# Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral *Montastraea faveolata*

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ABSTRACT: The lack of detailed studies on the earliest life stages in corals currently limits the understanding of coral population dynamics. Although pre- and postsettlement processes both play a role in structuring coral populations, their relative importance and interaction are not well understood. By lowering seawater salinity (range: 28 to 36 psu), we created an artificial environmental gradient and followed the responses of *Montastraea faveolata* (Ellis & Solander, 1786) planulae during their pre- and postsettlement phases. Decreased salinity increased pre- and postsettlement mortality and altered larval behavior and substrate choice upon settlement. The effect of lowered salinity on the survival of *M. faveolata* planulae was mainly expressed during the pelagic life-phase. Reduced salinity levels increased the mobility of planulae, and reduced the duration of the planktonic period and their selectivity among available habitats for settlement. Regardless of salinity, planula behavior changed over time. During the early planktonic phase (0 to 52 h) the proportion of moving and positively geotactic planulae within a population increased towards lower salinity and under dark conditions. Thereafter (>67 h), most planulae (>60%) became positively geotactic, regardless of salinity. Settlement started after 144 h and salinity had no effect on settlement rate, i.e. the number of planulae settling per unit of time. As variable pelagic histories influence planular survival and habitat choice upon settlement, the number and distribution of coral settlers was related to their earlier pelagic experiences. This finding experimentally shows that the distribution and subsequent performance of corals early after settlement depends at least partly on their presettlement history and highlights the potential importance of presettlement processes in structuring coral populations.

KEY WORDS: Stress · Planulae · Settlement · Behavior · Plankton · Life-history

## INTRODUCTION

In the study of population dynamics, 2 major objectives are to determine the processes underlying the abundance and distribution of individuals. Despite its obvious importance, detailed information on natural processes that control post- and especially presettlement mortality is scarce for scleractinians (stony corals). For other sessile marine invertebrates the crucial role of presettlement (i.e. pelagic) processes in structuring benthic adult populations has been clearly demonstrated. Several authors (e.g. Alexander & Roughgarden 1996, Lasker et al. 1998) have even suggested that presettlement processes could be the main determinants of abundance and structure of adult populations. There are 2 modes of coral reproduction: (1) broadcast–spawning, whereby adult colonies release gametes and fertilization is external, and (2) brooding, whereby fertilization is internal and colonies release competent planulae. Regardless of reproductive mode, planulae have to contend with pelagic conditions for some period of time before they settle. The fact that

coral planulae are primitive larvae with limited mobility and no specialized organs (Harrison & Wallace 1990) has led to the assumption that their dispersal and survival is a predominantly passive, stochastic process (Scheltema 1986, Garrison 1999, Mundy & Babcock 2000). However, recent studies have shown that coral planulae move both actively and passively during dispersal and exhibit complex larval behavior during settlement (Babcock & Mundy 1996, Raimondi & Morse 2000, Stake & Sammarco 2003). When considering larval behavior, one should be aware that life-history elements (i.e. growth, behavior and maintenance) are not independent, since energetic resources of invertebrate larvae are limited (Richmond 1987, Pechenik 1990, 1999, Hoegh-Guldberg & Emlet 1997, Bertram & Strathmann 1998, Pechenik et al. 1998, Mundy & Babcock 2000). Differential allocation of resources among various life-history elements in response to variable environmental conditions provides the opportunity to optimize survival for an individual without means to replenish spent resources (Pechinek 1990). Individuals that invest energy in dispersal benefit from reduced intraspecific space-competition, reduced likelihood of inbreeding and reduced local extinction risk. On the other hand, distant dispersers face increased risk of mortality due to resource depletion (Stearns 1992, Skelly 1995). Resources spent during the presettlement period are also not available for activities that require energy during and immediately after settlement: habitat selection, metamorphosis or repair of tissue damage. Thus, the number of settling planulae, their spatial organization, and probability of survival are likely to depend on their use of energetic resources during the presettlement phase. It is, however, unknown whether sublethal stress during the presettlement phase affects the number of coral settlers and their behavior at settlement.

*Montastraea faveolata*, a common reef-building coral in the Caribbean region, releases bundles containing egg and sperm once a year. Bundles float to the surface, where they break apart and fertilization takes place (Szmant 1986, Van Veghel & Bak 1993, Van Veghel 1994). The resulting lecithotrophic planulae have a pelagic phase that lasts at least 3 d before settlement occurs. Variations in salinity due to large-scale hydrodynamic processes or rainfall are likely to be a potential natural stressor during this life-phase, as members of the lower invertebrate groups, including the cnidarians, are not capable of osmoregulation (Hoegh-Guldberg & Smith 1989). Salinity affects the biology of many marine organisms (Lyster 1965, Mann et al. 1991, Metaxas & Young 1998, Simpson & Hurlbert 1998, Garrison 1999) and most corals have a narrow salinity tolerance (Muthiga & Szmant 1987, Porter et al. 1999, Mundy & Babcock 2000). Although salinity stress does

