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ORIGINAL PAPER

Ecological and biogeographic implications of *Siderastrea* symbiotic relationship with *Symbiodinium* sp. C46 in Sal Island (Cape Verde, East Atlantic Ocean)

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Abstract The relative abundance of the genus *Siderastrea* and its relationship with temperature and irradiance was assessed around Sal Island (Cape Verde). In some of the surveyed sites, these corals accounted for 80–90 % of the living cover, making it a biotope-dominant organism. Unlike *Siderastrea* corals from West Atlantic and Caribbean locations, genetic analyses of the dinoflagellate symbiotic partner revealed high specificity between *Siderastrea* sp. in Cape Verde and the *Symbiodinium* type C46. Biotope restriction of the ecological success of *Siderastrea* in Cape Verde may be explained in part by this host–symbiont partnership, resulting locally in a small optimum ecological niche with specific light intensity regimes. Distinctively, West Atlantic and Caribbean *Siderastrea* associates with a much broader range of *Symbiodinium* diversity, suggesting that these symbioses exhibit some flexibility under differing environmental conditions where these corals occupy a wider range of ecological niches. Geographic isolation and/or long-standing environmental conditions are probably responsible for such adaptions and coral–dinoflagellate symbioses. Additional genetic analyses on Clade C *Symbiodinium* associated with *Siderastrea* were conducted with the hyper-variable plastid

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psbA minicircle to resolve phylogeographic patterns that indicate the relative connectivity and/or isolation of these symbionts throughout the tropical Atlantic.

Keywords Coral reef · Siderastrea · Symbiodinium · Diversity · Biogeography · Endosymbiosis

Introduction

Reef-building photosymbiotic scleractinians rely on endosymbiotic dinoflagellates (genus *Symbiodinium*) to meet their energy requirements and to enhance calcification rates and skeletal growth (Hallock 1981; Muscatine et al. 1981; Muller-Parker and D'Elia 1997; Hoegh-Guldberg 2004; Stanley 2006). The successful construction of massive coral reef structures greatly depends on rapid calcification (Veron and Stafford-Smith 2000) in corals, which is attributed to the photosynthesis of the endosymbiont partner (Pearse and Muscatine 1971; Muscatine et al. 1981; Stanley 2006; Colombo-Pallotta et al. 2010).

Advances in molecular tools and techniques and the generalization of the use of genetic markers have revealed that the genus *Symbiodinium* is much more diverse than early researchers had ascertained using morphology. The lack of diagnostic morphological traits misled early studies to identify most symbiotic dinoflagellates as a single pandemic species, *Symbiodinium microadriaticum* Freudenthal, 1962 (Trench 1993; Stat et al. 2006), and still hampers species recognition and validation. An interim taxonomy of the groups based on genetic evidence uses alphanumeric designations to classify *Symbiodinium* into evolutionarily distinct, ecologically functional entities (LaJeunesse 2002; Pochon et al. 2004; Rodriguez-Lanetty et al. 2004; Sampayo et al. 2007, 2009; LaJeunesse et al. 2010). Grouped into distinct phylogenetic “clades” (e.g., A, B, C, etc.), nucleotide sequence phylogenies based on rDNA internal transcribed spacers 1 and 2, plastid genes, and microsatellite flanker regions identify numerous lineages well below the “clade” level, corresponding to operational taxonomic units (OTUs) (Sampayo et al. 2009), and exhibiting unique ecological and biogeographic distributions (Baillie et al. 2000; LaJeunesse 2002; Sampayo et al. 2007; LaJeunesse et al. 2010).

The study of these obligate symbioses over large geographic scales can provide important data regarding how isolation, environment, and host biology have influenced their coevolution (LaJeunesse 2005; Finney et al. 2010) and also reveal the variation and/or persistence of particular partner combinations from region to region. Such studies also provide insight into mechanisms underlying the hosts' resilience and ecological restrictions to their distribution and abundance. Furthermore, the study of coral–dinoflagellate associations and diversity are crucial to assess the possibility that partner recombination, involving changes in host–symbiont specificity, offer a mechanism for rapid physiological adjustment to changing environmental conditions (Baker et al. 2004; Berkelmans and van Oppen 2006).

Atlantic siderastreids (Siderastreidae: *Siderastrea*) can be major reef builders (Foster 1980; Oigman-Pszczol and Creed 2004; Castillo et al. 2011) and are the primary contributor to reef frameworks found in Cape Verde (Moses et al. 2003; Monteiro et al. 2009). They have proven to be remarkably resilient and resistant to a number of stress factors such as low salinity, sediment deposition, and burial (Lewis 1989; Lirman et al. 2002; Lirman and Manzello 2009).

Considering the importance of the coral–dinoflagellate associations, it is likely that the diversity of *Symbiodinium* associating with *Siderastrea* is, at least partially, responsible for their resilience and resistance to stressors. Atlantic *Siderastrea* species are known to associate with different *Symbiodinium* partners (LaJeunesse 2002; Thornhill et al. 2006a, b; Costa et al. 2008; Finney et al. 2010), which may be linked to their geographic distributions and ecological abundance.

This study investigates the diversity of *Symbiodinium* associating with *Siderastrea radians* (Pallas, 1766) in Cape Verde, the most abundant scleractinian coral in the archipelago, and explores the ecological and phylogeographic implications of such diversity. In Sal Island (Cape Verde), local environmental conditions such as depth, temperature, and light exposure were monitored to determine if local factors influence relative abundance and distribution of *S. radians* and/or *Symbiodinium sp.* diversity. Finally, the diversity from Cape Verde is compared to associations found in siderastreids from Brazil (new data) and from locations in the Caribbean (comprising published and unpublished data). Biogeographic patterns and *Symbiodinium* diversity associated with *Siderastrea* spp. is discussed from the perspective of environmental conditions, geographic distance, potential for dispersal, and host species identity.

