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RESEARCH ARTICLE

S. Brooke · C. M. Young

Embryogenesis and larval biology of the ahermatypic scleractinian *Oculina varicosa*

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Abstract The ivory tree coral *Oculina varicosa* (Leseur, 1820) is an ahermatypic branching scleractinian that colonizes limestone ledges at depths of 6–100 m along the Atlantic coast of Florida. This paper describes the development of embryos and larvae from shallow-water *O. varicosa*, collected at 6–8 m depth in July 1999 off Fort Pierce, Florida (27°32.542 N; 79°58.732 W). The effect of temperature on embryogenesis, larval survival, and larval swimming speed were examined in the laboratory. Ontogenetic changes in geotaxis and phototaxis were also investigated. Embryos developed via spiral cleavage from small (100 μm), negatively buoyant eggs. Ciliated larvae developed after 6–9 h at 25°C. Embryogenesis ceased at 10°C, was inhibited at 17°C, and progressed normally at 25°C and 30°C. Larval survival, however, was high across the full range of experimental temperatures (11–31°C), although mortality increased in the warmest treatments (26°C and 31°C). Larval swimming speed was highest at 25°C, and lower at the temperature extremes (5°C and 35°C). An ontogenetic change in geotaxis was observed; newly ciliated larvae swam to the water surface and remained there for approximately 18 h, after which they swam briefly throughout the water column, then became demersal. Early larvae showed no response to light stimulation, but at 14 and 23 days larvae appeared to exhibit negatively phototactic behavior. Although low temperatures inhibited the development of *O. varicosa* embryos, the larvae survived temperature extremes for extended periods of time. Ontogenetic changes in larval behavior may ensure that competent larvae are close to the benthos to facilitate settlement. Previous experiments on survival, swimming speeds, and observations on behavior of *O. varicosa* larvae from deep-water adults indicate that there is no difference between larvae of the deep and shallow populations.

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S. Brooke (✉) · C. M. Young
Harbor Branch Oceanographic Institution,
5600 US1 North, Fort Pierce, FL, USA
E-mail: sbrooke@darkwing.uoregon.edu
Fax: +1-541-8883250

Present address: S. Brooke
Oregon Institute of Marine Biology,
PO Box 5389, Charleston, OR 97420, USA

Introduction

The ivory tree coral *Oculina varicosa* occurs in a range of habitats along the south central region of Florida's Atlantic coast. At depths of 70–100 m along the edge of the Florida shelf, this species forms extensive reef systems, composed of thickets of delicate azooxanthellate colonies. These deep-water *O. varicosa* systems support communities of fish and invertebrates that are as diverse as those of tropical coral reefs, and also provide spawning habitat for a number of commercial fisheries species (Koenig et al. 2000). The deep-water reefs exist only on the shelf edge off eastern Florida, and stretch over 90 nautical miles (167 km) from Fort Pierce to Daytona Beach (Macintyre and Milliman 1970; Avent et al. 1977; Reed 1980).

Abundant facultatively zooxanthellate colonies of *O. varicosa* inhabit the near-shore limestone ledges that occur at depths from 6 to 30 m off the Atlantic coast of Florida. The most common scleractinian species on these near-shore ledges are *O. varicosa* and *O. diffusa*, with occasional occurrence of *Cladocora arbuscula*, *Siderastrea siderea*, and grouped polyps of *Phylangia* sp. and *Astrangia* sp. Shallow populations of *O. varicosa* have been reported as far north as South Carolina and as far south as the Caribbean. However, the taxonomy of the Oculinidae of the western Atlantic is somewhat confused (Dr. S. Cairns personal communication), so the descriptions of distribution may be incorrect.

O. varicosa is a gonochoristic, broadcast-spawning species with small eggs (~100 μm diameter) and a high

fecundity (Brooke 2002). The gametogenic cycle begins in the early summer, and spawning occurs during July and August in the shallow populations and in September in the deep populations, with no obvious relationship to lunar or tidal phase. Embryos and larvae of *O. varicosa* could be exposed to a wide range of environmental conditions during their development. Visibility on the shallow ledges generally ranges from 1 to 10 m, but during periods of phytoplankton bloom or storm activity, can be reduced to a few centimeters. Particles from the water column are deposited during calm conditions, producing a thick layer of fine sediment on the substratum. Temperature over the shallow habitats varies from 7°C to 29.5°C, partly from seasonal changes, but also because of periodic upwelling events that cause cold deep-ocean water to inundate the near-shore habitats (Smith 1981), subjecting both deep and shallow *O. varicosa* populations to rapid temperature fluctuations. Upwelling events during the summer months, when the Florida Current flows closer to the Florida shelf, can cause the water temperature to decrease rapidly in both deep and shallow habitats (Smith 1981, 1983, 1987).

Physiological tolerances of the dispersive stages may strongly influence recruitment patterns and genetic exchange among *Oculina eulina varicosa* populations. The optimum temperature for growth and survival of most adult scleractinians is 25–29°C (Crossland 1981), although a number of corals in temperate and deep-water habitats live at much lower temperatures (Rogers 1999; Brooke and Young 2003). There is little information available, however, on environmental tolerances of coral embryos and planulae. Abnormal embryos of the tropical scleractinian *Diploria strigosa* were observed at temperatures >30°C (Bassim et al. 2002), and elevated temperature (33°C) increased mortality, reduced larval longevity, and caused premature metamorphosis in *Porites astreoides* larvae (Edmunds et al. 2001). Alternatively, larval life (therefore dispersal potential) may be extended at sub-lethal low temperatures, which has implications for distribution and genetic homogeneity of populations. Invertebrate larvae cannot swim against oceanic currents, but they can use behavioral responses to physical stimuli (Edmondson 1946) to regulate their vertical position in the water column. Larvae can avoid predation, optimize feeding, control dispersal distance, and regulate spread with respect to siblings and adults by modifying their behavior. The two major vectors to which larvae orient in the marine environment are light (phototaxis) and gravity (geotaxis) (Young 1995). The effect of intensity and spectral quality of light on the settlement of six species of scleractinian corals (*Goniastrea favulus*, *G. aspera*, *Acropora tenuis*, *Oxypora lacera*, *Montipora peltiformis*, and *Platygyra daedalea*) with contrasting depth distributions was examined in laboratory trials by Mundy and Babcock (1998). Light-dependent settlement was shown by planulae from five of the six species examined, and settlement patterns shown by planulae from all six species were consistent with the vertical distribution patterns of adults in the field. Planulae of *Achrelia horrescens*, *Euphyllia glabrescens*, *Pocillopora damicornis*, and *Seriatopora hystrix* all exhibited negative geotaxis and positive phototaxis, but became negatively phototactic in bright light (Kawaguti 1941). Larval phototactic response varied among species and correlated well with larval zooxanthella density and the observed distributions of adults.

