Patterns of resistance and resilience of the stress-tolerant coral *Siderastrea radians* (Pallas) to sub-optimal salinity and sediment burial

Diego Lirman a,⁎, Derek Manzellob

a University of Miami, Rosenstiel School of Marine and Atmospheric Science, Marine Biology and Fisheries Division, 4600 Rickenbacker Cswy., Miami, Florida 33149, USA

b Atlantic Oceanographic and Meteorological Laboratory, National Oceanic and Atmospheric Administration, Miami, Florida 33149, USA

**Abstract**

The coastal lagoons of south Florida, U.S., experience fluctuating levels of sedimentation and salinity and contain only a subset of the coral species found at the adjacent reefs of the Florida Reef Tract. The dominant species within these habitats is *Siderastrea radians*, which can reach densities of up to 68 colonies m⁻² and is commonly exposed to salinity extremes (<10 psu to >37 psu) and chronic sediment burial. In this study, we document the patterns of resistance and resilience of *S. radians* to sub-optimal salinity levels and sediment burial in a series of short-term, long-term, acute, chronic, single-stressor, and sequential-stressor experiments. *S. radians* displayed remarkable patterns of resistance and resilience and mortality was documented only under prolonged (>48 h) continuous exposure to salinity extremes (15 and 45 psu) and chronic sediment burial. A reduction in photosynthetic rates was documented for all salinity exposures and the decrease in photosynthesis was linearly related to exposure time. Negative impacts on photosynthetic rates were more severe under low salinity (15 psu) than under high salinity (45 psu). Corals exposed to intermediate, low-salinity levels (25 psu), exhibited initial declines in photosynthesis that were followed by temporary increases that may represent transient acclimatization patterns. The impacts of sediment burial were influenced by the duration of the burial period and ranged from a temporary reduction in photosynthesis to significant reductions in growth and tissue mortality. The maintenance of P/R ratios >1 and the rapid (<24 h) recovery of photosynthetic rates after burial periods of 2-24 h indicates that *S. radians* is able to resist short-term burial periods with minor physiological consequences. However, as burial periods increase and colonies become covered at multiple chronic intervals, sediment burial resulted in extended photosynthetic recovery periods, reduced growth, and mortality. Under normal conditions (i.e., no salinity stress), *S. radians* was very effective at clearing sediments, and >50% of the colonies’ surface area was cleared within 1 h. However, clearing rates were influenced by physiological status, and prior exposure to sub-optimal salinity significantly reduced the clearing rates of stressed colonies. The response of *S. radians* to disturbance documented in this study characterizes this species as highly stress-tolerant and provides an explanation for its present high abundance in both reef and marginal environments. Moreover, the key life-history attributes of *S. radians*, such as brooding reproductive strategy, small colony size, high stress-tolerance, and high recruitment rates, suggest the potential for this species to replace reef-building taxa under increased disturbance scenarios in Florida and elsewhere in the region.

© 2008 Elsevier B.V. All rights reserved.

**1. Introduction**

Coral reefs have undergone a drastic decline in diversity, abundance, and condition in the recent past that has focused attention on the impacts of single and multiple stressors on coral abundance, distribution, and condition (e.g., Gardner et al., 2003; Hughes et al., 2003; Pandolfi et al., 2003; Wilkinson, 2004). While patterns of decline have been widespread across spatial scales and taxonomic groups, reviews of the impacts of coral disturbances based on correlational and experimental studies indicate that the response of corals to both chronic and acute stress can be highly species-specific (e.g., Jokiel and Coles, 1990; Coles and Jokiel, 1992; Fabricius, 2005). In fact, the species-specific susceptibility of corals to disturbances is reflected in the patterns of coral decline observed in the Caribbean, which have been characterized by the loss of the main reef-building coral taxa (Hughes, 1994; Hughes and Tanner, 2000; Kramer, 2003) and corresponding increases in the relative cover of stress-resistant, weedy coral species (Green et al., 2008).