Methods

Cape Verde study sites and environmental monitoring

Conducted between April and December 2009, fieldwork was restricted to Sal Island (Cape Verde), where well-established coral communities, over a rocky (basaltic) reef and sedimentary terraces (hereafter referred to as ‘bedrock’), had been previously reported (Laborel 1974; Morri and Bianchi 1995; Moses et al. 2003; Monteiro et al. 2009). In order to compare variability surrounding Sal, the island was divided into 10 sections by imposing a 7-km grid, and each section was assigned a code (Fig. 1). The two most northern sections (NW and NE) were not easily accessible and were not included in this study. At each remaining section, we have deployed

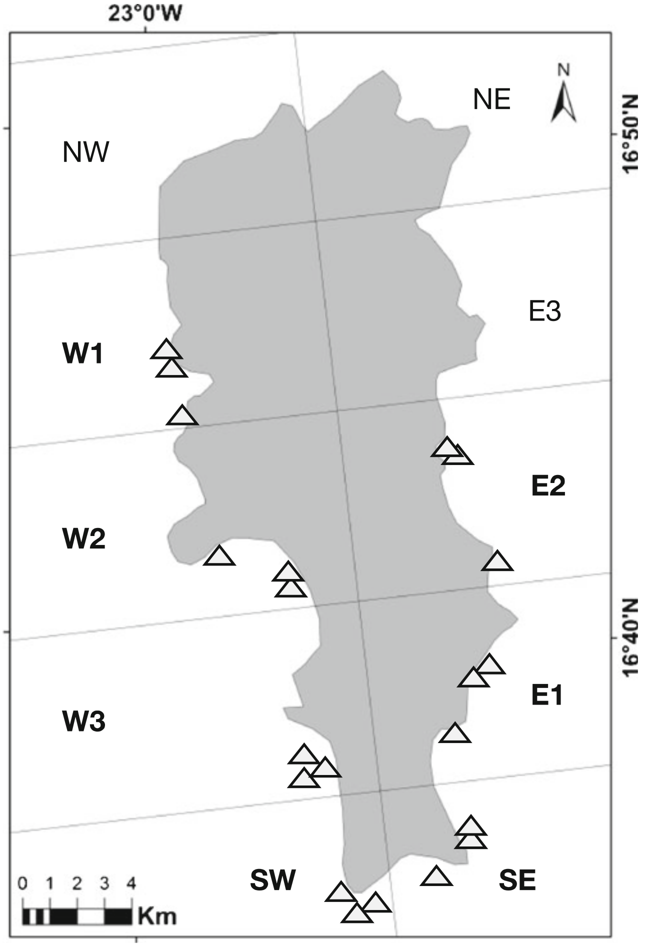

Fig. 1 Sal Island (Cape Verde) divided in 10 sections: monitoring survey sites (*triangles*) in sections where fieldwork was possible (sections W1, W2, W3, SW, SE, E1, and E2)

an Onset HOBO-Pendant® Temperature/Light Data Logger at 5–6 m and at 10–11 m depth, to collect information on temperature and light intensity every 15 min. Every 15–20 days, data were downloaded and loggers were cleaned to avoid fouling. One additional logger was set up inland for surface light intensity monitoring where no structures would shade it and influence its readings. Assuming light intensity values of the logger set at the surface as 100 % of light intensity reaching the surface, one can calculate the average percentage of light reaching the several logger sets. This "relative light intensity" excludes daily and seasonal fluctuations and allows a better comparison between sites. The logger set deployed at section E3 was lost, which, together with the lack of coral cover in initial surveys, led to the exclusion of this section from the study.

On a larger geographical scale, remote sensing data were used to assess and compare broad environmental conditions across several locations where *Siderastrea* corals occur. Sea surface temperature (SST) and aerosol mass concentration time series were generated in Giovanni, a web-based application developed and maintained by the NASA GES DISC, that provides a simple and intuitive way to visualize, analyze, and access vast amounts of Earth science remote sensing data. Monthly SST data (11 μm/day) and aerosol mass concentration ($\mu\text{g.cm}^{-2}$) between January 2001 and December 2009 was compiled for Cape Verde, south and north Brazil, and several other locations in the Greater Caribbean (where samples had been collected). For each location, compiled data was averaged by month and by year for comparison.

Siderastrea radians relative abundance assessment

Siderastrea radians relative abundance in Sal Island was assessed over hard nature, horizontal and near horizontal substratum, where reef-building corals occur, using photoquadrat surveys. Two depth categories were considered: 4–6 m and 10–12 m. In each of the seven remaining sections of the island (W1, W2, W3, SW, SE, E1, and E2), three randomly distributed survey dives were conducted for each depth category in locations where coral communities were present, making a total of 54 survey dives. Each survey had three sets of five photoquadrats taken (a total of 15 quadrats with >1 m^2 each), using an underwater photography system (Nikon D80 with 10–20 mm lens inside an Aquatica aluminum housing), assembled on a custom-made "quadpod" structure, to assure constant distance and angle at which the images were captured. All quadrats were randomly placed, following a random number table (adapted from Wallenstein et al. 2008) and depth-tagged. All images were white balance-adjusted and labeled according to their sampling station. Compiled photoquadrat imagery was analyzed with Coral Point Count with Excel extensions (CPCe) software (Kohler and Gill 2006) using a custom-made list of categories and subcategories. This list compiled observed taxa plus other, necessary, non-biological categories/subcategories, such as 'sand', 'pavement' and 'rubble'. Each photoquadrat was scaled (using the "quadpod" structure as reference) and had a total of 144 points overlaid in random-stratified manner—six random points over 24 (4 rows×6 columns) equal cells (20,5×20,5 cm), over an area of 101 cm^2. Taxa and other subcategories (e.g., sand, pavement) were assigned to each point over the CPCe interface. Random placements of points result in points overlaying the quadrat structure or shade areas where valid categorical taxon assignment was impossible. Non-valid categories were excluded from subsequent analysis. Live cover (%) and the relative abundance of *S. radians* (in relation to living coverage) was averaged and estimated for both depth categories in each section.