occur, it is unlikely that it creates altered environmental conditions for prolonged periods of time, since hydrodynamic processes constantly mix large bodies of seawater. Nevertheless, salinity changes could be a useful semi-natural factor to represent stress in the presettlement phase of corals that can be used to experimentally explore its effect on coral early life-history dynamics. In this study, we thus investigated presettlement and postsettlement processes and their potential interaction using lowered salinity as an experimental stress factor. We were interested in the following questions: (1) Do planulae behavior and survival change in response to variable environmental conditions? (2) Do altered presettlement behavior and survival affect the number and behavior of planulae at settlement, i.e. the start of their benthic life-phase?

## MATERIALS AND METHODS

**Study site and organism.** All planulae in this study were obtained from Key Largo Dry Rocks (25° 07′ 59″ N, 80° 17′ 91″ W), a small (0.085 km$^2$) shallow (<10 m) patch reef, within the Florida Keys National Marine Sanctuary. The reef is dominated by the coral *Montastraea faveolata* and wide sea grass fields surround the reef on all sides. Salinity varies between 31.8 and 38.4 (median 36.2, Boyer & Jones 2002), while temperature ranges from 20.6 to 30.6°C (NOAA National data buoy center; www.ndbc.noaa.gov; station MLRF1) with a yearly maximum around October/November.

*Montastraea faveolata* (Ellis & Solander, 1786) is a dominant reef-building coral throughout the tropical West Atlantic and one of the best-studied corals in the region (e.g. Barnes 1973, Dustan 1975, Knowlton et al. 1992, Lopez et al. 1999, Medina et al. 1999, Sanchez et al. 1999, Lesser et al. 2000, Levitan et al. 2004). The species is part of the *M. annularis* species complex. The status of the 3 species in this complex is the subject of ongoing investigation (Knowlton et al. 1992, 1997, Van Veghel & Bak 1993, 1994, Van Veghel 1994, Lopez et al. 1999, Medina et al. 1999, Fukami et al. 2004, Levitan et al. 2004). All *Montastraea* species participate in the yearly mass spawning, which occurs twice between Days 6 and 8 after the full moon in August through November, depending on latitude within the Caribbean (Van Veghel 1994, Szmant et al. 1997). Around 22:00 h small (<2 mm) sperm-egg bundles are released simultaneously from large areas of the colony. Bundles float towards the surface where they break apart and fertilization occurs. After settlement, colonies grow between 6.8 and 7.3 mm yr$^{-1}$ (Van Veghel & Boscher 1995), reaching an average living surface area of 0.2 m$^2$ (Meesters et al. 2001).

**Collection of gametes and larval rearing.** Eggs and sperm were collected during the 2002 coral spawn (22:00 h; 28 August 2002). We netted (mesh size 0.8 mm) 30 haphazardly chosen *Montastraea faveolata* colonies (>60 cm) in a depth range between 2 and 7 m, and collected floating sperm/egg bundles in plastic removable cups at the top of each net. Collected gametes, with a total volume of nearly 2 l, were mixed in a 10 l container to increase fertilization rates, and left for 3 h to allow egg/sperm bundles to break up and fertilization to take place. Mixing decreases the 'colony effect', whereby potential differences in colony fitness (i.e. maternal malnutrition) are transferred on to the planulae and mask the influence of factors under investigation (Bertram & Strathmann 1998). To minimize natural variation in larval condition before the experiment started, we took subsamples of 200 similarly sized, healthy–looking larvae (Age 3 to 5 h) and transferred them to standard Petri dishes (∅ 9 cm) containing 40 ml of filtered seawater (Whatman 0.2 µm). To enhance planulae survival, their density was kept low, with a surface to volume ratio of water inside each Petri dish of 63.6 cm$^2$ to 40.0 cm$^3$. Planulae never occupied more than 0.0005 % of the total water volume. Low planulae densities prevent the build-up of bacterial concentrations that thrive on the substances released (mainly lipids) by planulae that die in Petri dishes.

**Experimental treatment.** We subjected planulae to 5 salinity treatments (28, 30, 32, 34 and 36 psu) using 4 replicates (except the 28 psu salinity treatment, which had 3 replicates) and studied their behavior and survival (see next subsection) along this simulated environmental gradient. The 36 psu salinity treatment represents the natural salinity on the reef, and deionized water was used to dilute filtered seawater to the desired salinity prior to adding the planulae. All seawater was filtered prior to use (GF/F; pore-size 0.7 µm). During the first 144 h water was refreshed every day, and thereafter every second day until the experiment was terminated after 3 mo. Approximately 95 % of the water was removed using a Pasteur pipette to remove dead planulae and debris. The remaining water contained all planulae and fresh seawater, premixed for the desired salinity, was then gently added to the original volume. The entire experiment was carried out in a shaded outdoor laboratory, subjecting planulae to a natural daily temperature cycle (range 26.0 to 28.5°C). Planulae were easily observed by the naked eye and survival and behavior was examined at approximately 5 h intervals during the first 72 h and at longer intervals thereafter. In addition to the salinity treatments, the behavior of planulae under dark and light conditions was observed in the presettlement period during the first 144 h.