In Florida, declines of up to 95% in the cover of *Acropora* spp. and *Montastraea* spp. have been reported, underscoring the high susceptibility of these taxa to increased temperature, coral diseases, and hurricane impacts (Jaap et al., 1988; Dustan, 1999; Dustan et al., 2001;
Miller et al., 2002; Palandro et al., 2003). In the Caribbean region, high mortality and limited sexual recruitment of reef-building taxa has resulted in the increased predominance of stress-tolerant, early colonizing taxa like Porites and Agaricia on natural (Hughes and Connell, 1999; Kramer, 2003; Green et al., 2008) and artificial substrate (Lirman and Miller, 2003; Vermeij, 2005).

South Florida’s Biscayne Bay and Florida Bay experience extreme and highly variable levels of sedimentation and salinity. Hardbottom habitats within these lagoons contain coral communities with only a subset of the species found at the adjacent reefs of the Florida Reef Tract. Siderastrea radians, which can reach densities of up to 68 colonies m⁻², is the dominant Scleractinian in these habitats (Lirman et al., 2003). In Biscayne Bay, S. radians colonies are found in shallow (<2 m) nearshore habitats influenced by the inflow of freshwater from canal structures that can cause salinities to drop dramatically (to <5 psu) over a period of hours and remain well below oceanic values for extended periods of time. The shallow nature of this basin and the limited water turnover can also create hypersaline (>37 psu) conditions during the dry season (Jan-April) (Lirman et al., 2008). Lastly, high sedimentation and sediment migration rates in these basins can cause >45% of colonies to be completely buried at any given time (Lirman et al., 2003).

In addition to being the dominant species in the coastal lagoons of southeast Florida, S. radians is a ubiquitous component of coral communities of the Florida Reef Tract where it usually occupies high-sedimentation, low-lying locations within these habitats (Chiappone and Sullivan, 1994; Lirman and Fong, 2007). The high recruitment potential of this species makes it a very successful early colonizer on newly available substrate such as reef restoration structures (Miller and Barimo, 2001; Lirman and Miller, 2003) and wrecks (Vermeij, 2005). Finally, high abundance of this species in disturbed or marginal environments has also been documented by Lewis (1989) in Barbados and by Moses et al. (2003) in the Cape Verde Islands.

In this study, we document the patterns of resistance (i.e., the intensity and duration of a stressor needed to elicit a significant negative response) and resilience (i.e., the rate of return to a pre-disturbance state) of Siderastrea radians exposed to sub-optimal salinity levels and sediment burial, two stress factors commonly encountered by this species in its natural lagoon habitat in a series of short-term, long-term, acute, chronic, single-stressor, and sequential-stressor experiments. The response of S. radians to single and multiple stressors documented in this study characterizes this species as highly stress-tolerant and provides an explanation for its high abundance in both reef and marginal non-reef environments.

2. Materials and methods

Colonies of Siderastrea radians (<4 cm in diameter) were collected from Biscayne Bay, Florida, and kept in outdoor tanks for an acclimation period of 2–3 weeks. All the experiments were conducted under ambient light in a water table for temperature control and colonies were kept in flow-through outdoor tanks during all recovery periods. The stressor levels and exposure times were chosen to cover the range of sub-optimal conditions encountered by corals in Biscayne Bay, especially in those habitats influenced by freshwater inflow from water management canals (Lirman et al., 2003, 2008).