Symbiodinium diversity associating with *Siderastrea*

S. radians samples ($n=17$) were collected from eastern and western sites surrounding Sal Island (Cape Verde) in 2007 and 2009. Corals were identified in the field and pivot samples were collected to confirm taxonomic identification following Veron and Stafford-Smith (2002). In Brazil, *Siderastrea* samples (n=24) were collected in intertidal and subtidal zones ,by mask and snorkel and SCUBA in late November 2008, at several sites in the province of Paraíba (north) and in the province of Bahia (south). Brazilean siderastreids comprise *S. stellata* and *S. radians*, two closely related species, which can be morphologically very similar (Neves et al. 2008). Sampled corals were identified in the field and have been grouped under *Siderastrea* spp. (*radians/stellata*) due to their similarity and difficulty in making a reliable identification to species level.

Samples from small fragments of tissue from each individual were preserved in 20 % DMSO preservation buffer (Seutin et al. 1991) and stored at −20 °C (in Mueller Lab, Department of Biology, Pennsylvania State University, USA). Skeletal fragments (approximately 10–20 mm^2 tissue) were mechanically disrupted using a Biospec Beadbeater (Bartlesville, OK, USA) for 1 min at maximum speed. Nucleic acids were then extracted using a modified Wizard DNA extraction protocol developed by Promega (Madison, WI, USA); see LaJeunesse et al. (2003, 2010) for protocol details. The ITS2 region was analyzed by denaturing gradient gel electrophoresis (DGGE) fingerprinting as previously described (LaJeunesse 2002; Sampayo et al. 2009; LaJeunesse et al. 2010). Amplified ITS2 fragments were separated on a CBScientific DGGE system (Del Mar, CA, USA) using 8 % poly-acrylamide gels (40:1 acrylamide/bis) with an internal gradient 45–80 % (formamide and urea were used as denaturants). Gels were electrophoresed at 110 V for 15–16 h, stained for 20 min with 1× SYBR Green (Molecular Probes, Eugene, OR, USA) in 1× TAE running buffer, and photographed using a Fotodyne (Hartland, WI, USA) imaging system. For identification and/or identity confirmation of a symbiont type, diagnostic bands from denaturing gels were excised, eluted, re-amplified using the non-GC reverse primer, and directly sequenced as described in LaJeunesse (2002). Chromatograms were visually inspected for accuracy in base calling (Sequence Navigator) and edited sequences aligned by eye. *Symbiodinium* ITS2 diversity associating with *Siderastrea* from Cape Verde and Brazil was compared with that found in other locations (described in LaJeunesse 2002; Thornhill et al. 2006a; Warner et al. 2006; Finney et al. 2010).

Fine-scale differences among *Symbiodinium* diversity associating with *Sideastrea* was assessed using sequences of the non-coding region of the psbA minicircle (*psbA*$^{\mathrm{ncr}}$), following the protocol and primers specified by Moore et al. (2003), and included archived samples from various hosts and regions in the Caribbean including Carry Bow Cay, Belize; Lee Stocking and Abaco, Bahamas; St Croix; Barbados, Curacao, and the Flower Garden Banks in the Gulf of Mexico (LaJeunesse 2002; Thornhill et al. 2006a, b; Finney et al. 2010; unpublished collections). All samples were sequenced using Big Dye 3.1 reagents (Applied Biosystems, USA) at the DNA Core Facility (Pennsylvania State University). Chromatograms were visually inspected for accuracy in base calling (Sequence Navigator) and the edited sequences aligned by eye.

Phylogenetic reconstructions using PAUP (v.4.0b10; Swofford 2000) under the criterion of Maximum Parsimony (MP) and Distance under default settings were generated using *psbA*$^{\mathrm{ncr}}$ partial sequences. Insertions and deletions (indels) were analyzed as a 5th character state. All bootstrap values testing the statistical support of internal branches were calculated based on 1,000 replicates.

Results

Local environmental conditions

Local monitoring of temperature and light intensity was only possible in 7 of the 10 sections of Sal Island. Data loggers were unable to be deployed on the NE section, they were unable to be recovered on the NW section, and they disappeared from section E3. Light intensity (lux) and temperature (°C) data from the remaining sites were collected for 21 weeks, from July to December 2009. Light intensity for the daily period between 1030 and 1530 hours, excluding the night period and periods of low-angled light incidence, was compiled for each depth category at each section and averaged over each month (July–December). Temperature data were compiled and monthly averaged for each section for the full 21 weeks period (Fig. 2).

Comparison of monthly average light intensity between sections does not reveal a clear and obvious pattern or gradient in relation to N–S or E–W (Fig. 2). However, relative light intensity values suggest higher intensities on west sections (Fig. 2), and average light intensity of all west sections (over the 21 weeks) is slightly higher than that of the east sections (data not shown).

Water temperature data, collected over the 21-week period, revealed no major differences between depth categories, with differences between depth categories only ranging between 0.0 and 0.2 °C. Average, maximum, and minimum temperature data reveals northern sections of the island have slightly lower temperatures than southern sections (Fig. 2)

Environmental conditions: comparing geographic regions

Environmental conditions were not monitored across locations, allowing a broad geographical assessment. A comparison of different conditions over different geographic locations relied on remote sensing data. Compiled Sea Surface Temperature and Aerosol Mass Concentration time series from the "Giovanni online data system" (Acker and Leptoukh 2007), were averaged (yearly and monthly) for Cape Verde, Brazil (north and south) and several locations in the Greater Caribbean

