Papéis Avulsos de Zoologia
Museu de Zoologia da Universidade de São Paulo

Volume 54(16):199-208, 2014
www.mz.usp.br/publicacoes
www.revistas.usp.br/paz
www.scielo.br/paz
ISSN impresso: 0031-1049
ISSN *on-line:* 1807-0205

Morphological variation in the atlantic genus *Siderastrea* (Anthozoa, Scleractinia)

Natalia Menezes[1,3]
Elizabeth Neves[1]
Ruy K.P. Kikuchi[2]
Rodrigo Johnsson[1]

ABSTRACT

Siderastrea *is a small genus of scleractinian corals, composed by zooxanthellate massive colonial forms. Besides contributing to the consolidation of the reef structure, represent a group with significant resistance to environmental stress. Until the 70's, its taxonomy was a complicated task, limited by the difficulty in identifying morphotypes. More recently, interspecific boundaries were redefined for 'Atlantic* Siderastrea *Complex'. However, despite new perspectives, including the occurrence of* S. radians *and* S. siderea *for Brazil, morphological patterns are still poorly studied and inconspicuous for several coastal areas. In order to characterize levels of intraspecific and interspecific morphological variation in* S. stellata *and* S. radians, *morphometric analysis were carried out in colonies from Bahia State coast. Samples were taken in Todos-os-Santos Bay and North Coast. We applied the Canonical Discriminate Analysis upon six corallite characters to evaluate the different levels of variation. The tests revealed that diameter of corallites, columella depth and number of septa varied among populations. Number of septa was the most important character for the species differentiation.* Siderastrea stellata, *with three different morphological patterns, was more variable than* S. radians.

Key-Words: Systematics; Modular organism; Morphotypes; Zooxanthellate coral; South Atlantic.

INTRODUCTION

Siderastrea is a small genus of scleractinian corals, composed by zooxanthellate, massive colonial forms. Besides contributing to consolidation of the reef structure, representes a group with wide environmental distribution and high resistance to environmental stress (Leão, 1986; Leão *et al.* 2003). In fact, it is commonly observed in the reef plateau where they usually occupy pools and semi-exposed areas (Laborel, 1967; Veron, 2000; Neves, 2004). Five species represents this group, of which, *Siderastrea savignyana*

---

[1] Universidade Estadual de Campinas, Instituto de Biologia, Departamento de Genética e Evolução, Laboratório de Diversidade Genética. Cidade Universitária Zeferino Vaz, Barão Geraldo, CEP 13083-970, Campinas, SP, Brasil.

[2] Universidade Federal da Bahia, Instituto de Geociências, Departamento de Oceanografia, Grupo de Pesquisa em Recifes de Corais e Mudanças Globais. Rua Barão de Jeremoabo, 147, Campus Ondina, CEP 40170-115, Salvador, BA, Brasil.

[3] E-mail of the corresponding author: menezes.natalia@gmail.com

http://dx.doi.org/10.1590/0031-1049.2014.54.16

Edwards & Haime, 1850 and *Siderastrea glynni* Budd & Gúzman, 1994 are restricted to the Indo-Pacific region (Laborel, 1969/70), and the other three occur abundantly in the Atlantic Ocean and represent the 'Atlantic *Siderastrea* Complex' (Veron, 1995). *Siderastrea stellata* Verril, 1868 is endemic to Brazilian coast (from Parcel do Manuel Luis to northern coast of Rio de Janeiro) (Leão, 1986; Amaral *et al.,* 2007). *Siderastrea radians* (Pallas, 1766) and *Siderastrea siderea* (Ellis & Sollander, 1789) are some of the most common corals in the Caribbean region (Neves, 2004) and, recently, they were also registered in Brazilian coast (Neves *et al.,* 2006, 2008, 2010; Menezes *et al.,* 2013).

According to Laborel (1974), given the notable variation and overlap of diagnostic characters, the taxonomy of *Siderastrea* is a complicated task, limited by difficulties in identifying morphotypes and in determining interspecific boundaries. Recent studies with a broad taxonomic approach have maintained the identity of these species based on the following main characteristics: *Siderastraea siderea* is an hermaphroditic spawning specie while *Siderastrea radians* and *Siderastrea stellata* are gonogoric brooder species (Szmant, 1986; Duerden, 1904; Neves & Silveira, 2003); *S. radians* and *S. stellata* from Brazil presented exclusive alleles for each specie in a population genetic studies (Neves *et al.,* 2008); divergence among the three species was revealed in a phylogenetic study based on ITS sequence (Forsman *et al.,* 2005); and morphological traits also indicate differences among species (Neves, 2004; Neves *et al.,* 2010). However, morphological variability is still an unexplored issue. Considering the presence of many quantitative characteristics in *Siderastrea* diagnosis and its overlap, identify morphotypes is an important task.

The morphological similarity between *S. stellata* and *S. radians,* in particular, are currently considered an important problem because of its occurrence in sympatry in Brazilian coast and the inability to *in situ* identification (Neves *et al.,* 2010). Werner (1996) synonymizes *S. stellata* and *S. radians* based on statistical analysis of morphology. Santos *et al.* (2004) also studied the Brazilian and Caribbean species and founded high morphological variability. However, both cited studies did not consider the occurrence of *S. radians* and *S. siderea* in Brazilian coast. Supposedly, the observed variability could be related to interference of other species on their morphometric results, as suggested by Neves *et al.* (2010).

