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Longevity, competence and energetic content in planulae of the soft coral *Heteroxenia fuscescens*

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Abstract

The longevity and competence period of the azooxanthellated planulae of the soft coral *Heteroxenia fuscescens*, a common shallow-reef inhabitant on the Red Sea reefs, were studied for the first time. The caloric content of the planulae in the course of their life is determined and its possible significance for the longevity and competence periods is considered. *H. fuscescens* planulae are able to metamorphose immediately upon release and tend to settle adjacent to their parent colonies. The current study presents evidence for absence of a pre-competence period. A maximal longevity of 50 days and a competence of 49 days were recorded, providing an effective dispersal time which encompasses virtually the entire lifespan of the planulae. A monthly variation was found in longevity and competence, possibly temperature related; significantly higher metamorphosis rates occurred during the hotter months of the year, indicating the occurrence of additional temporal variations related to the species reproduction. During late stages of the experiments most of the planulae underwent partial metamorphosis, probably due to a lack of necessary inducers for settlement. It is hypothesized that these polyps may obtain zooxanthellae through their mouth opening, thus acquiring the energy to extend their pelagic life, until they encounter such settlement inducers. Two-day old planulae had a caloric content of 0.58 ± 0.05 cal × planula^{-1}; which decreased gradually with age, to a minimum of 0.35 ± 0.005 cal × planula^{-1} in 16-day old planulae. *H. fuscescens* has a wide distribution along the eastern coast of Africa, probably due to the longevity and competence of its planulae.

Keywords: Competence; Energetic content; *Heteroxenia fuscescens*; Longevity; Metamorphosis; Octocorallia; Planulae

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1. Introduction

Red Sea soft corals of the family Xeniidae (Octocorallia: *Alcyonacea*) are represented by five genera: Anthelia, Cespitularia, Heteroxenia, Sympodium and Xenia, comprising 29 species that provide dense coverage over large reef areas below the surf zone (Benayahu, 1990). The soft coral *Heteroxenia fuscescens* is common on shallow-reefs in the northern Red Sea (Benayahu, 1985). The colonies possess zooxanthellae and are characterized by polyp dimorphism, having two kinds of polyps, autozooids and siphonozooids, in adult colonies (Achituv and Benayahu, 1990). *H. fuscescens* demonstrates continuous gametogenesis and planulation throughout the year in the northern Red Sea (Benayahu, 1991). The immature planulae develop within the autozooids and are later translocated externally to the intersiphonozooid spaces, where they mature (Benayahu et al., 1989a). Upon release, the planulae (Fig. 1a) lack zooxanthellae and the primary polyps are infected by symbiotic algae during the third day of metamorphosis in the field (Benayahu et al., 1989b).