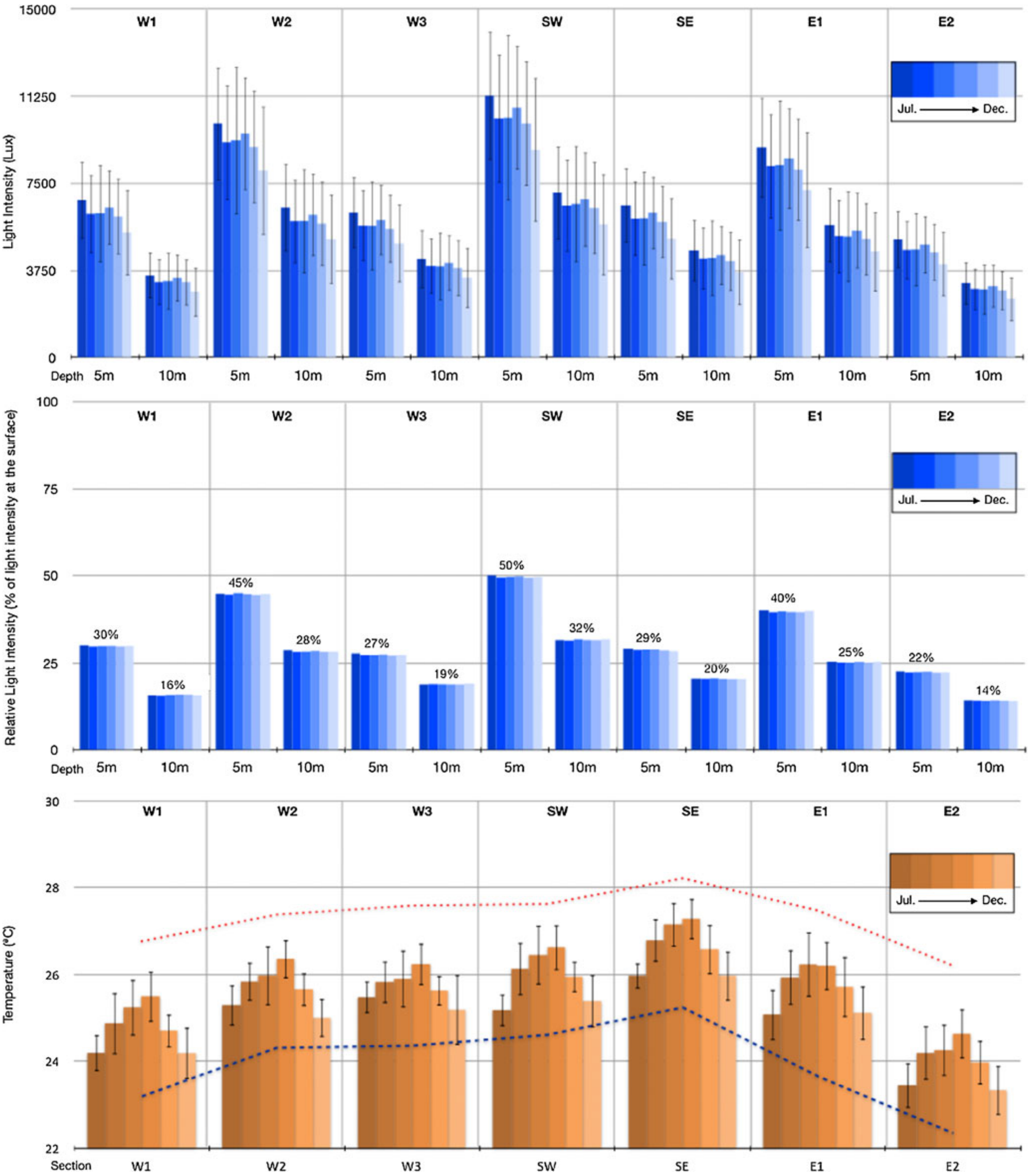

Fig. 2 Monthly average of light intensity (*top*), relative light intensity (*middle*) and water temperature (*bottom*) for the period July–December in sections W1, W2, W3, SW, SE, E1 and E2 of Sal Island. *Top* monthly average light intensity (lux) and standard deviation at depths of 5 and 10 m. *Middle* relative light intensity (5 and 10 m), percentage of light intensity at the surface. *Bottom* monthly average water temperature (°C) and standard deviation (*columns*), and maximum (-- *red line*) and minimum (-- *blue line*) temperatures (averaged)

region (Fig. 3). Yearly averaged SST in Cape Verde is 1–3 °C lower than other locations; however, minimum average temperatures (February–March) are above minimum average temperatures from Florida Banks. Aerosol mass concentration (the total aerosols mass in a vertical column of atmosphere) has a proxy indicator for light intensity attenuation, assuming the

