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Effects of temperature and ammonium on larval development and survivorship in a scleractinian coral (*Diploria strigosa*)

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Abstract Increases in ambient water temperature on coral reefs around the world, along with regional nutrient enrichment, have been a growing concern in coral reef ecology. We studied the effects of seawater temperature and ammonium concentrations on the azooxanthellate planular larvae of *Diploria strigosa* Dana, 1846 (Cnidaria: Scleractinia) over a period of 9 days. We did this to determine whether increases in these environmental variables affect coral larval development and survival. Settlement frequencies were also examined. Larvae were placed in water baths at 28°C, 30°C, and 32°C (ambient temperature at time of sampling was ~29°C). Larvae in 30°C and 32°C suffered approximately 50% and 70% greater mortality, respectively, than those at 28°C. At each of the three temperatures, separate groups of larvae were exposed to a 20 μM l^{-1} concentration of NH_4^+ (as NH_4Cl), a concentration similar to that measured on certain reefs in the Florida Keys. Seawater temperatures of 30–32°C slowed or halted development in the later stages of larval development. At 32°C, time spent by larvae in a swimming/searching mode was observed to be higher than that at 28°C or 30°C. In the 28°C and 30°C treatments, *D. strigosa* planulae exhibited phototactic responses similar to those of other scleractinian corals–positively phototactic initially and then negatively so after ≥50 h; at seawater temperatures of 32°C, planulae became immediately negatively phototactic. In general, an increase in the seawater temperature caused a significant decrease in ciliary activity (motility) and rate of settlement in the larvae in a manner proportional to temperature. The presence of ammonium also caused a significant decrease in these variables, and these effects were additive with respect to those of increased temperature. The lack of symbiotic algae (which can assimilate ammonia) may have contributed to the observed increased mortality levels under conditions of enriched NH_4^+. Calculation of isochrons (distances which a larva may traverse within a given period of time) for planulae exposed to conditions of increased temperature and/or ammonium concentrations suggests that a resultant decrease in larval longevity could potentially decrease distance of larval dispersal.

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Introduction

Recent studies suggest that average global atmospheric temperature is increasing with time (Houghton et al. 1990; Atmospheric Environmental Service 1994; Keeling et al. 1996; Mortsch and Quinn 1996; also see Vitousek 1994). Mean sea surface temperatures (SSTs) also appear to be increasing in tropical seas (Glynn and d'Croz 1990; Hayes and Goreau 1991; Goreau and Hayes 1994; A. Strong, NOAA, personal communication). The potential increase in air temperature has been predicted to range from 0.5°C to 4.5°C by the year 2100 (Houghton et al. 1990; Atmospheric Environment Service 1994). It has also been predicted that recent sea-warming is the result of global warming that will increase SSTs by 1–2°C on average by 2030–2050 AD (Mitchell 1988; Manabe et al. 1991). Results from a coupled ocean–atmospheric model appear to indicate that most coral reef regions lying between 25°N and 25°S latitudes will experience SST increases of between 1°C and 2°C (Mitchell 1988; Manabe et al. 1991). Results of other modelers

forecast somewhat lower rates of warming than the previous references, but these rates are still ca. five times greater than those which have occurred during the past 100 years (Houghton et al. 1990; Wigley and Raper 1992).

Coral reefs exist within a narrow temperature range. The optimum temperature for adult scleractinian corals is between 25°C and 29°C; the minimal temperature appears to be 18°C (Stoddart 1969). At SSTs only several degrees above local average maxima, corals may bleach (Brown 1990; Goreau and Hayes 1994) or exhibit increased mortality (Jokiel and Coles 1977, 1990; Glynn and d'Croz 1990; Glynn 1993). The production of heat-shock proteins (e.g. Sharp et al. 1997) and the expulsion of zooxanthellae are typical coral responses to increased SSTs. "Hot spots" are now known to exist in the tropics in regions bearing coral reefs, causing mass bleaching and mortality in scleractinian corals (Glynn 1991; Hayes and Goreau 1991; Goreau and Hayes 1994; Huppert and Stone 1998).

Increases in temperature can depress success of fertilization, slow embryonic development, and cause abnormal development in the planulae of scleractinian corals (Bassim et al. 2002). This is important because the planulae spend a portion of their development period in the upper layers of the water column, where SSTs can reach high levels (Harrison and Wallace 1990). Vertical movement in fully developed coral planulae is known to be affected by ambient light conditions (phototaxis; Atoda 1947a,b; 1951a,b,c, 1953; Szmant-Froelich et al. 1980, 1985; Heyward and Babcock 1986). To date, however, the effects of variation in SST on scleractinian coral larvae have received little if any attention. SST could potentially affect the dispersal and success of settlement in corals by diminishing larval survivorship. Small geographically isolated reef systems may depend on upstream sources for new recruits (Sammarco and Andrews 1988; Sammarco 1994). Earlier studies have related larval survivorship to potential dispersal. Specifically, potential dispersal distances have been calculated for coral larvae on the basis of known larval longevities and bioenergetic reserves (Richmond 1982, 1987, 1988). Any factor that limits larval dispersal could contribute to isolation of a reef, decreasing its ability for regeneration via recruitment from a remote reef after a major environmental perturbation. The question arises as to whether SSTs above those normally experienced by coral planulae over an extended period of time can be detrimental to their later stages of development and survivorship.

Sources of environmental stress generally do not act alone. An increasing amount of attention is now being given to the effects of multiple stressors in the environment acting simultaneously on reef organisms (e.g. temperature and salinity; Porter et al. 1999). One increasing environmental perturbation being experienced in coastal waters on a world-wide basis is nutrification, commonly associated with coastal urban areas (Maragos 1972; Maragos et al. 1985; see Miller 2000 for overview). Many coral reefs exist within coastal waters. Thus, this problem may have strong negative effects, since corals generally occur in oligotrophic waters.

D'Elia and Wiebe (1990) have reported that dissolved inorganic nitrogen (total DIN, including NO_3^- and NO_2^-) concentrations reported at or near coral reefs range globally from 0.22 μM (forereef, Pago Bay, Guam) to >8.04 μM (backreef, Tuman Bay, Guam; Marsh 1977); the average, however, is 1.404 μM (reviewed by D'Elia and Wiebe 1990). The pore waters found within reefs associated with Key Largo, Florida, USA, have been found to far exceed these concentrations, reaching 67 μM DIN (Shinn et al. 1994). Corals may become stressed by dissolved nitrogen concentrations above those to which they are adapted. The general effects of ammonium on marine animals, which can result in mortality include the following (reviewed by Withers 1992): direct effects on the nervous system, changes in membrane permeability that affect iono- and osmo-regulation, inhibition of Na^+ uptake by an Na^+–NH_4^+ exchange pump, effects on O_2 transport capacity of hemocyanin; effects on carbohydrate metabolism, and effects on the acid–base balance.

