555

ELSEVIER

Journal of Experimental Marine Biology and Ecology
288 (2003) 181–201

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Effects of pressure on swimming behavior in planula larvae of the coral *Porites astreoides* (Cnidaria, Scleractinia)

Joel L. Stake*, Paul W. Sammarco

Department of Biology, University of Louisiana at Lafayette, Lafayette, LA 70504, USA
Louisiana Universities Marine Consortium (LUMCON), 8124 Hwy. 56, Chauvin, LA 70344, USA

Received 8 August 2002; received in revised form 20 November 2002; accepted 15 December 2002

Abstract

Mechanisms governing the behavior of coral planulae are not well understood, particularly those manifesting themselves between the time when the larvae are released and when they settle. Larvae from the hermatypic coral *Porites astreoides* Lamarck were exposed to different levels of hydrostatic pressure—103.4, 206.9, 310.3, 413.8, and 517.1 kPa (including ambient pressure). Data were collected at stops of the above pressures for 15 min each, respectively. This was done in both an increasing sequence and a decreasing one. When exposed to increases in pressure from 103.4 kPa, larvae swam upward (negative barotaxis) in a spiraling motion. Upon exposure to decreasing pressure from 517.1 kPa, larvae moved downward (positive barotaxis), but the magnitude of the vertical movement was much less than in the case of increasing pressure. This suggests that these larvae are more sensitive to increased pressure than decreasing pressure. High variance was also observed in the responses of these larvae at both the intra- and inter-colony levels. Thus, this behavioral trait is variable within the population. The trait may be genetically based, and thus may be susceptible to alteration by natural selection, although this remains to be demonstrated. This study is the first to document these behavioral mechanisms in coral larvae.

Keywords: Coral; Planula; Pressure; Larval behavior; *Porites astreoides*; Barotaxis

* Corresponding author. Department of Biology, University of Louisiana at Lafayette, Lafayette, LA 70504, USA. Tel.: +1-337-482-5246; fax: +1-337-482-5834.
E-mail addresses: jstake@yahoo.com (J.L. Stake), psammarco@lumcon.edu (P.W. Sammarco).

0022-0981/03/$ - see front matter © 2003 Elsevier Science B.V. All rights reserved.
doi:10.1016/S0022-0981(03)00018-2

1. Introduction

One of the means by which scleractinian corals maintain their populations is through the release of swimming larvae that are carried by currents to settle and establish nearby reefs, as well as to help maintain the natal reefs from which they were released (Sammarco, 1994b). Swimming larvae can act as a means of dispersal in many marine benthic organisms (Thorson, 1961, 1964; Doyle, 1975), particularly sedentary or sessile organisms (Harrison and Wallace, 1990). Such dispersal can provide a means by which to colonize new habitats, recolonize old habitats, and promote gene flow (Thorson, 1961; Scheltema, 1977; Gerrodette, 1981; Ayre et al., 1997).

The impact of planktonic dispersal, however, has been the subject of controversy. One view is that reefs are dependent upon each other for larval recruits (Harrison et al., 1983, 1984; Williams et al., 1984; Babcock and Heyward, 1986), and the other is that many larvae are retained on their natal reef (Done, 1982; Sammarco and Andrews, 1988). This apparent controversy has been reviewed in detail by Sammarco (1994a,b); he has demonstrated, in fact, that both short- and long-distance dispersal can be simultaneously occurring. The many questions regarding what happens to these larvae between the time they are released and the time that they are cued to settle remains open.

Much research has been performed on adult coral reproduction, particularly over the past 20 years (e.g. Rinkevich and Loya, 1979; Kojis and Quinn, 1980; Fadlallah and Pearse, 1982; Fadlallah, 1983; Chornesky and Peters, 1987; Harrison and Wallace, 1990; Richmond and Hunter, 1990; McGuire, 1997; Shlesinger et al., 1998), and larval dispersal mechanisms (e.g. Richmond, 1987; Sammarco and Andrews, 1988, 1989; Harrison and Wallace, 1990; Sammarco, 1994a,b, 1996). Research on physical oceanographic mechanisms has provided for prediction of larval dispersal (Sammarco, 1994b).

There are many modes of reproduction in the Scleractinia (see Sammarco, 1982; Harrison and Wallace, 1990), but two are generally used in this order. The first is the release of gametes followed by external fertilization, generally termed "broadcasting". The second is the development of planula larvae within the polyp followed by release of fully developed larvae, termed "brooding". Once formed, either by broadcast spawning or brooding, the planula larva is simple in structure. Similar to the adults, they consist of only two cell layers, an ectoderm and an endoderm (Barnes et al., 1993). The composition and internal structures of the larvae have been identified by Permata et al. (2000).

The majority of studies conducted on planulae have been performed on brooding species (Atoda, 1953; Harrigan, 1972; Fadlallah, 1983). The planula's biochemical composition has been found to contain large amounts of lipids (70% by dry weight), protein (17%), and carbohydrates (13%; Richmond, 1987). Development periods differ between broadcast and brooded larvae. For broadcast larvae, a minimum of 48–72 h is required before they are competent to settle (Hodgson, 1985; Babcock and Heyward, 1986). Brooded larvae are fully developed at release, and a minimum of only ~4 h is required until they are competent to settle (Harrigan, 1972). Larvae derived from either form of reproduction, however, may have a larval period of up to 90 days (Richmond, 1987) (although some investigators believe 90 days is an overestimate; Mundy and Babcock, 1998).

After release, the ciliated planulae can swim through the water column in any direction, and a number of swimming patterns have been described (Harrigan, 1972; Rinkevich and Loya, 1979). Planular swimming rates average from 1 to 5 mm s^{-1} (Atoda, 1951a,b,c; Harrigan, 1972; Tranter et al., 1982; Fadlallah, 1983). Direction of movement can be horizontal or vertical. At a horizontal swimming rate of 5 mm s^{-1}, however, this velocity would be exceeded by several orders of magnitude by the current velocity of the water in which it is swimming; for example, current velocities of 8–10 cm/s have been commonly measured in the central region of the Great Barrier Reef. Thus, a planula is under the primary influence of currents in the horizontal plane, as are many planktonic larvae (Sammarco, 1994b).

Many planktonic larvae have the ability to regulate their vertical position (Mileikovsky, 1973). Mileikovsky concludes that because some pelagic larvae can swim at reasonable speeds (>1 cm min^{-1}), they are able to control, to some degree, their vertical distribution in the water column. This allows them to position themselves vertically even in areas with strong tidal currents such as estuarine and marine nearshore areas.

Mass mortality of corals has been documented at an increasing rate in recent decades (Antonius, 1985; Munro, 1983; Bythell and Sheppard, 1993; Ohman et al., 1983; Miller, 1996; Sammarco, 1996; Santavy and Peters, 1997; Green and Bruckner, 2000; White et al., 2000; Porter et al., 2001; Riegl, 2001). In some cases, this has been attributed to increased sea surface temperatures (SSTs) and the resultant bleaching of corals (Brown, 1990; Goreau and Hayes, 1994; Huppert and Stone, 1998). Because higher seawater temperatures generally occur in shallow depths, an understanding of any behavior that assists a coral larva to regulate its depth becomes important. Recruitment of coral planulae to a disturbed area is critical to the reestablishment and recovery of reef ecosystems. Thus, understanding the factors that influence these larvae as they are dispersed is also critical to predicting reef regeneration processes.

1.1. Sensitivity to pressure

Some larvae are known to be sensitive to changes in hydrostatic pressure at certain developmental stages (Rice, 1964; Knight-Jones and Morgan, 1966; Morgan, 1984). In general, larvae move up when pressure is increased and move down when pressure is decreased (Forward, 1989). It is possible that coral planulae have similar sensitivities and behaviors, although to date, this has not been investigated. Some researchers suggest that, because a coral species is found generally at 6–8 m depth on inshore fringing reefs and rarely found below 20 m on the outer continental shelf, biological factors—such as settlement behavior—rather than physical factors may be limiting their distribution (Mundy and Babcock, 1998). Information on the effects of hydrostatic pressure on vertical swimming behavior in coral planulae would provide valuable information on the sensory abilities of coral planulae, i.e., whether they are able to perceive and react to pressure in their surrounding environment.