**Planula behavior and survival.** For each replicate we counted (1) the number of surviving planulae, (2) the number of planulae moving in the water column, (3) the number of planulae moving along the bottom, and (4) the number of settled planulae. The number of moving planulae within the population was determined by counting all planulae that moved during 5 consecutive counts. Consecutive counts never differed by more than 2 %, and their average was taken to represent the proportion of moving individuals. Since the initial number of planulae added to each Petri dish varied slightly, the proportion of surviving planulae was expressed as a percentage of this initial value.

**Settlement behavior.** After 96 h, a small piece of crustose coralline algae (CCA; *Porolithon* sp. and *Paragoniolithon* sp.) and a small terracotta chip (approx. 8 × 5 × 1 mm length × width × height) were added to each Petri dish to induce and facilitate settlement. Substrates were not added earlier (i.e. <96 h) to (1) reduce the possibility that planulae obtained zooxanthellae, (2) standardize the substrates among treatments, (3) facilitate precise planulae counts, (4) prevent additional contamination that could increase mortality rates. Settlement rate was determined by examining the Petri dish surface with a dissecting microscope and gently rotating the added CCA and terracotta chips with forceps to score the number of settlers. Settlers were easily visible, so handling the chips did not add to settler mortality (e.g. by touching, or squashing a settler while rotating the chip). A planula was quantified as a settler only when it had started calcifying. Settlement densities were standardized to the total density of planulae present during the observation.

To test whether energetic resources were differentially depleted among treatments, we compared the size of planulae in the various treatments. Changes in planula size reflect resource use for planulae, as there are no known means to renew used energy reserves such as possession of endosymbiotic algae (zooxanthellae) or uptake of dissolved organic material (Isomura & Nishihara 2001). Using a calibrated microscope equipped with a digital camera, settled planulae were photographed and their size was determined from digitized images using image analysis software (Scion Image 2000). Only planulae that settled on the Petri dish were photographed since the topographical complex surface of the CCA and terracotta chips prevented accurate size measurements. Swimming speeds were determined by setting the speed of the camera to 1 s, photographing the swimming planulae against a black background, and then measuring the length of the trail in a 2-dimensional plane against a standardized grid photographed under the same conditions.

**Statistics.** Since comparisons are for the same planulae over time, successive comparisons over time are not independent. Therefore, we compared the effect of salinity on the (1) survival, (2) mobile fraction and

(3) settled fraction of planulae using repeated-measures ANOVAs, whereby salinity was the single fixed factor. Mortality rates were calculated separately for the presettlement (0 to 144 h) and the postsettlement (144 to 600 h) periods by plotting the percentage of surviving planulae versus time on a natural log scale. Assuming a simple exponential mortality function, i.e. $N_{(t)} = N_{(0)}e^{\mu t}$, the slope of this linear relationship represents the intrinsic mortality rate ($\mu$). Differences in mortality values between pre- and postsettlement periods and between salinity treatments were tested using ANOVA. No comparisons between pre- and postsettlement mortality rates were made after 600 h since all planulae in the 28 salinity treatment had died and mortality rates had become constant in all other treatments. Prolonging the postsettlement interval would thus reduce meaningful differences among treatments during the preceding phase. All post-hoc comparisons were made using the Tukey Honestly Significant Difference (HSD) test for unequal sample sizes (Spjotvoll & Stoline 1973) since the 28 salinity treatment had only 3 replicates whereas all other treatments had 4.

To assess the effect of light on the proportion of moving planulae in a population, a multiple regression analysis was performed using light ($\mu$mol m$^{-2}$ s$^{-1}$) and salinity as separate predictor variables. Settlement preference, i.e. the ability to distinguish between 3 available substrate types, was determined using chi-square analysis. The observed distribution of planulae over the 3 substrates was compared against a distribution assuming random settlement, with the number of settlers on a substrate type being proportionate to the available area of that substrate type. Both distributions were compared using a 5 × 3 matrix representing the 5 salinity treatments and the 3 substrate types.

Size of the planulae upon settlement was compared among salinity treatments using a 1-way ANOVA.