Among marine invertebrates, settlement and subsequent metamorphosis of larval

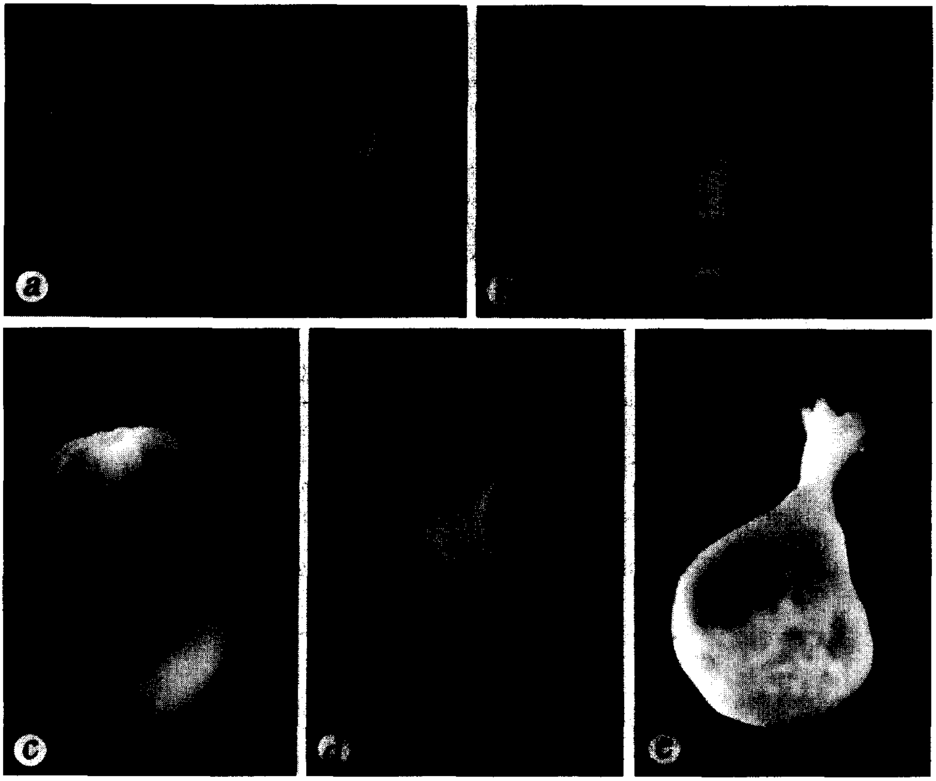

Fig. 1. *Heteroxenia fuscescens*. (a) 5-day old planulae; (b) 1-month old primary polyp; (c–e) Partially metamorphosed planulae: (c) 2-day old (d) 7-day old (e) 14-day old.

stages constitute major events in their life cycle. Many sessile organisms release large numbers of free-swimming propagules into the water that settle after dispersal (Crisp, 1984). Free swimming larvae have the potential to link populations and may play a major role in determining probabilities of extinction and speciation (Pechenik, 1990; Pechenik and Cerulli, 1991). For marine invertebrate larvae, competence is operationally defined as the ability to metamorphose following exposure of larvae to a demonstrated natural inducer. This definition, while functional and ecologically appropriate, does not account for the factors and steps which may intervene between initial induction of settlement behavior and subsequent metamorphosis (Coon et al., 1990). Larvae become competent to metamorphose at a certain stage of their development, which may occur either before their release into the water or, alternatively, after a certain period of free swimming (Pechenik, 1990; Harrison and Wallace, 1990). Numerous chemical and physical factors can influence the patterns of initial larval settlement; in their absence metamorphosis may be delayed, but the capacity to metamorphose remains (Chia and Bickell, 1978; Pechenik and Eyster, 1989; Pechenik, 1990; Walters, 1992). The ability to postpone metamorphosis in the absence of suitable conditions allows the larvae to choose habitats most likely to support their future survival and successful reproduction (Crisp, 1974; Paige, 1988; Pechenik, 1990; Pechenik and Cerulli, 1991; Walters, 1992). Several studies have suggested that bacteria can induce settlement and metamorphosis of such larvae and, therefore that antibiotics prevent it (Neumann, 1979; Richmond, 1987; Fitt et al., 1989; Johnson et al., 1991; Pawlik, 1992; Leitz, 1993)

Most of the available data on metamorphosis, competence and delayed metamorphosis of marine invertebrate larvae are derived from laboratory studies (Pechenik, 1990). Only a few attempts have been made to determine larval capacity to delay metamorphosis; the intent of most research on this topic was aimed rather at discovering which factors best trigger the process (Crisp, 1974, 1984; Butman, 1987; Pechenik, 1990). Field studies carried out by Hadfield, 1978 and Pechenik, 1986 presented evidence for sporadic delayed metamorphosis in some plankton samples. The potential for export of large numbers of coral planulae from Kaneohe Bay, Hawaii is considered high, but whether they delay metamorphosis while remaining capable of recruiting on reefs outside the bay is yet to be determined (Hodgson, 1985). Both metamorphosis and competence have been shown to be related to the larval energy content (Lucas et al., 1979; Richmond, 1987, 1988; Pechenik, 1990; Qian et al., 1990; Harms, 1992; Jaeckle and Manahan, 1992; Havenhand, 1993).

