Coral Reefs (2008) 27:485–490
DOI 10.1007/s00338-008-0392-5

NOTE

Effect of aragonite saturation state on settlement and post-settlement growth of *Porites astreoides* larvae

R. Albright · B. Mason · C. Langdon

Received: 3 March 2008 / Accepted: 13 May 2008 / Published online: 4 June 2008

Abstract In response to the increases in pCO_2 projected in the 21st century, adult coral growth and calcification are expected to decrease significantly. However, no published studies have investigated the effect of elevated pCO_2 on earlier life history stages of corals. *Porites astreoides* larvae were collected from reefs in Key Largo, Florida, USA, settled and reared in controlled saturation state seawater. Three saturation states were obtained, using 1 M HCl additions, corresponding to present (380 ppm) and projected pCO_2 scenarios for the years 2065 (560 ppm) and 2100 (720 ppm). The effect of saturation state on settlement and post-settlement growth was evaluated. Saturation state had no significant effect on percent settlement; however, skeletal extension rate was positively correlated with saturation state, with ~50% and 78% reductions in growth at the mid and high pCO_2 treatments compared to controls, respectively.

Keywords Coral · Aragonite saturation · Larvae · Climate change · Ocean acidification · Growth

Introduction

Over the past several decades, global degradation of coral reef ecosystems has resulted in unprecedented loss of adult corals (Hoegh-Guldberg 1999; Hughes et al. 2003). The persistence and recovery of coral reefs require that levels of recruitment keep pace with the loss of adult individuals (Richmond 1997; Hughes and Tanner 2000). Unfortunately, recently conducted recruitment surveys (Porter and Meier 1992; Hughes and Tanner 2000) and settlement plate studies (Shearer and Coffroth 2006) indicate low levels of sexual recruitment throughout the Florida Keys and the Caribbean. Low levels of sexual recruitment, in conjunction with high rates of adult mortality, denote an alarming trend that is altering the structure and function of coral reefs as a marine ecosystem. It is therefore important to understand the potential roles of various environmental factors that may affect sexual recruitment.

Recruitment is influenced by both pre-settlement and post-settlement processes. Environmental factors known to influence planktonic development and survivorship, as well as various aspects of settlement, include nutrients (Harrison and Ward 2001; Bassim et al. 2002), anthropogenic contaminants (Negri and Heyward 2001; Negri et al. 2005), salinity (Vermeij et al. 2006), temperature (Edmunds et al. 2001), and exposure to ultra-violet radiation (UVR) (Wellington and Fitt 2003; Gleason et al. 2006). Post-settlement survivorship has been shown to be influenced by habitat choice (Miller et al. 2000, Harrington et al. 2004), water quality (Koop et al. 2001; Villanueva et al. 2006), sedimentation (Hunte and Wittenberg 1992; Babcock and Smith 2002), and indirect (allelopathy, Kuffner and Paul 2004; shading, Box and Mumby 2007) and direct competition with algae (Box and Mumby 2007) and other sessile organisms. Despite recent efforts to constrain relationships between a variety of environmental factors and early life history stages of corals, no studies to date have investigated the effect of increasing levels of ocean acidification on larval settlement, growth, or survivorship.

Communicated by Guest Editor Dr Katharina Fabricius

R. Albright (✉) · B. Mason · C. Langdon
Division of Marine Biology and Fisheries, Rosenstiel School of Marine and Atmospheric Science, 4600 Rickenbacker Causeway, Miami, FL 33149, USA
e-mail: ralbright@rsmas.miami.edu