The present study describes the embryology and larval development of shallow-water *O. varicosa*. We present data on the survival of embryos and larvae over a range of temperatures, observations on the effect of temperature on larval swimming speed, and experimental evidence for larval responses to light and gravity. The results of similar experiments on larvae from deep-water *O. varicosa* are reported elsewhere (Brooke and Young 2003).

Materials and methods

Embryogenesis and larval development

During periods of potential spawning activity (July and August 1999), small pieces from several (6–12) colonies of *Oculina varicosa* (Leseur, 1820) were collected from shallow (6–8 m) limestone ledges, approximately 500 m offshore from Pepper Park (27°32.542 N; 79°58.732 W), in Fort Pierce, Florida. The samples were maintained at ambient light and temperature (~25°C) in a 1-l glass bowl containing 20-μm-filtered seawater. When spawning occurred, gametes were collected immediately using glass pipettes and transferred to small (200 ml) glass bowls of 0.45-μm-filtered seawater (FSW) for fertilization. The fertilized embryos were observed throughout embryogenesis, and photographs of each stage were taken using an Optronics digital camera attached to an Olympus light microscope. Stock cultures of embryos and larvae were maintained in 2-l glass jars of FSW (35 ppt) at 25°C (ambient water temperature at the time of sample collection) at a density of 3–5 ind. ml^{-1}.

Since the eggs, embryos, and larvae are all small and negatively buoyant (dead embryos were observed to sink in all stages), we attempted to determine if the larvae were planktotrophic. Subsamples of larvae were offered various types of food, including different concentrations of algal cultures (*Isochrysis galbana* and *Nanochloropsis* sp.), crushed *Artemia salina* nauplii, and coarsely filtered (80 μm) natural seawater.

Samples of embryos were taken at each developmental stage and preserved in 2.5% glutaraldehyde. Ciliated larvae were preserved at weekly intervals. The age of embryos was measured from time of fertilization, and larval age was recorded from the onset of swimming. Samples were observed under a light microscope and a scanning electron microscope to document embryonic and larval development. Larval swimming behavior was described from observations under an Olympus SZH10 dissecting microscope at ×20 magnification.

Water temperatures

To determine the range of temperatures that embryos and larvae might encounter during dispersal, we deployed a HoboTemp temperature logger near the shallow (6 m deep, Pepper Park, Ft. Pierce, Florida) habitat and a coastal 2D-ACM current/temperature meter at the deep (80 m deep, Jeff's Reef) *O. varicosa* reef (Fig. 1). The shallow-water instrument was deployed and recovered by SCUBA. The shallow record spanned a period of 20 months, with a mid-winter gap caused by bad weather. A submersible was used for deployment and recovery of the deep instrument, which recorded for a full year. The data loggers were programmed to record temperature every half hour and every 2 h at the shallow and deep sites, respectively, and the data are reported as weekly averages.

Effect of temperature on embryogenesis

Samples of 100 newly fertilized eggs (fertilized at ~25°C) were placed in 16 scintillation vials, each containing 20 ml of FSW. Four replicate vials were incubated at each of four temperatures (11°C, 17°C, 25°C, and 30°C) in an aluminum temperature gradient block (Baker 1974; Stanwell-Smith and Peck 1998). Treatment temperatures were maintained using two water baths at opposite ends of the block: one set at 5°C and the other at 35°C. Embryonic developmental stage was scored as the number of embryos at each stage after 3 h, to document the effect of temperature on early embryos, and after 18 h to determine longer term effects on development. The data were translated into percentages and arcsine-transformed before applying a two-way ANOVA to the 3-h and 18-h data separately.

Effect of temperature on larval survival

Samples of 40 larvae (age 4 days) were placed in 20 ml scintillation vials of FSW. Three replicate vials per treatment were incubated in the aluminum temperature gradient block at 11°C, 17°C, 22°C, 26°C, and 31°C. Larvae were counted and placed into clean FSW every 3–5 days for 24 days. The data were analyzed using the Kaplan–Meier survival estimation (Lee 1992), which estimates the distribution of survival times from independent samples under different experimental treatments. The survival estimates were calculated for each temperature, where the probability of survival was calculated at the end of each time interval. The null hypothesis states that all the samples at the different temperatures have the same survival function. The log-rank test compares the equality of survival functions for the different temperatures.

Effect of temperature on larval swimming speed

Three replicate scintillation vials of FSW, each containing 100 larvae (age 12 days), were placed in incubators and acclimated to the experimental temperatures (5–35°C in increments of 5°C) for 6 h prior to data collection. The larvae were then removed from the vial and placed in a small (5 cm diameter) Petri dish under an Olympus SZH10 dissecting microscope at ×50 magnification. Larval swimming was recorded for 2 min onto Hi-8 videotape using a camera connected to the microscope. The recording was then terminated to avoid artifacts of temperature change. Once a larva had crossed the field of view, it was removed from the dish with a glass pipette to avoid re-sampling. A scale was included with each recording for assessment of distance. The tapes were replayed on a 29 cm video monitor, and for each treatment replicate the distance traveled by each of 20 individuals was recorded at 2-s intervals until the larva disappeared from view. An average swimming speed was computed for each treatment, and a one-way ANOVA (analysis of variance) was applied to determine the effect of temperature on larval swimming speed.