The zooxanthellae within coral tissue, however, take up ammonium (NH_4) and nitrate (NO_3) (e.g. Muscatine and Porter 1977; Muscatine 1980; Wilkerson and Trench 1986; Muscatine et al. 1989; Stambler et al. 1991; Snidvongs and Kinzie 1994; Hoegh-Guldberg and Williamson 1999). Hoegh-Guldberg and Williamson (1999) found that the exposure of zooxanthellate corals to 20 μM NH_4, a concentration 7–90× greater than the average values reported for reefal waters (see above), commonly results in increased zooxanthellar density, but only rarely in mortality. It is possible that coral planulae lacking zooxanthellae may be more sensitive to increased nutrient concentrations than adults, because the zooxanthellae may buffer the animal against the ill effects of the high nutrient concentrations. The question arises as to how coral planulae may respond to increases in nutrients in the surrounding seawater, to which they may become exposed, and more specifically, how these increases may affect development and survivorship.

In order to examine these phenomena, we used an externally fertilizing ("broadcasting"), hermaphroditic, scleractinian coral (*Diploria strigosa*). This species is one of the most common corals in the tropical western Atlantic, found in Bermuda (Wyers 1985), the Gulf of Mexico, and on reefs of the NOAA Flower Garden Banks National Marine Sanctuary (FGB; 93°49.0′·W; 27°52.6′·N). In the experiments described here, we tested the following null hypotheses.

- Temperatures of 28–30°C have no effect on coral planular survival; thermal stress does not occur at these temperatures.
- Ammonium concentrations increased beyond those found in the environment from which the larvae came have no effect on the survival of azooxanthellate coral planulae.

- These same temperatures and ammonium concentrations have no effect on the swimming ability of coral planulae or on their ability to settle and metamorphose into newly settled juveniles.
- *D. strigosa* larvae exhibit random patterns of vertical movement in response to temperature and increased ammonium, as well as to light.

Materials and methods

Gametes of the scleractinian coral *Diploria strigosa* (Scleractinia: Faviidae) were collected at 2030 h on 8 September 1996. Collection took place during the annual mass coral spawning at the NOAA Flower Garden Banks National Marine Sanctuary. The FGB encompasses a series of offshore reefs and banks associated with topographic highs (salt domes; diapiric or piercement structures in which there are central, equi-dimensional salt plugs; Parker 1989) in the northwestern Gulf of Mexico (Fig. 1). The M.V. *Fling* was used to access the FGB. On the vessel, the gametes from three different colonies were combined (out-crossed). The techniques of Heyward and Babcock (1986) (including agitation) were used to enhance fertilization success. After spawning and collection of gametes, gametes from each colony were placed in separate containers, so as to avoid inter-colony contamination of samples. The gametes of each colony were then divided into two equal volumes. Each of these volumes was placed in a 1-l bottle. The bottles were then filled with seawater that had been collected prior to the spawning period, to insure the absence of gametes. One-third of the volume from each of these two source containers was then combined in a new container, to achieve fertilization of eggs using six permutations of two colonies each – A×B, A×C, and B×C (out-crossed), and A×A, B×B, and C×C (self-fertilized).

The zygotes and embryos were then transported in aerated ice-chests to the Woody J. DeFelice Marine Center (Louisiana Universities Marine Consortium, LUMCON). The chests were modified to a control temperature slightly below that of ambient (~27°C; Bassim 1997) during transport. This process, from collection of gametes to delivery to Louisiana, required ~68 h.

The experiment (Fig. 2) followed a three-way, balanced, random-blocks, replicated ANOVA design (see Sokal and Rohlf 1981). The first experimental factor considered was temperature. There were three water baths, each kept at a different temperature: 28°C, 30°C, and 32°C. The second experimental factor was ammonium enrichment at two levels: 0 (control) and 20 μM added. Only two concentration levels were used in order to obtain gross effects of the treatment, and to reduce the size of the experimental design and number of replicates that needed to be monitored, to a manageable size. Each trial was replicated four times in space. The third factor was the random blocks. The entire above design was replicated twice in space (multiple tanks). SST at the FGB at the time of sampling was ~29°C. Mean ammonium concentration in this region during the summer has been measured to be 0.23 μM (SD = 0.21, $n = 35$, June 1995; S. Gittings and K. Deslarzes, NOAA Flower Garden Banks, Nat. Mar. Sanctuary, personal communication).

Approximately 72 h after fertilization, embryos were placed in artificial seawater with 0 μM NH_4 in four 25-ml vials – one set within each tank at each experimental temperature ($n_t = 4$). The number of embryos in each vial varied from 4 to 45, with a mean of 12. (The small size of the embryos and their adhesion to each other due to their mucus coat made it difficult to allocate a specific number of embryos to each vial. The mucus dissipated rapidly with time, however, and the developing embryos broke apart from each other.) Four additional vials were prepared with 20 ± 3 μM of reagent-grade ammonium chloride in solution ($n_T = 4$). These were introduced into tanks held at each experimental seawater temperature. The concentrations of ammonia in the experimental controls and in the enriched-ammonium-chloride-treatments were verified to be 0 and 20 μM (mean value), respectively, by a standard colorimetric test (Strickland and Parsons 1972). The samples were compared with a series of standards, to test the precision of concentrations within the experimental vials, particularly since we were using artificial seawater.

