PLANULA RELEASE AND REPRODUCTIVE SEASONALITY OF THE SCLERACTINIAN CORAL *PORITES ASTREOIDES* IN BERMUDA, A HIGH-LATITUDE REEF

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ABSTRACT

Planula release from the scleractinian coral *Porites astreoides* Lamarck, 1816 at a high-latitude reef in Bermuda primarily occurred in the summer months of July and August, when the average seawater temperature for the lunar cycle preceding planulation exceeded 26.5 °C. Within the reproductive season in Bermuda, optimal planulation temperatures for *P. astreoides* are narrow. The release of fewer planulae was correlated with higher temperatures and there was significant variation in reproductive effort in colonies collected from sites across the 18-km wide Bermuda lagoonal seawater temperature gradient during this 2-yr study. The annual reproductive period of this species lengthens with a decline in latitude, which corresponds to a decrease in the range of annual seawater temperatures. Reproductive effort, as measured by the percentage of the population that is reproductive and number of planulae released per colony, is similar or slightly higher in Bermuda compared to conspecifics at lower latitudes. However, the shortened reproductive season results in a lower overall annual reproductive effort in Bermuda. Lunar synchrony of planula release peaked a few days before the new moon, slightly earlier than conspecifics in Florida, which peak during the new moon. Colonies from the Inner Lagoon peaked in planula release a few days earlier than those from other zones. We attribute spatial variation in lunar periodicity of planula release to differences in the timing of fertilization or planula maturation that may be influenced by environmental factors such as temperature and turbidity.

Knowledge of coral reproductive cycles and recruitment is fundamental to understanding ecological processes of coral reefs. Scleractinian coral reproductive modes can be classified into either broadcast spawning, which is the release of gametes followed by external fertilization and planula development, or brooding, whereby gamete fertilization and planula development occur internally (Harrison and Wallace 1990, Baird et al. 2009). Globally, broadcast spawning is the dominant reproductive mode in scleractinian corals; although, in the Caribbean, there is almost an equal number of species that are documented as brooders vs broadcast spawners (Baird et al. 2009). The potential for self-fertilization and for successful reproduction to occur even in low population densities, as well as the capacity for rapid recruitment, may explain why brooding coral populations have begun to dominate some Caribbean reefs following degradation from a combination of natural and anthropogenic disturbances (e.g., overfishing, hurricane damage, and coral disease) in the 1980s and 1990s (Hughes 1994, Mumby 1999, Knowlton 2001). Therefore, understanding the reproductive characteristics of brooding corals may provide further insight into reef dynamics and the potential for recovery after major disturbances.

A wide range of proximate and ultimate factors control the annual reproductive cycles of corals. The main documented environmental factors are sea surface temperature, photoperiod (day length), and solar insolation, with finer scale controls of
monthly cycles by lunar day (Harrison and Wallace 1990, Richmond and Hunter 1990, Baird et al. 2009). These cues constrain and synchronize the physiological events that lead to internal gamete development, culminating in either the annual spawning events of broadcasting species or the development of brooded planulae and their subsequent release. High-latitude reefs can provide interesting insights into the study of factors controlling reproductive cycles since there is a wider range in environmental parameters within subtropical waters, such as lower seasonal seawater temperature and shorter photoperiod in the winter, and many species are at their distribution extreme (Perry and Larcombe 2003). If environmental cues are good predictors of the timing and duration of coral reproductive schedules, species at high-latitude reefs will either show a more pronounced seasonality or a widening of optimal ranges over which reproduction can occur.