Ontogenetic changes in geotactic and phototactic responses

Newly ciliated larvae (< 12 h post-ciliation) from a single culture were divided into groups of 50 and placed in 50-ml acrylic tissue-culture vials (10 cm×5 cm×2 cm),

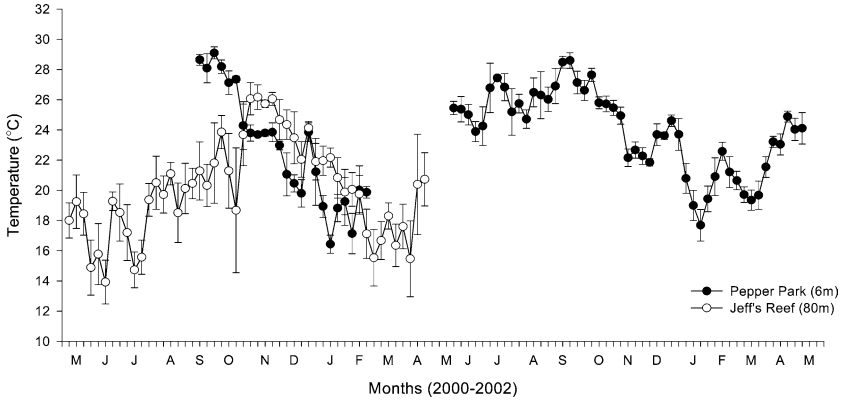

Fig. 1 Seasonal changes in mean weekly bottom water temperature (°C) at the deep (80 m) and shallow (6 m) study sites, Jeff's Reef and Pepper Park, respectively, for 2000–2002. Data collected by the authors using a "hobotemp" temperature datalogger at Pepper Park and a 2D-ACM acoustic doppler current meter at Jeff's Reef

containing FSW. The vials were flat on all sides, and five equal horizontal sections (2 cm apart) were marked on the walls. Three replicate vials were placed in an incubator at 25°C in the dark and examined under red light at noon and midnight for the first 48 h (to establish any diurnal changes) and, thereafter, at approximately 2-day intervals for a period of 14 days. The number of larvae in each of the five sections of the vial was counted; those in the top section were scored as negatively geotactic, and those in the bottom were scored as positively geotactic. Those in the other sections were considered neutral and categorized as "middle".

An ordinal logistic regression model was applied to the counts of larvae found in the top, middle, and bottom sections of the experimental vials for each value of age and tested for goodness of fit with the score test for the proportional odds assumption. The null hypothesis that larval position is independent of age was tested with the likelihood ratio test. The intercept values and the coefficient for the effect of age on the log scale were estimated with maximum likelihood and then entered into an equation to generate a predicted cumulative probability model of larval position at each age.

Phototaxis experiments were conducted using larvae at ages of 12 h, 24 h, 8 days, 14 days, and 23 days. For each trial, 50 larvae were dark-adapted for 3 h at 25°C, and all experiments were done between 1200 and 1600 hours to reduce any behavioral variation that might be caused by diel rhythms. A slide projector with a 300-W lamp provided light stimulus for this experiment. The light was filtered with a hot mirror (Baird Atomic) and an infrared-radiation-absorbing filter to remove heat. Light intensity was controlled using neutral density filters and measured with a radiometer (EG&G model 500). A small Lucite trough (15 cm×3 cm×3 cm) containing FSW was placed inside a water bath (to reduce light reflection off the back wall of the trough), and removable partitions were inserted to divide the trough into five equal sections. Under dim red light, the dark-adapted larvae were gently placed in the center section with a glass pipette, and, upon light stimulation, the partitions were removed allowing the larvae to swim freely in the trough. After a 5-min exposure to light, the separator grid was inserted into the trough, and the number of larvae in each section was scored. A larva was scored as exhibiting positive phototaxis if it was found in the section closest to the light source and negative phototaxis if it was in the section farthest from the light. Five different light intensities were used as well as a control in which the experiment was run in complete darkness.

The response of larvae of different ages to various light levels was analyzed with logistic regression. The null hypothesis states that larval position is independent of age and light level. The overall effect of these two factors was first tested with a Chi-squared likelihood ratio. Maximum likelihood was then applied to estimate the coefficients for the independent variables (age and light), and tests for significance of the coefficients were performed with the Wald Chi-squared test. Separate Chi-squared tests were applied to each age to determine whether there were any significant differences between the responses of the observed and expected (dark control) larvae.

Results

Embryogenesis and larval development

Observations of embryonic and larval development were made using stock cultures at 25°C and 35 ppt. *Oculina varicosa* sperm observed under a light microscope (×40) have a simple conical head, and newly spawned eggs were negatively buoyant, small (~100 μm in diameter), and spherical, with germinal vesicle breakdown occurring either prior to release or shortly thereafter. A single polar body was extruded within 30–60 min of spawning, but since the male and female gametes were not collected separately, it was unclear whether polar body extrusion occurred prior to or after fertilization. Cleavage occurred at intervals of approximately 45 min until the embryos reached the 32-cell stage, when the cleavage pattern became complex and difficult to track. Cell division was equal and holoblastic in both animal and vegetal poles, and embryos developed in a spiral cleavage pattern until the hollow blastula formed 4–5 h later. Gastrulation occurred by invagination, with the endodermal cells folding inwards from an essentially spherical blastula. During gastrulation, the blastulae became flattened and concave; however, they re-formed into a spheroid shape and produced normal planula larvae (Fig. 2A–F), which were fully ciliated. This stage was reached after ~18 h at 25°C and 30°C, but the presence of algal foods, ground up *Artemia* sp. larvae, and coarsely filtered seawater had no positive effect on survival or development, and merely caused the culture water to foul more rapidly. Larvae developed well in FSW, suggesting that these larvae could be lecithotrophic despite their small size and dense tissues. However, the experiments were not conclusive, and the mode of nutrition for this species remains unresolved.