The purpose of this investigation was to determine whether planulae from the scleractinian coral *Porites astreoides* Lamarck are sensitive to changes in hydrostatic pressure, and to determine the effects of variation in pressure on the vertical swimming behavior of the larvae. The results of this study provide insight into the evolution and

adaptive significance of this behavioral trait and should open questions regarding associated sensory mechanisms. This study may also provide insight into physiological mechanisms contributing to depth-dependent settlement of coral planula larvae.

2. Materials and methods

A total of 20 adult colonies of *P. astreoides* were collected from a depth of 1–4 m on bridge supports and sea walls in the lower Florida Keys. *P. astreoides* is known to occur at depths ranging from 1 to 50 m, but is most frequently found at 1–10 m. The channels and areas used as sample sites were Little Duck–Missouri Channel, Spanish Harbour Channel, Bahia Honda Channel, Moser Channel, and Ohio–Missouri Channel. All *P. astreoides* colonies were of the "green" morph. Coral colonies were collected ~10 days before the new moon, to allow collection of larvae from adult colonies upon their release, which normally occurs at or near the new moon (McGuire, 1998).

Colonies were maintained at the Mote Marine Laboratory—Center for Tropical Research, Summerland Key, FL, in 10- and 20-gal aquaria outdoors on wet tables. Maxi-jet® powerheads were used to provide water flow and aeration in each of the aquaria. Colonies were kept outside to expose them to natural lunar reproductive cues. Water tables were covered with 60% shade cloth to reduce the amount of solar irradiation. Aquaria temperatures were maintained at a mean of 26 ± 2 °C. Temperature was maintained by using chilled seawater to cool the tanks and heated seawater to heat them, when necessary. Salinity was kept between 34 and 37 ppt and maintained by addition of freshwater to decrease salinity.

Nylon mesh derived from stockings was used to collect coral larvae. The mesh was placed on pyramidal PVC frames for support. Adult colonies were covered with the nets each evening for 7 days before and after the new moon and were checked each morning for larvae. Larvae were removed by pipetting, placed in separate holding chambers, one for each colony, and counted. Larvae were held in glass vials and placed in a water bath to help maintain a constant temperature. Each vial was aerated from a single air pump. Larvae were labeled according to parent colony and date of release.

The pressure chamber (Fig. 1) was constructed from transparent PVC pipe, 0.80 m in length (O.D. = 7.62 cm; I.D. = 6.99 cm). It was sealed at the bottom using a PVC end cap secured with Oatey® Clear PVC cement. The top was sealed using PVC bushings, again glued with Oatey® Clear PVC cement. A 2.54-cm hole in the cap served as both an access point for the introduction and removal of larvae, and an attachment point for tubing from the pressure regulator and air source. The side of the apparatus was fitted with a metric ruler as a reference guide for recording the vertical position of each larva. Compressed air from a SCUBA tank was used to regulate pressure in the chamber. A Victor® SR250 single-stage regulator was used to control chamber pressure. The first stage of the regulator was used to reduce the air pressure from 19,300 to < 1379 kPa. A second stage was also used as a pressure-release valve.

The experiment followed a one-way ANOVA design using repeated measures. The experimentally varied factor was pressure. The response variable was the vertical position of the larvae in the tank. The pressures used were 103.4, 206.9, 310.3, 413.8, and 517.1.1

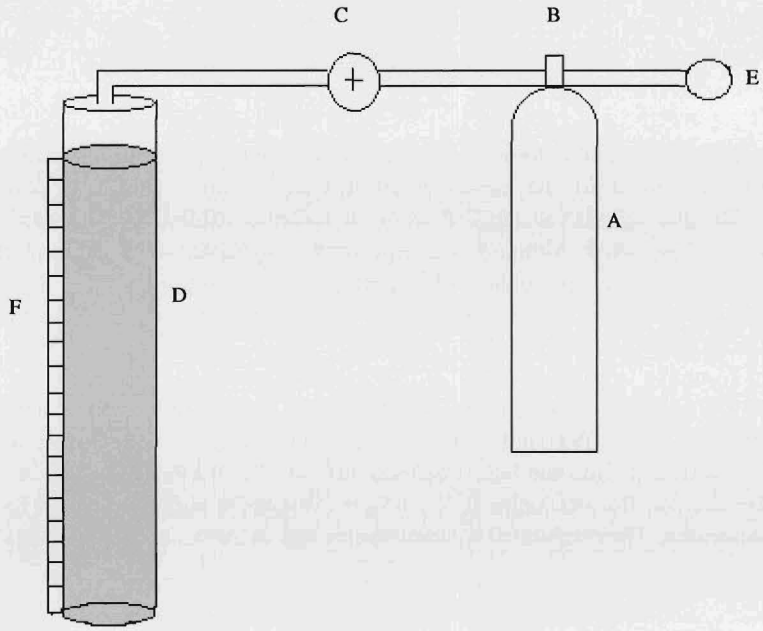

Fig. 1. Experimental pressure chamber. (A) Compressed air cylinder at 19,300 kPa. (B) SCUBA first stage, reducing pressure to 1379 kPa. (C) Second stage regulator, for fine control of air pressure (103.4–517.1 kPa). (D) Observation chamber. (E) SCUBA second stage, used as release valve. (F) Metric ruler, used as reference for vertical position of larvae.

kPa (total pressure, including ambient). The pressures were applied stepwise in ascending and descending order. The experiment was repeated 10 times, using planulae from separate colonies each time ($n_i = 10$).

Larvae <24 h old were used for the experiment, to ensure that they were all at approximately the same stage of development. Ten randomly selected larvae from one adult colony were placed inside the pressure apparatus, which was filled with seawater. The larvae were permitted 15 min to acclimate. At the end of this 15-min period, a timer was started and observations were taken. The vertical position of each larva was recorded every 5 min starting at 0 min and ending at 130 min. Qualitative observations were also made regarding planular swimming behavior. During this time, the pressure was increased by 103.4 kPa every 15 min until a maximum of 517.1 kPa (the equivalent of 40 m depth) was attained. After this pressure had been reached and the 15 min was allowed for a response to that pressure, the pressure was reduced by 103.4 kPa every 15 min until it once again reached ambient. Larvae were only used once, and no colony was used as a source of larvae more than once during the experiment.

The data were analyzed using repeated-measures ANOVA for both individual trials and pooled data. Data were log-transformed before analysis for purposes of normalization (Sokal and Rohlf, 1995). Statistical details may be found in figure legends. Only significant results will be discussed.

3. Results

3.1. Effects of increasing pressure

Larvae derived from all colonies exhibited a significant response to increasing pressure (significant movement of the larvae either upward or downward was considered a response). On average, larvae derived from all colonies exhibited an upward response as pressure was increased. Although the response was variable, no larvae from any single colony exhibited an average downward response to increasing pressure.

Larvae from a number of colonies exhibited similar response trends to the stepped treatments. In particular, larvae from colonies 2, 3, 4, and 5 all exhibited a highly significant response to pressure (Fig. 2). As pressure increased, larvae generally moved upwards in the chamber steadily until ~310 kPa was reached, after which they remained at a depth of 3–4 cm. Post hoc comparisons showed that each treatment was highly significantly different from the base treatment (103.4 kPa; 0 kPa plus ambient pressure).