Two types of experiments were performed: (1) single-exposure experiments where corals were exposed to a treatment for different lengths of time; and (2) multiple-exposure experiments where corals were exposed to treatments for 24 h at weekly intervals over a period of three months. Coral condition was assessed as tissue coloration and polyp appearance (retracted or extended). Colony coloration was classified as normal (normal pigmentation throughout the colony), pale (lighter coloration in the coral theca and coenosteum), and bleaching (white coloration throughout the colony) (Lirman et al., 2002). The surface area of each colony was measured with calipers assuming a hemispherical shape, and growth or partial mortality were assessed by documenting changes in live tissue area over time. To measure photosynthesis and respiration rates, corals were placed in clear and opaque 1-liter containers sealed to prevent gas diffusion. Concurrently, control light and dark containers without corals were used to account for photosynthesis and respiration due to the plankton and bacterial components of seawater as described by Manzello and Lirman (2003). Corals were kept within the sealed containers for 2 h, after which dissolved oxygen was measured. Photosynthesis and respiration rates were always measured under experimental conditions during the last 2 h of the exposure period. For example, for a 4-hr exposure to 25 psu, corals were kept in 20-1 containers at 25 psu for the first 2 h. After the initial 2 h, the corals were transferred to dark and light 1-1 containers filled with water at 25 psu for the remainder of the exposure period (i.e., 2 h), over which photosynthesis and respiration rates were measured. The water used for all the 1-1 containers was drawn from a single, well-mixed batch so that initial conditions were similar for all corals. Lastly, to reduce the amount of variability due to daily variations in photosynthetic rates as well as the variable light intensity during incubation times, the parameters obtained for each experiment were compared only to those obtained for control corals that were run simultaneously. Photosynthetic rates were expressed as: (1) net photosynthesis (i.e., changes in mg O₂ cm⁻² hr⁻¹); and (2) relative photosynthesis. Relative photosynthesis was calculated as the deviation from the mean value obtained for the corresponding coral controls, allowing for comparisons among data collected at different dates and times (Manzello and Lirman, 2003). Differences in mean photosynthetic, respiration, and growth rates were tested with Wilcoxon rank-sum tests (2 groups) and Kruskal-Wallis tests (>2 groups) due to non-conformity to the normality assumption required for parametric tests (Sokal and Rohlf, 1995). Recovery was deemed complete when no significant differences in net photosynthetic rates were found between exposed and control corals.

2.1. Single-Exposure Experiments

Salinity Exposure: Colonies of S. radians (n = 10 colonies per treatment) were exposed to treatments of 15, 25, 35 (oceanic controls), and 45 psu in a series of short-term (2, 4, 6, 24, 48 h) and long-term (7 and 21 d) exposure experiments. Salinity levels were adjusted by adding freshwater to compensate for evaporation and the water was changed every 3 d during long-term exposure experiments. High-salinity treatments (45 psu) were created using seawater concentrated through evaporation. After exposure, corals were returned to outdoor mesocosms and photosynthesis and coral survivorship and photosynthesis and respiration rates were measured as described.

Sediment Burial: Colonies of S. radians (n = 10 colonies per treatment) were buried completely under sediments for 1, 4, 24, and 48 h. Sediments were collected from Biscayne Bay, rinsed with freshwater, and dried for 48 h prior to the experiments. Enough sediment was added to ensure that the corals would not be able to uncover any portion of the colony during the exposure period. After the burial time, corals were rinsed to remove sediments and photosynthesis and respiration were measured as described. The photosynthetic rates of previously buried corals were monitored after 24 h, 48 h, and 7 d to document recovery patterns. Control corals were buried concurrently with experimental corals, but sediments were removed immediately for these controls. Photosynthesis and respiration rates of control corals were determined as described for the exposed corals.

A second experiment was conducted to document sediment clearing rates and to evaluate whether sediment clearing rates in S. radians are influenced by colony shape. For this experiment, hemispherical colonies (sphericity index = mean height-to-diameter = 0.55, n = 15) and flat colonies (sphericity index = 0.4, n = 6) were used (Riegel, 1995). Dead hemispherical colonies (n = 8) were used as controls. Containers with sediments spread evenly over the bottom were placed in an outdoor tank. Corals were placed on the surface of the sediments and slowly
covered with additional sediments until the colonies were no longer visible. Clearing of the sediments commonly occurred from the top of the colony in a circular pattern, increasing gradually in diameter. The surface area of the cleared tissue was measured every hour and used to calculate the percent of total surface area of each colony cleared over time (Weber et al., 2006).

2.2. Multiple Exposure Experiments

*S. radians* colonies (*n* = 10 colonies per treatment) were exposed to salinity treatments (15, 25, 35 (oceanic controls), and 45 psu) and sediment burial for 24 h at weekly intervals for up to three months. Corals were placed in outdoor tanks between exposure periods. Coral growth and partial mortality were assessed every 4 weeks.

2.3. Salinity and Sediment Burial

To evaluate the impacts of prior exposure to sub-optimal salinity on the sediment-clearing response of *S. radians*, sediment-clearing trials were conducted following 24 h of exposure to 20 psu (n = 16 colonies), 25 psu (n = 16 colonies), 35 psu (controls, n = 15 colonies), and 45 psu (n = 12 colonies). While 15 psu was used as the lowest salinity treatments in all previous experiments, salinity levels reached 20 psu during the sediment clearing experiment. All of the colonies used were hemispherical. A second sediment-clearing trial was performed 24 h and 5 d after the initial experiment to document the recovery of the sediment clearing response after return to control oceanic salinity conditions.