Early planulae (Fig. 3A) were completely ciliated and slightly elongated along the anterior–posterior axis. Newly developed planulae moved towards the water surface, where they swam rapidly in a spiral fashion, rotating around the longitudinal axis. As the larvae developed, the oral pole became slightly wider than the aboral pole (Fig. 3C), which was directed forward whilst swimming. *O. varicosa* planulae were composed of ectoderm and endoderm cell layers, separated by an acellular mesoglea. The ectoderm was comprised of a layer of columnar epithelial cells containing well-developed nematocyst cells, which fired in response to a physical stimulus (Fig. 3F). At age 24 h, the mean length (±SD) of the planulae was 141.6 ± 16.5 μm. After 2–4 days, the larvae began swimming throughout the water column following straight directional, large circular, and sigmoidal tracks. After 14 days (Fig. 3C) larvae became more elongated [mean length (±SD): 216.7 ± 27.7 μm]. The cilia at the

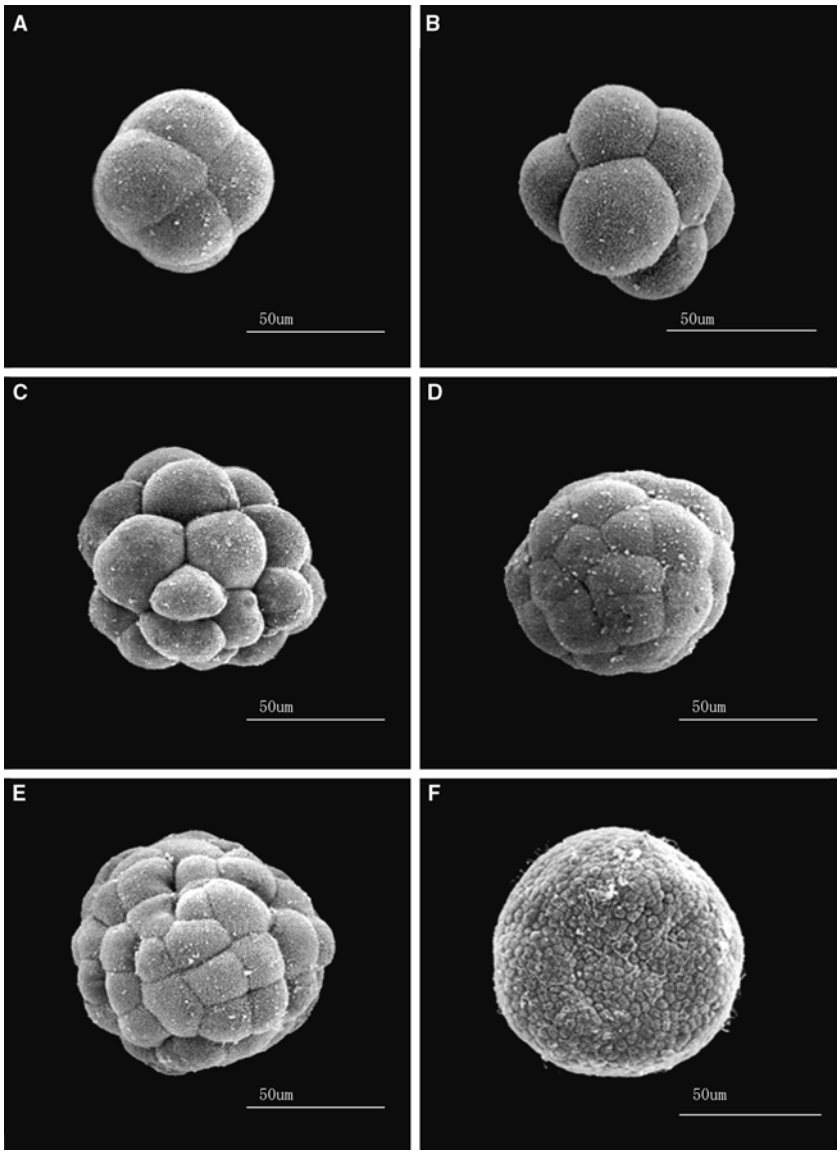

Fig. 2A–F *Oculina varicosa*. Scanning electron micrographs of different embryonic stages: **A** 4-cell, **B** 8-cell, **C** morula, **D** early blastula, **E** late blastula, and **F** late gastrula

aboral pole were noticeably longer than the other cilia, and the larvae displayed an apparent benthic probing or creeping behavior. The planulae were very flexible and often changed shape during this phase. Some attached temporarily to the substratum by the aboral pole, but began to swim freely again shortly afterwards. The planulae were azooxanthellate for the duration of their larval life, as are the deep-water *O. varicosa* planulae. The few planulae that underwent metamorphosis did so after approximately 21 days at 25°C. The polyps were small [mean diameter = 85.7 ± 14.0 μm (SD)] and had two to six extended tentacles.

Ambient temperatures

Mean weekly water temperature in the shallow *O. varicosa* habitats ranged from 16°C to 29.5°C over the course of the year, but only from 24°C to 29.5°C during the period (July through September) when embryos and larvae are likely to be in the water column (Fig. 1). Mean water temperature at the deeper *O. varicosa* habitat ranged from 14°C to 26°C, with breeding season temperatures ranging from approximately 15°C to 22°C. Historical data (Smith 1983) shows that July–September temperatures may sometimes be as low as 10°C at 80 m and 18°C at 10 m during upwelling events.