## RESULTS

### Mortality

Over the entire study period, planulae survival decreased significantly with decreasing salinity and over time (Table 1, Figs. 1 & 2). Post-hoc tests indicated that mortality rates differed among treatments with a >2 psu salinity difference (Tukey-HSD; $p < 0.05$). For example, survival in the 30 psu treatment was not significantly different from that in the 28 and 32 psu salinity treatments. However, between the 28 and 32 psu salinity treatments, where the difference between treatments was 4 psu, survival rates differed significantly. The highest mortality occurred in the lowest

Table 1. *Montastraea faveolata.* Effect of salinity and time on planula survival rates, mobility and settlement (repeated-measures ANOVA). ns: not significant

| Effect | df | MS | *F* | p |
|---|---|---|---|---|
| **Proportion of planulae surviving** | | | | |
| Salinity | 4 | 3098 | 46.21 | <0.001 |
| Error | 14 | 67 | | |
| Time | 14 | 13865 | 447.85 | <0.001 |
| Time × Salinity | 56 | 72 | 2.31 | <0.001 |
| Error | 196 | 31 | | |
| **Proportion of planulae moving** | | | | |
| Salinity | 4 | 1714.4 | 14.14 | <0.001 |
| Error | 14 | 121.3 | | |
| Time | 12 | 5581.2 | 97.31 | <0.001 |
| Time × Salinity | 48 | 334.0 | 5.82 | <0.001 |
| Error | 168 | 57.4 | | |
| **Proportion of planulae settling** | | | | |
| Salinity | 4 | 645.04 | 2.18 | ns (0.12) |
| Error | 14 | 296.06 | | |
| Time | 2 | 29769.81 | 109.62 | <0.001 |
| Time × Salinity | 8 | 181.39 | 0.67 | ns (0.71) |
| Error | 28 | 271.58 | | |

salinity treatment, 28 psu, and exponentially decreased ($r = -0.82$, $p < 0.001$, $n = 19$) with increasing salinity.

### Survival: presettlement versus postsettlement phase

The presettlement period was defined as the first 144 h after spawning, prior to which most planulae were moving near the bottom. Presettlement mortality was significantly different among salinity treatments
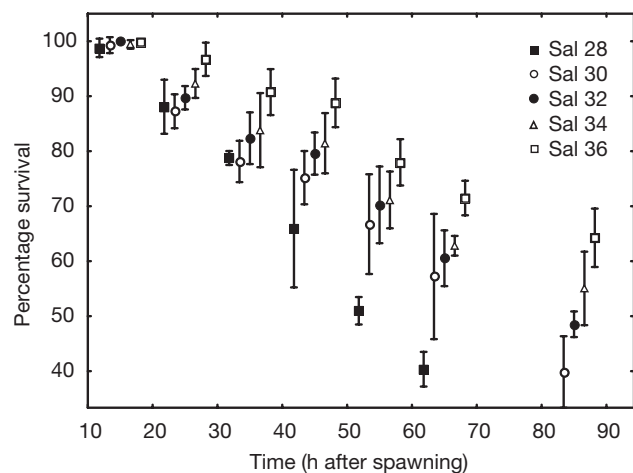


Fig. 1. *Montastraea faveolata.* Survival (mean ± SD) of planulae at various salinities (range 28 to 36 psu) during first 100 h after spawning (n = 4). Data offset for clarity: this does not represent differences in time when measurements where taken. Note that data points for 28 psu salinity treatment continue below x-axis after time ($t$) = 63 h
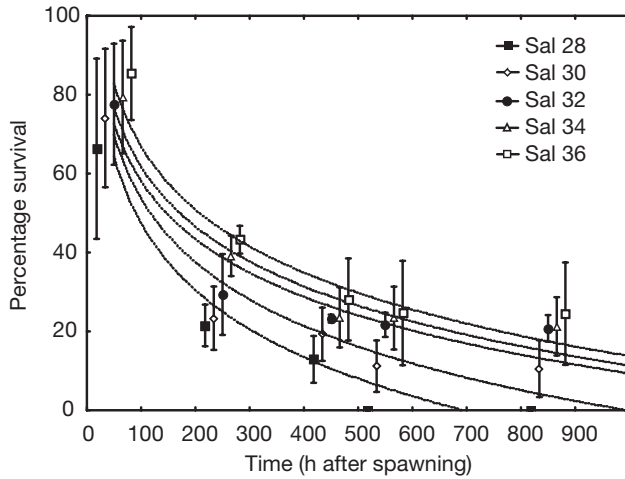
Fig. 2. *Montastraea faveolata.* Survival (mean ± SD) of planulae at various salinities (range 28 to 36 psu) during first 800 h after spawning (n = 4). Data offset as for Fig. 1



Fig. 3. *Montastraea faveolata.* Pre- (●) and postsettlement (□) mortality (mean ± SD) of planulae under various salinities (range 28 to 36 psu). See 'Materials and methods' for calculation of mortality rates

($F_{4,14}$ = 24.67, p < 0.001). Subsequent post-hoc analyses showed that the high mortality in the 28 psu salinity treatment was mainly responsible for the overall difference among treatments. With the 28 psu salinity treatment excluded, significant differences still existed among the other treatments (30 to 36 psu), but differences decreased over time and disappeared after 456 h.