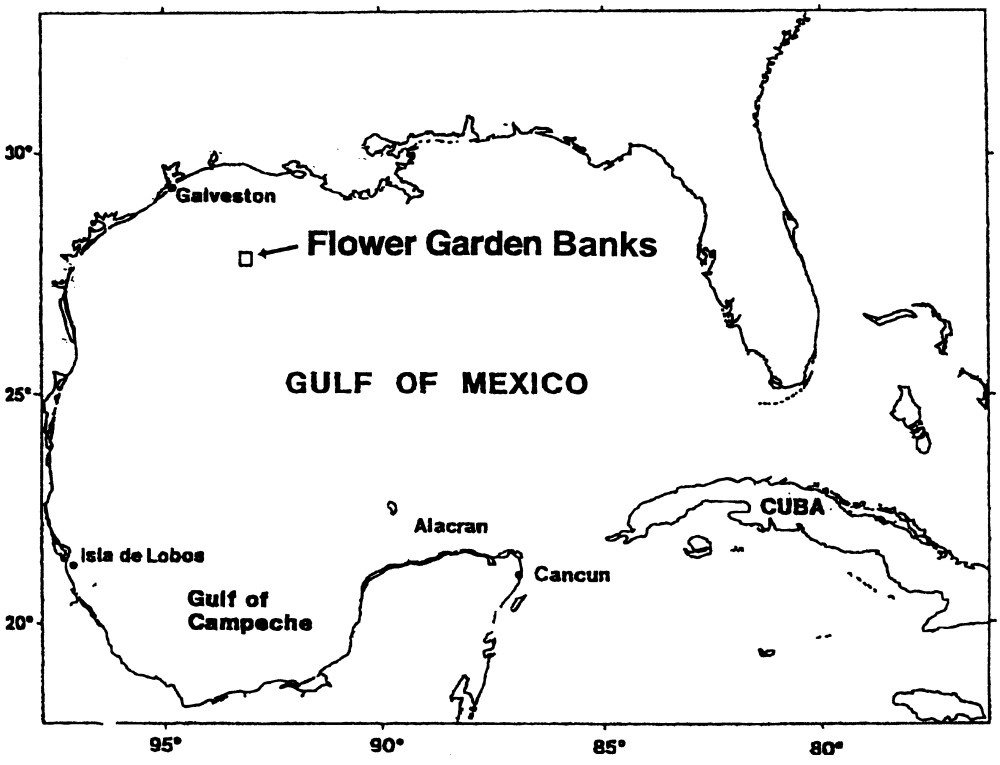

Fig. 1 Map of Gulf of Mexico, indicating location of the Flower Garden Banks National Marine Sanctuary (reprinted from Rezak et al. 1990, with permission)

Ammonium Enrichment (in μM)	Random Block	Temp in °C 28	30	32
0	A			
	B			
20	A			
	B			

$n_t = 4$ (per cell)

Fig. 2 Experimental design. The experiment followed a three-way, balanced, random-blocks, replicated ANOVA design (see Sokal and Rohlf 1981). First experimental factor: *temperature*, three water baths (10-US-gallon aquaria) kept at 28°C, 30°C, and 32°C. Second experimental factor: *ammonium enrichment*, at 0 (control) and 20 μM concentrations. Each trial was replicated four (n_t) times (using 25-ml culture vials). Third factor: two *random blocks* of aquaria (A, B)

A 10-gallon glass aquarium with a 100-W submersible heater was used for each bath (total = 6 tanks). The sides of the tanks were wrapped with black polyethylene so that the light sources would only be perceived as coming from above to simulate natural conditions. All of the tanks rested upon an insulating mat to decrease heat loss. Directly above the baths were two 48-W fluorescent fixtures with daylight-spectrum bulbs, timed to be synchronous with the corresponding daylength at the FGB. A rheostat-controlled incandescent bulb above the aquaria was also time- and brightness-regulated (0.05–0.1 M m^{-2} s^{-1}) to simulate lunar irradiance. Irradiance was verified with a Li-Cor model LI-193SA spherical underwater quantum sensor, and compared to irradiance data from the FGB. During the day, the corals received natural solar radiation for natural daylength periods, with appropriate shading to protect the colonies from exposure to excess UV irradiation.

We sampled at shorter time intervals during the beginning of the experiment than later. Initial sampling periods varied between every 2–7 h (at $t = 0$–26 h). For the next 24 h of the experiment, sampling was conducted every 8 h; sampling for the remainder of the experiment (2–9 days) was every 12 h. Sampling for survivorship and ciliary motility consisted of examining the vials from above through a dissecting microscope. The number of live larvae and the number with active ciliary movement were also counted. A decrease in the latter was assumed to be an indicator of physiological stress. Individual counts were taken within clumps as best possible, where clumps of embryos existed. In most cases, it was possible to discern time at which the embryo entered its next developmental stage (1, 2, 4 cells, etc.), and this was also recorded. "Time observed dead" and "time last observed alive", often used in larval survivorship studies such as this, were recorded to generate survival curves using a Kaplan–Meier product-limit analysis (Fernandez-Pato et al. 1992; Parmer and Machin 1995). A Weibull regression (Chatfield 1978; Parmer and Machin 1995) was calculated using the same survival data used for the Kaplan–Meier analysis, a regression analysis often used on data such as these. Settlement of larvae on the bottom and sides of the vials was also observed and quantified. A larva was considered to have successfully settled if it attached to the substratum and began secreting a calcium carbonate skeleton.

The vials used for the experiment were 2.0 cm in diameter and 9.0 cm in length. The relative position of the planulae in the vial were recorded through time. Since coral planulae are "coarse-grained" organisms (as defined by Levins 1968), they are only able to perceive their surrounding environment spatially in a limited manner. Assuming a larval diameter of 0.5 mm, the vial would be 40×180 body lengths – an adequate size to assess movement and position. The depth was coded so that the top of the vial corresponded to 1.0, the middle, to 2.0, and the bottom, or "floor", to 3.0. Intermediate depths were graded accordingly. This produced a continuous variable that could be analyzed for differences among treatment groups by multivariate analysis of variance (MANOVA). For all statistical analyses, higher order interactions will only be discussed if significant.

The survivorship results of these experiments were used to estimate potential dispersal distances from three known coral reefs in the Gulf of Mexico, using current data from Leipper (1954). Since SST changes occur more broadly across ocean waters than increases in nutrient concentrations, these projections were considered primarily in relation to the potential effects of temperature on larval dispersal.

Results

Precision tests for nutrient concentrations

Colorimetric tests used to test the precision of concentrations within the experimental vials yielded Pearson's product-moment correlation coefficients of between 99.9% and 100.0%, indicating a very high level of precision. The use of artificial seawater had no observable effects on the experimental results. Although bacteria may have been present during the experiment, they did not appear to be present in excess, if at all, nor did they appear to cause any problems. The larvae showed little mortality in the 28°C controls. The amount of ammonium excreted by the organism was not considered here.