The susceptibility of scleractinian corals to elevated carbon dioxide levels has been a central issue in the context of global climate change. The concentration of carbon dioxide in the atmosphere is currently increasing at a rate of approximately 0.5% per year and is projected to increase to double pre-industrial levels by the year 2065 (IPCC 2007). This increase will cause ocean surface waters to become more acidic and result in alterations in the saturation state of aragonite, Ω_{arag} (Broecker et al. 1979; Caldeira and Wickett 2003). The projected changes in tropical surface seawater involve a reduction in pH from 8.08 to 7.93 (with a doubling of CO_2), and a reduction in Ω_{arag} from 4.0 ± 0.2 (mean ± 1 SD) to 3.1 ± 0.2 by the year 2065 and 2.8 ± 0.2 by 2100 (Kleypas et al. 1999). This reduction in saturation state will likely cause a global reduction in the rates of reef accretion, as the deposition of $CaCO_3$ by corals and other reef organisms is partially controlled by the saturation state of $CaCO_3$ in seawater (Gattuso et al. 1998; Langdon et al. 2000, 2003; Leclercq et al. 2000, 2002; Marubini et al. 2001, 2002; Reynaud et al. 2003; Langdon and Atkinson 2005; Fine and Tchernov 2007). While recent research efforts aim to constrain the mechanisms and effects (both physiological and ecological) of elevated pCO_2 on adult scleractinian corals, studies evaluating the response of earlier life history stages are lacking. The objectives of the present study were to investigate the effects of aragonite saturation on the settlement and early post-settlement growth of a common Caribbean reef coral *Porites astreoides.*

Materials and methods

Collection of larvae

Adult colonies of the brooding species *P. astreoides* were collected from The Rocks, an inshore patch reef near Tavernier, Florida (FL, USA), several days prior to the new moon in May and June 2007 and maintained in a closed recirculating seawater system for approximately 1 week during the predicted period of larval release. Colonies were stored in mesh-lined containers during the nights of release. Following release, larvae were transferred to sterile containers with filtered seawater and transported to the University of Miami's Rosenstiel School of Marine and Atmospheric Science (RSMAS). Approximately 700 larvae were collected in May and 400 in June.

Experimental set-up

A flow-through seawater system was used to create and maintain three aragonite saturation states: $\Omega_{arag} = 3.2$ (control), $\Omega_{arag} = 2.6$ (mid), and $\Omega_{arag} = 2.2$ (low) (based on projected pCO_2 scenarios for the years 2065 and 2100, respectively, as determined by the Intergovernmental Panel on Climate Change (IPCC) 3rd Assessment Report (IPCC 2001). Seawater was pumped into a 240,000 l settling tank, filtered through sand to remove particulate matter, and piped to three tanks where the carbonate system was manipulated. Total alkalinity (TA) and pH were adjusted via constant-drip 1 M HCl additions and control of seawater flow rates. Treated water was then introduced to experimental aquaria (18 l) at a constant rate. Duplicate aquaria were used for each treatment, and the treatment water was used for both settlement and growth experiments. Water temperature was maintained at 26.6 ± 0.8°C (mean ± 1 SD) and 25.4 ± 0.3°C during May and June experiments, respectively. Ambient lighting was not artificially supplemented in order to discourage algal overgrowth of juvenile corals. Light intensity ranged from 1 to 191 $\mu mol\ m^{-2}\ s^{-1}$, averaging less than 10 $\mu mol\ m^{-2}\ s^{-1}$ over the course of 12.5 h of daily illumination. Water samples from treatment aquaria were analyzed for TA and pH. TA was determined in duplicate using an automated Gran titration (Dickson et al. 2007, SOP3b), and accuracy was checked against certified seawater reference material (A. Dickson, Scripps Institute of Oceanography). pH was determined using an Orion Ross combination pH electrode. Concentrations of CO_3^{2-}, Ca^{2+}, and Ω_{arag} were computed from TA, pH, temperature, and salinity using the program CO2SYS (E. Lewis, Brookhaven National Laboratory), and dissociation constants for carbonate determined by Mehrbach et al. (1973) as refit by Dickson and Millero (1987), and dissociation constant for boric acid determined by Dickson (1990). pH is reported on the seawater scale, the scale on which K1 and K2 were determined in the Gran functions.