The reproductive seasons of corals with a brooding reproductive mode range from species that show distinct seasonality to those that planulate year round. Seasonality in brooding periods is species-specific and the duration and rate of planulation can vary among species within a location (e.g., Szmant 1986, Villanueva et al. 2008). The timing and duration of the brooding periods of some species also vary across latitudinal gradients, as can be observed by the coral species *Pocillopora damicornis* (Linnaeus, 1758) and *Stylophora pistillata* (Esper, 1797). These species planulate year-round on equatorial reefs in Palau (Atoda 1947a,b), but show greater seasonality at higher latitudes, with brooding periods restricted to warmer seawater temperatures (Rinkevich and Loya 1979 for *S. pistillata*, Stoddart and Black 1985 for *P. damicornis*, Tanner 1996 for both species). However, reproductive seasonality of a population is not always dependent on latitude: *P. damicornis* also planulates year-round at the mid-latitude reef of Hawaii (21°N, Richmond and Jokiel 1984) and shows strong seasonality at Lizard Island on the Great Barrier Reef (14°N, Harriott 1983). Such geographic variation in coral brooding seasons may reflect adaptations to local environmental conditions and cues (Richmond and Hunter 1990). Latitudinal variation in seawater temperature is well known to define the breeding seasons of many marine invertebrates, including corals (Orton 1920, Stoddart and Black 1985, Kojis 1986, Oliver et al. 1988, Olive 1995).

Within coral reproductive seasons, the lunar cycle is the primary proximate cue for the timing of gamete and planula release over specific days for many coral species, with the associated tides and currents for dispersal being cited as the ultimate cause (Harrison and Wallace 1990). Brooding corals show various degrees of lunar periodicity from no pattern to tight synchrony in planula release over a few days (Harrison and Wallace 1990, Richmond and Hunter 1990). Similar to variation in the timing and duration of brooding seasons, there are interspecific differences in synchrony to the lunar cycle within a location and even intraspecific differences across locations, implying that there is no single universal environmental cue (Richmond and Jokiel 1984, Tanner 1996, Vermeij et al. 2003, Zakai et al. 2006, Villanueva et al. 2008).

Bermuda is the most northerly coral reef in the Atlantic (32°N) and provides an opportunity to examine coral reproductive cycles on a high-latitude reef to gain insight into possible environmental controls. Studies from Bermuda have reported a distinct seasonality in reproductive timing, which is restricted to the summer period for the broadcast spawning corals *Diploria* spp. and *Montastraea* spp. (Wyers 1985, Wyers et al. 1991), the brooding coral *Favia fragum* (Esper, 1795) (Goodbody-Gringley and de Putron 2009), and the gorgonian *Pseudoplexaura porosa* (Houttuyn,
1772) (de Putron and Ryland 2009). In this study, we extend the documentation of coral reproduction in Bermuda by examining the spatial and temporal patterns of sexual reproduction of the brooding coral species *Porites astreoides* Lamarck, 1816 (Scleractinia: Poritidae), with comparison to conspecific patterns at lower latitudes in the Caribbean. Previous studies on the reproductive cycle of this common species have been conducted in Puerto Rico (Szmant 1986), Jamaica (Chornesky and Peters 1987), Panama (Soong 1991), and the Florida Keys (McGuire 1998). These studies have shown that the length of the reproductive season varies with geographic location, occurring over 4–5 mo in Florida compared to 9 mo or year-round at the lower latitudes in the Caribbean (McGuire 1998). Planula release is synchronized to the new moon in Florida (McGuire 1998). Histological sampling in the other studies also revealed weak synchrony peaking around the new moon (Chornesky and Peters 1987, Soong 1991), although the limited field sampling regime makes determining true periodicity difficult in comparison to laboratory monitoring of collected colonies.

In the present study, we document the brooding season of *P. astreoides* in Bermuda, the relationship of planula release to the lunar cycle, and the reproductive effort of colonies each month over two summers. We selected study sites within the different reef zones of the Bermuda reef platform that vary in temperature and turbidity levels to gain insight into possible environmental controls on reproductive patterns within this species in Bermuda.