The only published studies on the competence period of coral planulae are by Richmond, 1987, 1988, who reported values of 20 and 100 days for planulae of the stony corals *Acropora tenuis* and *Pocillipora damicornis*, respectively, and further claimed that the energetic content of the planulae determined the obtained results. The high energetic content of *P. damicornis* planulae along with the presence of zooxanthellae that furnish photosynthetic carbon, enables the longer competence period. This in turn increases their dispersal period (Richmond, 1988). A maximum competence period of at least 58 days was found in a recent study on planulae of the Red Sea soft coral *Dendronephthya hemprichi* (Dahan and Benayahu, in prep.). The present study examines for the first time the longevity and competence period for planulae of the soft coral *H. fuscescens*. The caloric content of the planulae in the course of their life was also determined, and its possible significance for longevity and competence is considered.

2. Materials and methods

2.1. Collection of corals and larvae

Colonies of *H. fuscescens* were sampled on the coral reef in front of the Marine Biology Laboratory (MBL) at Eilat (Red Sea) during April 1992–November 1993. Sexually mature colonies were placed in containers with running seawater flowing at a rate of 2 l × min^{-1}. Prior to sunset the colonies were transferred to aerated aquaria and examined the following morning for the presence of released planulae. The planulae were collected and placed in 500 ml PVC containers, filled with Millepore-filtered (0.45 μm) seawater (FSW) containing Ampicillin at a concentration of 50 $\mu g \times ml^{-1}$. The obtained planulae (1–2 days old) were transported to Tel-Aviv for the experiments, all conducted in natural Red Sea water. The number of planulae available varied throughout the year and dictated the experimental design. All following experiments, throughout the study period, were conducted in water temperature corresponding to the ambient Red Sea temperature.

2.2. Natural settlement of the planulae

On August 1992 five batches of 150 freshly released planulae were placed in aquaria in the MBL, each containing 5 l of seawater (26°C) and natural reef substrata (fragments of dead *Stylophora pistilata* colonies). Settlement and metamorphosis of the planulae were monitored every few hours during the first 2–3 days, and then every 3–5 days for a total of 20 days.

2.3. Determination of the standard antibiotic mixture

In order to obtain an antibiotic mixture that would not harm the planulae, yet would prevent their settlement and metamorphosis, on April 1992 the following antibiotics were tested: (a) Ampicillin sodium salt (50 $\mu g \times ml^{-1}$; Strathmann, 1987); (b) Rifampicin (5 $\mu g \times ml^{-1}$; Morse and Morse, 1991); (c) a mixture of Penicillin-G potassium salt, Neomycine sulfate and Streptomycin sulfate (100 $\mu g \times ml^{-1}$ each; Fitt et al., 1992), subsequently referred to as PNS. In addition FSW (0.2 μm; Strathmann, 1987) was examined and microbial tests were conducted to check its sterility by placing drops of water on marine agar plates. Longevity, time to 50% mortality, percentage of metamorphosis and metamorphosis rate of 150 *H. fuscescens* planulae were tested in each of these antibiotic mixtures and the FSW. All tests were conducted at 22°C.

2.4. Longevity of the planulae

Planulae were washed with FSW (0.45 μm) to remove organic debris, and later placed in batches of up to 250 planulae in Erlenmeyer flasks, each containing 300 ml FSW (0.45 μm) with Ampicillin (50 $\mu g \times ml^{-1}$). Six experiments were run, in June, July, August, October and November 1992 and April 1993, with 500, 485, 977, 350, 380 and 470 planulae respectively. The flasks were placed in a temperature room corresponding to the ambient Red Sea water-temperature (21–26°C). The planulae were transferred to clean flasks with fresh FSW containing Ampicillin every 2–3 days. Planulae were counted every 5 days and their survival was recorded.