Survival

The first fully developed planulae were observed 4 days after fertilization. Examination of the planulation by fluorescence microscopy confirmed that the planulae of *Diploria strigosa* were azooxanthellate.

Mortality rates in coral planulae increased with increasing experimental temperatures (Fig. 3). In the 28°C treatment, after an initial 10% mortality (possibly caused by transportation-induced stress), there were no significant changes in survivorship for the remainder of the experiment. In the 30°C and 32°C treatments, survival decreased rapidly at first but then became asymptotic. At the end of the experiment (9 days), survivorship was 56% at 28°C. On the other hand, only 27% of the planulae survived after this period at 30°C, and 15% survived at 32°C. Survivorship was further depressed by the addition of ammonium chloride. Averaged across all experimental temperatures, survivorship was 57% at 0 μM NH_4, but dropped to 8% at 20 μM (Fig. 4). The negative effects of increased temperature and increased ammonium concentrations on larval survivorship were highly significant ($P < 0.001$ between temperatures, $P < 0.001$ between nutrient and control, Kaplan–Meier

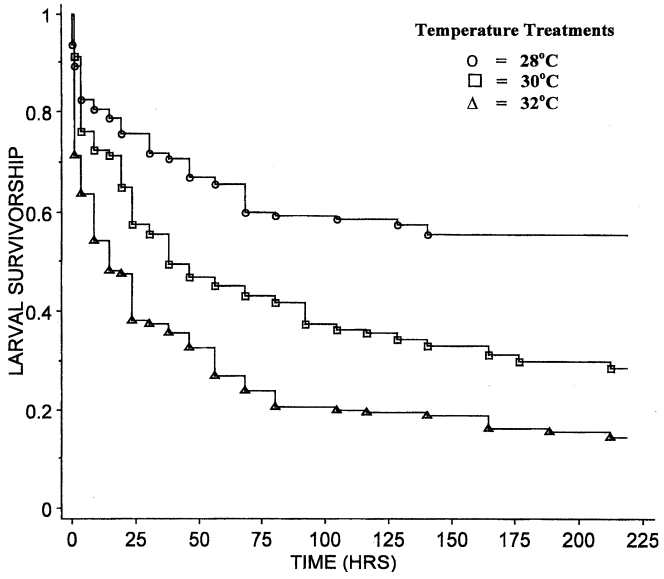

Fig. 3 *Diploria strigosa*. Survivorship in larvae under conditions of three experimental seawater temperatures (28°C, 30°C, and 32°C) through time. Step-wise curves calculated and generated using Kaplan–Meier product-limit analysis (see Parmer and Machin 1995; also see Fernandez-Pato et al. 1992 for explanation). Data pooled over ammonium-enriched treatments and shown as a function of time after exposure. Significant difference between temperature treatments (Breslow–Gahan–Wilcoxon rank test, $P < 0.001$)

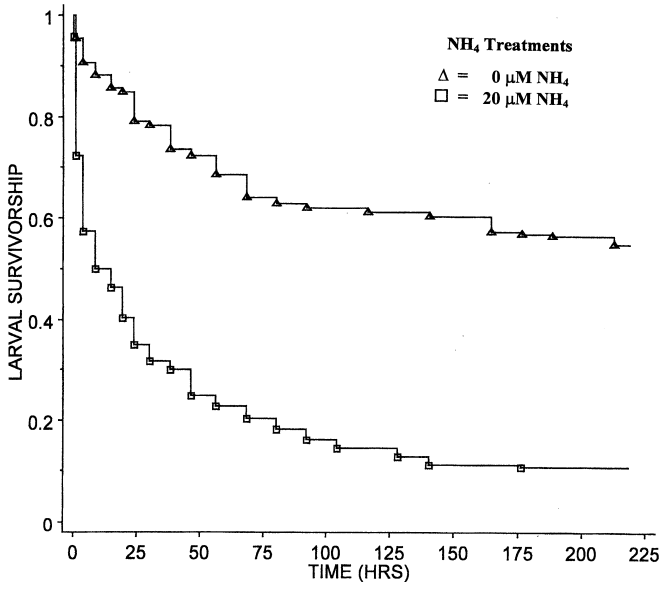

Fig. 4 *Diploria strigosa*. Survivorship in larvae under control and ammonium-enriched conditions. Curves calculated and generated using Kaplan–Meier product-limit analysis (see Parmer and Machin 1995; also see Fernandez-Pato et al. 1992 for explanation). Data pooled over temperatures and shown as a function of time after exposure. Significant difference between nutrient treatment and control (Breslow–Gahan–Wilcoxon rank test, $P < 0.001$)

product analysis; Figs. 3, 4). There was no significant difference between blocks ($P > 0.05$, Kaplan–Meier).

Weibull regressions are particularly well suited to curve-fitting in distributions of high initial mortality followed by slower rates, as observed here, and can be very useful predictive tools. Differences between experimental temperatures were also significant when fitted to a Weibull distribution and analyzed ($P < 0.001$). The Weibull regression coefficient of –0.683 calculated from our data shows that an increase of 2°C will accelerate mortality, by a factor of $e^{2(-0.683)} = 0.26$, i.e. by ~74%. In other words, the time to death for those larvae in 32°C seawater is estimated to be 74% shorter, on average, than for those in 30°C seawater.

Standard parametric analyses also revealed significant differences between experimental temperatures and ammonium concentrations, but no significant higher-order interactions were found between the effects of temperature and ammonium enrichment (Fig. 5).

Motility

Larval motility, as indicated by visible, active, ciliary movement, varied significantly between different experimental temperatures (under 0 μM NH_4^+ conditions; $P < 0.05$, repeated-measures MANOVA). At the end of the experiment, larval motility dropped to 56% in the 28°C treatment, ~10% at 30°C, and ~8% at 32°C. This slowing of motility observed under conditions of increasing temperature (28–32°C) was significantly further depressed with the addition of ammonium to the seawater ($P < 0.05$; Fig. 6). Under conditions of 20 μM NH_4^+ concentrations, motility dropped through time from 10% to 1% at 28°C, 3% to 0% at 30°C, and 10% to 0% at 32°C. Larvae at the higher ammonium concentration exhibited no ciliary motion after 141 h at 28°C and after 33 h at 30°C and 32°C.