### 3. Results

#### 3.1. Salinity Exposure

The immediate reaction of corals exposed to salinity stress was polyp retraction and tissue paling. Net photosynthesis of *S. radians* was significantly lower following 2, 4, 6, and 8 h of exposure to 15 psu compared to controls (*p* < 0.05 for all tests). In corals exposed to 15 psu for 24 h, 48 h, and 7 d, respiration rates exceeded photosynthesis (Table 1; Fig. 1). While respiration rates for corals exposed to 15 psu were lower than those of the controls for exposures of 2, 4, 6, and 8 h, these declines were only significant for corals exposed for 6 and 8 h (*p* < 0.05 for both tests). In contrast, longer exposures (24 h, 48 h, and 7 d), resulted in an increase in respiration rates of exposed corals in comparison to controls, and Pg/R values that were < 1 (Table 1). Two of the colonies exposed for 48 h died. After one week of exposure to 15 psu, all corals were completely bleached and 4 of the 10 colonies died. After 3 weeks of exposure, all of the colonies in the 15 psu treatment died.

Recovery of photosynthetic rates took 24 h for the corals exposed for 2 h, 5 d for the corals exposed for 4 and 6 h, and 7 - 10 d for corals exposed for 8, 24 and 48 h. The relative photosynthetic rates of the surviving corals exposed for 7 d were still depressed compared to controls after 21 d of recovery. Coloration of the surviving colonies exposed to 15 psu for 7 d returned to normal after 6 weeks of recovery.

Photosynthetic rates of *S. radians* exposed to 25 psu were significantly lower than the corresponding controls for all exposure periods from 2 h - 7 d (*p* < 0.05 for all tests) (Table 1; Fig. 1). The recovery of photosynthetic rates took 24 h for corals exposed for 2-24 h, 48 h for corals exposed for 48 h, and 9 d for corals exposed for 7 d. Photosynthesis always exceeded respiration and no tissue mortality was observed for any of the short-term exposures. While tissue paling was observed after exposures of 24 h - 7 d, complete bleaching was not observed. No tissue mortality was observed during long-term exposures and normal tissue coloration returned within 6 weeks of recovery.

Photosynthetic rates of *S. radians* exposed to 45 psu were lower than the corresponding controls for all exposure periods from 2-48 h, but significant decreases were only observed for exposures of 8-48 h (*p* < 0.05 for all tests) (Table 1; Fig. 1). Photosynthesis always exceeded respiration and no tissue mortality was observed for any of the treatments. The recovery of photosynthetic rates took longer for corals exposed to 45 psu than any of the previous exposure experiments (15-25 psu). Recovery of photosynthetic rates took 7 d for the corals exposed for 8 h, 14 d for the corals exposed for 24 h, and 21 d for corals exposed for 48 h. Tissue coloration was pale after 7 d and 21 d and recovered fully for 21 d of recovery.