Planulae derived from colonies 6, 9, and 10 exhibited a slightly delayed response to pressure increases. They exhibited upward swimming in response to increasing pressure

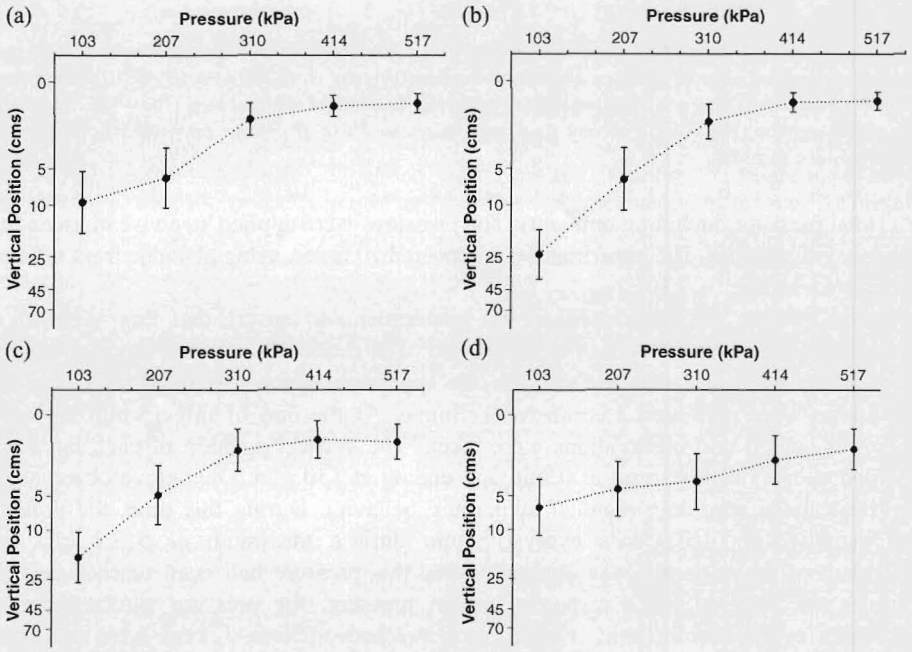

Fig. 2. Mean depth (cm) of planulae in experimental apparatus, under conditions of increasing pressure from 103.4 to 517.1 kPa. Exposure duration = 15 min for each step. Mean shown with 95% confidence limits. Data log-transformed for purposes of normalization (Sokal and Rohlf, 1995). Data shown for colonies (a) 2 (b) 3 (c) 4 and (d) 5. Significant differences between pressures (H–F adj. p value <0.001, one-way ANOVA with repeated measures). Post hoc contrasts significant between the first treatment and all others (103.4 vs. 206.9, 310.3, 413.8, and 517.1 kPa, respectively; $p<0.001$ in all cases).

(Fig. 3); however, the change in vertical position between the first and second treatments (206.9 and 310.3 kPa) was less pronounced than in the previous group (post hoc contrast, $p < 0.05$). Post hoc contrasts between the first vs. third, fourth, and fifth treatments were significantly different.

The larvae derived from colonies 1 and 8 also elicited a significant but somewhat delayed response to increasing pressure (Fig. 4). The initial differences in response between treatments 1 and 2 were not significant ($p > 0.05$). All other post hoc comparisons between treatment 1 and the others were highly significantly different ($p < 0.001$).

Larvae from colony 7 also showed a significant response to increasing pressure by swimming upward (Fig. 5), but post hoc contrasts indicated no significant change in vertical position until the onset of treatment 4. This difference was significant, but less pronounced than in previous colonies ($p < 0.05$). Treatments 1 and 5 were also highly significantly different ($p < 0.001$).

An analysis of larvae from all 10 colonies combined demonstrated that, as a group, all larvae responded significantly to increases in pressure by swimming upward (Fig. 6). There was also a highly significant difference in response between larvae derived from different colonies ($p < 0.001$). Post hoc contrasts showed that the baseline treatment was significantly different from all other treatments ($p < 0.001$).

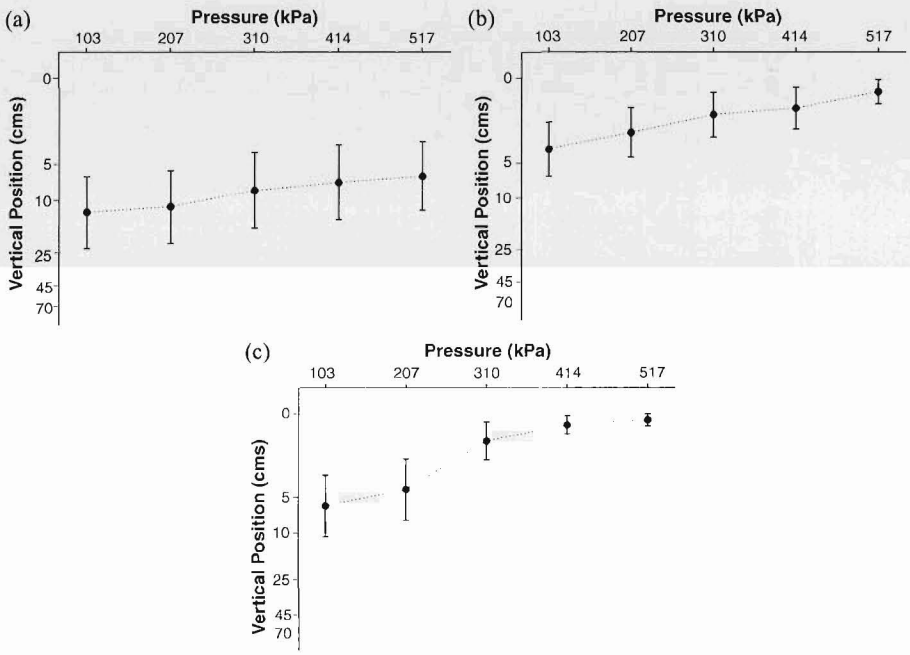

Fig. 3. Mean depth (cm) of planulae in experimental apparatus, under conditions of increasing pressure from 103.4 to 517.1 kPa. Data shown for colonies (a) 6 (b) 9 and (c) 10. Mean shown with 95% confidence limits. Significant differences between pressures (H–F adj. $p < 0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p < 0.001$), except for treatment 1 vs. treatment 2, which were significant at a lower level ($p < 0.01$).

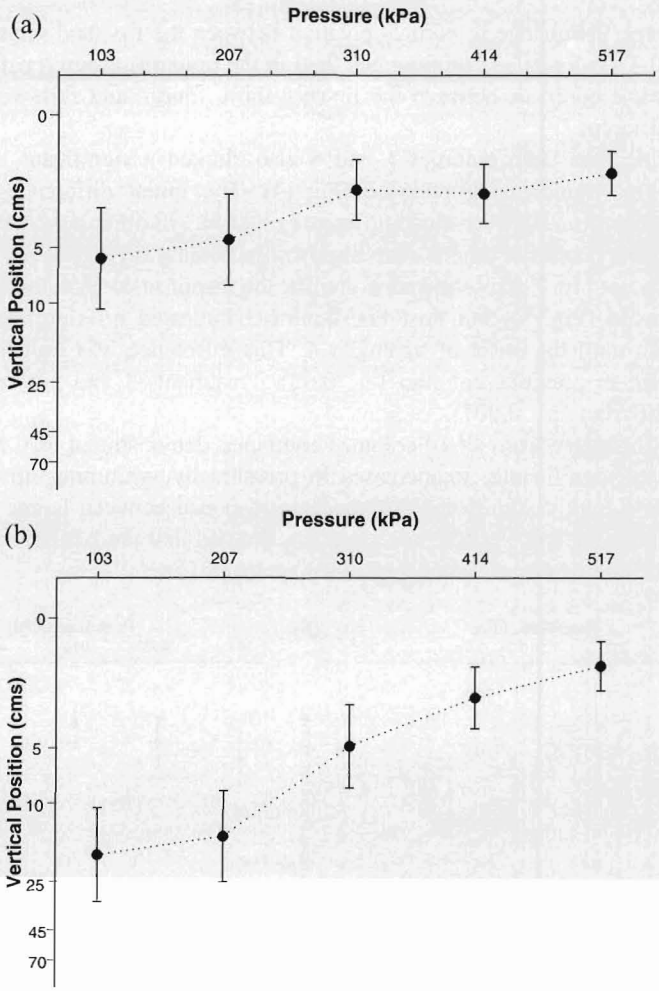

Fig. 4. Mean depth (cm) of planulae in experimental apparatus, under conditions of increasing pressure from 103.4 to 517.1 kPa. Data shown for colonies (a) 1 and (b) 8. Mean shown with 95% confidence limits. Significant differences between pressures (H - F adj. $p < 0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p < 0.001$), except for treatment 1 vs. treatment 2, which were not significant.

3.2. Effects of decreasing pressure

Larvae from individual colonies showed high within-colony variability and also high between-colony variability under conditions of decreasing pressure. Larvae from all of the colonies except two (colonies 3 and 6) were found to exhibit a significant response to decreasing pressure. The movements of larvae derived from any given colony were highly variable. On the average, however, the larvae moved significantly downward. In no case were planulae observed to move upward when pressure was decreased.