Vertical position of larvae

In the 28°C and 30°C treatments, changes in depth within the test vials were marked by an initial ascent to the top of the vial by the majority of the larvae; this was followed by a descent after 50 and ~100 h, respectively (Fig. 7). The response was different in the 32°C treatments. There, the initial trend was immediately downward. The majority of the planulae in the 32°C treatment spent most of their time near the bottom of the vials.

Settlement

Seventy percent of those larvae which survived to full development successfully settled within the 28°C vials (no ammonium enrichment). This occurred within 9 days, or 12 days after fertilization. Approximately 65% of the survivors in the 30°C treatment (no ammonium) also settled successfully (see Fig. 8). In the 32°C treatment (no ammonium), however, only 4% of the survivors successfully settled. The addition of ammoni-

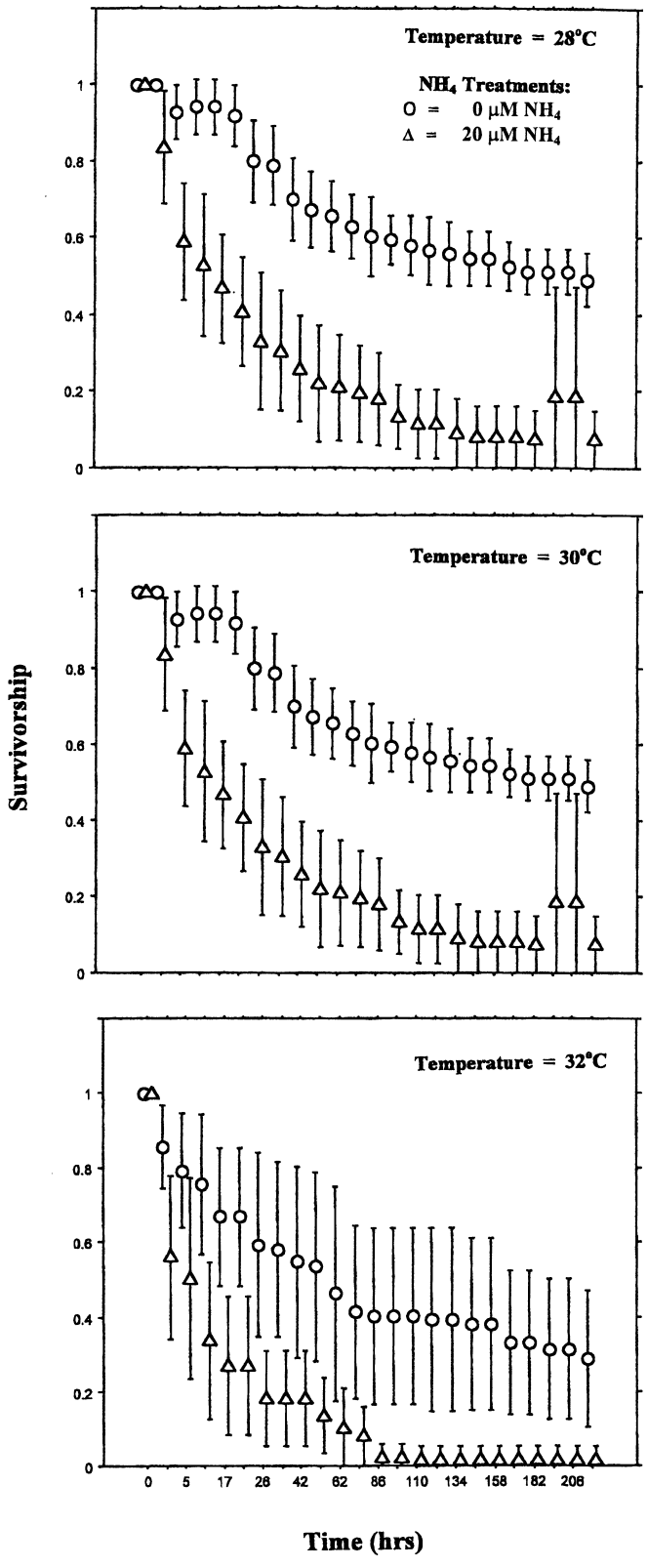

Fig. 5 *Diploria strigosa*. Survivorship of larvae at 28°C, 30°C and 32°C, as a function of time. Effects of the addition of NH_4^+ (and control) also shown. Data presented as proportions of larvae surviving through time. *Error bars* represent 95% confidence limits. No significant difference between blocks ($P > 0.05$, Kaplan–Meier test); block means have been averaged