### Table 1

<table>
<thead>
<tr>
<th>Time</th>
<th>Type</th>
<th>Photosynthesis</th>
<th>Respiration</th>
<th>Pg/R</th>
<th>Photosynthesis</th>
<th>Respiration</th>
<th>Pg/R</th>
<th>Photosynthesis</th>
<th>Respiration</th>
<th>Pg/R</th>
<th>Photosynthesis</th>
<th>Respiration</th>
<th>Pg/R</th>
</tr>
</thead>
<tbody>
<tr>
<td>2 h</td>
<td>exp.</td>
<td>0.029 (0.004)</td>
<td>0.019 (0.002)</td>
<td>2.5</td>
<td>0.015 (0.006)</td>
<td>0.009 (0.002)</td>
<td>2.7</td>
<td>0.022 (0.006)</td>
<td>0.009 (0.004)</td>
<td>2.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>0.07 (0.019)</td>
<td>0.022 (0.007)</td>
<td>4.2</td>
<td>0.039 (0.018)</td>
<td>0.008 (0.003)</td>
<td>5.9</td>
<td>0.027 (0.006)</td>
<td>0.005 (0.004)</td>
<td>6.4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4 h</td>
<td>exp.</td>
<td>0.024 (0.006)</td>
<td>0.014 (0.008)</td>
<td>2.7</td>
<td>0.022 (0.006)</td>
<td>0.005 (0.002)</td>
<td>5.4</td>
<td>0.018 (0.006)</td>
<td>0.014 (0.007)</td>
<td>2.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>0.06 (0.002)</td>
<td>0.019 (0.004)</td>
<td>4.2</td>
<td>0.036 (0.009)</td>
<td>0.01 (0.006)</td>
<td>4.6</td>
<td>0.027 (0.011)</td>
<td>0.009 (0.003)</td>
<td>4.0</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6 h</td>
<td>exp.</td>
<td>0.009 (0.006)</td>
<td>0.009 (0.004)</td>
<td>2.0</td>
<td>0.016 (0.005)</td>
<td>0.008 (0.003)</td>
<td>2.0</td>
<td>0.017 (0.004)</td>
<td>0.019 (0.005)</td>
<td>1.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>0.041 (0.001)</td>
<td>0.025 (0.009)</td>
<td>2.5</td>
<td>0.039 (0.006)</td>
<td>0.012 (0.005)</td>
<td>4.3</td>
<td>0.023 (0.009)</td>
<td>0.013 (0.003)</td>
<td>2.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>8 h</td>
<td>exp.</td>
<td>0.002 (0.002)</td>
<td>0.006 (0.006)</td>
<td>1.3</td>
<td>0.017 (0.008)</td>
<td>0.015 (0.025)</td>
<td>2.1</td>
<td>0.011 (0.003)</td>
<td>0.023 (0.021)</td>
<td>1.5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>0.046 (0.01)</td>
<td>0.027 (0.011)</td>
<td>2.7</td>
<td>0.038 (0.003)</td>
<td>0.013 (0.01)</td>
<td>3.9</td>
<td>0.026 (0.004)</td>
<td>0.016 (0.005)</td>
<td>2.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>24 h</td>
<td>exp.</td>
<td>-0.004 (0.01)</td>
<td>0.027 (0.021)</td>
<td>0.8</td>
<td>0.025 (0.008)</td>
<td>0.022 (0.009)</td>
<td>2.1</td>
<td>0.016 (0.012)</td>
<td>0.026 (0.004)</td>
<td>1.6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>0.054 (0.02)</td>
<td>0.012 (0.007)</td>
<td>5.5</td>
<td>0.041 (0.009)</td>
<td>0.009 (0.002)</td>
<td>5.6</td>
<td>0.071 (0.013)</td>
<td>0.039 (0.038)</td>
<td>2.8</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>48 h</td>
<td>exp.</td>
<td>-0.006 (0.021)</td>
<td>0.019 (0.014)</td>
<td>0.7</td>
<td>0.014 (0.003)</td>
<td>0.004 (0.003)</td>
<td>4.5</td>
<td>0.029 (0.019)</td>
<td>0.022 (0.069)</td>
<td>2.3</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>0.036 (0.013)</td>
<td>0.013 (0.01)</td>
<td>3.8</td>
<td>0.051 (0.014)</td>
<td>0.018 (0.005)</td>
<td>3.8</td>
<td>0.098 (0.032)</td>
<td>0.025 (0.02)</td>
<td>4.9</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7 days</td>
<td>exp.</td>
<td>-0.004 (0.017)</td>
<td>0.023 (0.013)</td>
<td>0.8</td>
<td>0.018 (0.005)</td>
<td>0.01 (0.003)</td>
<td>2.8</td>
<td>2 - 7d - - -</td>
<td>7 d - - - - -</td>
<td>- - - - - -</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>control</td>
<td>0.042 (0.015)</td>
<td>0.016 (0.026)</td>
<td>3.6</td>
<td>0.032 (0.01)</td>
<td>0.013 (0.01)</td>
<td>3.5</td>
<td>2 - 7d - - -</td>
<td>7 d - - - - -</td>
<td>- - - - - -</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Figure 1. Relative photosynthesis of *Siderastrea radians* exposed to different salinity treatments. *p* < 0.05 for all tests. Photosynthesis always exceeded respiration and no tissue mortality was observed for any of the treatments.
80% of colonies after 6 weeks of recovery. After 21 d of exposure, 2 colonies from the 45 psu treatment exhibited partial tissue losses of 40% and 55% of the original live tissue surface area.