Effect of temperature on embryogenesis

There was a positive relationship between temperature and embryonic development time. When maintained at 25°C and 30°C, embryos developed rapidly, reaching the morula stage after 3 h of incubation. In the 17°C culture, 16% of the embryos progressed to the 8-cell stage after 3 h, but most remained at the 4-cell stage. Cultures incubated at 10°C were composed primarily of embryos

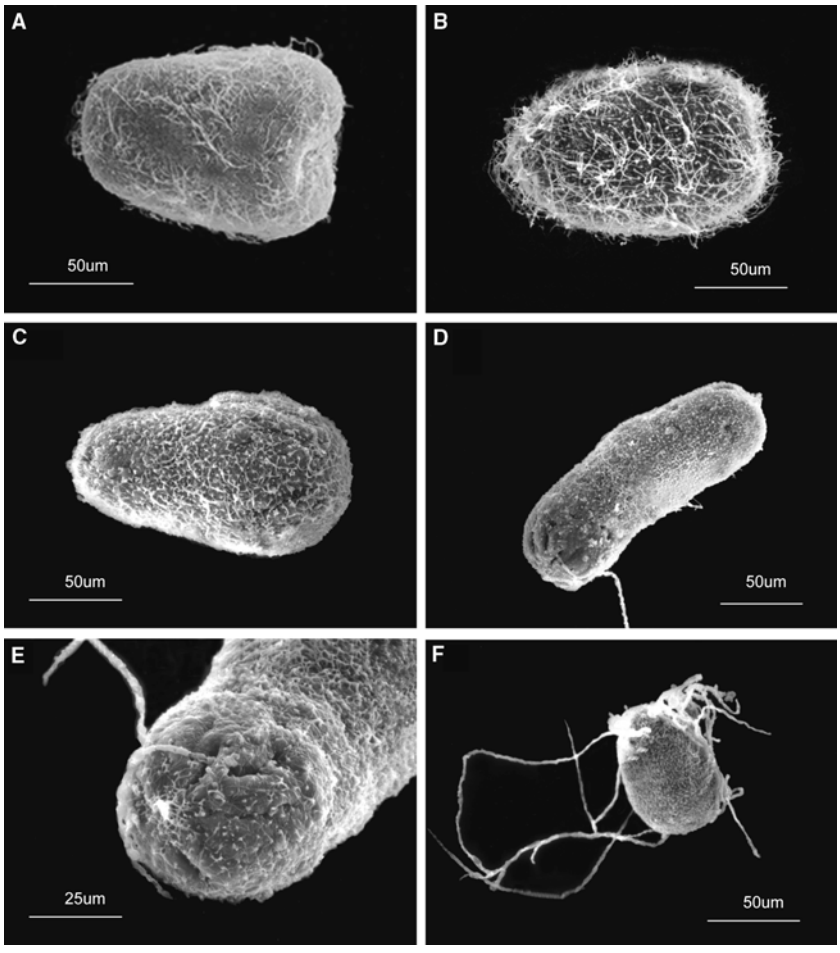

Fig. 3A–F *Oculina varicosa*. Scanning electron micrographs of larval stages maintained at 25°C: **A** 24 h post-ciliation, **B** 7 days, **C** 14 days, **D** 21 days, **E** detail of nematocyst on larva, age 21 days, and **F** numerous nematocysts fired on larva, age 10 days

with two and four cells, with $<2\%$ attaining the 8-cell stage (Fig. 4A).

After 18 h, all of the cultures at 25°C and 30°C contained 100% actively swimming larvae. Embryos in the 17°C treatment were at the morula stage, and those at 10°C had not progressed beyond eight cells (Fig. 4B). The cultures with arrested embryonic development were incubated at 25°C to see whether they would develop further. Embryos from the 17°C culture proceeded to develop, and, after a further 18 h, cultures contained 39% apparently normal, but very slow-swimming planulae, and 61% abnormal embryos. Embryos from the 10°C culture did not develop, and all were either abnormal or dead after 36 h of incubation at 25°C.

Results from a two-way ANOVA on arcsine-transformed data revealed no significant effects of temperature ($F=0.02$, $P=0.99$) on embryonic development after 3 h. The 18-h data set failed the test for normality and was not analyzed.

Effect of temperature on larval survival and swimming speed

For the first 15 days of the experiment, larval survival was high ($>80\%$) in all treatments; however, increased mortality was observed over time with increasing temperature (Fig. 5). Larval settlement was not observed in any of the experimental treatments, and lethal high and low temperatures were not determined.

The Kaplan–Meier analysis of larval survival over time at different temperatures (Table 1) revealed a significant effect of treatment on survival function ($\chi^2=36.67$, $P<0.0001$) over the duration of the experiment, despite the high number of survivors ($>60\%$ in all treatments) after 24 days. A one-way ANOVA showed that temperature had a significant effect ($F=63.58$, $P<0.001$) on larval swimming speed. Swimming speed approximately doubled between 5°C and 25°C (Q_{10}: ± 1.98), and motility was lowered at the experimental extremes of 5°C and 35°C. The estimated position of the larvae in the water column after 12 h of vertical swimming was calculated using the average speed at each temperature (Fig. 6), demonstrating that larvae could easily undergo daily migrations to the surface in the shallow habitat, even at the most extreme temperatures.

Larval geotactic and phototactic responses

The score test for the proportional odds assumption ($\chi^2=0.04$, $P=0.83$) indicates that the ordinal logistic

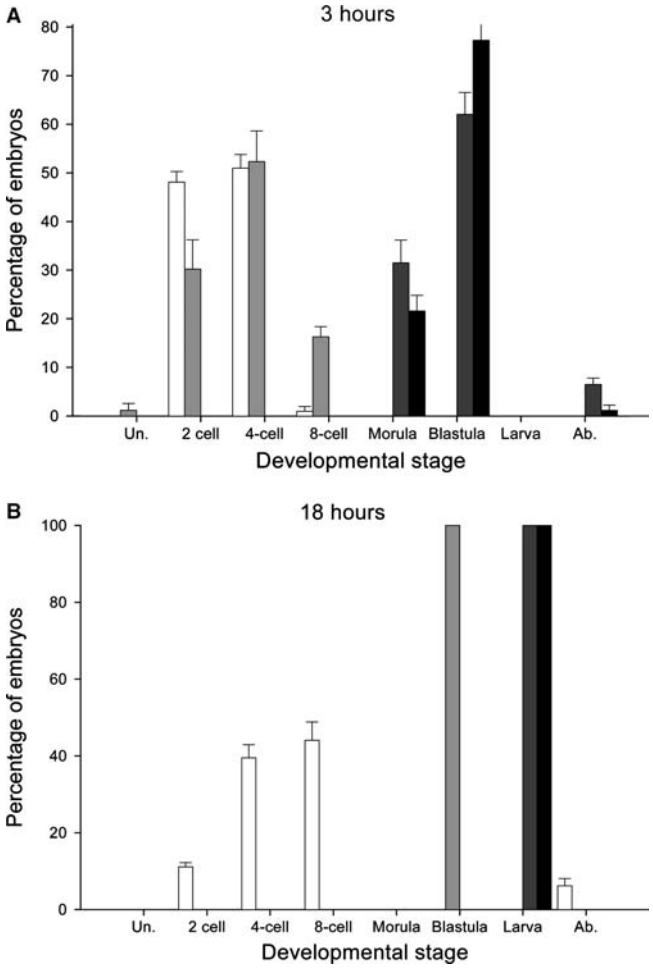

Fig. 4A, B *Oculina varicosa*. Effect of four temperatures on embryonic development after: **A** 3 h and **B** 18 h. *Error bars* represent SE of the mean of four replicate vials with 100 embryos vial^{-1} (*Un*. undeveloped; *Ab*. abnormal)