Settlement experiments

Settlement experiments were conducted in 300 ml plastic solo cups, maintained in a water bath at a constant temperature of 25°C. Each cup contained three 1 cm^2 limestone tiles that were pre-conditioned for approximately 1 month in situ. Tiles were nested in clean, baked silica sand to force larvae to settle on the flat, upper surface of the tile, ensuring accurate growth measurements. Silica sand was used to avoid the potential buffering effects of limestone sediments. Cups were randomly assigned to treatments, 250 ml of treatment water and a known number of larvae were added to each cup, and larvae were allowed 1 week to settle. Settlement cups were un-aerated and tightly covered with a sheet of Plexiglas to prevent gas exchange. Water was exchanged every 48 h taking care not to disturb larvae. In May, 12 settlement cups were prepared for each treatment, with 20 larvae introduced into each cup. In June, eight cups were used, with 15 larvae per cup. Settlement was confirmed by examining juveniles under a dissecting microscope.

Juvenile growth rates

Once settlement was assessed; limestone tiles were introduced to treatment aquaria containing water corresponding to the treatment in which they were settled. Juvenile growth rates were determined by measuring the change in surface area over the course of 21 days in May and 28 days in June. Juveniles were photographed under a dissecting microscope at the start and end of each experiment. SPOT© software was used to measure total surface area (defined as the outermost extent of visible skeleton). Growth rates were calculated as the rate of change in surface area (mm^2 $month^{-1}$). Data were square root transformed to meet assumptions and analyzed using a One-Way ANOVA.

Results and discussion

Chemical conditions

The chemical conditions in each of the treatments are summarized in Table 1.

Settlement

Saturation state did not significantly affect the settlement rates of *P. astreoides* larvae (Table 2); however, the high within-treatment variance meant that the power to detect subtle treatment effects was limited. Although other environmental factors (e.g., salinity, UVR, nutrients, temperature) have been shown to negatively impact early life history stages of corals, the lack of a significant treatment effect in the present study suggests that saturation state did not directly influence larval development, settlement, and metamorphosis. These findings are consistent with observations from earlier studies, indicating that while the positive correlation between coral calcification and saturation state is well-documented, other physiological processes such as tissue growth (i.e., increase in biomass) (Fine and Tchernov 2007) and photosynthesis (Leclercq et al. 2002; Reynaud et al. 2003; Langdon and Atkinson 2005) remain unaffected or may even be augmented. As coral larvae are not actively calcifying while in the plankton, it seems unlikely that saturation state would affect pre-settlement physiology. Should an effect of aragonite saturation on settlement exist, the mechanism of this effect would likely be indirect.

Table 2 Percent larval settlement and juvenile growth rate (mm^2 $month^{-1}$) of *Porites astreoides*[a]

	Control $\Omega_{arag} = 3.2$	Mid $\Omega_{arag} = 2.6$	Low $\Omega_{arag} = 2.2$
Percent settlement			
May	34.72 ± 7.29 (12)	41.94 ± 8.82 (12)	26.39 ± 5.83 (12)
June	12.50 ± 4.95 (8)	16.67 ± 4.88 (8)	13.33 ± 3.56 (8)
Growth rate			
May	0.32 ± 0.03 (58)	0.14 ± 0.03 (73)	0.09 ± 0.05 (30)
June	0.44 ± 0.08 (14)	0.24 ± 0.03 (16)	0.07 ± 0.02 (10)

[a] Mean ± 1 SE (*n*)

Substrata quality and benthic community composition are known to be critically important in determining settlement. Studies indicate that settlement and metamorphosis of some coral species are induced by chemicals associated with microbial biofilms and/or crustose coralline algae (CCA) (Morse et al. 1988; Negri et al. 2001; Webster et al. 2004). CCA precipitates high-magnesium calcite 13–15% $MgCO_3$ (Agegian and Mackenzie 1989), a mineral phase of calcium carbonate that is 1.2–5 times as soluble as aragonite (Plummer and Mackenzie 1974; Morse et al. 2006). Recent work showed a 78% reduction in CCA recruitment associated with conditions mimicking a doubling of atmospheric CO_2 (Kuffner et al. 2008). Such changes in substrate community composition may affect the settlement and sexual recruitment of coral larvae.