2.5. Competence of the planulae

Planulae were similarly maintained as for the longevity experiments. They were removed at various time intervals and washed with FSW (0.45 μm) to remove residual antibiotics. They were then placed in 24-well tissue-culture plates, each well containing 2.5 ml water. The number of planulae that metamorphosed were recorded, and their competence period determined. Planulae were considered to have metamorphosed only after they had settled and developed a mouth opening and tentacle buds (Fig. 1b). Seven experiments were performed, in June, August, September, October, November 1992, and March and April 1993 with 360, 530, 270, 200, 243, 200 and 260 planulae respectively.

2.6. Calorimetric analysis

The caloric content of planulae and primary polyps was measured by a Phillipson Microbomb Calorimeter in August 1992. Batches of 250 freshly released planulae, planulae of 2, 6, 13 and 16 days and primary polyps were analyzed (two replicates for each stage). Calibration curves for the Microbomb Calorimeter work were calculated using benzoic acid samples (Scott and Marlow, 1982). The daily average energy loss was calculated according to the equation: $El = (Ec_1 - Ec_2) \cdot \Delta dt^{-1}$, where El is the daily average energy loss, Ec_1 is the energy content in calories at the beginning of a period, Ec_2 is the energy content at the end of the period, and Δdt is the number of days for each period.

3. Results

3.1. Natural settlement of the planulae

Among the planulae of *H. fuscescens* 40% ($n = 5$) were competent to metamorphose upon their release into the water. Freshly released planulae tended to sink immediately after release to the bottom of the experimental aquaria, settling on the dead fragments of *S. pistilata* or adjacent to their parent colonies. In all these experiments 50% of the planulae settled and metamorphosed during the first 2–3 days, and the remainder in the

Table 1
Longevity and time to 50% mortality for planulae of *Heteroxenia fuscescens* tested in different conditions

	Ampicillin	Rifampicin	PNS	FSW
Longevity (days)	43	32	27	18
Time to 50% mortality	27	17	17	17

course of the following two weeks. By the end of the experiments, which ran for 17 days, the average percent metamorphosis was 86±8.6%.

3.2. Determination of the antibiotic mixture

Planulae became deformed in the PNS mixture, changing in shape from their normal elongated form to an irregular one, and developing blisters on the surface. Planulae underwent partial metamorphosis in all the antibiotic mixtures i.e., Ampicillin, Rifampicin and PNS and also in FSW, and developed tentacle buds and a mouth opening but did not settle (Fig. 1c–e). These polyps lived freely in the water until exposed to natural substrata, on which they settled and continued to develop normally.

The longevity and time to 50% mortality of the planulae, as obtained in each of the four tested media, are presented in Table 1. Planulae lived the longest (43 days) in Ampicillin treatment, while in Rifampicin, PNS and FSW they lived only for 32, 27 and 18 days, respectively. The time to 50% mortality of the planulae was 27 days in Ampicillin, but it was only 17 days in all other treatments. The percentage of metamorphosis in all the media is presented in Fig. 2. No planulae metamorphosed for the first 10 days in these experiments. The lowest metamorphosis (12%) was obtained in FSW (Fig. 2), with a total mortality of the planulae by day 18 of the experiment.

The microbial tests conducted on day 10 of the experiment showed that the FSW contained at least seven strains of bacteria. Antibiotics were used to control bacterial growth and, therefore, to prevent settlement and induction of metamorphosis of the planulae without damaging them. Planulae took longer to metamorphose in the

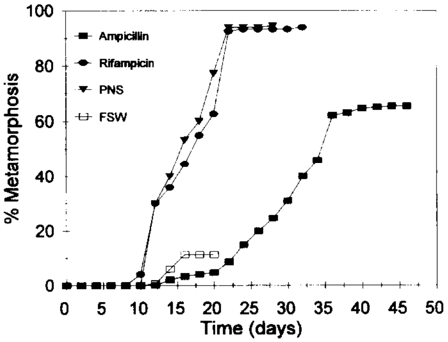

Fig. 2. Percentage of *Heteroxenia fuscescens* planulae which metamorphosed with time at 22°C in each of the antibiotic mixtures ($n = 1$, with 150 planulae per treatment).