3.2. Sediment Burial

Tissue paling was observed for all colonies buried regardless of burial time. No significant impacts on photosynthesis or respiration were documented after burial periods of 1 and 2 h ($p > 0.05$). However, when the burial period increased to 4 and 24 h, significant declines in photosynthesis were documented ($p < 0.05$). No significant differences in respiration rates were observed for any of the burial periods. After the longest burial period (48 h), respiration exceeded photosynthesis (Fig. 2). S. radians colonies that were buried for 24 h recovered full photosynthetic ability after 48 h, and colonies buried for 48 h recovered fully after one week.

Hemispherical colonies of S. radians showed a rapid sediment-clearing response and were able to uncover 56.8% (±6.8) of their surface area within 1 h and 92.7% (±4.2) within 4 h (Fig. 3). In contrast, flat colonies cleared a significantly lower percentage of their surface area (36.4% (±15.1) after 1 h and 57.4% (±13.8) 4 h) ($p < 0.05$). None of the dead control colonies cleared any sediment during the 4 h burial experiment.

3.3. Multiple Exposure Experiments

No significant differences in growth were documented for S. radians colonies exposed to 15 psu (mean radial growth=0.28 mm mo$^{-1}$ ±0.14), 25 psu (0.34 mm mo$^{-1}$ ±0.13), 35 psu (controls, 0.33 mm mo$^{-1}$ ±0.11), and 45 psu (0.22 mm mo$^{-1}$ ±0.22) for 24 h at weekly intervals for 30 d ($p > 0.05$). However, after 60 d (i.e., 8 exposures) the growth rates of corals in the extreme treatments, 15 psu (0.34 mm mo$^{-1}$ ±0.16) and 45 psu (0.37 mm mo$^{-1}$ ±0.17), were significantly lower than the growth rates of the controls (0.57 mm mo$^{-1}$ ±0.12) ($p < 0.05$). No tissue mortality was observed during these chronic exposures.

The growth of S. radians colonies buried under sediments for 24 h at weekly intervals (0.14 mm mo$^{-1}$ ±0.12, n=10) was significantly reduced after 30 d (i.e., 4 exposures) ($p < 0.05$) compared to control corals (0.39 mm ±0.13). Furthermore, 50% of the experimental colonies suffered complete mortality after 3 months, while control colonies showed no signs of partial mortality over the same period.

3.4. Salinity and Sediment Burial

Prior exposure to salinity extremes (45 and 20 psu) had a significant effect on the ability of S. radians to clear sediments (Fig. 3). Control colonies were able to clear a significantly larger percentage of their surface area compared to corals that were previously exposed to sub-optimal salinity treatments ($p < 0.01$). Four hours after burial, 41% and 36% of the surface of colonies exposed to 45 and 20 psu, respectively, were clear of sediments. In contrast, corals exposed to 25 psu and ambient salinity (35 psu) had 62% and 92% of their surface cleared respectively. S. radians colonies exposed to 25 and 45 psu recovered the ability to clear sediments efficiently (i.e., no significant differences between exposed and control corals) after 24 h of recovery, but it took considerably longer (5 d) for those colonies previously exposed to 20 psu to clear sediments as fast as control corals.

