature does not operate as a proximate cue for the timing of reproductive activity in the stony coral *Echinopora lamellosa* in Taiwan, and that its spawning season may reflect the environmental conditions favoring the survival of its planktonic planulae. McClintock and Watts (1990) showed in the tropical sea urchin *Eucidaris tribuloides*, and Vernon et al. (1993) in the irregular echinoid *Clypeaster ravenelii* from the Gulf of Mexico, that day length may serve as an exogenous proximate cue for gametogenesis and/or spawning. Fadlallah (1996), who monitored synchronization in spawning of the stony coral *Acropora clathrata* for 6 years, noted that the only constant and predictable annual factor was day length. Similarly, it was found for three species of the stony coral *Montastrea* that simulation of an early sunset for several days could reset the spawning event (Knowlton et al. 1997). Reproduction may also be related to seasonal fluctuations in food availability, as shown for *Alcyonium digitatum* by Hartnoll (1975) and the stony coral *Astrangia danae* by Szmant-Froelich and Pilson (1984). Photosynthetically fixed carbon plays a major energetic role in growth and reproduction of corals (Sutton and Hoegh-Guldberg 1990; Brown and Ogden 1993). During summer, when temperature and light levels are higher, more photosynthetically derived energetic resources are available (Falkowski et al. 1990). Therefore, we suggest that in summer more resources are also allocated to reproduction.

In the Gulf of Eilat seasonal changes in the abiotic features of the water may have an impact on reproduction in *Heteroxenia fuscescens*. During summer, primary productivity reveals a distinctive maximum up to a depth of about 40 m (Genin et al. 1995). The winter mixing water brings up nutrients from the depths into the upper 200 m, especially into the major primary productivity zone, thereby triggering the annual phytoplankton bloom. There are two algal blooms per annum: the major bloom which starts in February and lasts for almost 2 months, and the minor fall bloom which starts in mid-September and lasts for about 3 months. The former starts with the onset of the summer thermocline, and the latter with the fall erosion of the thermocline and the beginning of winter mixing (REEFLUX 1991; Genin et al. 1995). Since colonies of *H. fuscescens* gain nutritional benefit from the uptake of organic material dissolved in the water as well as by carbon fixation by zooxanthellae (Schlichter and Liebezeit 1991) and, presumably, do not in any way directly benefit from the abundance of phytoplankton in the water, we suggest that the seasonal fluctuations in its reproductive features are related to these changes in nutrient and light levels. The winter nutrient enrichment may intensify gonad development and thus lead to a later increased planulation during summer. This high production of planulae is further enhanced in summer by the high carbon fixation resulting from the appropriate light and temperature regimes.

In summer 1992 the fecundity of *Heteroxenia fuscescens* was the highest recorded in the entire monitoring period, and colonies released up to 2000 planulae per colony per night. In the winter of 1992 an unusual vertical mixing event occurred in the Gulf of Eilat, extending to >850 m depth and thus resulting in an increased supply of nutrients to the surface waters, which fuelled extraordinarily large benthic algae and phytoplankton blooms (Genin et al. 1995). No similar event has occurred since. Moreover, the thermocline has not deteriorated, probably causing a cumulative deficit in nutrient levels of the surface water (B. Lazar, personal communication). Consequently, these conditions may have led to a gradual decrease in the fecundity of *H. fuscescens* (Fig. 2). Further data on nutrient uptake and the energetic investment in planulae production are still needed in order to better understand the factors regulating long-term variation in reproductive features of *H. fuscescens*.

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