Ampicillin treatment. In Rifampicin and PNS media 94% metamorphosis was achieved on day 23 of the experiment demonstrating a metamorphosis rate of 6.4% per day from day 10 onwards. By 33 days, in the presence of Ampicillin, only 64% of the planulae had metamorphosed, with a metamorphosis rate of only 1.9% per day between day 10 and day 43 of the experiment (Fig. 2). The above results (Table 1, Fig. 2) indicated the use of Ampicillin in FSW for the following experimental work, to keep the planulae alive for the longest possible time.

3.3. Longevity of the planulae

Planulae lived the longest for 50 days in October and November 1992, while in the other months lower values of 40 or 41 days were obtained (Fig. 3). During June, July, August 1992 and April 1993, the time to 50% mortality ranged between 33–37 days, and in October and November 1992 lower values of 24 and 21 days, respectively, were found (Fig. 3). The survivorship curves demonstrate the same pattern in all the experiments: a high survivorship during the first phase, followed by a decrease of 60–80% in planulae within a short period, and terminating with a few planulae only, which finally die (Fig. 3). Some of the planulae underwent partial metamorphosis on about day 35 of the experiments (see Fig. 1c–e).

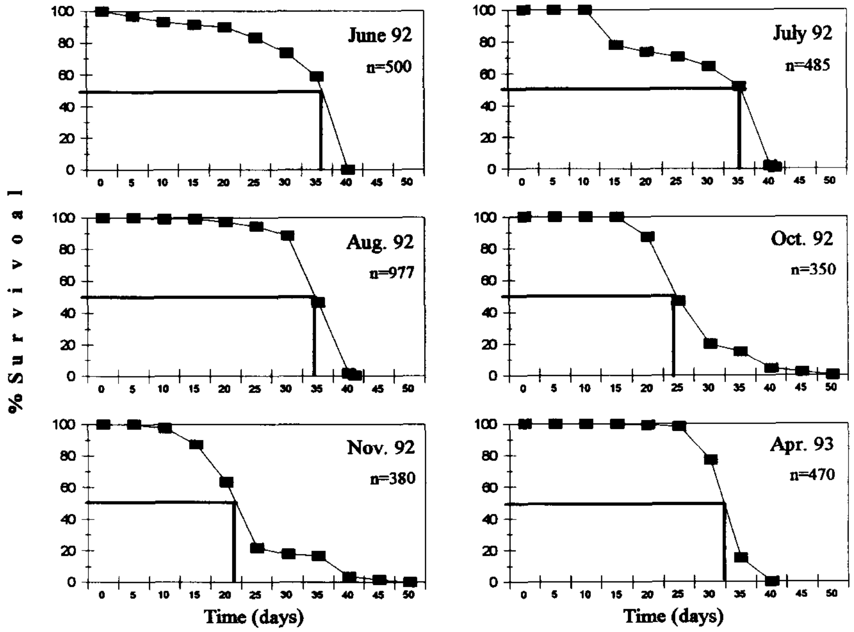

Fig. 3. Survival curves of *Heteroxenia fuscescens* during different months of the study, in Ampicillin at 21–26°C. Day 0 indicates planula release. Bold line indicates time to 50% mortality.

3.4. Competence of the planulae

Competence in *H. fuscescens* planulae to metamorphose was assessed by calculating the percentage undergoing metamorphosis with time. Metamorphosis started 5–10 days after terminating the Ampicillin treatment and accelerated sharply during the ensuing days. The average competence period was 34±7 days in all seven experiments (Fig. 4). The maximum competence period was recorded in November 1992, when four planulae remained competent for 49 days; in August 1992, 16 planulae were competent on day 38 of the experiment. The highest metamorphosis was obtained in June, August, September 1992 and April 1993, averaging 97.8±1.3%. Lower values were obtained in October, November 1992 and March 1993, averaging 52.3±16.1% (Fig. 4). The difference between these two averages is significant (*t*-test, $p<0.05$).