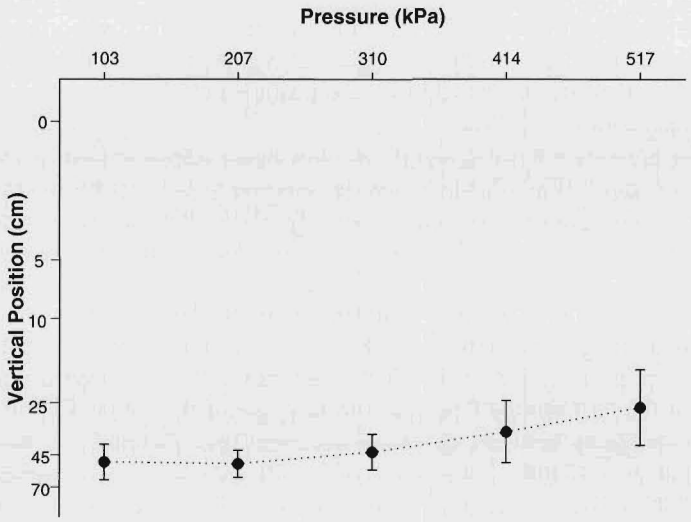

Fig. 5. Mean depth (cm) of planulae in experimental apparatus, under conditions of increasing pressure from 103.4 to 517.1 kPa. Data shown for colony 7. Mean shown with 95% confidence limits. Significant differences between pressures (H–F adj. $p < 0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p < 0.001$), except between treatment 1 vs. treatments 2 and 3.

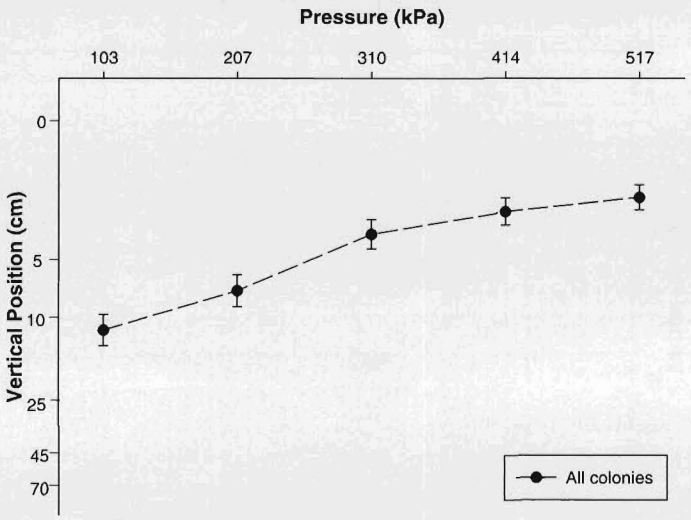

Fig. 6. Mean depth (cm) of planulae in experimental apparatus, under conditions of increasing pressure from 103.4 to 517.1 kPa. Data shown for all coral colonies exposed to this set of treatments. Mean shown with 95% confidence limits. Significant differences between pressures (H–F adj. $p < 0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p < 0.001$).

Larvae derived from colony 2 showed an overall significant downward response when exposed to decreasing pressure (Fig. 7). This trial was the only one to show a significant difference between all treatments and the base treatment (517.1 kPa) when examined via post hoc comparisons ($p < 0.001$).

Decreasing pressure elicited a significant downward response from planulae derived from colonies 5 and 8 (Fig. 8). Movement in response to the first treatment (413.8 kPa) was, however, non-significant for both colonies ($p > 0.05$). Post hoc comparisons between treatment 1 vs. treatments 3, 4, and 5 revealed significant downward movement ($p < 0.001$).

Planulae derived from colonies 9 and 10 also responded significantly to decreasing pressure by swimming downward, but with a slightly weaker response in colony 10 (Fig. 9). A post hoc comparison indicated that the response to the first two treatments was not significantly different from the base pressure in either of the colonies ($p > 0.05$). Similar post hoc comparisons between the base treatment and treatment 3, however, were significant, but at a slightly lower level of significance than the colonies considered above ($p < 0.05$). There were highly significant differences, however, in post hoc comparisons between treatments 1 and 4 ($p < 0.001$ for colony 9, and $p < 0.01$ for colony 10, respectively), and between treatments 1 and 5 ($p < 0.001$ and $p < 0.01$, respectively).

Planulae from colonies 1 and 7 also showed a significant response to decreasing pressure by actively swimming downward (Fig. 10). Post hoc comparisons between treatment 1 vs. treatments 2 and 3 revealed no significant differences for either colony

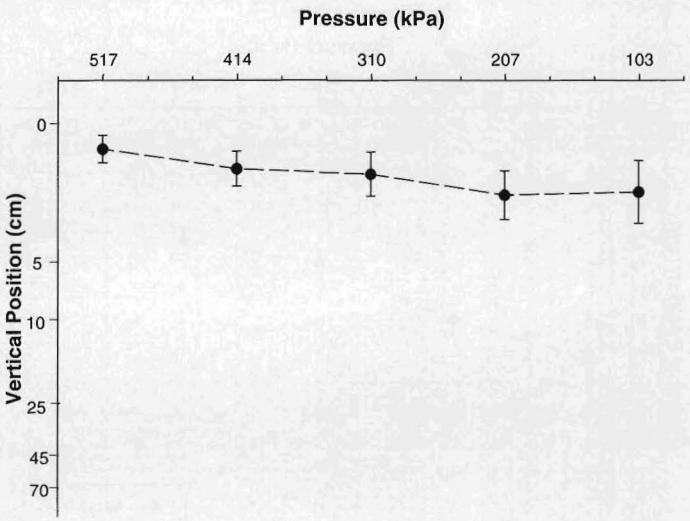

Fig. 7. Mean depth (cm) of planulae in experimental apparatus, under conditions of decreasing pressure from 517.1 to 103.4 kPa. Exposure duration = 15 min for each step. Mean shown with 95% confidence limits. Data log-transformed for purposes of normalization (Sokal and Rohlf, 1995). Data shown for colony 2. Significant differences between pressures (H–F adj. $p < 0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p < 0.001$).

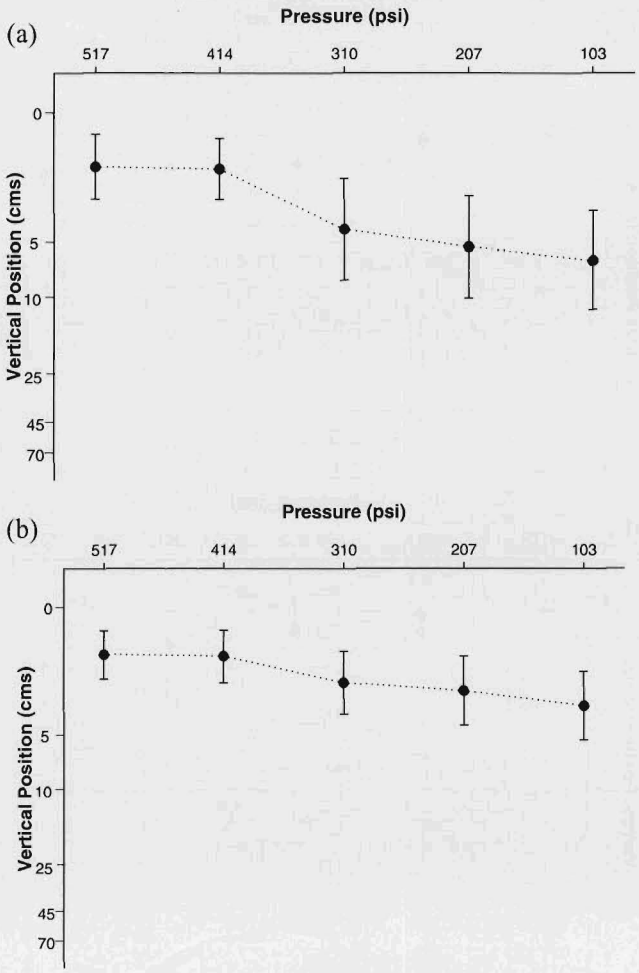

Fig. 8. Mean depth (cm) of planulae in experimental apparatus, under conditions of decreasing pressure from 517.1 to 103.4 kPa. Data shown for colonies (a) 5 and (b) 8. Mean shown with 95% confidence limits. Significant differences between pressures (H–F adj. $p<0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p<0.001$), except between treatment 1 vs. treatment 2.

($p>0.05$). Post hoc comparisons did demonstrate a significant difference between the base treatment and treatment 4 for both colonies, although the level of significance was different for each colony ($p<0.05$ for colony 1 and $p<0.001$ for colony 7). This was also true for comparisons between treatments 1 and 5 ($p<0.01$ and $p<0.001$, respectively).