When planulae started settling, the survival curve flattened (Fig. 2) and mortality rates dropped on average by a factor of 24.0 (SD ± 39.6; Fig. 3). The average decrease in mortality rates, defined as the presettlement mortality rate divided by the postsettlement mortality rate, was negatively linearly correlated with increasing salinity (r = 0.92; p < 0.05). This suggests that planulae in lower salinities obtained an increasingly higher benefit from settling. Postsettlement mortality rates also increased with decreasing salinity ($F_{4,14}$ = 7.08, p < 0.01). Differences between the 28 and the 32 and 34 psu salinity treatments mainly contributed to this overall difference in mortality rates. The smaller differences among treatments in postsettlement rates indicated that the effect of salinity variation on planulae survival was reduced after they settled.

By 600 h, all planulae in the 28 psu salinity treatment had died. In the other treatments, not all individuals had settled by this time, although some had already started calcifying. Interestingly, in all treatments, settled planulae sometimes vacated their skeletons and settled nearby (<1 cm), a phenomenon known as 'polyp bail-out' (Sammarco 1982). Most settled individuals at 600 h (96.6 % ± 3.4 SD) in the 30 to 36 psu salinity treatments survived until the experiment was terminated after 3 mo.
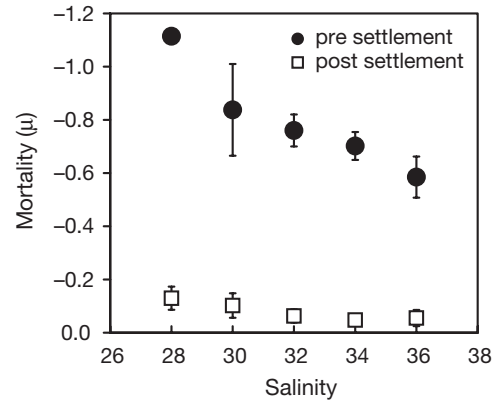
## Planula behavior

### Movement

Initially all planulae floated passively at the surface, but 14 h after fertilization an increasingly larger proportion of the population started moving (Fig. 4). During the first 24 h, the mobile proportion of planulae was related, albeit weakly, to the daily light cycle (hourly averages, µmol m$^{-2}$ s$^{-1}$), with more planulae moving at night ($R^2$ = 0.20, $F_{(2,225)}$ = 29.70 p < 0.001). Planulae in the 28 psu salinity treatment showed a similar cycle during the following evening (41 to 52 h), while in all other treatments
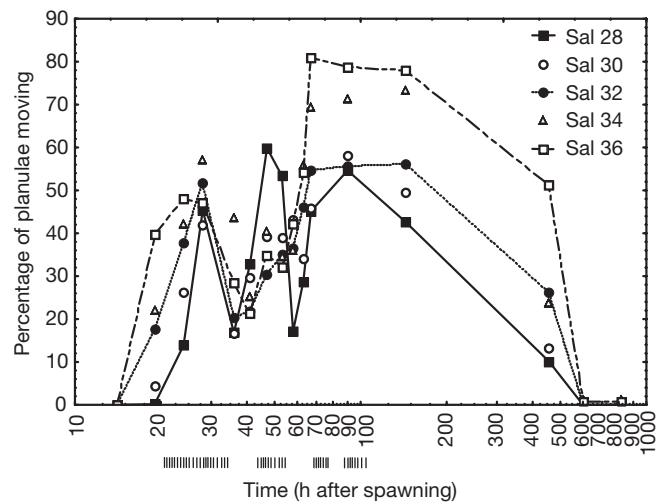


Fig. 4. *Montastraea faveolata.* Movement of planulae at various salinities (range 28 to 36 psu) during first 800 h after settlement, defined as percentage of planulae alive and moving. Standard deviations omitted for clarity; see 'Results' for statistical details. Lined areas below *x*-axis indicate periods between dusk and dawn for the first 100 h

Table 2. *Montastraea faveolata.* Effect of salinity and light on proportion of moving planulae (ANOVA). ns: not significant

| Effect | df | MS | *F* | p |
|---|---|---|---|---|
| **Proportion of planulae moving** | | | | |
| Salinity | 4 | 1159.83 | 32.07 | <0.001 |
| Light | 1 | 175.47 | 4.85 | <0.05 |
| Salinity x Light | 4 | 13.23 | 0.37 | ns (0.83) |
| Error | 28 | 36.17 | | |

the proportion of moving planulae increased steadily until settlement, independent of light (Fig. 4). To determine whether the daily cycle observed was related to light and not another diel factor (e.g. temperature), we tested the effect of a small light (20 W) on nighttime movement of planulae 24 h after spawning. Under artificial lighting, planulae movement decreased and was significantly different from values measured 1 h later under completely dark conditions (Table 2).