4. Discussion

Siderastrea radians displayed remarkable patterns of resistance and resilience to the stressors tested in this study and tissue mortality was documented only under prolonged (≥48 h) continuous exposure to salinity extremes (15 and 45 psu) and chronic sediment burial. Acute and shorter-term exposures resulted in only a transient depression of photosynthetic rates. The response of S. radians to increasing levels of disturbance followed a progression that included: (1) polyp retraction; (2) reduced photosynthesis and either increased or decreased respiration; (3) tissue paling; (4) bleaching; (5) reduction in growth rates; and finally (6) tissue mortality. Polyp retraction as an immediate reaction to stress decreases the surface area of the tissue in contact with the surrounding environment was also observed for S. siderea (Muthiga and Szmant, 1987), Porites astreoides (Lirman, 2001), P. furcata (Manzello and Lirman, 2003) and numerous other species of Caribbean (Bak and Elgershuzien, 1976) and Australian (Stafford-Smith and Ormond, 1992) corals. Changes in coloration (i.e., paling) are also commonly reported as a signal of stress for corals subject to salinity, sedimentation, and other stressors, and the progression from polyp retraction to paling to bleaching under extended or more severe stress has been previously reported by Coles and Jokiel (1992), Stafford-Smith (1993), and Wessling et al. (1999). Philipp and Fabricius (2003) concluded that the change in coloration of corals exposed to sediments was likely due to the expulsion of zooxanthellae from the host tissue, a response that was also documented for corals under hypo-osmotic stress by Kerswell and Jones (2003).

4.1. Salinity Stress

The sudden exposure to sub-optimal salinity levels caused a consistent decrease in photosynthetic rates of S. radians. In contrast, the response of respiration rates to changes in salinity was highly
variable as described by Vernberg and Vernberg (1972) for both marine and estuarine species. The decrease in photosynthesis relative to controls for corals exposed to salinity extremes was linearly related to exposure time, but negative impacts on coral photosynthetic rates were more severe under low salinity (15 psu) than under high salinity (45 psu). In contrast, photosynthetic recovery took longer for corals exposed to higher salinity.

A reduction in photosynthesis is the most commonly documented effect of salinity stress on corals (reviewed by Coles and Jokiel, 1992) and the decrease is often directly proportional to the magnitude or duration of the salinity change (Muthiga and Szmant, 1987). However, the impacts of salinity stress appear to be highly species-specific. In Florida, patterns of high tolerance to sub-optimal salinity were recorded for S. siderea and Porites furcata, which were able to withstand sudden and extended changes in salinity without lethal impacts (Muthiga and Szmant, 1987; Manzello and Lirman, 2003). The reef-building coral Montastraea annularis was able to sustain autotrophy and showed no tissue mortality after exposure to 40 psu for 36 h (Porter et al., 1999), but P. porites showed high mortality after 5 d of exposure to 15 and 45 psu (Marcus and Thouraug, 1981). For S. radians, P/R ratios were maintained >1 under most experimentally stressful conditions and full photosynthetic recovery was documented for all but the most extreme salinity treatments, establishing the resilience of this species to salinity stress at both ends of the osmotic spectrum encountered in Biscayne Bay.

Little information is presently available on the osmoregulatory mechanisms of corals exposed to salinity stress. Nevertheless, previous studies have shown that a limited number of euryhaline coral species are in fact able to withstand and quickly recover from osmotic stress (Coles and Jokiel, 1982). In the present study, corals exposed to intermediate, low-salinity levels (25 psu), exhibited initial sharp declines in photosynthesis that were followed by temporary increases that may represent transient acclimatization patterns. This pattern was also observed by Manzello and Lirman (2003) for P. furcata, suggesting that corals commonly exposed to rapid environmental fluctuations may exhibit a limited capacity for osmoregulation (Mayfield and Gates, 2007). The mechanisms involved in the response of corals to osmotic stress, which clearly warrant further examination, may include behavioral responses such as polyplyp retraction to limit water and gas exchange with the external medium and physiological responses through the production of organic osmolytes to protect cell volume regulation (Mayfield and Gates, 2007). While it is not yet known what mechanisms specifically confer S. radians its high levels of resilience and resistance to stress, it is clear that a further understanding of how unusually hardy coral species can thrive in marginal environments will provide important insights into the future ability of corals to persist through large-scale habitat modifications and climate change.

4.2. Sediment Burial

The impacts of sediment burial on S. radians were influenced by the duration of the burial period and ranged from a temporary reduction in photosynthesis to significant reductions in growth and tissue mortality. The maintenance of P/R ratios >1 and the rapid (i.e., ∼24 h) recovery of photosynthetic rates after burial periods of 2–24 h indicates that S. radians is able to resist short-term burial periods with minor physiological consequences. However, as burial periods increase and colonies become covered at multiple chronic intervals, the impacts of sediment burial can become significant, resulting in extended photosynthetic recovery periods (7 d for a 48 h burial), reduced growth, and, ultimately, colony mortality.