Planulae from colony 4 showed an overall significant downward swimming response to decreasing pressure, but less pronounced than that exhibited by larvae from the other colonies (Fig. 11). Post hoc contrasts only revealed significant differences between treatments 1 and 2 ($p<0.01$); all other comparisons were non-significant ($p>0.05$).

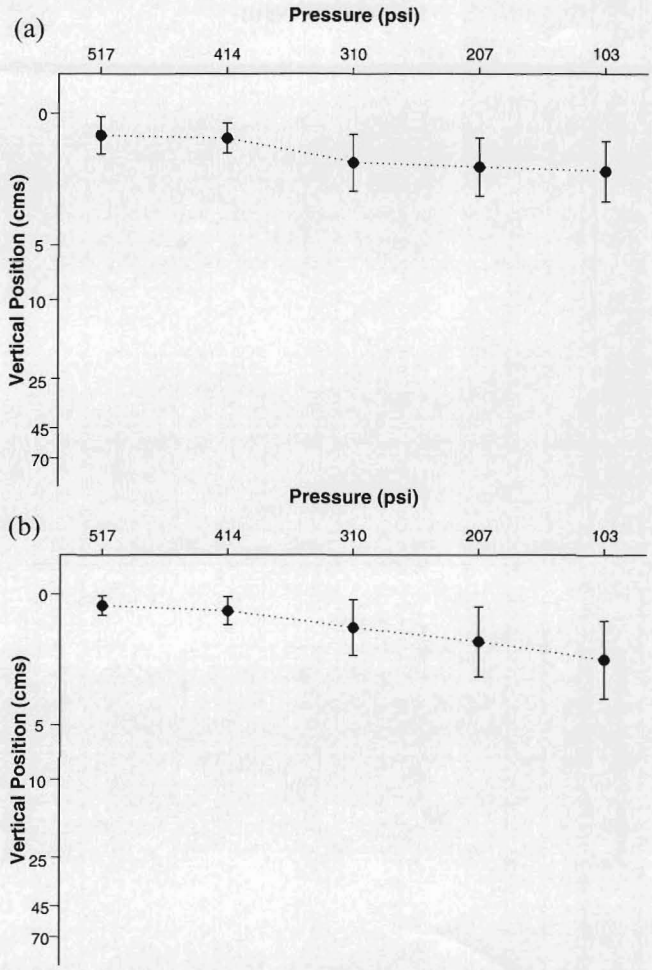

Fig. 9. Mean depth (cm) of planulae in experimental apparatus, under conditions of decreasing pressure from 517.1 to 103.4 kPa. Data shown for colonies (a) 9 and (b) 10. Mean shown with 95% confidence limits. Significant differences between pressures (H–F adj. $p < 0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p < 0.001$), except between treatment 1 vs. treatment 2. Post hoc contrast between treatment 1 vs. treatment 3 is less significant ($p < 0.05$) than other comparisons.

When data from the larvae of all colonies were pooled, the repeated-measures ANOVA revealed a highly significant downward swimming response to decreasing pressure (Fig. 12). There was a highly significant difference between the responses of larvae derived from different colonies. In addition, a significant two-way interaction was detected between pressure and parent colony ($p < 0.001$). That is, planulae responded significantly to pressure changes, but the nature of that response varied highly significantly between colonies. Post hoc comparisons revealed a significant difference between treatment 1 and all other treatments ($p < 0.001$). Larvae were also demonstrated to exhibit a significant downward

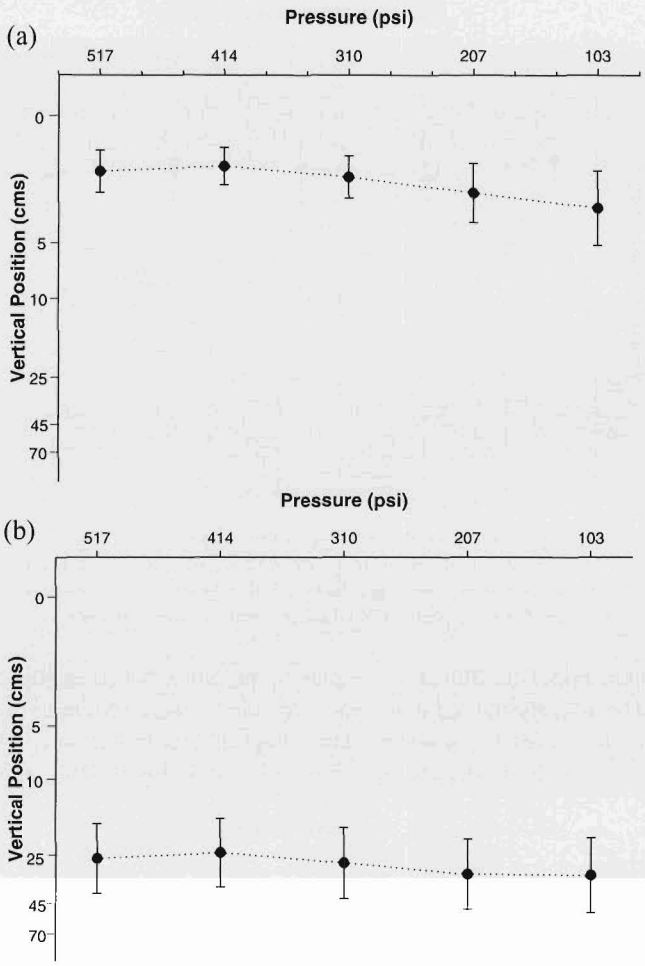

Fig. 10. Mean depth (cm) of planulae in experimental apparatus, under conditions of decreasing pressure from 517.1 to 103.4 kPa. Data shown for colonies (a) 1 and (b) 7. Mean shown with 95% confidence limits. Significant differences between pressures (H- F adj. $p < 0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p < 0.001$), except for treatment 1 vs. treatments 2 and 3.

swimming response (vs. simple random movement) in association with decreasing pressure (Kendall's coefficient of rank correlation, τ, $p < 0.001$, for all treatments).

3.3. Planular swimming behavior

When exposed to increases in pressure, planulae began to actively swim toward the surface in a spiraling motion. Although not all larvae were observed swimming in this pattern, for those traveling longer distances, a spiraling pattern was most frequently observed. Larvae were clearly not moving toward the surface passively, but actively

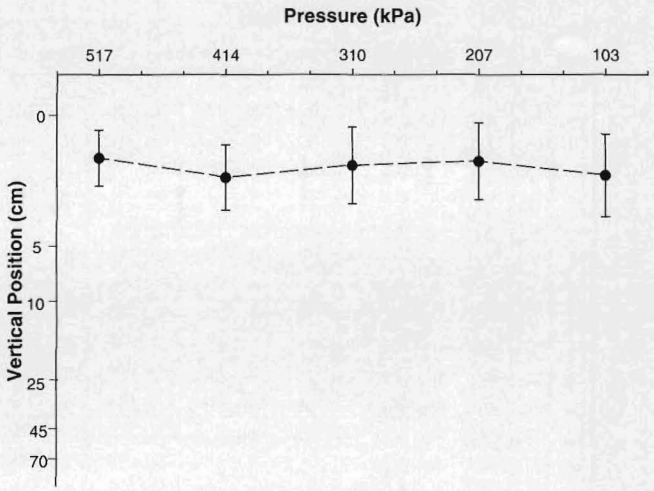

Fig. 11. Mean depth (cm) of planulae in experimental apparatus, under conditions of decreasing pressure from 517.1 to 103.4 kPa. Data shown for colony 4. Mean shown with 95% confidence limits. Significant differences between pressures (H–F adj. $p<0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between treatments 1 and 2 ($p<0.001$); all other contrasts non-significant.

swimming upward under conditions of increasing pressure. When exposed to decreasing pressure, planulae actively moved downward. No larvae were observed to sink passively under conditions of decreasing pressure. This suggests that larvae actively regulate their position in the water column depending upon which stimulus is being applied.