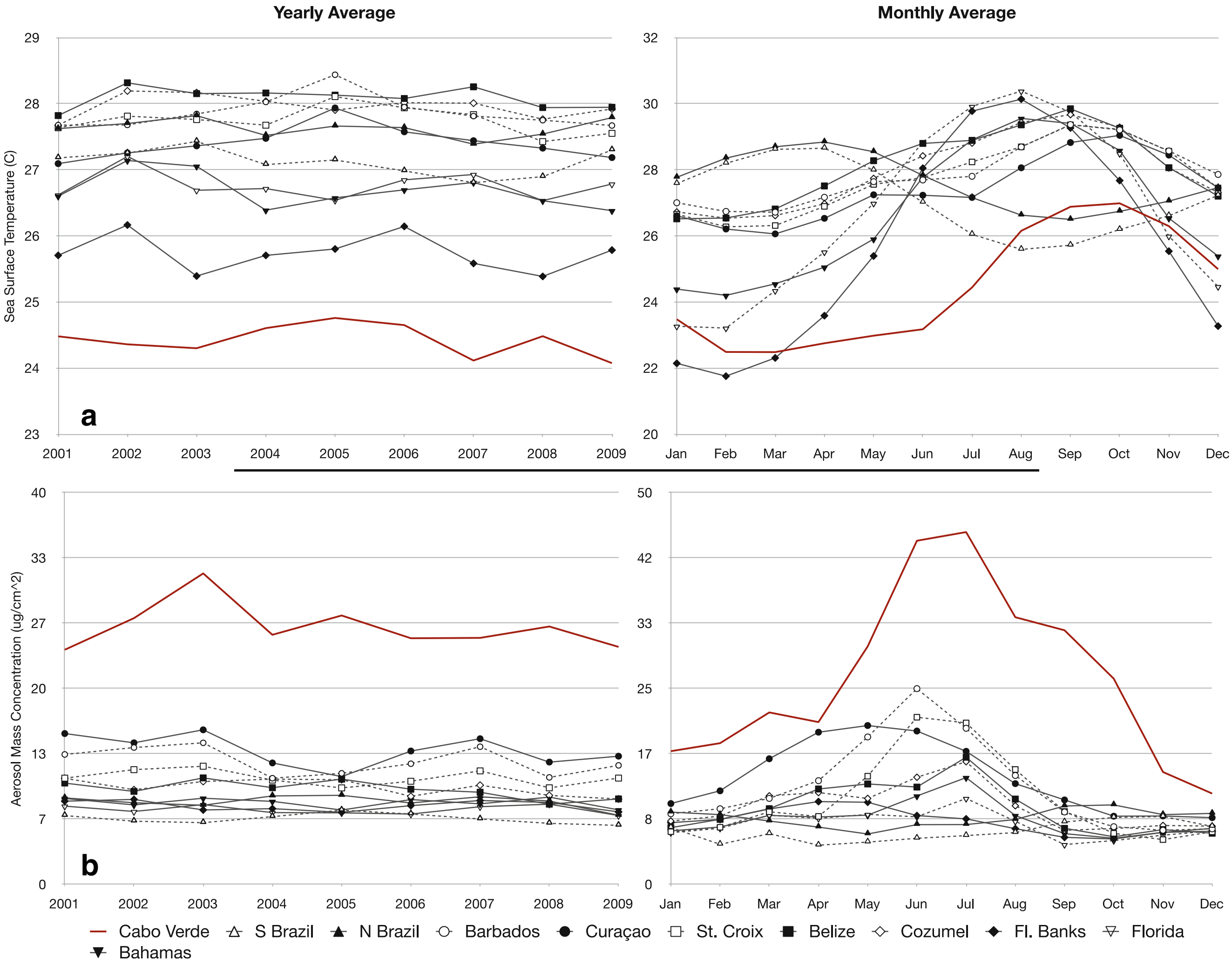

Fig. 3 Sea surface temperature: 11 µm day (**a**) and aerosol mass concentrations (**b**) regimes in Cape Verde (*red lines*) and other locations (*black lines*). Yearly and monthly averages (*left* and *right*, respectively) compiled from MTMOSST.001 using the Giovanni online data system (Acker and Leptoukh 2007)

effect of aerosols in dispersing and scattering light (in air) and the increase of water turbidity from aerosol fallout (Bohren and Huffmann 1983; Li et al. 1996). Peaking between July and August, Cape Verde yearly and monthly average values are consistently higher than other locations, probably due to its proximity to the Sahara desert and its seasonal dust plumes (Garrison et al. 2003).

Siderastrea radians relative abundance in Sal Is. (Cape Verde)

Photoquadrat surveys and imagery analysis results reveal different coral live coverage and *S. radians* relative abundances across the sections of Sal Island (Figs. 1, 4), with lower values in the eastern shoreline (windward). *Siderastrea radians* abundance in relation to the total coral live cover (Fig. 4) varies between 23 and 91 %. In some sites, *S. radians* colonies form a pavement morphology (similar to the one described in Moses et al. 2003), and are the dominating organism. No further statistical analysis was performed, however, comparing *S. radians* relative abundance and its variation between depth categories reveals no clear patterns. In some sections, *S. radians* is higher at −10 m and in other sectionsat −5 m. Higher abundances were observed in sections/depths where the average light intensity (between 10:30 and 15:30 hours) was between 5,500 and 6,500 lx (Fig. 5).

Symbiodinium diversity associating with *Siderastrea*

All ITS2-DGGE fingerprints of *Siderastrea radians* samples collected in Cape Verde (n=17) had the same single prominent band, typical of an association with a single, dominant, *Symbiodinium* type. Unlike *Siderastrea* corals from Brazil and the Great Caribbean, which can associate with different types of *Symbodinium*, all samples from Cape Verde associated with a single type: *Symbiodinium* C46.

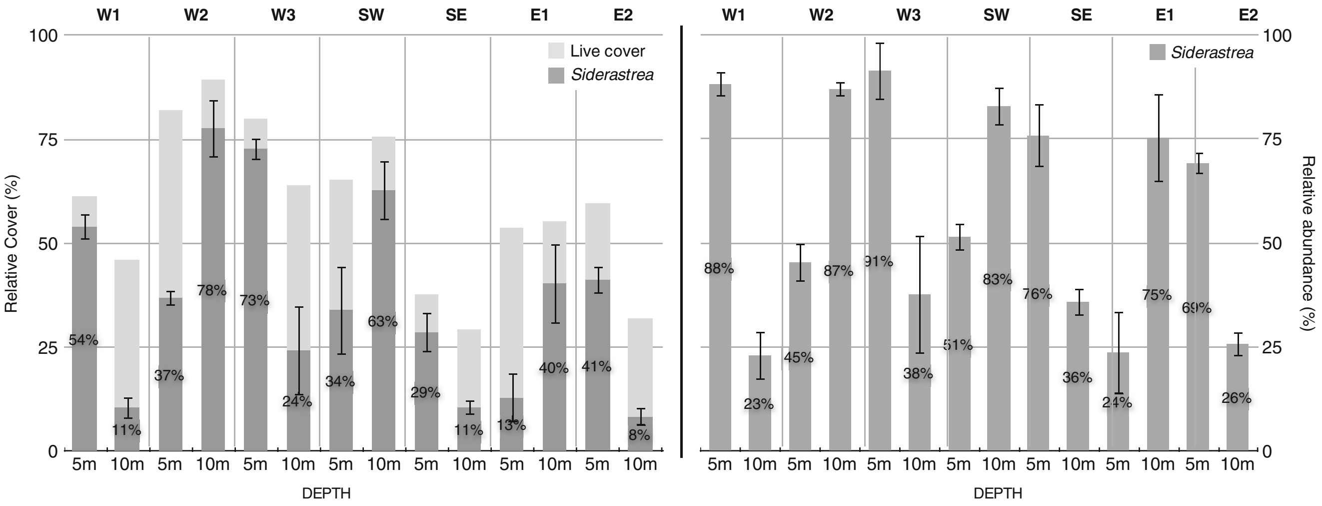

Fig. 4 *Siderastrea radians* and living cover (*left*) and S. radians relative abundance (*right*) at −5 and −10 m over horizontal and near horizontal hard substratum in sections W1, W2, W3, SW, SE, E1, and E2 of Sal Island. Values estimated from imagery using CPCe (Kohler and Gill 2006), from 3 sets of 5 photoquadrats (1 m^2 each)