3.5. Calorimetric analyses

Two-day old planulae of *H. fuscescens* had a caloric value of 0.58±0.05 $\text{cal} \times \text{planula}^{-1}$ ($n=2$, with 250 planulae per replication). The caloric content of the planulae gradually decreased with age to a minimum of 0.35±0.005 $\text{cal} \times \text{planula}^{-1}$ in 16-day old planulae (Fig. 5), representing a daily energy loss of 0.016 $\text{cal} \times \text{planula}^{-1} \times \text{day}^{-1}$ over the entire experimental period. At this stage, the yield of planulae was too low for further caloric measurements. Between day 2 and 6 the calculated daily average loss was

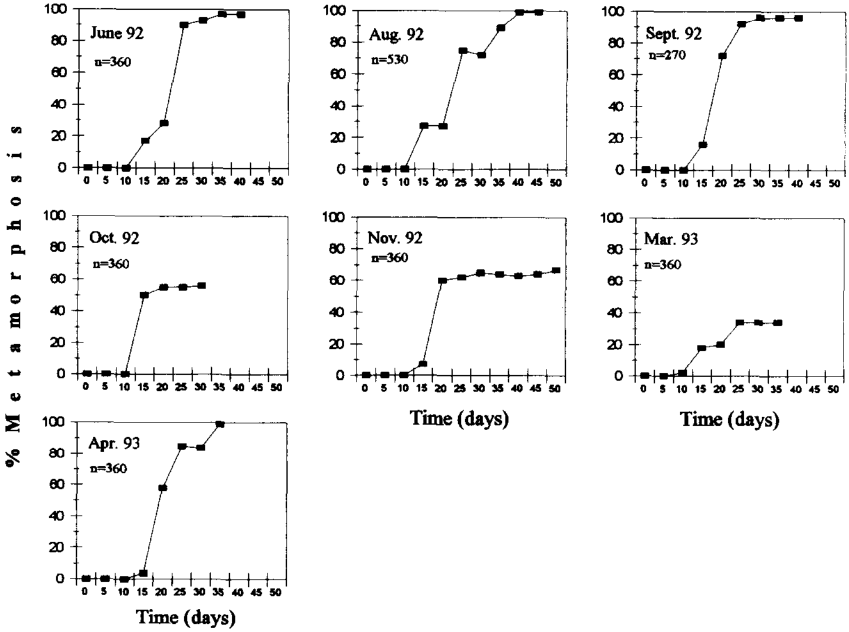

Fig. 4. Percentage of metamorphosis in *Heteroxenia fuscescens* planulae with time during the study at 21–26°C. Day 0 indicates planula release.

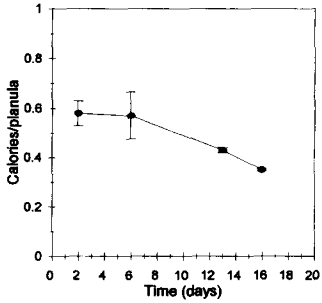

Fig. 5. The average caloric content of the *Heteroxenia fuscescens* planulae measured during the study (two replicates for each stage, $n = 250$).

0.0025 cal×planula^{-1}×day^{-1}; between day 6 and 13 they lost 0.019 cal×planula^{-1}× day^{-1}; and between day 13 and 16 they lost 0.028 cal×planula^{-1}×day^{-1}. These results show that newly-released planulae lost energy more slowly than the older ones. The caloric value of 2–4 day old primary polyps averaged 0.22±0.01 cal×polyp^{-1} ($n = 2$).