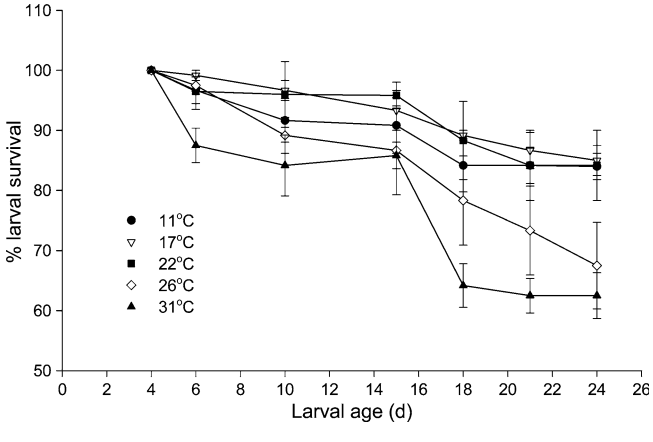

Fig. 5 *Oculina varicosa*. Effect of five temperatures on percent larval survival over 24 days. *Error bars* represent SE of the mean of three replicate vials with 40 larvae vial^{-1}

regression model adequately describes the experimental data for position of larvae over time. The likelihood ratio test indicates that age is a significant predictor of

Table 1 *Oculina varicosa*. Log-rank statistics and log-rank test of equality between survival functions of larvae at different temperatures

Temperature (°C)	Log-rank
11	−11.95
17	−10.24
22	12.563
26	−10.33
31	19.967

Log-rank test: $\chi^2 = 36.67$; $df = 4$; $P < 0.0001$

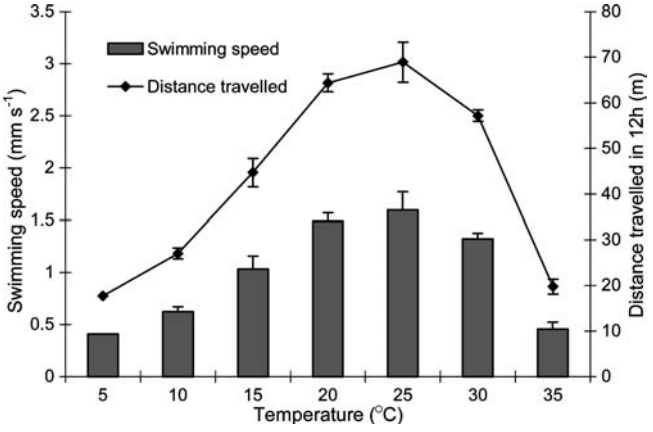

Fig. 6 *Oculina varicosa*. Effect of temperature on larval swimming speed (mm s^{-1}), and estimated position of larvae in the water column after 12 h of vertical migration. *Error bars* represent SE of the mean of three replicate vials containing 100 larvae vial^{-1}

larval position ($\chi^2 = 273.81$, $P < 0.0001$); therefore, the null hypothesis that position is independent of age was rejected. The predicted and actual larval positions (Table 2) were presented graphically for comparison (Fig. 7). Larvae exhibited negative geotactic behavior for the first 12 h after ciliation, with ~90% swimming at the water surface. Between 24 and 48 h, larvae became more evenly distributed throughout the vial. After 48 h the larvae were observed in increasingly high numbers in the lower section of the vial, and by age 14 days, <90% of the larvae were swimming close to the bottom.

The likelihood ratio test (Table 3) indicated that in the overall model, light and age together are not significant predictors of larval tactic response ($\chi^2 = 4.04$, $P = 0.133$). Level of light does not appear to have a significant effect ($\chi^2 = 0.20$, $P = 0.63$). However, when age was entered into the model by itself, its effect on the probability of a positive response to light approached significance ($\chi^2 = 3.84$, $P = 0.05$). Ciliated larvae (24 h old) showed little horizontal dispersal from the center of the light exposure trough where they were initially placed. They swam to the water surface, and most larvae remained in the middle sections. At ages 1 and 8 days, Chi-squared analyses (Table 4) showed almost no significant difference between the expected (dark control data) and observed numbers of larvae exhibiting phototactic behavior (Fig. 8). At age 14 days (Fig. 8) and

Table 2 *Oculina varicosa*. Predicted and actual larval positions in the experimental vial at each age. Numbers represent percent larvae at each position. Actual data represent mean (±SE) of three replicate vials

Age (days)	Top		Middle		Bottom	
	Predicted	Actual	Predicted	Actual	Predicted	Actual
0.5	60.8	90.7 (2.70)	14.1	7.4 (0.77)	25.1	2.0 (1.96)
1	56.5	62.7 (7.11)	14.9	15.6 (7.57)	28.6	21.6 (5.15)
2	47.5	21.5 (5.16)	16.0	21.2 (0.81)	36.6	57.3 (5.95)
4	30.5	2.6 (2.56)	15.2	14.5 (0.74)	54.3	82.9 (3.06)
6	17.5	31.1 (1.23)	11.5	12.8 (3.08)	71.0	56.1 (1.95)
8	9.3	9.5 (4.21)	7.2	6.4 (1.07)	83.5	84.2 (3.20)
14	1.2	5.4 (3.21)	1.0	1.7 (1.71)	97.8	92.9 (3.57)