In Brazil, *Siderastrea* samples were identified as *Siderastrea* sp. (*radians/stellata*). Sampled colonies associated with *Symbiodinium* B5, C3, C3+B5, C46, C46+B5 and C1 (the former only found in samples collected in tidal pools). There were some differences in the diversity of *Symbiodinium* found in the two regions of Brazil. Except for those in intertidal pools, *Siderastrea* colonies sampled in south Brazil associated with *Symbiodinium* C46. In Paraíba (north), colonies could also associate with C3, B5, and some of sampled colonies co-hosted different *Symbiodinium* types: C3+B5 and C46+B5. Such results reveals that: (1) C46 occurs in both East and West side of the Atlantic, and (2) that it can be found in *Siderastrea* corals co-hosting multiple symbiont types or as a single dominant type.

Previous studies (described in LaJeunesse 2002; Thornhill et al. 2006a; Warner et al. 2006; Finney et al. 2010) in several locations in the Caribbean also report associations of *S. radians* with C1, C3, C46, B5, and D1a. In fact, the analysis of the symbiosis displayed by *S. radians* in the Atlantic shows a complex "mosaic" of associations with different symbiont types (Fig. 6).

Phylogenetic analyses

Because of its high mutational rate, the phylogeny based on the non-coding region of the psbA minicircle ($psbA^{\text{ncr}}$) allows the exploration of the relationships of closely related species (Barbrook et al. 2006; LaJeunesse and Thornhill 2011). The *psbA* non-coding region sequences for type *C46* (from Cape Verde and Brazil) and for type *C3* (from Brazil and the Greater Caribbean) each form divergent monophyletic lineages (Fig. 7). The *Symbiodinium C46* lineage comprises *psbA* haplotypes whose phylogenetic relationships suggest that populations in Brazil and Cape Verde may be intermixed, whereas *C3* lineage exhibits substantial sequence divergence between Brazil and the Greater Caribbean locations (Fig. 6). Sequences of *Symbiodinium* samples from Cape Verde (C46) could not be aligned with sequences from other clades (A, B, and D) or with C1 sequences from *Siderastrea* hosts of other geographic locations, suggesting they have diverged to such an extent that, to study this relationship, a more conservative region of the genome should be explored.

Discussion

Atlantic siderastreids (*S. radians, S. siderea*, and *S. stellata*) associate with different *Symbiodinium* types depending on

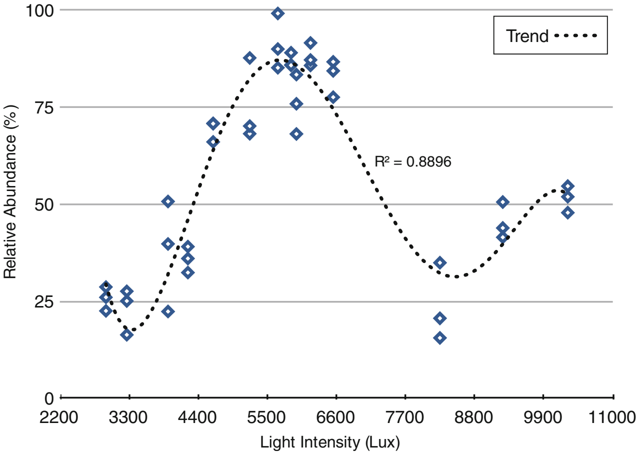

Fig. 5 Average light intensity versus *Siderastrea radians* relative abundance: average light intensity values estimated from 1030–1530 hours readings for the period July–December; relative abundance and *quintic* polynomial trendline estimated from photoquadrats at each dive survey site (see above for description)

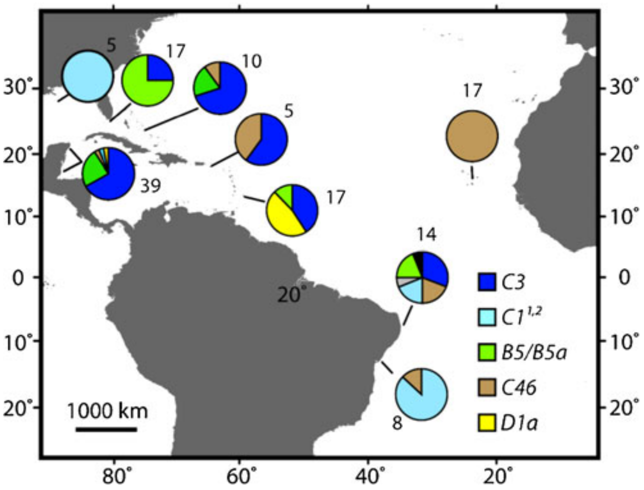

Fig. 6 Geographic patterns of *Symbiodinium* types associated with the genus *Siderastrea* in regions throughout the Atlantic. The numbers of colonies sampled in each location are listed next to each pie graph. Some *Siderastrea* colonies in Brazil hosted combinations of *Symbiodinium* types (C3+B5 in *black* and B5+C46 in *gray*) The existence of a particular type may also depend on depth. For example, B5/B5a occur only in shallow water colonies (1–5 m)

geographic location and depth (Finney et al. 2010; this study). In Cape Verde, however, *S. radians* was found to associate only with *Symbiodinium* C46, a host specialist known to occur only with colonies from this genus (LaJeunesse 2005; Finney et al. 2010). The interplay of factors shaping these coral–algae associations is complex (Iglesias-Prieto et al. 2004; LaJeunesse et al. 2004a, 2010; Sampayo et al. 2007; Goulet et al. 2008), and the exclusive association of *S. radians* with *Symbiondinium* C46 may be influenced by environmental conditions, biogeographic barriers, host specificity, or some combination of these factors. Diversity and distribution patterns of *Symbiodinium* in Atlantic Siderastreids (this study; LaJeunesse 2002; Thornhill et al. 2006a; Warner et al. 2006; Finney et al. 2010) indicate that: (1) C46 occurs exclusively in *Siderastrea* colonies, in both the Eastern and Western Atlantic; (2) *Siderastrea* colonies from Western Atlantic locations can harbor several different *Symbiodinium* "types"; and (3) *Symbiodinium* C46 is the only species found in *Siderastrea* colonies from the Tropical Eastern Atlantic.