4. Discussion

Most *H. fuscescens* planulae are able to metamorphose immediately upon release and tend to settle adjacent to the parent colonies (Benayahu et al., 1989b; this study). Previous studies on planulae of both soft corals and stony corals described a pre-competence period of a few days (Sebens, 1983; Farrant, 1986; Harrison and Wallace, 1990; Morse et al., 1988). The current study, however, presents for the first time evidence for the absence of a pre-competence period among corals. The soft corals *Alcyonium digitatum* and *A. siderium* have a maximum longevity of 245 days and 194 days at 13°C±1°C, respectively (Hartenoll, 1975; Sebens, 1983). A period of planulae competence of 15 days has been reported for *A. digitatum* (Mathews, 1917), 49 for *A. siderium* at 13°C±1°C (Sebens, 1983), >30 for *Capnella gaboensis* (Farrant, 1986) and 20 for *Lobophytum crassum* at 25°C±2°C (Uehara et al., 1987). As all these results were obtained while keeping the planulae in non-sterile conditions, and in the presence of various natural substrata, it is probable that the longevity and competence values obtained were underestimates of the actual ones. In the present study the possibility of natural induction was eliminated by using the ampicillin mixture (Table 1, Fig. 2). This procedure permitted the determination of a maximum longevity of 50 days (Fig. 3) and a competence period of 49 days for *H. fuscescens* planulae (Fig. 4). The same procedure was also employed by Richmond, 1987, 1988, for stony corals, providing competence periods of 20 days for *A. tenuis* and 100 days for *P. damicornis*.

Pechenik (1990) suggested that environmental factors such as temperature and salinity influence the precompetent and competent periods. Our results indicate a monthly variation in longevity (Fig. 3) and competence (Fig. 4) which might be temperature related and which, in turn, may affect the energy expenditure of H. fuscescens planulae.

The significantly higher metamorphosis rates found during the spring and summer months (June, August and September 1992 and April 1993) (Fig. 4) imply further temporal variations in the breeding activity and the nature of the planulae. The year round planulation of *H. fuscescens* thus provides a unique opportunity to examine annual differences in the longevity and competence of planulae in relation to fluctuating environmental factors such as temperature and nutrient availability.

In the absence of specific environmental signals, larvae of many marine invertebrates are known to delay their metamorphosis. This ability is generally considered to be an advantage as it allows the larvae prolonged time to locate a habitat suitable for post-metamorphic development (Crisp, 1974; Paige, 1988; Pechenik, 1990; Pechenik and Cerulli, 1991; Walters, 1992). The time spent as an effective dispersal propagule depends on the length of time that larvae require to become competent and the amount of time that passes before they encounter the stimuli required to initiate their metamorphosis (Pechenik, 1990). In planulae of *H. fuscescens* the effective dispersal time encompasses virtually their entire lifespan, i.e., the competence period starts at their release and continues until death.

Most of the *H. fuscescens* planulae underwent partial metamorphosis at late stages in the experiments (see results), suggesting that despite lack of appropriate external triggers for settlement, progressed time lead to the scenario. A similar phenomenon has been found in larvae of the oyster *Crassostrea gigas* in which L-DOPA can induce both their settlement and metamorphosis, while epinephrine and norepinephrine only induces metamorphosis, without settlement (Coon et al., 1985). Different responses to natural and artificial inducers have been found in larvae of the gastropod *Phestilla sibogae* which exhibited partial metamorphosis in the presence of certain catecholamines. In some of the experiments carried out with low concentrations of catecholamines, larvae completed metamorphosis when transferred to water containing a natural inducer (Hadfield, 1984). We suggest that partial metamorphosis of *H. fuscescens* planulae resulted from the lack of necessary inducers for their settlement and is endogenously controlled. The ability of the metamorphosed polyps to maintain the potential to settle when exposed to a suitable substratum increases their likelihood of finding sites appropriate for normal settlement. We hypothesize that partially metamorphosed polyps may acquire zooxanthellae through their mouth opening (see Benayahu et al., 1989b), and these in turn furnish them with energy to extend their pelagic life, until they encounter inducers for settlement.