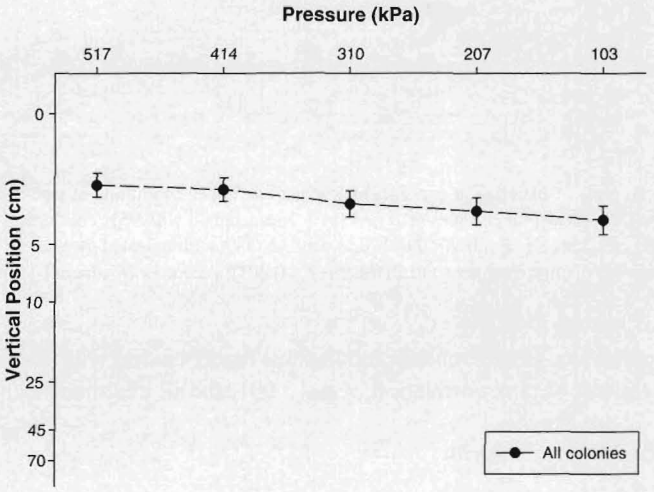

Fig. 12. Mean depth (cm) of planulae in experimental apparatus, under conditions of decreasing pressure from 517.1 to 103.4 kPa. Data shown for all coral colonies exposed to decreasing pressure. Mean shown with 95% confidence limits. Significant differences between pressures (H–F adj. $p<0.001$, one-way ANOVA with repeated measures). Post hoc contrasts were significant between the first treatment and all others ($p<0.001$).

4. Discussion

The results of this study indicate that, when exposed to increases in pressure, coral planulae respond on the average by actively swimming upward in the water column. When exposed to decreases in pressure, they also show a significant downward swimming response, although to a lesser extent. The general response of barokinesis and/or negative barotaxis (actively moving away from increased pressure) has been demonstrated in several planktonic animals, including planktonic larvae (e.g. Rice, 1964; Knight-Jones and Morgan, 1966; Schembri, 1982; Morgan, 1984; Forward, 1989; Tankersley et al., 1995). Before this study, however, this behavior had never been demonstrated in the larvae of scleractinian corals. These data indicate that pressure may well be a factor that influences coral dispersal and settlement, and that settlement of coral larvae may not be simply light- or substrate-limited (Mundy and Babcock, 1998) but may also be heavily influenced by pressure or depth. That is, the planulae may have control over the depth to which they will be transported by currents and in which they will settle. Their response to pressure is not simply a passive buoyancy-controlled response, but rather an active swimming movement of the larva to ascend under conditions of increasing pressure (negative barotaxis) and descend under conditions of decreasing pressure (positive barotaxis). The larvae actively swim up in a spiraling motion to regulate their vertical position with regard to increasing pressure. With respect to decreasing pressure, larvae do not passively sink, but rather swim in a simple fashion to a suitable deeper position in the water column.

4.1. Negative barotaxis

Most planktonic animals are dependent upon food found in the shallower euphotic zone for survival. Field as well as theoretical studies have shown that it is essential that many planktonic animals spend at least some of their time in or near the surface layer, and therefore, must exercise some level of active depth regulation (Raymont, 1963; Enright and Hamner, 1967; Vlyman, 1970). Coral planulae and, more importantly, adult corals are dependent upon the euphotic zone because of their need for solar energy to drive photosynthesis in their zooxanthellae (Muscatine, 1980, 1990; Cook, 1983; Falkowski et al., 1984; Leletkin et al., 1996; Goodson et al., 2001). If the larvae either actively swim or are carried to waters too deep, photosynthesis within their zooxanthellae becomes light limited. Non-feeding zooxanthellate planulae, dependent upon these symbiotic dinoflagellates for energy, may not survive, particularly if their lipid stores are inadequate to support them for long periods of time (Richmond, 1987).

In waters where corals exist, there are two factors that may act as environmental indicators of depth: light and pressure. As depth increases in the ocean, light decreases in intensity and changes in spectral composition, due to absorbance by the water and particles therein. This relationship, however, is dynamic and can be highly variable over short periods of time. For example, light is affected naturally by diurnal/nocturnal shifts, clouds blocking the sun during the day, storms causing periods of low light, etc. Changes in turbidity can also heavily influence the relationship between light and depth. In the long term, light intensity and quality is affected by season, day length, and turbidity. The natural dynamics of atmospheric light are probably too variable to serve as a reliable indicator of

depth for larvae. Under very low light conditions (e.g. night), light is of little or no use as a depth indicator (Rice, 1964), except perhaps in the presence of strong lunar light.

In contrast to light, the relationship between depth and pressure is highly predictable. This consistency may allow behavioral responses to pressure to be operating at all times—equally so during the day and night. Pressure provides an accurate measure of vertical position in the water column, irrespective of light conditions.

Negative barotaxis may serve to keep larvae from moving below depths where suitable settlement substratum may be found and below the euphotic zone, where sufficient photosynthetically active radiation exists to enable their survival (Shick et al., 1995). It provides a means by which larvae that have been swept too deep by currents may return to their preferred depth. If larvae were using only light as a depth indicator under similar conditions, they may not be able to reorient and return to the euphotic zone before the consumption of energy reserves, required for respiration, exceed the rate of production of energy products derived from zooxanthellar photosynthesis. If increases in pressure stimulate coral planulae to actively move upward, then pressure may serve as a lower depth-limiting factor for settlement. Pressure and light may work together to provide a depth limit for settlement in some species.

4.2. Positive barotaxis

The response of larvae to decreasing pressure was, on the average, to move downward when exposed to decreasing pressure. Although the response was not as great in magnitude as it was for increasing pressure, it was nonetheless significant. This difference in level of response to increasing vs. decreasing pressure may be indicative of an upper limit for preferred depth of coral larvae. The results suggest that larvae, when too close to the surface layer, actively swim toward deeper waters. This would allow them to maintain a position at an optimal depth where environmental factors are more suitable for survival. Such behavior might enable them to avoid the surface layer of the water, which can be too warm for survival (Bassim, 1997; Bassim et al., 2002; Bassim and Sammarco, 2003). It can also keep the larvae out of shallow depths where harmful ultraviolet radiation can penetrate and cause mortality. The response of larvae to decreasing pressure was significant, but it was characterized by high variance between planulae. It is possible that additional experimentation using larger numbers of larvae per run may provide a better estimate of variance.

4.3. Evolutionary implications

The high variance in planular behavior observed here is similar to high variance observed in morphological and physiological characters in coral larvae (Isomura and Nishihira, 2001; F. Yohannes, unpublished data). Analyses have shown that different colonies produced larvae with different biochemical compositions as well as different numbers of zooxanthellae per larvae. It is also known that the density of zooxanthellae in the parent colony and its larvae are not correlated (F. Yohannes, unpublished data). There is also a high degree of variation in the size of planulae produced by a colony, as well as comparative sizes between conspecific colonies (Isomura and Nishihira, 2001). If different colonies are producing differently sized larvae with different amounts of protein and lipid

content, and zooxanthellar densities, then these differences may well contribute to the observed variance of other traits dependent upon these factors, including behavior.

In addition, the high variance observed in this behavior indicates that it may well be susceptible to natural selection if it is genetically based. The adaptive value of an upward swimming response to an increase in pressure is clear keeping the larva in the euphotic zone. The high variability in this response, however, indicates that this may not always be adaptive. Perhaps upward movement sometimes carries larvae into surface layers that are too warm or where salinity is too low, causing mortality. Thus, lack of response may be selected for at times, characteristic of normalizing selection (Futuyma, 1998). This was particularly evident through intra-colony variance where larvae derived from the same colony demonstrated a wide range of responses to pressure, as well as through intercolony variance where planulae from some colonies exhibited marked responses, and others more subdued ones.

4.4. Sensory mechanisms

One mechanism by which planula larvae may be able to sense pressure is through lipid vacuoles, which may also act as buoyancy devices. Although larvae from different colonies have significantly different lipid content, the lipid/protein ratio remains consistent between colonies (F. Yohannes, unpublished data). The most common types of lipids found in corals are wax esters and triacylglycerol, with the most common fatty acid being palmitic acid (a.k.a. hexadecanoic acid; see Yamashiro et al., 1999). Because organic compounds such as palmitic acid vary from other organic compounds and from seawater in their isothermal compressible characteristics (Lide, 1991), it is possible that the lipid vacuoles may expand or contract in response to pressure differentially with respect to the aqueous environment around them. This could provide a cue indicating that the planula should swim up or down. The compression coefficients of these compounds may be sufficiently disparate to provide a signal to the larva for depth change. The mechanism by which planulae sense depth and regulate their vertical position at this point remains unknown.