**Materials and Methods**

**Study Sites.**—The Bermuda reef is an elliptical, atoll-like formation situated in the North Atlantic (32°20’N, 65°50’W; Fig. 1). The shallow North Lagoon of the platform can be divided into at least three physiographic reef zones before the reef shelves away to the deeper terrace reefs: the Inner Lagoon, Outer Lagoon, and Rim Reef (Fig. 1), which exhibit gradients of temperature, turbidity, and wave intensity (Bodungen et al. 1982, Logan 1988, CARICOMP 1997, Smith 1999). The outer Rim Reef is a shallow (2–6 m), annular coral reef where wave energy is high and turbidity is low, with annual Secchi measurements ranging from 10 to > 50 m (CARICOMP 1997, de Putron 2003). Inshore of the Rim Reef, within the enclosed shallow lagoon, are many patch reefs that can be roughly divided into those close to land (1–2 km offshore, Inner Lagoon), which experience the highest levels of turbidity and annual Secchi measurements ranging from 5 to 10 m, and those at the Outer Lagoon (10–15 km offshore), which have moderate to low levels of turbidity and annual Secchi readings from 5 to 18 m (CARICOMP 1997, de Putron 2003). *Porites astreoides* is ubiquitously distributed across these reef zones, allowing for collection sites within each zone. The annual seawater temperature on the reef at the three study sites was monitored over 1999 and 2000 with in situ calibrated data loggers (Onset Stowaway, accuracy ± 0.05 °C, resolution ± 0.02 °C). Data were logged every 88 min and a daily average was calculated.

**Collection of Corals and Monitoring of Planulation.**—Initial observations of freshly collected *P. astreoides* colonies in aquaria (SR Smith, Bermuda Natural History Museum, unpubl data) showed that they did not release planulae in the winter and spring months in Bermuda. In the present study, adult colonies (15–20 cm maximum diameters) were randomly collected by SCUBA divers using a hammer and chisel at least 10 d before the new moon of each month from June until September 1999 and from June until October 2000 to encompass the summer reproductive seasons. The total sample size was 204 colonies: in 1999, five colonies were collected from each site within the three reef zones in June, July, and September, and eight colonies were collected per reef zone in August; in 2000, 10 colonies
were collected per reef zone per month, except in October, when five colonies per reef zone were collected.

All corals were transported back to the laboratory in coolers of ambient seawater. The corals were maintained at the outdoor wet bench facility at the Bermuda Institute of Ocean Sciences. Each colony was placed inside a “planulae collector,” a clear Tupperware® container (2.5 L, 18 cm × 12 cm deep) with a water flow inlet at the base and a 200 μm Nitex mesh lid to promote circulation through the container while retaining any planulae released within the container. The planulae collectors were placed within large aquaria of flowing seawater to help maintain a constant temperature; in situ data loggers showed that seawater temperatures in the aquaria were within a consistent range as that of the Inner Lagoon reef zone. *Porites astreoides* release planulae after sunset (McGuire 1998, Edmunds et al. 2001, pers obs), so the collectors were checked each morning and any planulae were removed using a pipette and counted. The lids to the collectors were left off during the day to encourage water flow around the colonies and reduce shading effects. At the end of the 20 d monitoring period (encompassing 10 d on either side of the new moon), the total surface area of each colony was measured using the aluminium foil technique (Marsh 1970). Polyp density of the colonies was measured by counting the number of corallites under a dissecting microscope using a 1 × 1 cm grid. Five replicate counts were made from skeletons of each of five colonies. The colonies were returned to their respective reefs and cemented in place, and new coral colonies were collected for the next month, such that every colony was brought into the laboratory only once for observation.