Table 1 Physical and chemical conditions during settlement and growth experiments[a]

	Salinity	Temperature (°C)	TA ($\mu mol\ kg^{-1}$)	pH_{SWS}	CO_3^{2-} ($\mu mol\ kg^{-1}$)	[b]Ca^{2+} ($mmol\ kg^{-1}$)	Ω_{arag}
May							
Control	36 ± 1	26.6 ± 0.8	2348 ± 4	7.95 ± 0.02	198 ± 7	10.6 ± 0.3	3.1 ± 0.1
Mid	36 ± 1	26.6 ± 0.8	2206 ± 34	7.88 ± 0.02	165 ± 6	10.6 ± 0.3	2.61 ± 0.09
Low	36 ± 1	26.6 ± 0.8	2138 ± 44	7.80 ± 0.02	135 ± 7	10.6 ± 0.3	2.2 ± 0.1
June							
Control	34 ± 1	25.4 ± 0.3	2422 ± 14	7.99 ± 0.02	202 ± 8	10.0 ± 0.3	3.2 ± 0.1
Mid	35 ± 1	25.4 ± 0.3	2224 ± 55	7.91 ± 0.01	166 ± 3	10.3 ± 0.3	2.62 ± 0.04
Low	35 ± 1	25.4 ± 0.3	2181 ± 9	7.84 ± 0.02	141 ± 4	10.3 ± 0.3	2.23 ± 0.08

[a] Mean ± 1 SD

[b] Calculated based on 10.28 mmol kg^{-1} of Ca^{2+} at a salinity of 35

Growth and survivorship

Saturation state exhibited a significant treatment effect on growth rates of *P. astreoides* juveniles (May: ANOVA, $F_{2,159} = 8.61$, $P < 0.001$; paired comparisons by Tukey HSD, significant differences, $P < 0.05$; June: ANOVA, $F_{2,38} = 10.46$, $P < 0.001$; paired comparisons by Tukey HSD, significant differences, $P < 0.05$). Growth, as measured by lateral skeletal extension, was positively correlated with saturation state ($P = 0.007$) (Fig. 1). Juveniles reared in the mid saturation state treatment grew an average of 45% (June) to 56% (May) slower than controls, while those reared in low saturation state treatments grew an average of 72% (May) to 84% (June) slower than controls. These findings are consistent with the hypothesis that saturation state controls calcification and, ultimately, growth, as has been documented for several adult scleractinians and an experimental reef community (Gattuso et al. 1998; Langdon et al. 2000, 2003; Leclercq et al. 2000, 2002; Marubini et al. 2001, 2002; Reynaud et al. 2003; Langdon and Atkinson 2005; Fine and Tchernov 2007).

Declining growth rates may have implications for rates of juvenile mortality. Risk of mortality has been shown to be inversely proportional to juvenile growth rate and colony size (Hughes and Jackson 1985; Babcock 1991; Babcock and Mundy 1996) with up to a 20% increase in survivorship associated with a 0.5-mm increase in diameter of 4-month-old juveniles of certain species (Babcock and Mundy 1996). Although post-settlement mortality was not observed in either the present or other laboratory studies that have mimicked ocean acidification (Fine and Tchernov 2007), it is important to note that mortality rates observed in this study do not approximate survivorship of juveniles in situ. Under laboratory conditions, factors known to affect early survivorship on the reef (e.g., competition with algae and other benthic organisms, sedimentation effects, predation) were controlled or eliminated in order to minimize influences on growth other than the desired treatment effect. Therefore, survivorship in this study likely overestimates survivorship that would be expected on the reef.