Initially, planulae moved around in the water column, but after 36 h an increasingly larger proportion became positively geotactic. The proportion of planulae observed moving differed between the various salinity treatments and over time (Table 1). The relative proportion of planulae moving near the bottom (0.0 to 0.5 mm) increased with decreasing salinity during the period 36 to 52 h after spawning (Fig. 5). After 52 h this relationship was reversed and the mobile proportion of planulae near the bottom increased exponentially with increasing salinity. Between 70 and 90 h, planulae moved at an average speed of 1.1 mm s$^{-1}$ (SD ± 0.4; n = 50; all treatments pooled). At this time, exploratory behavior near the bottom reached its maximum, with 53 and 87% of the moving planulae in the 28 and 36 salinity treatments, respectively, and there-
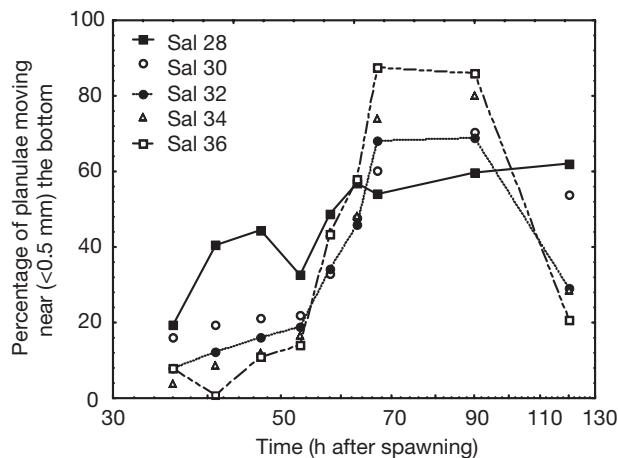


Fig. 6. *Montastraea faveolata.* Settlement curves (mean ± SD) for planulae reared under various salinity conditions (range 28 to 36 psu). Data offset as for Fig. 1

after decreased as planulae started settling at 144 h. All planulae had either settled or died by 456 h, except for 2 planulae in the 36 and the 34 psu salinity treatment that moved near the bottom for 800 h.

## Settlement

At 162 h, soon after planulae were first observed swimming near the bottom, settlement occurred in the lower salinity treatments (28 and 32 psu; Fig. 6). Settlement did not start until 200 h after spawning in the 34 and 36 psu salinity treatments.

The distribution of planulae over available substrate types was not random ($\chi^2$ = 201.62; df = 14, p < 0.001; Fig. 7), suggesting that planulae preferred certain substrate types for settlement. In all treatments, planulae showed preference for natural substrate, i.e. small chips of natural limestone covered with CCA and semi-natural terracotta chips, each of which comprised <1% of the total available substrate. The proportion of planulae that started skeleton formation on substrate consisting of limestone covered with CCA increased with increasing salinity (r = 0.72; p < 0.001), while the number of planulae settling on the plastic Petri dish decreased (r = –0.74; p < 0.001). The proportion of planulae settling on the terracotta tiles was independent of salinity (r = 0.01; p = 0.96). When combined, these relationships suggested that at lower salinities settling planulae showed altered preference for substrate type.

## Planula size upon settlement

Initially (i.e. 21 h after spawning), planulae did not differ in size among treatments (ANOVA; $F_{4,245}$ = 0.33, p = 0.86). After settlement, planulae formed a flat basal



Fig. 5. *Montastraea faveolata.* Percentage of moving planulae observed near or at bottom (<0.5 mm) of Petri dish during first 120 h after settlement. Standard deviations omitted for clarity; see 'Results' for statistical details
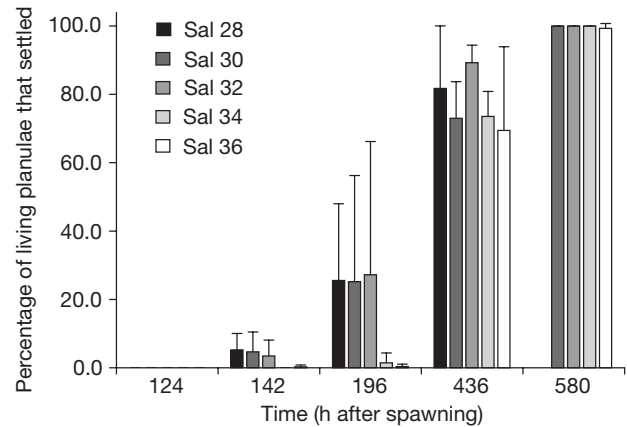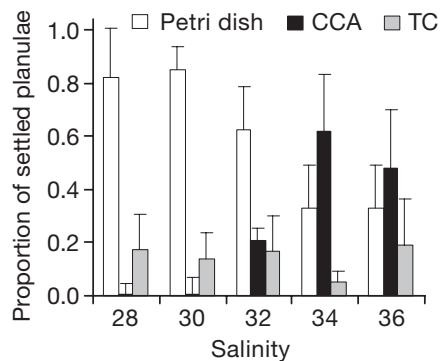
Fig. 7. *Montastraea faveolata.* Proportion (mean + SD) of planulae with preference for various types of settlement substrata in relation to water salinity. In each treatment, surface available to settling planulae comprised ~98% of bottom of the Petri dish, ~1% of terracotta chips (TC) and ~1% of natural substrate covered with crustose coralline algae (CCA)