Niche restrictions

The success of *S. radians* in Cape Verde suggests that this slow-growing scleractinian coral is well adapted to the region's environmental conditions. Unlike what is usually observed in other geographic regions, *S. radians* in Cape Verde can have diameters >100 cm across, and in some locations they can form a pavement-like morphology and become a dominant organism (this study; Moses et al. 2003; Monteiro et al. 2009). However, data suggest that *S. radians* dominance in Sal Is. is site-restricted (Figs. 1, 4).

S. radians association with a single *Symbiodinium* type (Fig. 6) suggests that this host specialist is also well adapted to the region's environmental conditions, but the low diversity of *Symbiodinium* associating with *S. radians* in the region may be contributing to the restriction of the animal's realized niche. *Symbiodinium* can be differently adapted to various ranges of irradiance and temperature (Iglesias-Prieto and Trench 1994; Rowan et al. 1997; Iglesias-Prieto et al. 2004; LaJeunesse et al. 2004a; Thornhill et al. 2006b). In such cases, it is not only *Symbiodinium* types that can be better adapted to specific ranges, as they have different tolerances to changes in irradiance and temperature. Conclusions from previous studies (Iglesias-Prieto et al. 2004; LaJeunesse et al. 2004a; Warner et al. 2006; Bongaerts et al. 2010; Finney et al. 2010) have suggested that depth (and irradiance attenuation) influences the partitioning of compatible *Symbiodinium* to certain coral colonies. In Brazil and in the Caribbean (see above), differences in predominant assemblages suggest a relation between changes in *Symbiodinium* diversity associating with *Siderastrea* and the hosts' ability to thrive in different ecological niches. In contrast, the exclusive association between *Siderastrea* and *Symbiodinium* C46 in Cape Verde may limit the hosts' distribution to a narrow range of habitat. Variation in the relative abundance of *S. radians* around Sal Island (Cape Verde) appears to be influenced by irradiance (Figs. 4, 5), decreasing where average light intensity is lower or higher than an optimum range. Harboring a single predominant *Symbiodinium* type, this coral thrives at different depths, but preferably where average light intensity (between 1030 and 1530 hours, when the Sun is closer to its azimuth) is between 5,500 and 6,500 lx (Fig. 5). The preference of this coral host for locations with a specific range of light intensity suggests that *Symbiodinium* C46 may be better adapted to a specific light (intensity and/or quality) regime and may influence the hosts' local distribution and restrict the host's ecological niche. Furthermore, the exclusivity of this association in Cape Verde may constrain *S. radians* tolerance and resilience to changing environmental conditions. Corals with a higher diversity in *Symbiodnium* associations are expected to better withstand changing conditions, as symbionts differ in their tolerance thresholds (Fitt et al. 2001; Kemp et al. 2006; Goulet et al. 2008; Oliver and Palumbi 2010). Physiological experimentation is required to verify this hypothesis.

Phylogeographic patterns

The geographic and ecological distributions of *Symbiodinium* are sometimes complex, because they are affected by local and regional environmental factors and by their dispersal capability (as "free-living" cells or with the host, either carried by rafting colonies or by the brooded larvae released to the water column). Sea surface temperature and aerosol mass concentration in the Cape Verde geographic region are consistently different than other locations where *S. radians* associates with other symbionts (Fig. 3). Lower average water temperatures could be one of the factors contributing to the exclusion of other *Symbiodinium* associations with *S. radians* in Cape Verde. However, despite the overall lower temperature, SST monthly averages (Fig. 3a) reveal a reasonably low seasonal temperature fluctuation and within the range of variation of other locations. Average photosynthetically active radiation, the amount of light available for photosynthesis (data not shown), is not significantly different between locations (Acker and Leptoukh 2007); however, aerosol mass concentration is considerably higher in Cape Verde (Fig. 3b). This high concentration of aerosols in the region is a reflection of its proximity to the African continent. Seasonal dust plumes rise from the Sahara desert (Shinn et al. 2000; Garrison et al. 2003; Gill et al. 2006) and are pushed west by prevailing and harmatan winds (Braby 1913; Wilke et al. 1984; Griffin et al. 2001; Zazo et al. 2007). Dust and aerosols fall out across the Atlantic influencing light reaching the surface and increasing water turbidity (Braby 1913; Bohren and Huffmann 1983). The prevailing longitudinal gradient in aerosol mass concentration is an indicator of different light regimes that can be contributing to the shaping of coral–symbiont associations.

Geographic isolations may explain in part the absence of other *Symbiodinium* types or species (ITS2) associated with *S. radians* from Cape Verde. Unlike fishes with amphi-Atlantic distribution (Floeter et al. 2007; Monteiro et al. 2008; Rocha et al. 2008), coral larvae and “free-living” cells are dispersed passively, which limits their ability to disperse across the mid-Atlantic Barrier. The geographic distance separating regions and local currents, such as the Amazonas outflow, act as barriers to reef-coral dispersal and gene flow. Indeed, populations of *Siderastrea sideraea* and *S. radians* show some genetic partitioning between the Caribbean, Brazil, and Africa (Nunes et al. 2011). However, the presence of *Symbiodinium* C46 in coral hosts from Cape Verde, Brazil, and Caribbean locations indicates that there is some connectivity between these major Atlantic provinces.