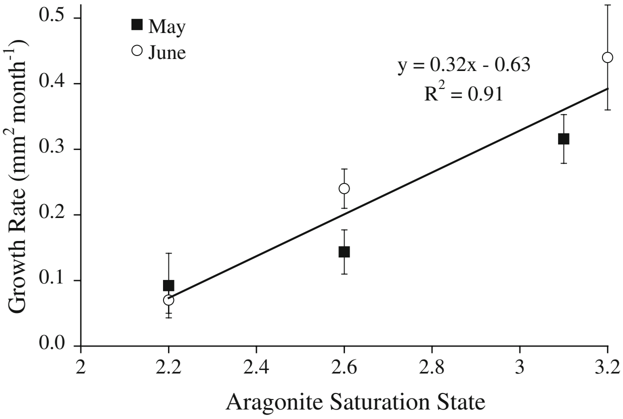

Fig. 1 Effect of saturation state on skeletal growth rate (±SE) of *Porites astreoides* juveniles ($P = 0.003$)

In addition to potential increases in juvenile mortality, both the onset of sexual maturity (Chornesky and Peters 1987; Szmant 1991) and fecundity (McGuire 1998; Babcock 1991; De Barros and Pires 2006) of reef-building corals are known to be a function of colony size. Therefore, depressed growth would likely result in longer time spent in juvenile (non-reproductive) life stages, which, in combination with adult loss, would shift population structures toward dominance by smaller size classes, ultimately reducing effective population sizes, population fecundity, and the resilience of reef-building corals.

This study indicates that increasing atmospheric carbon dioxide and the associated reductions in aragonite saturation of tropical surface waters have the potential to accelerate the degradation of coral reefs by affecting multiple life history stages and ecological processes critical to reef persistence and resilience. These effects may occur via both direct (e.g., depressed calcification) and indirect (e.g., changes in substrate conditions that favor settlement) pathways. Slowed growth may trigger numerous other repercussions, including, but not limited to: elevated juvenile mortality and reduced recruitment success; and shifts in population size structure and lower reproductive output. There is a need to further investigate the ability of corals to acclimatize and/or adapt to elevated $p\mathrm{CO}_2$ given prolonged exposure, as well as the possibility of taxonomic differences in sensitivity. Focusing efforts on the protection and cultivation of more adaptable species may improve the effectiveness of coral preservation and restoration efforts.

Acknowledgments This project was funded in part by a grant awarded by Mote Marine Laboratory's Protect Our Reefs specialty license plate. Permit FKNMS-2007-009 was provided by the Florida Keys National Marine Sanctuary for the collection of coral colonies. Field and laboratory assistance was provided by M. Miller and W. Cooper. Constructive review of the manuscript by M. Miller and D. Manzello is greatly appreciated.

References

Agegian CR, Mackenzie FT (1989) Calcareous organisms and sediment mineralogy on a mid-depth bank in the Hawaiian Archipelago. Pac Sci 43:55–66

Babcock RC (1991) Comparative demography of three species of scleractinian corals using age- and size-dependent classifications. Ecol Monogr 61:225–44

Babcock R, Mundy C (1996) Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians. J Exp Mar Biol Ecol 206:179–201

Babcock R, Smith L (2002) Effects of sedimentation on coral settlement and survivorship. Proc 9th Int Coral Reef Symp 1:245–248

Bassim K, Sammarco P, Snell T (2002) Effects of temperature on success of (self and non-self) fertilization and embryogenesis in *Diploria strigosa* (Cnidaria, Scleractinia). Mar Biol 140:479–488

Box SJ, Mumby PJ (2007) Effect of macroalgal competition on growth and survival of juvenile Caribbean corals. Mar Ecol Prog Ser 342:139–49

Broecker WS, Takahashi T, Simpson HJ, Peng TH (1979) Fate of fossil fuel carbon dioxide and the global carbon budget. Science 206:409–418

Caldeira K, Wickett MF (2003) Anthropogenic carbon and ocean pH. Nature 425:365

Chornesky EA, Peters EC (1987) Sexual reproduction and colony growth in the scleractinian coral *Porites astreoides*. Biol Bull (Woods Hole) 17:161–77

De Barros MML, Pires DO (2006) Aspects of the life history of *Siderastrea stellata* in the tropical Western Atlantic Brazil. Invertebr Reprod Dev 49:237–44

Dickson AG (1990) Thermodynamics of the dissociation of boric acid in synthetic seawater from 273.15 to 318.15°K. Deep-Sea Res 37:755–766

Dickson AG, Millero FJ (1987) A comparison of the equilibrium constants for the dissociation of carbonic acid in seawater media. Deep-Sea Res 34:1733–1743