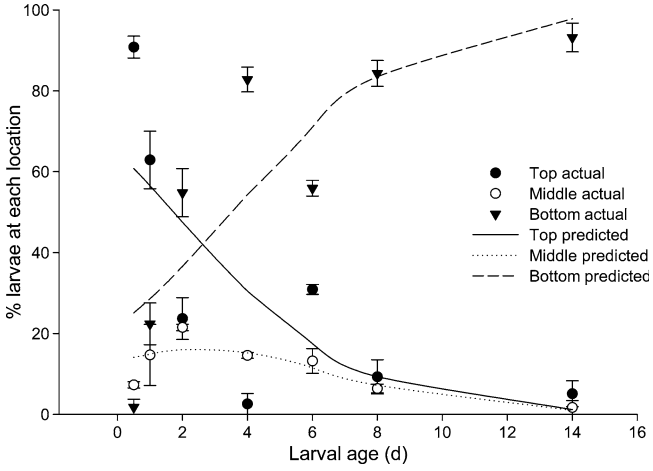

Fig. 7 *Oculina varicosa*. Ontogenetic change in larval geotactic response (% larval response). *Error bars* represent SE of the mean of three replicate vials with 100 larvae vial^{-1}

Table 3 *Oculina varicosa*. Analysis of maximum-likelihood estimates. Coefficients based on daily effects of each parameter on larval response

Parameter	*df*	Estimate	SE	χ^2	*P*
Intercept	1	−0.195	0.150	1.675	0.196
Age	1	−0.018	0.009	3.962	0.047
Light	1	0.030	0.066	0.203	0.653

Table 4 *Oculina varicosa*. Larval Chi-squared values for phototactic response to a range of light intensities by larvae of different ages. Significant differences between dark control larvae and those exposed to light are represented by *asterisks*: $*P<0.05$ and $**P<0.01$

Photoresponse	1 day	8 days	14 days	23 days
Positive	9.44	9.24	16.52*	35.15**
Negative	6.66	15.89*	295.37**	104.13**

23 days (Fig. 8), there were significant differences between dark controls and light-exposed larvae.

Discussion

Larvae of shallow-water *Oculina varicosa* showed tolerance to a wide range of temperatures for extended periods in the laboratory, although there was a decrease in survival over time, especially at the higher temperatures. The larvae may have exhausted their energy supplies earlier in the warmer treatment as a result of increased metabolic demand. Despite possible laboratory artifacts, the results show that *O. varicosa* larvae are physiologically capable of surviving a range of temperatures wider than the range they would have encountered over the bathymetric and latitudinal areas in which adults occurred during the 2 years of our study. On this basis, one might be tempted to conclude that the limits of distribution for this species are set by factors other than thermal tolerances. However, in some years, upwelling events can cause the summer temperature at the deep *O. varicosa* sites to drop below 10°C (Smith 1981), which would cause abnormal development or death to developing embryos in deep water. Thus, variation in recruitment between years could be related to the strength and timing of upwelling events.

Scleractinian corals are neither diverse nor abundant on the central Florida shelf, and *O. varicosa* is the most abundant species in this habitat. The ability of larvae to tolerate a very wide range of temperatures in a system where seasonal upwelling may quickly change the water temperature during the dispersal period may be one reason that this species is so successful. Larvae from deep-water and shallow-water colonies showed similar thermal tolerances (Brooke and Young 2003), an indication that larvae from each habitat can potentially colonize the other.

In contrast with brooding scleractinians such as *Favia fragrum* (Szmant et al. 1985) and *Monomyces rubrum* (Heltzel and Babcock 2002), embryogenesis is typically rapid in externally fertilizing species, with swimming larvae developing within 6–8 h (20–22°C) in the temperate species *Astrangia danae* (Szmant-Froelich et al. 1980) and within 48 h in the tropical species *Platygyra sinensis* (Babcock and Heyward 1986). The embryos of *O. varicosa* conformed in both type and speed of development with other broadcast-spawning species. Heltzel and Babcock (2002) postulated that externally fertilized embryos (e.g. *A. danae* and *P. sinensis*) progressed rapidly to the swimming larval stage, which minimized the time spent in the plankton and facilitated