Reproductive effort for each colony during each new moon period was recorded as the total number of planulae released cm$^{-2}$ d$^{-1}$. Mean reproductive effort per reef zone per month
was related further to the average seawater temperature in each zone for the 30 d preceding the new moon. Planula development to maturity through brooding in *P. astreoides* takes approximately 2 wks after fertilization that occurs around the full moon (Chornesky and Peters 1987); therefore, 30 d prior to the new moon encompasses the period of final gamete maturation, spawning, and planula development (similar to methods by McGuire 1998). The differences in coral colony size of reproductive and non-reproductive (no planula release observed) colonies were tested using one-way ANOVA; data were Log$_{10}$-transformed to obtain normality and variance homogeneity. The relationship between daily planula release and coral colony size was assessed using a Pearson product-moment correlation with Log$_{10}$-transformed data. Interannual and among-zone variation in reproductive effort was tested using a one-way nested ANOVA on arc-sine transformed data. Post-hoc tests of differences between monthly and reef zone means were performed using the TK, GT2, and T’ tests. The relationship between reproductive effort and seawater temperature was assessed using linear regression on arc-sine transformed data. All statistics were carried out using BIOMstat3.3.

**Results**

**Inter-annual and Inter-zone Variation in Reproductive Effort.**—No planula release occurred from all of the colonies collected from each of the reef zones in either June of each year or October 2000. There were also no planulae released from colonies collected from the Inner Lagoon sites in September of each year or from the Outer Lagoon sites in September 1999. The planulation period of *P. astreoides* in Bermuda from July through August/September corresponds to the period of maximum seawater temperature (Fig. 2). During this summer maximum, there was variation in temperature for each year among zones: the offshore Rim Reefs, buffered by oceanic waters, only reached temperatures in excess of 29 °C for 6 d in 1999, whereas temperatures at the Inner Lagoon site reached a summer maximum > 29 °C for over 2 mo and > 30 °C for 16 d. In addition, inter-annual variation in seawater
temperature occurred with generally cooler summer temperatures in 2000 (Fig. 2). For example, the maximum temperature at the Rim Reef and Inner Lagoon in 1999 was 29.1 and 30.7 °C, respectively. By comparison, in the summer of 2000, the Rim Reef never reached 29 °C (max 28.2 °C), and the Inner Lagoon did not exceed 29 °C until the end of July, remaining above 29 °C for just over 2 weeks and only attaining a maximum of >30 °C for a few days.

Reproductive effort (planulae released cm⁻² d⁻¹) varied with month and reef zone of collection (Fig. 3). Significant differences in overall reproductive effort per month (mean number of planulae released cm⁻² d⁻¹, combining the planula release data from colonies at all the reef zones each month; Fig. 3) were detected (one-way nested ANOVA: P = 0.006). Post-hoc testing revealed the overall reproductive effort in August 2000 was significantly higher (TK, GT2, and T¹ tests: P < 0.05) than that in September 2000 and August and September 1999 (Fig. 3). In addition, the overall reproductive effort in September 1999 and 2000 was each significantly lower (P < 0.05) than that in July 1999 and 2000 (Fig. 3). In addition to the variation in monthly overall reproductive effort, there was variation in the combined reproductive effort of the colonies collected from the different reef zones (Inner Lagoon, Outer Lagoon, and Rim Reef) over the time scales (months to years, Fig. 3). The combined reproductive effort of the colonies across all of the months in 1999 and 2000 was significantly different among the reef zones (one-way nested ANOVA: P = < 0.0001).
tests revealed that the overall reproductive effort from the Rim Reef colonies was significantly greater (TK, GT2, and T’ tests: P < 0.05) than overall reproductive effort from the Inner Lagoon colonies. There was no significant difference in the number of planulae released from colonies collected from the individual zones and separated out by months (one-way nested ANOVA: P = 0.195, Fig. 3).