disc on the substrate, calcification began, and polyps developed. The size of the basal disc differed among salinity treatments (ANOVA; $F_{4,65}$ = 19.39, p < 0.001) with exponentially increasing sizes towards the higher salinities (r = 0.67; p < 0.001). In planar view, settled planulae in the 36 salinity treatment had an average area of 0.302 mm$^2$ (SD ± 0.010; n = 14), whereas settled planulae in the 28 salinity treatment measured 0.257 mm$^2$ (SD ± 0.013; n = 14). Post-hoc tests indicated that differences were significant between the 28 and 32 psu salinity treatments versus the 34 and 36 psu salinity treatments, but not within these groups.

## DISCUSSION

The extent to which pre- and postsettlement processes structure benthic populations of marine invertebrates has been a subject of ongoing controversy for at least 30 yr. Herein, we have shown that pelagic experiences for *Montastraea faveolata* planulae in the Florida Keys can affect the number of planulae settling in a given location and the distribution of settlers through changes in their ability to discriminate amongst habitat types. Environmental stress in the form of reduced salinity increased the geotactic mobility of planulae, decreased the duration of the presettlement phase, altered preference for natural substrates, and increased mortality rates. These results indicate that (1) planula behavior is complex and responds to changes in the environment and (2) that presettlement dynamics affect the earliest phases of coral population formation, i.e. settlement on the reef.

These observed behavioral changes and differences in survival could have implications for the population dynamics of *Montastraea faveolata*, as the natural

range in salinity for the Florida Keys reflects the salinity range considered in this study (Boyer & Jones 2002). The reproductive season during which broadcasting corals release their larvae coincides with the rainy season in the Florida Keys (Szmant 1986), and salinity fluctuations can occur while gametes and planulae are present in the water. Salinities as low as 28 psu do occur near the water surface after heavy rainfall (M. J. A. Vermeij pers. obs.) and occasional salinity differences up to 2 psu across 7 m of depth have been observed for the Florida Keys (Porter et al. 1999) indicating that, depending on local reef topography, lower salinities can even occur at the bottom. Nevertheless, periods of lowered salinity are much shorter than those in our study (NOAA National data buoy center; www.ndbc.noaa.gov; station MLRF1), and therefore are unlikely to represent realistic environmental conditions. Low salinity in our study should be regarded as a semi-natural and experimentally tractable stressor that was used to illustrate the presence of complex planular behavior governed by environmental conditions that link a coral's pre- and postsettlement life-phase. It remains to be determined if similar larval responses would accompany other, more realistic, field stressors such as high temperature or chemical pollutants.

With decreasing salinity, a larger proportion of planulae were active during the first 52 h after spawning, i.e. planulae swam sooner and were first and more frequently observed swimming near the bottom. Since low salinities occur predominantly at the surface of the water column due to density stratification, this suite of behavioral responses probably results in an escape from low salinity conditions in the field. However, increased mobility during the planktonic period bears associated costs, and energy resources are likely to be depleted faster than for less active planulae occurring in higher ambient salinities. Planulae of *Montastraea faveolata* possess no endosymbiotic algae that allow autotrophic feeding, nor any characteristics that could indicate the potential for heterotrophic feeding. The earlier onset of downward vertical migration could also serve to reach the reef substrate to obtain zooxanthellae that can then be used to restore lost energy reserves. Dissolved organic matter (DOM) can also serve as an additional food source (Jaeckle 1995), but we have no information whether absorption takes place. Although planulae could compensate for lost resources by uptake of DOM, levels of DOM were assumed to be potentially variable, but not limiting, across salinity treatments. For other invertebrates, uptake of DOM often comprises only a small fraction of the larval energy demand (0 to 11%; Hoegh-Guldberg 1994, BenDavidZaslow & Benayahu 2000, Wendt 2000) and uptake is believed to be more related to adjusting the planula's nitrogen budget than to energetic con-

straints for planulae of soft-corals (BenDavidZaslow & Benayahu 2000). Also, differences between treatments emerged soon after the start of the experiment, when planulae still possessed energetic resources. We therefore believe that the major patterns in our study result from differences in salinity rather than potential differences in DOM between treatments.