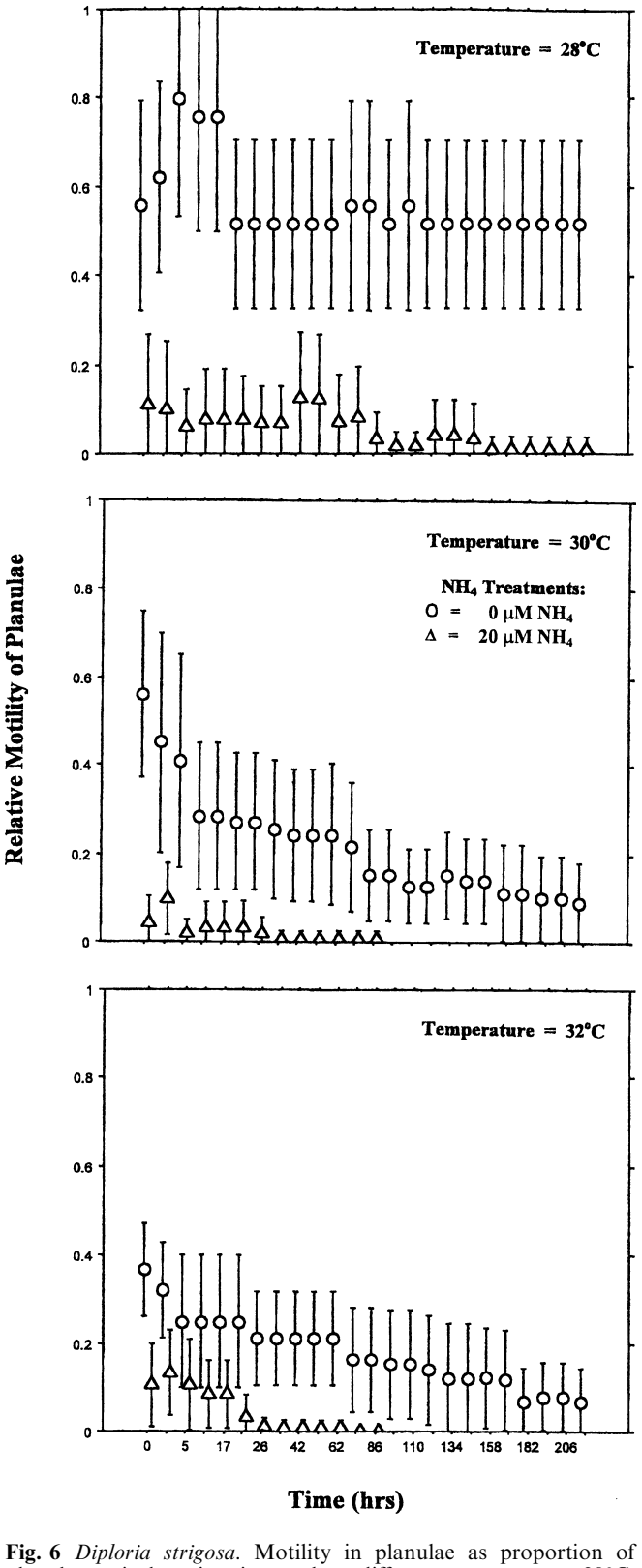

Fig. 6 *Diploria strigosa*. Motility in planulae as proportion of planulae actively swimming at three different temperatures: 28°C, 30°C, and 32°C through time. Effects of 0 and 20 μM NH_4^+ treatments also shown as *circles* and *triangles*, respectively, under each temperature. Significant differences between responses to different temperatures ($P < 0.05$, repeated-measures MANOVA) and ammonium levels ($P < 0.05$, repeated-measures MANOVA)

um to the seawater decreased settlement rates even further, at all experimental temperatures. At 32°C, there were few to no survivors.

Complete metamorphosis to a newly settled juvenile occurred in both ammonium-enriched and control groups. Frequency of complete metamorphosis was lower, however, in the nutrient-enriched treatments. The proportion of survivors undergoing metamorphosis in the 28°C non-ammonium-enriched treatment was 72%, slightly higher than that in the 30°C non-ammonium group (64%). Survivorship decreased dramatically, however, at 32°C (non-ammonium) to 4%. In the ammonium-enriched treatment, frequency of metamorphosis reached 0% at 32°C.

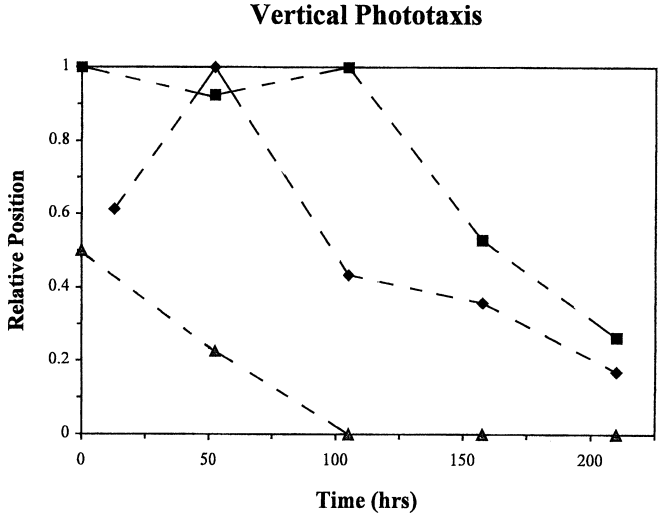

Fig. 7 *Diploria strigosa*. Vertical phototaxis in planula larvae. Vertical position in vials under experimentally varied temperatures of 28°C (*diamond*), 30°C (*square*), and 32°C (*triangle*) (0, lowest portion of vial; 1.0, highest portion). 1.0 also represents the direction from which light was transmitted; all other areas surrounded by black, light-absorbing material. 0 represents positions furthest away from light

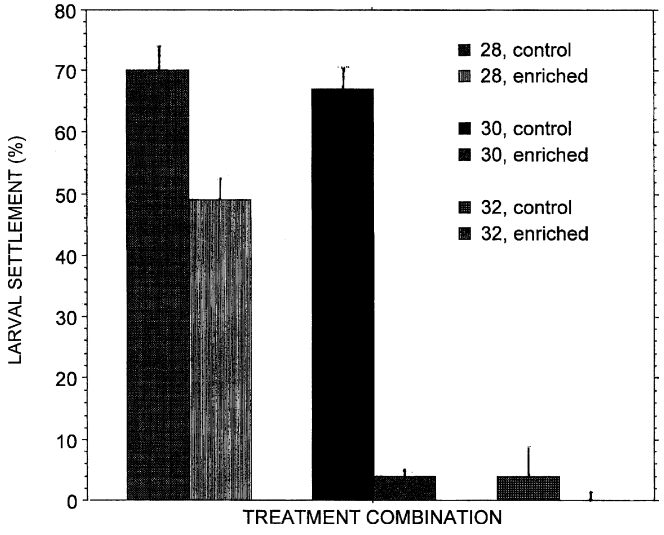

Fig. 8 *Diploria strigosa*. Survivorship of planulae which have undergone at least partial metamorphosis from planula to settled spat under control conditions and ammonium enrichment (20 μM NH_4^+ added). Data shown for planulae subjected to these conditions under three different temperature treatments (28°C, 30°C, 32°C)

Dispersal

Larval longevity can be translated into larval dispersal, if current velocities and directions are known for the region where spawning occurs. Using the larval survivorship data generated here, potential dispersal distances were calculated from two geographic starting points in the Gulf of Mexico. The resultant isochrons are shown in Fig. 9B. It was calculated that, at current velocities typical of the region under consideration (Leipper 1954; similar to velocities measured recently), a larva released from the Blanquilla Reefs at Isla de Lobos, Mexico, could potentially be advected ~84 km in 7 days in a