Reproductive effort of *P. astreoides* was related to variation in monthly and annual seawater temperatures at the three reef zones (Fig. 4). Planula release occurred only when mean temperature during the 30 d preceding the new moon (i.e., the period of internal planula development prior to release) exceeded 26.5 °C. In June and October of each year, the preceding seawater temperature was < 26.5 °C and no planula release occurred. By July of each year, the seawater temperature was between 26.5 and 27.5 °C, and planula release occurred. Planulation events in August over both study years (triangles, Fig. 4) showed the greatest range in preceding seawater temperatures (~3 °C) and was the only monthly data set to show a significant correlation with seawater temperature: the number of planulae released declined significantly with increasing seawater temperature (linear regression: r² = 0.75, P < 0.05, Fig. 4). Planula release was reduced in September when the seawater temperatures for the preceding month were generally > 28.2 °C. The highest temperatures in September were recorded from the Inner Lagoon reef zone and no planulae were released. Overall, there was a negative relationship between reproductive effort combined from all
reproductive months (July–September) and seawater temperature for the preceding month (linear regression: $r^2 = 0.6$, $P < 0.05$).

**Variation in Timing of Planula Release.**—Duration of planulation by *Porites astreoides* colonies ranged from the sporadic release of planulae over 1–4 nights to colonies that planulated for periods of up to 13 d. A few colonies planulated over two intervals that were 3–4 d long, separated by a short inactive period. Examination of the data by reproductive colonies only and combining all months and years of planulation for each reef zone revealed a peak in the percentage of colonies from the Rim Reef and Outer Lagoon reef zones planulating over the period of 5 d before new moon (BNM) until the night of new moon (Fig. 5). In contrast, colonies from the Inner Lagoon planulated earlier, 5–8 d BNM with 16% releasing planulae 10 d BNM (Fig. 5). Note that 10 d BNM was the start of the monitoring period for all the corals, thus planula release from the Inner Lagoon colonies may also have occurred earlier in the lunar cycle. This trend of an earlier release by the Inner Lagoon colonies occurred each year (graphs not shown): peak release in 1999 was 5–7 d BNM at the Inner Lagoon compared to 0–4 d BNM for colonies from the other reef zones; and 7–10 d BNM in 2000 compared to 2–6 d BNM for colonies from the other reef zones.

**Variation in Colony Reproductive Effort.**—In total, 124 colonies were monitored in the reproductive months (i.e., when planula release was observed from at least one colony), and of these, 93 (75%) were reproductive. There was no significant
difference between the mean surface area of the reproductive and non-reproductive colonies (one-way ANOVA: \( P = 0.679 \)). There was also no significant relationship between numbers of planulae released per day and the surface areas of the reproductive colonies monitored over the study period (Product-moment correlation: \( r = -0.033 \), \( N = 93 \), \( P = 0.755 \)).

The overall mean (± SD) number of planulae released from the 93 reproductively active \( P. astreoides \) colonies was 0.79 (± 1.38) planulae cm\(^{-2}\) of colony. Maximum planula release was 8.39 planulae cm\(^{-2}\) (total of 2099 planulae from one colony) and the minimum was 0.005 planulae cm\(^{-2}\) (two planulae released from one colony). It was estimated that the mean (± SD) polyp density of \( P. astreoides \) was 40.7 (± 0.9) polyps cm\(^{-2}\). Conversion of the mean number of planulae released per cm\(^{2}\) to the number of planulae released per polyp using this estimate of polyp density equates to a mean of 0.02 planulae polyp\(^{-1}\) and a maximum of 0.21 planulae polyp\(^{-1}\). Assuming that one polyp releases one planula per new moon period, the data suggest that a mean estimate of only 2% and a maximum of 21% of the polyps of \( P. astreoides \) colonies released planulae.

**Discussion**

Reproductive Seasonality.—\( P. astreoides \) planula release in Bermuda occurred in the summer months of July and August, with a small number of planulae released in September. The occurrence of gamete maturation and release during warmer seawater temperature has been documented in many other coral studies (Babcock et al. 1986, Glynn et al. 1991, Hayashibara et al. 1993, Vermeij et al. 2003, Wilson and Harrison 2003), with lower temperatures thought to delay the onset of gametogenesis (Harii et al. 2001) and subsequent planula development. In our study across all months, years, and reef zones in Bermuda, planula release in \( P. astreoides \) occurred when mean temperatures over the preceding lunar cycle each month were > 26.5 °C. The maximum seawater temperature range in Bermuda is approximately 10 °C offshore on the Rim Reef (range of ~19–29 °C) and 15 °C inshore at the Inner Lagoon site (range of ~15.5–30.5 °C). In June and October of each year, seawater temperature was < 26.5 °C and no planula release occurred, resulting in a relatively short brooding season.