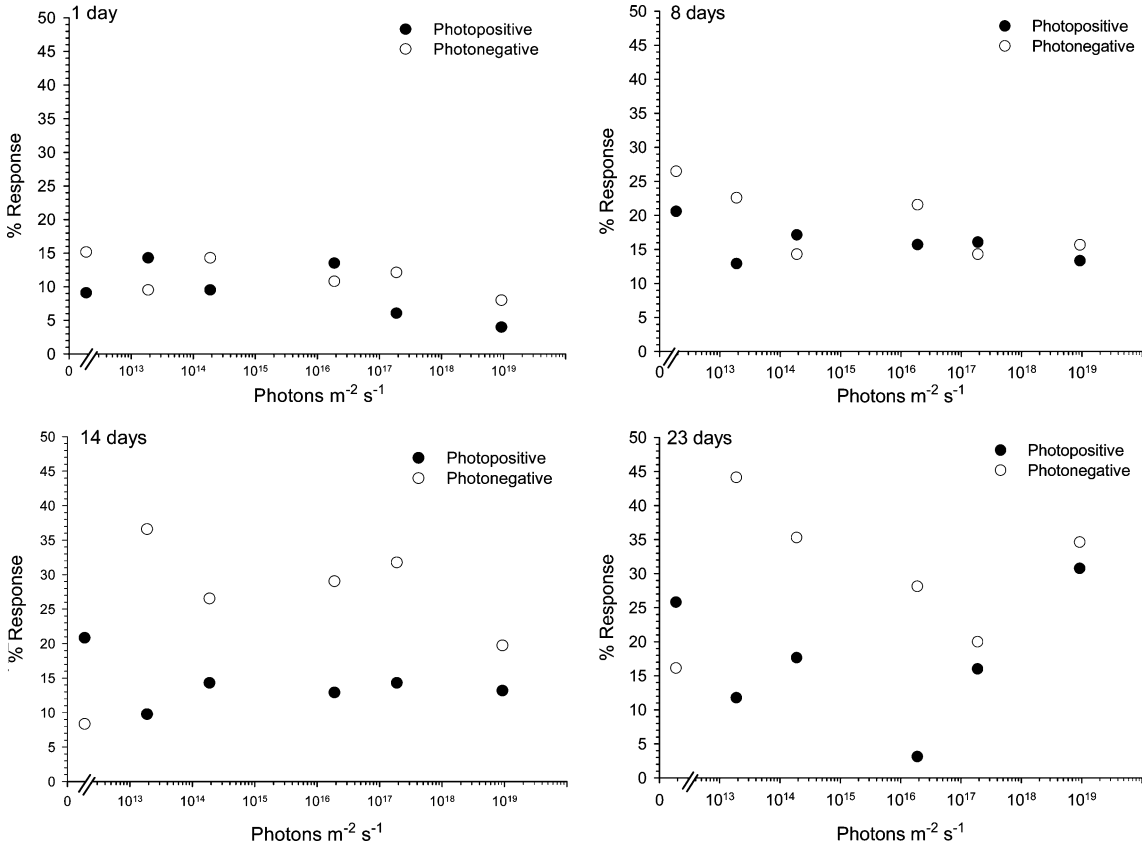

Fig. 8 *Oculina varicosa*. Phototactic responses of larvae to a range of light intensities at ages 1, 8, 14, and 23 days

faster settlement, thereby reducing overall mortality. This advantage is somewhat negated in species such as *O. varicosa* that produce long-lived larvae. These swimming planulae, however, have an advantage over the non-motile embryos in that they can control (to a limited extent) their position in the water column using behavioral and sensory mechanisms.

The few larvae that settled and metamorphosed in our study were all from the stock cultures at 25°C, and, since none of the larvae from the experimental treatments displayed settlement behavior, the effect of temperature on recruitment was not determined. Planulae from both deep- and shallow-water *O. varicosa* colonies were azooxanthellate, although the adults are facultatively zooxanthellate (even the deep-water colonies occasionally have zooxanthellae during the summer months). Symbionts are therefore acquired through some mechanism other than vertical transmission. It is still unclear whether *O. varicosa* larvae are planktotrophic, and, since they did not respond to provision of external food, neither the stock cultures nor the experimental larvae were fed. If these are planktotrophic larvae, the absence of an external energy source may have prevented successful metamorphosis. The absence of suitable substratum or appropriate light regime may also account for the observed low levels of metamorphosis.

Larval swimming speed slowed at lower temperatures, which is probably a result of the combined effects of higher water viscosity (viscosity at 20°C is 1.5 times the viscosity at 40°C) and slower metabolic rate with lower water temperatures. Larvae may have experienced respiratory inhibition above 25°C, as motility is reduced at the highest experimental temperatures. Impaired swimming speed reduces the ability of larvae to control their vertical position in the water column, which could, in turn, increase their risk of transport away from suitable habitat. Larvae spawned in shallow reef areas would be potentially capable of diurnal migrations in the water column, but whether this occurs in the field is unknown. Similar studies on larvae from deep-water *O. varicosa* adults showed no significant difference in swimming response to temperature from the "shallow" larvae. Vertical migration calculations indicated that larvae spawned by the deep *O. varicosa* habitat, even at the optimum temperature (25°C), would not reach the surface within 12 h (Brooke and Young 2003). These calculations ignore the effects of advective currents, but show that with the same physiological responses, larval migration patterns could vary between habitats. Differences in diel migration patterns undoubtedly have complex ecological consequences, but would require further study to determine how larval survival and dispersal might be affected.

Larvae showed no diel pattern of migration either when maintained in the dark or on a diurnal light/dark cycle. An age-related behavior, however, was consistently observed in laboratory cultures, where *O. varicosa*

larvae invariably swam towards the surface upon developing cilia and remained there for 12–24 h. After this time, they began to swim throughout the water column and subsequently became demersal. Although this behavior has been observed in other coral planulae (Harrigan 1972; Lewis 1974; Szmant-Froelich et al. 1985), and is usually attributed to changing phototaxis, most tactic responses have not been tested experimentally (Harrison and Wallace 1990). True geotactic behavior is driven by the ability of the organism to perceive gravity and orient themselves relative to the gravitational field through geo-receptive organs called statocysts. Larvae without statocysts use alternative orientation mechanisms. For example echinoplutei, veligers, and polychaete larvae all have uneven distributions of body mass and a low center of gravity, so ciliary action automatically results in upward motion. In organisms such as these that orient passively, swimming speed and frequency are under behavioral control and allow the larvae to control vertical distribution (reviewed by Young 1995). Anthozoan planulae do not have statocysts, but since eggs, embryos, and larvae of *O. varicosa* are all negatively buoyant, it is clearly a behavioral response rather than a change in buoyancy that causes young larvae to collect near the water surface and older larvae to become demersal.

Thorson (1964) observed that early stage larvae of many phyla are attracted to light in the laboratory. Later, Forward (1988) noted that most of the studies of phototaxis have been done using light regimes that bear little resemblance to those found in the field. He tentatively suggested that many positive light responses reported in the literature are laboratory artifacts and should not be used when inferring field behavior. Early larvae of *O. varicosa*, however, showed no significant response to light over a range of intensities, but older larvae (>8 days) showed negatively phototactic behavior. Although the data are not unequivocal and there are probably laboratory artifacts associated with these experimental observations, the general interpretation of the results makes sense in an ecological context. The early *O. varicosa* larvae swim towards the surface, which would carry them away from potential predators on the reef and into dispersive currents in the water column. In the later stages, the combination of positive geotactic and negative phototactic behavior would ensure that competent larvae approach the sea floor for settlement. Experiments on survival, swimming speeds, and observations on behavior of *O. varicosa* larvae from deep-water adults indicate that there is no difference between larvae of the deep and shallow populations (Brooke and Young 2003). This is not unexpected given that both populations of *O. varicosa* may experience similar environmental conditions, despite the differences in the depth of their habitats.

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