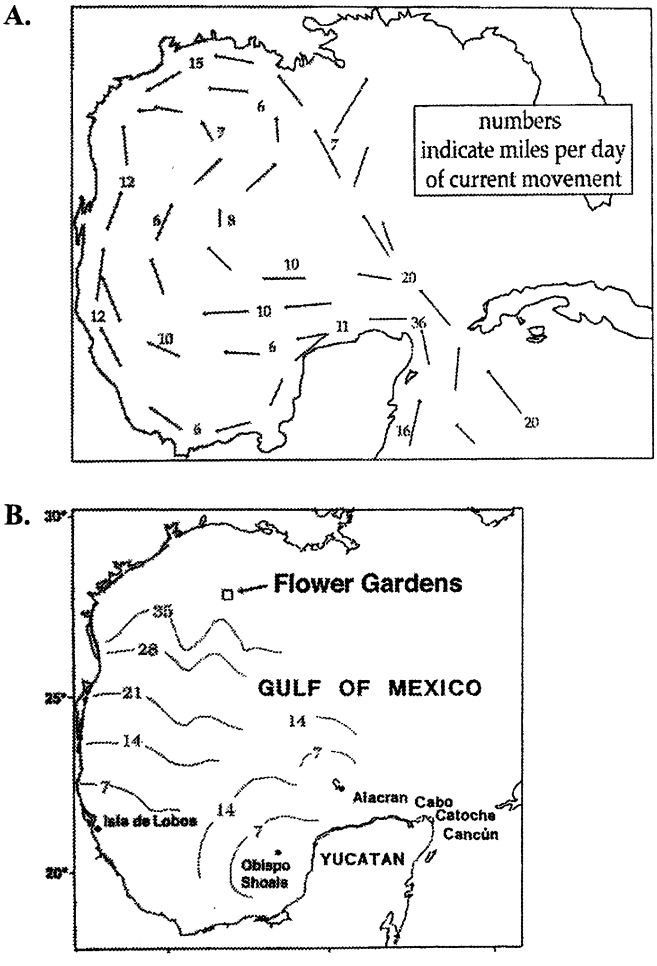

Fig. 9 **A** Average current velocities in the Gulf of Mexico in August (redrawn from Leipper 1954). **B** Isochrons in days representing the distances passive larvae would be advected from three selected sources: Isla de Lobos, Obispo Shoals, or Alacran Reefs, Mexico. Based on data derived from Leipper (1954); map adapted from Rezak et al. (1990)

variety of directions. If a larva died 14 days after release, it could have potentially traversed ~150 km, depending upon its starting point and direction.

Discussion

Elevated temperatures clearly reduced larval lifespan in *Diploria strigosa*. Reduced settlement frequencies evident later in the experiment at 30–32°C indicate, however, that competence to settle is also suppressed at increased temperatures. Larval motility, an indicator of physiological stress, was also observed at these temperatures. Delayed settlement capabilities automatically imply increased distant dispersal potential; however, it may be possible that stressed larvae such as these, although theoretically being able to disperse widely, may have a reduced ability to settle once they have reached a suitable site, or may have a decreased probability of survival after settling once arriving at a more distant site.

Given the warming of the atmosphere, which has been observed thus far (Houghton et al. 1990; Atmospheric Environmental Service 1994; Keeling et al. 1996; Mortsch and Quinn 1996) and is predicted to continue over the next century (Houghton et al. 1990; Atmospheric Environment Service 1994), it would appear that even slight increases in the SST may pose an important problem for successful reproduction, dispersal, and recruitment in scleractinian coral larvae. The highest rate of mortality observed here occurred early in the experiment, when buoyant, non-motile, developing embryonic larvae would be at the sea surface (Harrison and Wallace 1990). We predict that SSTs of ≥30°C may well induce the same effects in nature. Such SSTs are now commonly being observed on coral reefs in "hot spot" areas during strong El Niño years (Goreau and Hayes 1994; A. Strong, NOAA, personal communication).

We have considered specific rises in experimental temperature for larvae from one species of coral in a given region. We believe, however, that it may be the deviations from average local conditions and their associated variance which are important in causing these effects – not simple increases above some specific critical SST (Sammarco, Winter, and Stewart, in prep.); i.e. we believe that the frequency and duration of high SSTs will probably determine the response of the planulae. That critical SST will be different for different regions (e.g., the Red Sea vs. the Great Barrier Reef).

The higher mortality rates observed after the addition of 20 μM NH_4Cl indicate that nutrient enrichment in tropical and subtropical water presents an additional threat to coral larvae. At all experimental temperatures, survivorship was further reduced by the addition of ammonium. Numerous experiments have been performed in which adult corals have been exposed to these and higher concentrations of ammonia, without any visible, deleterious effects (Muscatine and Porter 1977; Muscatine 1980; Wilkerson and Trench 1986; Muscatine et al. 1989; Stambler et al. 1991; Snidvongs and Kinzie 1994). The most commonly observed results in these earlier studies were increases in the density of zooxanthellae.

From our results, we suspect that the toxic effects of ammonia/ammonium are reduced by symbiotic algae within scleractinian corals. The zooxanthellae may be acting to take up these compounds before they cause physiological stress, providing a buffering effect for the coral under conditions of elevated nutrient concentrations. If this were the case, the organism would not be protected from increases in ammonium concentrations in the absence of these endosymbionts. Bleached and azooxanthellate corals might be more vulnerable to ammonium toxicity than zooxanthellate ones. Moreover, early life history stages of various organisms, such as penaeid shrimp, are known to be particularly sensitive to the toxicity of ammonia (Ostrensky and Wasielesky 1995), and ammonium is known to be even more toxic than ammonia (Withers 1992). Hence, zooxanthellate planulae may be better protected from higher nutrient levels than azooxanthellate ones. These questions remain open for investigation.

Problems associated with ammonia/ammonium toxicity would most likely be found in near-shore, shallow-water, coral reef communities, such as those of the Florida Keys. Shinn et al. (1994) found that levels of ammonium across the reef ranged from 20.5 to 67.7 μM NH_4^+, reaching values three times greater than that examined experimentally here. Szmant and Forrester (1996) found much lower concentrations in the water column in the Florida Keys, e.g. ≤ 2.7 μM, although their estimates of total N reached ~52 μM. Our results imply that coral planulae in the vicinity of near-shore reefs affected by poor near-shore water quality could be negatively affected by increased concentrations of ammonium (also see Richmond 1993). This would include such developing areas as Central America, the Caribbean, Africa (Kenya), the Red Sea, the Indo-Pacific, and the USA (see Wells 1988a,b,c; Sammarco 1996; Birkeland 1997 for reviews).