Previous studies (Baillie et al. 2000; LaJeunesse et al. 2004a, b, 2010) have suggested that certain host–generalist and host–specialist symbionts may disperse long distances and across inhospitable environments while others are unable to do so. The absence of strong phylogeographic differentiation in the $psbA^{\text{ncr}}$ phylogeny among haplotypes of *Symbiodinium* C46 (Fig. 7) between Cape Verde and Brazil suggests occasional long-distance dispersal events. The non-coding region of psbA minicircle exhibits greater sequence divergence and considerably less overlap between intragenomic, inter-individual, and inter-specific variation found in ITS sequence data (LaJeunesse and Thornhill 2011). The significant sequence divergence between *C3* and *C46* associating with siderastreids (Fig. 7) clearly distinguishes these as independently evolving lineages (Avise

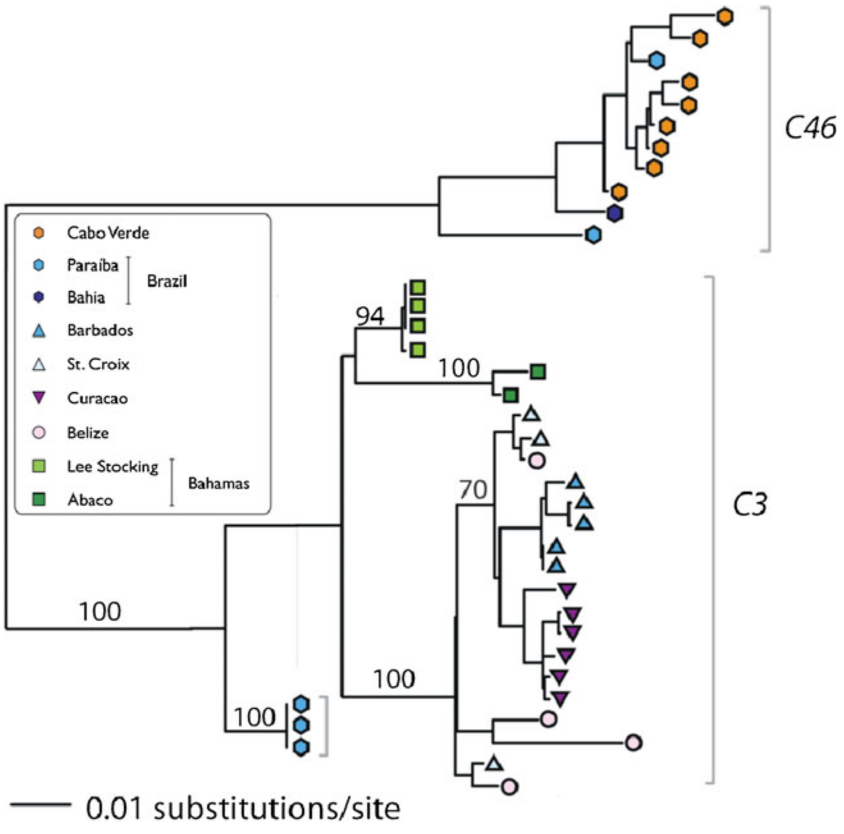

Fig. 7 Neighbor-joining tree using maximum parsimony inference of *Symbiodinium* C3 and C46 associated with *Siderastrea* from locations in the Atlantic based on partial sequences (~450–550 bases) of the $psbA^{ncr}$. *Symbiodinium* C3 comprises several geographically distinct lineages and indicates divergence between Brazil and the Caribbean. C46 from Cape Verde and Brazil comprise an independently evolved lineage specific to *Siderastrea stellata/radians*. Bootstrap values (>70), based on 1,000 replicates, are labeled above each branch

and Wollenberg 1997), despite the sequence similarity in ITS rDNA (LaJeunesse 2001; LaJeunesse et al. 2004a; Sampayo et al. 2009; Finney et al. 2010). Phylogenetic analysis of the non-coding *psbA* minicircle (Fig.7) indicates that *Symbiodinium C3* found in *Siderastrea* comprises cryptic lineages, not resolved by ITS sequence data, that exist in Brazil and various locations within the Caribbean. Geographic separation has clearly influenced the genetic make-up and *psbA* haplotype coalescence between C3 populations. In contrast, the *psbA* haplotypes of *Symbiodinium C46* from the Cape Verde and Brazil cluster together suggesting periodic mixing between populations of this symbiont from each region. In the light of laboratory experiments (Neves et al. 2008), in which *Siderastrea radians* planulae remained competent for only 24–48 h, it is unlikely that *S. radians* planulae would survive the journey across the Atlantic. Similarly, “free-living” cells of endosymbiotic *Symbiodinium* types are mainly benthic and usually absent from the water column or in very low densities (Littman et al. 2008; Pochon et al. 2010). Hoeksema et al. (2012) indicate that brooding corals can survive for periods that are long enough to enable trans-Atlantic dispersal through rafting (attached to drifting objects). The possibility that *S. radians* disperses by rafting remains speculative, but may explain in part its genetic similarity across the Atlantic (Nunes et al. 2011) and the broad distribution of *Symbiodinium* C46.

Summary

Cape Verde has a single *Siderastrea* species, which seems to associate with a single species of *Symbiodinium*. Besides very high relative abundance, *S. radians* colonies can reach sizes of over 100 cm across and dominate an entire area (Moses et al. 2003; Monteiro et al. 2009), in comparison with the 30 cm across seen in the Caribbean and Brazil (Veron and Stafford-Smith 2000). The local success of this coral suggests that this coral–dinoflagellate combination is well adapted to the environmental conditions in the region. In Sal Island, the distribution of *S. radians* is restricted by light intensity and possibly temperature.

The phylogenetic resolution provided by the psbA non-coding region enhances our understanding and appreciation of the ecological and geographic partitioning and suggests that *Symbiodinium* C46 undergoes periodic or sporadic exchange between Cape Verde and Brazil (Moore et al. 2003). These different patterns suggest that dispersal and/or gene flow may be considerable for some *Symbiodinium* types and therefore may significantly influence the ecology and evolution of particular host–symbiont combinations including rates of response to changing environmental conditions

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