Sedimentation is regarded as an increasing threat to coral reefs (reviewed by Fabricius, 2005). The impacts associated with sedimentation and sediment burial include reduced photosynthesis and increased respiration (Rieg and Branch, 1995; Philipp and Fabricius, 2003; Weber et al., 2006), tissue mortality (Rogers, 1983, 1990), reduced growth (Dodge et al., 1974; Rice and Hunter, 1992), and reduced fertilization, larval survivorship, and recruitment (Gilmour, 1999; Babcock and Smith, 2000). Previous research has identified the genus Siderastrea as a competent sediment remover (Hubbard and Pocock, 1972) and the tolerance of S. radians species to burial has been highlighted in the pioneer work by Mayer (1918) who reported that this species was only “half killed” after being covered by sediments for >73 h.

Under normal conditions (i.e., no salinity stress), S. radians was very effective at clearing sediments, and >50% of the colonies’ surface area was cleared within 1 h after burial. Rapid initial sediment clearing, followed by a slower response has been documented for numerous other corals species by Lasker (1980), Stafford-Smith (1993), and Rieg (1995). The clearing response of buried corals is potentially influenced by both active behavioral factors (e.g., tissue swelling, mucus production, tentacular and ciliary action) and factors influenced by colony shape (Hubbard and Pocock, 1972; Stafford-Smith and Ormond, 1992). In this study, we showed that both active and passive factors play a role in the clearing response of S. radians as only live colonies cleared sediments and hemispherical colonies cleared sediments faster than flatter colonies.

4.3. Sequential Stressors

S. radians was shown to be well-suited to resist and recover from single stressors. However, the sequential exposure of colonies to salinity and sediment burial highlighted the interactive negative influence of multiple stressors. The clearing rates of S. radians were influenced by the physiological status of colonies and prior exposure to sub-optimal salinity significantly reduced the clearing rates of stressed colonies that were unable to clear sediments efficiently. The energetic costs of sediment clearing can be considerable (Rieg and Branch, 1995), and the inability to clear sediments exposes corals to further stress as anoxic conditions under sediments can cause tissue bleaching and subsequent mortality (Weber et al., 2006). Thus, even highly resistant and resilient corals like S. radians can become susceptible to sequential stressors that would not normally cause long-term impacts when encountered individually. The impacts of sequential stressors and the effects of impaired physiological status on stress resistance and resilience are topics of renewed scientific and management interest as the frequency and intensity of both human and natural stressors increase over time. Some examples of the interactive effects of stressors include the higher susceptibility to elevated temperature of corals exposed to low salinity (Coles and Jokiel, 1978), the higher levels of bleaching in areas with high sedimentation (Nemeth and Sladek-Nowlis, 2001), and the increased prevalence of coral diseases in corals previously weakened by elevated temperatures and bleaching (Bruno et al., 2007; Whelan et al., 2007; Wilkinson and Souter, 2008).

The ecological niche of coral species is defined partly by patterns of resistance and resilience to stress. For example, the high resistance and resilience of S. radians to different coral stressors allows this species to thrive in habitats that commonly limit the diversity, abundance, growth, survivorship, and spatial distribution of more susceptible corals. The drastic decline in coral abundance reported for the Caribbean region over the past several decades (Gardner et al., 2003) has been characterized by the high mortality of the main reef-building coral genera like Acropora and Montastraea. In Florida, the high susceptibility of these taxa to hurricanes, diseases, and changes in water quality has resulted in significant declines in the condition and abundance of these keystone members of the reef community (Dustan et al., 1999; Miller et al., 2002; Palandro et al., 2003). Moreover, the lack of recruitment success of these genera raises concern about their long-term recovery potential. In contrast, more stress-tolerant taxa like Siderastrea and Porites continue to be both dominant components and successful recruiters on Florida reefs (Miller et al., 2002; Tougas and Porter, 2002; Lirman and Fong, 2007). These patterns may set up the stage for the relative increase of tolerant taxa and even the replacement of susceptible taxa by stress-tolerant species. Such scenarios have been predicted and documented by Aronson and Precht (2001), Aronson et al.