Porter and Meier (1992) monitored six reefs in the Florida Keys over a 7-year period and demonstrated that at least five of them exhibited a decline in percent-cover of living adult coral over that time. All reefs declined in number of species. There was no recruitment by any of the frame-building coral species during the study period either (Porter and Meier 1992), although successful recruitment had been noted in earlier years (Gittings et al. 1988, 1990) (also see Dustan 1977, for earlier observations and a discussion of diminished coral recruitment trends in the Florida Keys, and Jaap et al. 1994; Miller et al. 1995; Smith et al. 1995, for more recent information). If bottom concentrations are similar to those examined experimentally here, a possible contributing factor could have been the type of toxicity responses exhibited by planulae in these experiments, which may have played a role in the observed low

recruitment rates. This question remains unanswered at this time.

One mechanism that may explain the sensitivity to ammonium shown by planula larvae in these experiments is osmotrophy. The role of osmotrophy in coral larvae is not yet known. Some planktotrophic and lecithotrophic invertebrate larvae take up dissolved organic matter (DOM) directly from seawater (Manahan 1990), to increase biomass, or to meet the energetic needs of development. Uptake of amino acids by embryos and larvae has been demonstrated for anemones (Chia 1972), sea urchins (Manahan et al. 1983), and other taxa. Hermatypic scleractinian corals generally live in oligotrophic environments (Lewis 1973; Muscatine and Porter 1977; Muscatine 1980), and are probably adapted to take up nitrogenous compounds in very low concentrations. It is possible that coral larvae may not have a physiological mechanism to limit nutrient uptake in enriched environments, as D. Kinsey (personal communication) has hypothesized for adult corals. This represents one additional explanation for the increased rates of mortality shown by larvae of *D. strigosa* in ammonium-enriched treatments. Once again, this question could be addressed experimentally. Other factors such as light intensity and increases in UV-B variation may well be of significance for survival of coral planulae. Unfortunately, there was insufficient time and resources to consider such factors here.

Coral larvae have locomotive abilities. Because of their slow swimming speed (2–5 mm s^{-1}; Atoda 1953; also see Atoda 1951c; Fadlallah 1983), these abilities probably function more to control their vertical position in the water column rather than their horizontal position where comparatively high-velocity sea-surface currents exist (Sammarco 1994). Fully developed planulae also respond positively to light (positive phototaxis; Atoda 1947a,b, 1951a,b,c, 1953), which, for the larva, has more significance in a vertical plane than in a horizontal plane (Sammarco 1994). Planulae in the 28°C and 30°C treatments exhibited patterns of vertical movement through time consistent with earlier reports – initial positive phototaxis followed by negative phototaxis (see Atoda 1953; Szmant-Froelich et al. 1980, 1985; Heyward and Babcock 1986). Movement patterns at 32°C, however, indicated physiological stress from elevated temperatures. Many of the larvae observed at the bottom of the vials were dead. The immediate movement of planulae downward in the water when exposed to an environment where the SST was 32°C may well represent an adaptation of the larvae to seek deeper, cooler waters when exposed to this life-threatening situation.

Depressed ciliary activity resulting from ammonium enrichment and elevated temperature could affect the ability of planlulae to move vertically in the water column. This would be especially important in an environment like that of the FGB, where the minimum depth is 18 m and strong currents can easily transport larvae away from this highly isolated set of coral reefs. This would apply to any environment where substrate suitable for settlement is limited and the timing of settlement is critical.

Substratum selection and settlement preferences of scleractinian larvae have been tested quantitatively on several species in the laboratory (e.g. Morse 1991, 1994; Morse and Morse 1991, 1996; Morse et al. 1993, 1994, 1996; McGuire 1995). Those substrata "preconditioned" by submersion in seawater prior to use in experiments seem to serve as good settlement material for coral larvae (Harrigan 1972; Sammarco 1980, 1982, 1991; Sammarco and Andrews 1988, 1989; Harriott and Banks 1995; Richmond 1997). It was surprising, therefore, that such a large proportion of larvae settled on the glass. This may be due to a short larval duration in this species. Thigmotactic responses were evident from preferences for settlement of planulae in the corners of culture vials (also see Atoda 1947b; Carleton and Sammarco 1987). Planulae in this experiment were observed to settle close to one another and, in some cases, fuse together to form aggregated colonies. Aggregation has been observed previously (Atoda 1947a,b; Wallace and Bull 1981; Sammarco 1982; Richmond 1997), and is thought to be advantageous in reducing the size-dependent mortality rates of juvenile corals (Sammarco 1982; Harrison and Wallace 1990).

Embryos which successfully survive to later stages of development in nature may not successfully metamorphose into settling planulae at higher SSTs or elevated ammonium concentrations. Larval lifespan and competence of coral planulae to metamorphose and settle successfully are clearly decreased by both high temperatures and high concentrations of ammonium in the laboratory, and data exist to suggest that these results may be extended to the field (Hunte and Wittenberg 1992).

Larval dispersal potential is proportional to larval duration (Richmond 1987). As larval survivorship decreases with increased temperature or ammonium concentrations, so does potential distance of dispersal. This implies that regional warming of surface waters, such as those which occur as localized "hot spots" (Goreau and Hayes 1994), could reduce the dispersal range of *D. strigosa* if such occurs coincidentally with a spawning event. If repeated frequently, this could produce more locally isolated populations of corals. Regional nutrient enrichment could have similar effects. The two effects combined might even further decrease the dispersal potential of coral larval.

Conclusions

1. An experimental increase in seawater temperature from 28°C to 30°C or 32°C resulted in a significant decrease in the survivorship, ciliary activity (motility), and rate of settlement in planula larvae of the scleractinian coral *D. strigosa*. These effects were proportional to temperature.

2. Increasing the concentration of ammonium from < 1 to 20 μM resulted in a significant decrease in survivorship, ciliary activity, and rate of settlement in planula larvae of the scleractinian coral *D. strigosa*. These effects were additive with respect to the negative effects of increased temperature, described above.
3. At experimental seawater temperatures of 30–32°C, the later stages of larval development in *D. strigosa* planulae were slowed or halted. Searching behavior in the planulae was also extended at 32°C.
4. *D. strigosa* planulae exhibit phototactic responses similar to those described for the larvae of other scleractinian coral species, being positively phototactic initially and then negatively phototactic after ≥50 h in the 28°C and 30°C treatments. At experimental seawater temperatures of 32°C, planulae became immediately negatively phototactic.
5. We predict that if SSTs reach ≥30°C, larval survivorship, movement (primarily vertical), and recruitment in scleractinian corals may be negatively affected.

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