Dickson AG, Sabine CL, Christian JR (eds) (2007) Guide to best practices for ocean CO_2 measurements. PICES Special Publication 3, North Pacific Marine Science Organization. http://cdiac.ornl.gov/oceans/Handbook_2007.html

Edmunds PJ, Gates RD, Gleason DF (2001) The biology of larvae from the reef coral *Porites astreoides*, and their response to temperature disturbances. Mar Biol 139:981–9

Fine M, Tchernov D (2007) Scleractinian coral species survive and recover from decalcification. Science 315:1811

Gattuso J-P, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1998) Effect of calcium carbonate saturation of seawater on coral calcification. Glob Planet Change 18:37–46

Gleason DF, Edmunds PJ, Gates RD (2006) Ultraviolet radiation effects on the behavior and recruitment of larvae from the reef coral Porites astreoides. Mar Biol 148:503–12

Harrington L, Fabricius K, De'ath G, Negri A (2004) Recognition and selection of settlement substrata determine post-settlement survival in corals. Ecology 85:3428–3437

Harrison PL, Ward S (2001) Elevated levels of nitrogen and phosphorus reduce fertilization success of gametes from scleractinian reef corals. Mar Biol 139:1057–1068

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839–866

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–66

Hughes TP, Tanner JE (2000) Recruitment failure, life histories, and long-term decline of Caribbean corals. Ecology 81:2250–2263

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933

Hunte W, Wittenberg M (1992) Effects of eutrophication and sedimentation on juvenile corals. 2. Settlement. Mar Biol 114:625–631

IPCC (2001) Climate Change 2001: the scientific basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

IPCC (2007) Climate Change 2007: the physical science basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge

Kleypas JA, Buddemeier RW, Archer D, J Gattuso, Langdon C, Opdyke BN (1999) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. Science 284:118–120

Koop K, Booth D, Broadbent A, Brodie J, Bucher D, Capone D, Coll J, Dennison W, Erdmann M, Harrison P, Hoegh-Guldberg O, Hutchings P, Jones GB, Larkum AWD, O'Neill J, Steven A, Tentori E, Ward S, Williamson J, Yellowlees D (2001) ENCORE: The effect of nutrient enrichment on coral reefs synthesis of results and conclusions. Mar Pollut Bull 42:91–120

Kuffner IB, Paul VJ (2004) Effects of the benthic cyanobacterium *Lyngbya majuscula* on larval recruitment of the reef corals *Acropora surculosa* and *Pocillopora damicornis*. Coral Reefs 23:455–458

Kuffner IB, Andersson AJ, Jokiel PL, Rodgers KS, Mackenzie FT (2008) Decreased abundance of crustose coralline algae due to ocean acidification. Nature Geoscience [doi: 10.1038/ngeo100]

Langdon C, Atkinson MJ (2005) Effect of elevated pCO_2 on photosynthesis and calcification of corals and interactions with seasonal change in temperature/irradiance and nutrient enrichment. J Geophys Res 110, C09S07 [doi:10.1029/2004JC002576]

Langdon C, Broecker WS, Hammond DE, Glenn E, Fitzsimmons K, Nelson SG, Peng T, Hajdas I, Bonani G (2003) Effect of elevated CO_2 on the community metabolism of an experimental coral reef. Global Biogeochem Cycles 17:11–1 to 11–14

Langdon C, Takahashi T, Sweeney C, Chipman D, Goddard J, Marubini F, Aceves H, Barnett H, Atkinson MJ (2000) Effect of calcium carbonate saturation state on the calcification rate of an experimental coral reef. Global Biogeochem Cycles 14:639–654

Leclercq N, Gattuso J, Jaubert J (2000) CO_2 partial pressure controls the calcification rate of a coral community. Global Change Biol 6:329–334

Leclercq N, Gattuso J-P, Jaubert J (2002) Primary production, respiration, and calcification of a coral reef mesocosm under increased CO_2 partial pressure. Limnol Oceanogr 47:558–564