In general corals are regarded to have a nonfeeding larval stage (Crisp, 1984); however some exceptions do exist (Harrison and Wallace, 1990). The nonfeeding larvae are assumed to have ample nutritive content on which they rely and are, therefore, often called lecithotrophic (Crisp, 1984; Jaeckle and Manahan, 1989; Havenhand, 1993). However, no study has examined the possible uptake of dissolved organic material (DOM) by coral planulae, a resource known to be utilized by other marine larvae (Jaeckle and Manahan, 1989; Jaeckle, 1994). Absorption of DOM by planulae might contribute to their energy budget and thus extend their longevity and competence periods. Several studies have shown that these periods are related to the energy content of the released larvae and to the energy obtained during their planktonic phase (Richmond, 1987, 1988; Pechenik, 1990; Qian et al., 1990; Harms, 1992; Jaeckle and

Manahan, 1992; Havenhand, 1993). These energetic considerations are mostly suitable for species with lecithotrophic larvae, competent to metamorphose at release from the parent, or soon after (Pechenik, 1990). It has been concluded that knowledge of the initial amount of energy contained within a larva, the rate at which energy is expended under natural conditions, and the amount of energy that must be held in reserve to permit successful metamorphosis, will permit estimation of the length of time that metamorphosis can be delayed before the ability to metamorphose successfully is compromised (Lucas et al., 1979; Richmond, 1987, 1988; Pechenik, 1990; Jaeckle, 1994). For example, Cyprid larvae were shown to have the ability to swim for about four weeks at 10°C without utilizing reserves required for their metamorphosis, but the survival of larvae triggered to metamorphose beyond this period declined dramatically (Lucas et al., 1979). Jaeckle Jaeckle, 1994 found that larvae of the bryozoan *Bugula neritina* are generally capable of metamorphosis within 2 h of release, and that DOM transport provides the potential to extend their competence period by serving as an alternative source of energy. Two-day old planulae of *H. fuscescens* used in the present study possessed an average of 0.58 ± 0.05 $\mathrm{cal} \times \mathrm{planula}^{-1}$ and their energy expenditure during the next four days was minimal, 2.5×10^{-3} $\mathrm{cal} \times \mathrm{planula}^{-1} \times \mathrm{day}^{-1}$. The energy expenditure of the studied planulae increased with age (Fig. 5). Richmond, 1988 measured a caloric content of 0.74 $\mathrm{cal} \times \mathrm{planula}^{-1}$ and energy expenditure of 5.06×10^{-3} $\mathrm{cal} \times \mathrm{planula}^{-1} \times \mathrm{day}^{-1}$ in P. damicornis planulae and 0.29 $\mathrm{cal} \times \mathrm{planula}^{-1}$ and 2.93×10^{-3} $\mathrm{cal} \times \mathrm{planula}^{-1} \times \mathrm{day}^{-1}$ for *A. tenuis*. If one uses Richmond's equation (Richmond, 1988) predicting the competence period of planulae from energy content and rate of expenditure, a predicted competence period of 155 days is obtained for 2-day old planulae of *H. fuscescens* which is 3-fold greater than the duration actually found in the current study (49 days). The low experimental value may be due to increased energy expenditure actually measured with the aging of *H. fuscescens*.

Richmond, 1987, 1988 suggested that the competence periods calculated for the two stony coral species permit the prediction of their biogeographical distribution. *H. fuscescens* has a rather wide distribution along the eastern coast of Africa, extending from the Red Sea in the north (Benayahu, 1990) to South Africa in the south (Benayahu, 1993) and including localities on both sides of the equator: i.e., Kenya, Tanzania, Madagascar and Mozambique (Tixier-Durivault, 1966; Schlichter, 1982). This distribution along the coast of Africa and its adjacent islands is probably due to the dispersion of *H. fuscescens* planulae within a continuous geographical region. The longevity and competence of these planulae provide the species with its dispersive ability but do not permit distribution of the species to localities east of the tropical African coastline. Further comparative data is needed on the longevity and competence periods of other soft coral planulae to understand their dispersal and zoogeographical patterns.

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