There is a geographic difference in the length of the brooding season of \( P. astreoides \) (Table 1). In the Florida Keys, the highest proportion of \( P. astreoides \) colonies release planulae when water temperatures range from 24.5 to 28 °C during the preceding monthly lunar cycle (McGuire 1998). With an annual mean temperature range of ~6.5 °C, these favorable temperatures, as well as planulation, occur in the Florida Keys as early as April or May and continue throughout the summer (McGuire 1998, Table 1). With further decreases in latitude at Puerto Rico, Jamaica, and Panama, the annual temperature range is minimal (3–4 °C; CARICOMP 1997, D’Croz and Robertson 1997), and the brooding season of \( P. astreoides \) is extended in time (Table 1). The wide annual temperature fluctuation in Bermuda, along with a narrow water temperature over which planula release occurs (> 26.5 °C in Bermuda compared to > 24.5 °C in the Florida Keys), corresponds to a distinct seasonality and a restricted reproductive cycle, consistent with the studies on the brooding coral \( F. fragum \) (Goodbody-Gringley and de Putron 2009) and the broadcasting gorgonian \( P. porosa \) (de Putron and Ryland 2009). Similarly, in the Pacific, Stoddart and Black (1985) pro-
posed that the large seasonal variation in temperature of > 10 °C, at the southern distribution limit of the brooding coral *P. damicornis* in Western Australia, is a limiting factor for the reduced brooding season there, which occurs over a 5 mo period during spring and summer compared to a protracted reproductive season at Lizard Island, GBR, where the temperature range is only 4 °C. However, *P. damicornis* also exhibits year-round planulation at the mid-latitude reef of Hawaii (seawater temperature range of 7.7 °C), thus temperature variation among sites does not alone fully explain the distinct reproductive patterns of this species (Stoddart and Black 1985). Restricted reproductive seasons at some higher latitude locations have been documented for *S. pistillata* (Rinkevich and Loya 1979, Tanner 1996); although similar to *P. damicornis*, this is not always the case (Richmond and Jokiel 1984).

In comparison to the propensity for many brooding coral species to have multiple reproductive cycles per year, most broadcast spawning corals have just one gametogenic cycle per year and spawn over a discrete period of 1–2 mo (Baird et al. 2009). The broadcasting species that are an exception to this and have several reproductive cycles per year occur at various latitudes (van Woesik 2010). However, geographic differences in the timing (and not duration) of broadcast spawning events are hypothesized to reflect variations in temperature profiles (Willis et al. 1985, Dai et al. 1992, Hayashibara et al. 1993, Acosta and Zea 1997, Wilson and Harrison 2003). Some studies have shown that other factors are better predictors of spawning, such as solar insolation (Penland et al. 2004, van Woesik et al. 2006), photoperiod (Babcock et al. 1994, Fan and Dai 1998), spawning during calm wind periods (van Woesik 2010), and an interaction of rainfall and temperature (Mendes and Woodley 2002). Seasonal changes in photoperiod and solar insolation (Fan and Dai 1998, van Woesik et al. 2006) are pronounced at high-latitude reefs. The range in day-length hours in Bermuda is from ~14 hrs at the summer solstice to ~10 hrs at the winter solstice. Solar insolation summer maximum is in June at ~7.5 kWh m⁻² d⁻¹ and the minimum in December at ~3 kW m⁻² d⁻¹ (obtained from [http://eosweb.larc.nasa.gov/sse](http://eosweb.larc.nasa.gov/sse) with permission from the NASA Langley Research Center Atmospheric Science Data Center). The induction of planula development in Bermuda (in June for a July planulation event) is therefore correlated to maximum values or the switch to a negative rate of change in these parameters. A combination of these abiotic factors along with the optimum seawater temperature, as defined here, could synergistically control the induction of the planulating season of *P. astreoides* in Bermuda.