The smaller size of settled planulae at lower salinities supports our hypothesis that resources are more rapidly depleted under adverse environmental conditions, yielding inadequate resources to sustain metamorphosis and calcification (Marshall et al. 2003). Smaller size upon settlement has been shown to negatively affect future survival in many marine invertebrates: crustaceans (Clarke 1993, Guisande & Harris 1995), polychaetes (Qian 1994) and echinoderms (Hoegh-Guldberg & Emlet 1997). We observed a similar trend (Fig. 3), but higher than expected postsettlement mortality in the 36 salinity treatment caused this relationship to be non-significant.

Based on extrapolations of colony production rates, clone size and postsettlement survival rates, Lasker et al. (1998) suggested that recruitment of gorgonians (Octocorallia) is probably most sensitive to survival of larvae in the water column. Reduced availability of resources due to planktonic stress affects the number and performance of future developmental stages. This implies that the number of planulae and their risk of suffering postsettlement mortality depend not only on the local conditions at that moment (e.g. substrate availability, sedimentation), but also on its preceding history in the plankton. Relating the survival of coral settlers solely to small-scale local conditions can therefore result in misinterpretations if planulae fitness has already been compromised during their presettlement life phase.

## Mobility in early life stages: implications for distribution and dispersal

Planulae are capable of swimming as early as 14 h after spawning, with the development of cilia on their exterior surface. The swimming speeds observed in the present study ($<1.5$ mm s$^{-1}$) do not suggest that planulae could swim actively against currents common to the Florida Keys. The importance of swimming for planulae was suggested by Hodgson (1986), who noticed diurnal active migration in Hawaiian coral planulae, similar to our observations for *Montastraea faveolata*. Although this behavior can be related to predator avoidance (Acosta & Butler 1999), many studies on pelagic larvae have shown net directional movement due to an interaction of a larva's vertical positioning or behavior with local hydrodynamic conditions (Thorrold et al. 1994, Olivar & Sabates 1997, Higgs & Fuiman 1998, Jenkins et al. 1999). The light-related mobility of planulae (Fig. 4) is surprising given their supposed lack of photosensitive equipment. *M. faveolata* planulae are azooxanthellate; therefore, an algalmediated transfer of external light levels is impossible at this early stage. This leaves the presence of photosensitive organs or cells as the most parsimonious explanation (Gorbunov & Falkowski 2002).

The arrival of planulae at a favorable settlement site is without ecological significance if these planulae have passed the so-called 'point-of-no-return' or become 'living dead' (Raimondi & Morse 2000) such that, due to depleted energy reserves, metamorphosis becomes impossible (Raimondi & Morse 2000) or death inevitable (this study). Although larvae are still able to survive in the water column, their increased activity to escape an unfavorable environment (e.g. reduced salinity, but also unfavorable settlement depth; Raimondi & Morse 2000) results in loss of energy reserves which could be a problem for future developmental stages and, hence, survival.

## Importance of history

Many coral settlement studies investigate the ultimate factors that guide a planula to choose a certain site on which to settle (e.g. Van Moorsel 1988, Hunte & Wittenberg 1992, Smith 1992, Maida et al. 1994, 1995, Lasker & Kim 1996, Mundy & Babcock 1998). The ability to select optimal settlement sites on the reef is reduced when planulae experience suboptimal conditions in the preceding presettlement period. This suggests that the settlement process becomes opportunistic in nature in response to adverse planktonic conditions. This has fundamental implications for inferring information on substrate preference in corals: finding settlers at a 'wrong' site does not imply that they have no substrate preference. Opportunistic settlement is the only way to prevent dying, since settlement per se greatly reduces mortality rates, as indicated by the up to 24-fold average decrease in mortality rate after a planula settles (Fig. 3). It is possible that the quality of the CCA or their ability to produce compounds necessary to facilitate coral settlement may have been affected by the lower salinity treatments. However, the CCA fragments that were added to our treatments were covered with what appeared to be *Porolithon* sp. and *Paragoniolithon* sp., which are believed to be tolerant of low salinities (R. Steneck pers. comm.). In addition, no physiological degradation of the algae was observed during the duration of our experiment. We therefore believe that the observed reduction in settlement on CCA-covered areas with decreasing salinity can be attributed to altered planulae behavior and not to the changed physiological condition of the algae.

## CONCLUSION

Survival and appropriate habitat choice of a coral planula are not independent of its earlier experiences in the plankton. Coral planulae show behavioral responses during the presettlement period indicating that their survival and dispersal may not be solely determined by stochastic factors (e.g. currents, predation). It is premature to speculate on the implications of this laboratory behavior in the field, but the potential importance of presettlement processes should be carefully considered as an additional important factor in coral population dynamics.

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