It is also possible that the planulae are not responding to pressure, but to some other factor that is correlated with pressure. For example, in this experimental setup, pressure is varied by changing air or atmospheric pressure. This method introduces an oxygen gradient in the water, at least partially with respect to depth. It is possible that the larvae are responding to an oxygen gradient rather than pressure. If this were the case, however, the response to decreasing oxygen should be similar in intensity to that of increasing oxygen. This, however, was not the case. This question can be investigated in future experiments either by using nitrogen as the experimental gas, placing a diffusion barrier at the meniscus of the water, or by eliminating gases from the chamber by increasing pressure via a water pump.

The pressure changes implemented in this experiment were relatively rapid—on the order of 103.4 kPa over a 5- to 10-s interval. The probability of a coral larva encountering a similar change in the field is low, occurring only where there might be strong convergences or divergences, or possibly in connection with the breaking of large ocean waves. Therefore, some caution should be used when interpreting these laboratory results in terms of its direct application in the field. Nonetheless, we can say that when coral larvae of *P. astreoides* are exposed to increases in pressure—they will respond by actively swimming to

reach a shallower depth within the water column. When exposed to decreases in pressure, they will respond by actively swimming to reach a deeper depth. This represents the first study of its kind to demonstrate that coral larvae possess a mechanism by which to sense changes in pressure and respond to it through a swimming reaction.

Acknowledgements

We thank the following for their assistance in this project: D. Felder, P. Klerks, and J. Neigel for their advice and support during the project; J. Spring and E. Bartels for assistance in designing the pressure apparatus; and J. Hawkridge for assistance in collection and maintenance of the corals. J.L.S. also thanks his wife, K. Stake, for her unerring support during the project. Collections were made under provisions of NOAA Florida Keys National Marine Sanctuary (FKNMS) Permit no. 2001-011, and the Florida Fish and Wildlife Conservation Commission. This study was supported by a Link Foundation/Smithsonian Institution Graduate Fellowship, a Sigma Xi grant-in-aid, and University of Louisiana at Lafayette (ULL) Graduate Student Organization (GSO) Grant-in-Aid. This paper represents contribution no. 555 from the Smithsonian Marine Station at Fort Pierce, Fort Pierce, Florida. [SS]

References

Antonius, A., 1985. Coral diseases in the Indo-Pacific: a first record. Mar. Ecol. 6 (3), 197–218.

Atoda, K., 1951a. The larva and post-larval development of reef-building corals: III. *Acropora brueggmain* (Brook). J. Morphol. 89 (1), 1–13.

Atoda, K., 1951b. The larva and post larval development of the reef-building corals: IV. *Cralaxea aspera* Quelch. J. Morphol. 89 (1), 17–35.

Atoda, K., 1951c. The larva and postlarval development of the reef-building corals: V. *Seriatopora hystrex* Dana. Sci. Rep. Tohoku Univ., Ser. 4 19, 33–39.

Atoda, K., 1953. The larva and post larval development of the reef-building corals: VI. Sci. Rep. Tohoku Univ., Ser. 4 20, 105–121.

Ayre, D.J., Hughes, T.P., Standish, R.J., 1997. Genetic differentiation, reproductive mode, and gene flow in the brooding coral *Pocillopora damicornis* along the Great Barrier Reef, Australia. Mar. Ecol., Prog. Ser. 159 (1), 175–187.

Babcock, R.C., Heyward, A.J., 1986. Larval development in certain gamete-spawning scleractinian corals. Coral Reefs 5 (3), 111–116.

Barnes, R.S.K., Calow, P., Olive, P.W., Golding, D.W., 1993. The Invertebrates: A New Synthesis, 2nd ed. Blackwell, Oxford.

Bassim, K.M., 1997. Effects of temperature and ammonium on the early developmental stages of a scleractinian coral: implications for global warming and nutrient enrichment. MSc Thesis, Department of Biology, University of Louisiana at Lafayette. 51 pp.

Bassim, K.M., Sammarco, P.W., 2003. Effects of temperature and ammonium on larval development and survivorship in a scleractinian coral. Mar. Biol. 142 (2), 241–252.

Bassim, K.M., Sammarco, P.W., Snell, T., 2002. Effects of temperature on fertilization success and embryogenesis in *Diploria strigosa* (Coelenterata, Scleractinia). Mar. Biol. 140 (3), 479–488.

Brown, B.E. (Ed.), 1990. Coral Bleaching. Coral Reefs 8, 153–232.

Bythell, J., Sheppard, C., 1993. Mass mortality of Caribbean shallow corals. Mar. Pollut. Bull. 26 (6), 296–297.

Chornesky, E., Peters, E., 1987. Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. Biol. Bull. 172 (2), 161–177.

Cook, C.B., 1983. Metabolic interchange in algae–invertebrate symbiosis. Int. Rev. Cytol. Suppl. 14 (1), 177–210.
Done, T.J., 1982. Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1 (2), 95–107.
Doyle, R.W., 1975. Settlement of planktonic larvae: a theory of habitat selection in varying environments. Am. Nat. 109 (966), 113–126.
Enright, J.T., Hamner, W.M., 1967. Vertical diurnal migration and endogenous rhythmicity. Science 157 (3791), 937–941.
Fadlallah, Y., 1983. Sexual reproduction, development and larval biology in scleractinian corals. A review. Coral Reefs 2 (2), 129–150.
Fadlallah, Y., Pearse, J., 1982. Sexual reproduction in solitary corals: overlapping oogenic and brooding cycles, and benthic planulae in *Balanophyllia elegans*. Mar. Biol. 71 (3), 223–231.
Falkowski, P., Dubinsky, Z., Muscatine, L., Porter, J.W., 1984. Light and the bioenergetics of a symbiotic coral. BioScience 34 (11), 705–709.
Forward, R.B., 1989. Depth regulation of larval marine decapod crustaceans: test of a hypothesis. Mar. Biol. 102 (2), 195–201.
Futuyma, D.J., 1998. Evolutionary Biology, 3rd ed. Sinauer Associates, Sunderland, MA, USA.
Gerrodette, T., 1981. Dispersal of the solitary coral *Balanophyllia elegans* by demersal planular larvae. Ecology 62 (3), 611–619.
Goodson, M.S, Whitehead, L.F., Douglas, A.E., 2001. Symbiotic dinoflagellates in marine Cnidaria: diversity and function. Hydrobiologia 461 (1), 79–82.
Goreau, T.J., Hayes, R.L., 1994. Coral bleaching and ocean "hot spots". Ambio 23, 176–180.
Green, E.P., Bruckner, A.W., 2000. The significance of coral disease epizootiology for coral reef conservation. Biol. Conserv. 96 (3), 347–361.
Harrigan, J., 1972. The planula larva of *Pocillopora damicornis*: lunar periodicity of swarming and substratum selection behavior. PhD Thesis, Department of Zoology, University of Hawaii at Manoa. 319 pp.
Harrison, P., Wallace, C., 1990. Reproduction, dispersal, and recruitment of scleractinian corals. In: Dubinsky, Z. (Ed.), Ecosystems of the World 25. Coral Reefs Elsevier, Amsterdam, pp. 133–207.
Harrison, P., Babcock, R., Bull, G., Oliver, J., Wallace, C., Willis, B., 1983. Recent developments in the study of sexual reproduction in tropical reef corals. In: Baker, J.T., Carter, R.M., Sammarco, P.W., Stark, K.P. (Eds.), Proceedings: Inaugural Great Barrier Reef Conference, Townsville. James Cook University of North Queensland Press, Townsville, pp. 217–219.
Harrison, P., Babcock, R., Bull, G., Oliver, J., Wallace, C., Willis, B., 1984. Mass spawning in tropical reef corals. Science 223 (4641), 1187–1188.
Hodgson, G., 1985. Abundance and distribution of planktonic coral larvae in Kaneohe Bay, Oahu, Hawaii. Mar. Ecol. Prog. Ser. 26 (1–2), 61–71.
Huppert, A., Stone, L., 1998. Chaos in the Pacific's coral reef bleaching cycle. Am. Nat. 152, 447–459.
Isomura, N., Nishihira, M., 2001. Size variation of planulae and its effect on the lifetime of planulae in three pocilloporid corals. Coral Reefs 20 (3), 309–315.
Knight-Jones, E., Morgan, E., 1966. Responses of marine animals to changes in hydrostatic pressure. Oceanogr. Mar. Biol. Annu. Rev. 4 (2), 267–299.
Kojis, B.L., Quinn, N.J., 1980. Mode and timing of sexual reproduction in some members of the hermatypic coral family Faviidae. Am. Zool. 20 (4), 819.
Leletkin, V.A., Tittyanova, E.A., Dubinsky, Z., 1996. Photosynthesis and respiration of the zooxanthellae in hermatypic corals habitated on different depths of the Gulf of Eilat. Photosynthetica 32 (4), 481–490.
Lide, D.R. (Ed.), 1991. CRC Handbook of Chemistry and Physics. CRC Press, Boca Raton, FL.
McGuire, M.P., 1997. The biology of the coral *Porites astreoides*: reproduction, larval settlement behavior and responses to ammonium enrichment. PhD Dissertation, University of Miami. 177 pp.
McGuire, M.P., 1998. Timing of larval release by *Porites astreoides* in the northern Florida Keys. Coral Reefs 17 (4), 369–375.
Mileikovsky, S., 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. Mar. Biol. 23 (1), 11–17.
Miller, G., 1996. Living in the Environment: Principles, Connections and Solutions. 12th ed. Wadsworth Publishers, Belmont, CA.