**Temperature Effects on Reproductive Effort.**—Reproductive effort of the Bermuda population of *P. astreoides*, which was not influenced by colony size, varied significantly among months, years, and across the different zones of the reef platform. In addition, within the reproductive period, significantly fewer planulae were

<table>
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<th>Latitude</th>
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<th>Duration (mo)</th>
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<tr>
<td>Bermuda</td>
<td>32°N</td>
<td>July–August/September</td>
<td>2–3</td>
<td>Present study</td>
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<tr>
<td>Puerto Rico</td>
<td>18°N</td>
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released with higher temperatures during the month preceding planulation. The potential for small fluctuations in seawater temperature to affect reproductive effort is consistent with the earlier work of Jokiel and Guinther (1978), who reported that a change of just 1 °C from optimum significantly diminished the reproductive effort of *P. damicornis* colonies. Fecundity of colonies of the gorgonian *P. porosa* in Bermuda also showed significant variation over the summer months; however, in contrast to *P. astreoides*, there was a positive relationship between reproductive effort (gamete volume) of colonies and increasing seawater temperatures (de Putron and Ryland 2009). Similarly, there was a positive relationship between number of planulae released and temperature for several species of the Caribbean genus *Madracis* (Vermeij et al. 2003). Our observations of a negative relationship between seawater temperature and reproductive effort in *P. astreoides* suggest an upper thermal limit for successful gametogenesis and/or brooding in this species. Inhibition of reproduction by high summer temperatures has also been shown for *S. pistillata* populations in the Arabian Gulf, where the brooding season is in the spring outside of the summer temperature extremes (Fadlallah and Lindo 1988).

The observed shifts in the reproductive timing and fecundity of *P. astreoides* colonies across the 18 km-wide Bermuda lagoonal seawater temperature gradient demonstrate the important role temperature plays in controlling reproductive processes where many other factors, such as solar insolation and photoperiod, are constant. However, another environmental factor that is not constant across the reef zones is turbidity. Assuming that we did not underestimate reproductive effort due to reduced lunar synchrony in this zone (see below), the lowest reproductive effort of *P. astreoides* in this study was in the Inner Lagoon reef zone. This zone experienced both very high summer seawater temperatures and over three times greater turbidity levels compared to the other reef zones (Bodungen et al. 1982, Logan 1988, CARI-COMP 1997, Smith 1999, de Putron 2003). A similar result was shown for *Acropora palifera* (Lamarck, 1816) colonies in Papua New Guinea, where fewer planulae were produced in months when seawater temperatures were highest and at sites where turbidity was greatest, even when sites were < 10 km apart (Kojis and Quinn 1984). Turbidity caused by eutrophication was also related to depressed planula development and maturation in *Porites porites* (Pallas, 1766) in Barbados (Tomascik and Sander 1987). Studies have shown that reduction in irradiance and the stress of sediment removal can reduce energy allocation for growth and, potentially, reproduction (Riegel and Branch 1995, Phillip and Fabricius 2003).

**Variation in Lunar Periodicity of Planula Release.**—Planulation by *P. astreoides* colonies from all reef zones peaked several days before the new moon and diminished after the new moon. This is only in slight contrast to *P. astreoides* colonies in Florida where planula release showed a significant peak over the new moon and several days either side (McGuire 1998). Although variation in lunar periodicity of the same species at different geographic locations occurs for *P. damicornis* and *S. pistillata* (Tanner 1996, Zakai et al. 2006, Villanueva et al. 2008), it is unclear if the small differences between Bermuda and Florida are significant. Within Bermuda, colonies from the Inner Lagoon reef zone peaked in planula release a few days earlier than colonies from the Outer Lagoon and Rim Reef zones. A small percentage of the colonies from all zones planulated at low levels that continued over several days outside of the peak period, although this was more evident for the Inner Lagoon population. This atypical pattern of planula release at the Inner Lagoon site may reflect a
stress response (high temperatures, reduced illumination, sediment removal) that delayed fertilization and/or maturation of planulae, resulting in an extended release period for these colonies. Edmunds et al. (2001) showed that planulae released from colonies of *P. astreoides* on different days differed physiologically (variation in zooxanthellae density, photosynthesis, and respiration rate), and there were weak trends in mortality rate, all of which will affect fitness.