Marubini F, Ferrier-Pages C, Cuif JP (2002) Suppression of growth in scleractinian corals by decreasing ambient carbonate ion concentration: a cross-family comparison. Proc R Soc Lond Ser B Biol Sci 270:179–184

Marubini F, Barnett H, Langdon C, Atkinson MJ (2001) Dependence of calcification on light and carbonate ion concentration for the hermatypic coral *Porites compressa*. Mar Ecol Prog Ser 220:153–62

Mehrbach C, Culberson CH, Hawley JE, Pytkowicz RM (1973) Measurement of the apparent dissociation constants of carbonic acid in seawater at atmospheric pressure. Limnol Oceanogr 18: 897–907

McGuire MP (1998) Timing of larval release by *Porites astreoides* in the northern Florida Keys. Coral Reefs 17:369–375

Miller MW, Weil E, Szmant AM (2000) Coral recruitment and juvenile mortality as structuring factors for reef benthic communities in Biscayne National Park, USA. Coral Reefs 19:115–23

Morse DE, Hooker N, Morse ANC, Jensen RA (1988) Control of larval metamorphosis and recruitment in sympatric Agariciid corals. J Exp Mar Biol Ecol 116:193–217

Morse JW, Andersson AJ, Mackenzie FT (2006) Initial responses of carbonate-rich shelf sediments to rising atmospheric pCO_2 and "ocean acidification": role of high Mg-calcites. Geochim Cosmochim Acta 70:5814–5830

Negri AP, Heyward AJ (2001) Inhibition of coral fertilization and larval metamorphosis by tributyltin and copper. Mar Environ Res 51:17–27

Negri AP, Webster NS, Hill RT, Heyward AJ (2001) Metamorphosis of broadcast spawning corals in response to bacterial isolated from crustose algae. Mar Ecol Prog Ser 223:121–131

Negri AP, Vollhardt C, Humphrey C, Heyward A, Jones R, Eaglesham G, Fabricius K (2005) Effects of the herbicide diuron on the early life history stages of corals. Mar Pollut Bull 51:370–383

Plummer LN, Mackenzie FT (1974) Predicting mineral solubility from rate data: application to the dissolution of magnesium calcites. Am J Sci 274:61–83

Porter JW, Meier OW (1992) Quantification of loss and change in Floridian reef coral populations. Am Zool 32:625–640

Reynaud S, Leclercq N, Romaine-Lioud S, Ferrier-Pages C, Jaubert J, Gattuso J-P (2003) Interacting effects of CO_2 partial pressure and temperature on photosynthesis and calcification in a scleractinian coral. Global Change Biol 9:1660–1668

Richmond R (1997) Reproduction and recruitment in corals: critical links in the persistence of reefs. In: Birkeland C (ed) Life and death of coral reefs. Chapman & Hall, New York, pp 175–197

Shearer TL, Coffroth MA (2006) Genetic identification of Caribbean scleractinian coral recruits at the Flower Garden Banks and the Florida Keys. Mar Ecol Prog Ser 306:133–42

Szmant AM (1991) Sexual reproduction by the Caribbean reef corals *Montastrea annularis* and *M. cavernosa*. Mar Ecol Prog Ser 74:13–25

Vermeij MJA, Fogarty ND, Miller MW (2006) Pelagic conditions affect larval behavior, survival, and settlement patterns in the Caribbean coral *Montastraea faveolata*. Mar Ecol Prog Ser 310:119–28

Villanueva RD, Yap HT, Montano MNE (2006) Intensive fish farming in the Philippines is detrimental to the reef-building coral *Pocillopora damicornis*. Mar Ecol Prog Ser 316:165–174

Webster NS, Smith LD, Heyward AJ, Watts JEM, Webb RI, Blackall LL, Negri AP (2004) Metamorphosis of a scleractinian coral in response to microbial biofilms. Appl Environ Microbiol 70:1213–1221

Wellington GM, Fitt WK (2003) Influence of UV radiation on the survival of larvae from broadcast-spawning reef corals. Mar Biol 143:1185–1192