Morgan, E., 1984. The pressure-responses of marine invertebrates: a psychophysical perspective. Zool. J. Linn. Soc. Lond. 80 (2–3), 209–255.

Mundy, C., Babcock, R., 1998. Role of light intensity and spectral quality in coral settlement: implications for depth-dependent settlement? J. Exp. Mar. Biol. Ecol. 223 (2), 235–255.

Munro, J.L., 1983. The Composition and Magnitude of Trap Catches in Jamaican Waters. Caribbean Coral Reef Fishery Resources, 2nd ed. Int. Center for Living Aquatic Resources Mgt., Manila, Philippines, pp. 33–49.

Muscatine, L., 1980. Productivity of zooxanthellae. In: Falkowski, P.G. (Ed.), Primary Productivity in the Sea. Plenum, New York, pp. 381–402.

Muscatine, L., 1990. Flux of photosynthetic fixed carbon in corals. In: Dubinsky, Z. (Ed.), Ecosystems of the World 25. Coral Reefs Elsevier, Amsterdam, pp. 75–87.

Ohman, M., Rajasuriya, A., Lionden, O., 1983. Human disturbances on coral reefs in Sri Lanka: a case study. Ambio 22 (7), 474–480.

Permata, W.D., Kinzie, R.A., Hidaka, M., 2000. Histological studies on the origin of planulae of the coral *Pocillopora damicornis*. Mar. Ecol., Prog. Ser. 200 (1–2), 191–200.

Porter, J.W., Dustan, P., Jaap, W.C., Patterson, K.L., Kosmynin, V., Meier, O.W., Patterson, M.E., Parsons, M., 2001. Patterns of spread of coral disease in the Florida Keys. Hydrobiologia 460 (1), 1–24.

Raymont, J.E.G., 1963. Plankton and Productivity in the Oceans Pergamon, Oxford.

Rice, A., 1964. Observations on the effects of changes of hydrostatic pressure on the behavior of some marine animals. J. Mar. Biol. Assoc. U.K. 44 (1), 163–175.

Richmond, R., 1987. Energetics, competency, and long distance dispersal of planula larvae of the coral *Pocillopora damicornis*. Mar. Biol. 93 (4), 527–533.

Richmond, R., Hunter, C., 1990. Reproduction and recruitment of corals: comparisons among the Caribbean, the tropical Pacific and the Red Sea. Mar. Ecol. Prog. Ser. 60 (1–2), 185–203.

Riegl, B., 2001. Degradation of reef structure, coral and fish communities in the Red Sea by ship groundings and dynamite fisheries. Bull. Mar. Sci. 69 (2), 595–611.

Rinkevich, B., Loya, Y., 1979. The reproduction of the Red Sea coral *Stylophora pistillata*: I. Gonads and planulae. Mar. Ecol., Prog. Ser. 1 (2), 133–144.

Sammarco, P.W., 1982. "Polyp Bail-Out" in an Indo-Pacific coral: an escape response to environmental stress. Mar. Ecol. Prog. Ser. 10 (1), 57–65.

Sammarco, P.W., 1994a. The multi-team approach to scientific problem solving: an effective paradigm. In: Sammarco, P.W., Heron, M.L. (Eds.), The Bio-Physics of Marine Larval Dispersal. American Geophysical Union, Washington, DC, pp. 35–72.

Sammarco, P.W., 1994b. Larval dispersal and recruitment processes in Great Barrier Reef corals: analysis and synthesis. In: Sammarco, P.W., Heron, M.L. (Eds.), The Bio-Physics of Marine Larval Dispersal. American Geophysical Union, Washington, DC, pp. 35–72.

Sammarco, P.W., 1996. Comments on coral reef regeneration, bioerosion, biogeography, and chemical ecology: future directions. J. Exp. Mar. Biol. Ecol. 200 (1–2), 135–168.

Sammarco, P.W., Andrews, J.C., 1988. Localized dispersal and recruitment in Great Barrier Reef corals: the Helix experiment. Science 239 (4846), 1422–1424.

Sammarco, P., Andrews, J.C., 1989. The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals. Limnol. Oceanogr. 34 (5), 896–912.

Santavy, D., Peters, E., 1997. Microbial pests: coral disease in the western Atlantic. Proc. 8th Int. Coral Reef Symp. 1 (2), 607–612.

Scheltema, R.S., 1977. Dispersal of marine invertebrate organisms: paleobiogeographic and biostratigraphic implications. In: Kauffman, E.G., Hazel, J.E. (Eds.), Concepts and Methods of Biostratigraphy. Dowden, Hutchinson and Ross, Stroudsberg, PA, pp. 73–108.

Schembri, P.J., 1982. Locomotor, feeding, grooming and the behavioural responses to gravity, light and hydrostatic pressure in the stage I zoea larvae of *Ebalia tuberosa* (Crustacea: Decapoda: Leucosiidae). Mar. Biol. 72 (2), 125–134.

Shick, J.M., Lesser, M.P., Dunlap, W.C., Stochaj, W.R., Chalker, B.E., Won, J.W., 1995. Depth-dependent responses to solar ultraviolet-radiation and oxidative stresses in the zooxanthellate coral *Acropora microphthalama*. Mar. Biol. 122 (1), 41–51.

Shlesinger, Y., Goulet, T.L., Loya, Y., 1998. Reproductive patterns of scleractinian corals in the northern Red Sea. Mar. Biol. 132 (4), 691–701.

Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd ed. Freeman, New York.

Tankersley, R.A., McKelvey, L.M., Forward Jr., R.B. 1995. Responses of estuarine crab megalopae to pressure, salinity and light: implications for flood-tide transport. Mar. Biol. 122 (3), 391–400.

Thorson, G., 1961. Length of pelagic larval life in marine bottom invertebrates as related to larval transport by ocean currents. In: Sears, M. (Ed.), Oceanography, 67 (1). Am. Assoc. Adv. Sci., Washington D.C., pp. 455–474.

Thorson, G., 1964. Light as an ecological factor in the dispersal and settlement of larvae of marine bottom invertebrates. Ophelia 1 (2), 177–208.

Tranter, P.R.G., Nicholson, D.N., Kinchington, D., 1982. A description of the spawning and post-gastrula development of the cool temperate coral *Caryophyllia smithii* (Stokes and Broderip). J. Mar. Biol. Assoc. U.K. 62 (4), 845–854.

Vlyman, W.J., 1970. Energy expenditure of swimming copepods. Limnol. Oceanogr. 15 (3), 348–356.

White, A.T., Vogt, H.P., Arin, T., 2000. Philippine coral reefs under threat: the economic losses caused by reef destruction. Mar. Pollut. Bull. 40 (7), 598–605.

Williams, D.McB., Wolanski, E., Andrews, J.C., 1984. Transport mechanisms and the potential movement of planktonic larvae in the central region of the Great Barrier Reef. Coral Reefs 3 (4), 229–236.

Yamashiro, H., Oku, H., Higa, H., Chinen, I., Sakai, K., 1999. Composition of lipids, fatty acids and sterols in Okinawan corals. Comp. Biochem. Physiol. 122 (4), 397–407.