As is the case for all in vitro experiments, our planula release studies may have been influenced by stress to the colonies held in the aquaria. External light pollution was controlled with shades around the aquaria sides, with the tops open to the moonlight. Seawater temperature in the aquaria was not manipulated and was similar to the temperature of the Inner Lagoon reef zone. Thus, the aquaria temperature regime may have affected the colonies collected from the cooler Outer Lagoon and Rim Reef locations. However, new colonies were collected over each planulation period 10 d before the new moon; therefore, gametogenesis, spawning, and the majority of the planula development occurred in the natural setting. Consistent patterns of planulation among corals from the various zones were detected each month indicating that the common aquaria conditions were not highly disruptive to the pattern of final planula development and release. Wyers et al. (1991) did not detect any laboratory aquaria effects on lab spawning of *Diploria* spp. and *Montastraea* spp. vs field observations in Bermuda, and *P. astreoides* colonies monitored in the lab and in the field in Florida planulated over similar time periods (McGuire 1998). However, a comparative study of in situ vs laboratory methods of monitoring planula release in *S. pistillata* showed that lower numbers were released in the laboratory, a possible consequence of stress to the colonies (Zakai et al. 2006).

**Variation in Colony Reproductive Effort.**—Planula release occurred from 75% of the *P. astreoides* population in Bermuda (total of 124 colonies sampled during months when planula release was observed), which is only a slightly higher percentage than previously documented for this species. Planulation occurred in 61% of the 102 *P. astreoides* colonies sampled in the Florida Keys (McGuire 1998) and 69% of 52 colonies from Conch Reef in the Florida Keys (Edmunds et al. 2001). Soong (1991) found planulae in the tissues of 42%–56% of *P. astreoides* colonies examined in Panama and a comparable percentage of brooded planulae were in the sampled tissue of a Jamaican population (46%–50%, Chornesky and Peters 1987). Within reproductive *P. astreoides* colonies in Bermuda, a mean of 2% and maximum of 21% of the polyps released planulae. This is a higher maximum fecundity than McGuire’s (1998) observation that 1%–10% of the polyps of conspecific colonies in Florida released planulae.

**Implications for High-latitude Reefs.**—The high-latitude reef of Bermuda in the North Atlantic can be described as a marginal environment in terms of reproductive output from the brooding coral species *P. astreoides*. Even though the reproductive effort of *P. astreoides*, as measured by the percentage of the population that is reproductive and the number of planulae released per colony, is similar or higher than colonies in Florida and the Caribbean, the shortened reproductive season for this species in Bermuda implies an overall lower annual reproductive effort. A low, annual reproductive effort in Bermuda compared to the lower Caribbean also occurs in the brooding coral *F. fragum* (Goodbody-Gringley and de Putron 2009) and the broadcasting gorgonian *P. porosa* (de Putron and Ryland 2009), with colonies of the
latter also having a lower fecundity in Bermuda. The geographic isolation of many high-latitude reefs means that larval connections from tropical reefs may be limited (Miller and Ayre 2008, Gilmour et al. 2009), thus local reproduction is critically important for recruitment and the maintenance of genetic diversity. Coral species at high latitudes may therefore be more sensitive to disruptions occurring during the reproductive months (e.g., storms, bleaching episodes) compared to species at lower latitudes with longer reproductive seasons.

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