According to Gattuso *et al.* (1991), the morphological variation in Scleractinia depends of the adaptation to environmental heterogeneity and the mechanisms of genetic control. The modular development of these individuals is one important task to consider in morphological analysis, however usually ignored (Hageman, 2003; Davidson *et al.,* 2004; Eble, 2005). Best *et al.* (1983) propose a new dimension to the analysis in Scleractinia taxonomy when suggest that in fossil record and current species, within a geographically limited area, the intraspecific variation can be 'intracolonial', 'intrapopulation' and 'interpopulation'. Menezes *et al.* (2013) observe that intracolonial variation is not an important problem to differentiate *S. stellata* from *S. radians.* In the present study, we focus on the others categories of morphological variation, describing the intraspecific and interspecific variation of *S. stellata* and *S. radians* in Brazilian reef systems.

MATERIALS AND METHODS

The study was carried out in two distinct geographical sections of Bahia State (Brazilian northeastern littoral): the Todos os Santos Bay (TSB) and the North Shore (NS). The TSB is the second largest coastal bay in Brazil with an area of approximately 1,200 km^2, comprising a total of 91 internal islands, with coral reefs and mangroves as typical ecosystems (Cirano & Lessa, 2007). Founded in 1999 by the State Government, the 'Todos os Santos Bay Environmental Protected Area' aims to manage social and economic activities around the coast region (800 km^2). Nevertheless, despite its ecological importance, the bay has been critically impacted due to coastal development activities (Celino & Queiroz, 2006; Amado-Filho *et al.,* 2008; Felizzola *et al.,* 2008). NS is characterized by discontinuous coral banks distributed in 17 km along the coast in very shallow waters (Kikuchi, 2000). The resources have also been explored and are under degradation caused by domestic and industrial sewage, oil pollution, urban development, and intensive tourism (Costa *et al.,* 2000; Leão & Kikuchi, 2005).

Sampling was conducted in nine localities from 2006 to 2008 (Table 1): five around the TSB and four along the NS. Due to similarities between *S. stellata* and *S. radians,* field identification was not performed. In practice, this procedure prevents taxonomical misidentification, but is not favorable to homogenize sampling of sympatric species. Detailed information concerning total number of specimens *per* locality (n), georeferenced coordinates (lat/long), and additional sampling information are listed in Table 1, Fig. 1.

TABLE 1: Detailed data of collecting sites within two major sections of the Bahia State (Brazilian northeastern coast): the Todos os Santos Bay (TSB), and the North Shore (BS). Lat/Long = georeferenced coordinates, VCN = Vouchers catalogue number of deposited at the Zoology Museum of Universidade Federal da Bahia, Sp(n) = number of specimens per locality (Ss = *S. stellata,* Sr = *S. radians*).

Section	Localities	VCN	Lat/Long	Sp(n)		Date	Substrate
TSB	Maria Guarda Island	UFBA584	12°43'S/38°38'W	Ss(15)	Sr(3)	20 Ago 05 28 Apr 06	Rock, mud
	Paramana beach	UFBA575-577	12°45'S/38°37'W	Ss(15)	Sr(12)	28 Apr 06	Rock, mud
	Boa Viagem beach	UFBA578, 579, 594, 595	12°56'S/38°30'W	Ss(20)	—	27 Apr 06	Rock, sand
	Bahia Yacht Club	UFBA580-582	12°59'S/38°31'W	Ss(17)	—	27 Apr 06	Rock, sand
	Porto da Barra beach	UFBA583	13°00'S/38°32'W	Ss(14)	—	24 Apr 06	Rock, sand
NS	Genipabu-Abaí reef	UFBA 518, 519, 521, 522, 524, 529-532, 541	12°40'S/38°05'W	Ss(15)	—	20 Mar 07	Coral Reef
	Guarajuba reef	UFBA536, 539, 562	12°38'S/38°03'W	Ss(12)	Sr(3)	23 Nov 06 19 Mar 07	Coral Reef
	Itacimirim reef	UFBA587, 632	12°36'S/38°02'W	Ss(13)	Sr(2)	12 Jan 08	Coral Reef
	Praia do Forte reef	UFBA508, 610, 612, 619, 632	12°34'S/37°59'W	Ss(11)	Sr(4)	19 Nov 05 04 Nov 06 12 Jan 08	Coral Reef

Samples with at most 10 cm were haphazardly collected at a minimum distance of two meters. This measure was adopted to avoid the removal of clones due to the typical phylopatric pattern of *S. stellata* and *S. radians* during larvae recruitment. Colonies with evidence of disease or physiological senescence (irregular pigmentation, blemishes, whitening) were not considered. Samples were obtained from tide puddles of 0-30 cm deep or by free or SCUBA diving during low tide (no deeper than 3 m). Colonies were removed using hammer and ferrule, and placed in plastic bags for transportation. For corallum and corallite structure analysis, the colonies were submitted to a 2,0% sodium hypochlorite solution. Identifications followed Neves (2004). Morphometric analyses were carried out with the use of ocular micrometric on NIKON SMZ1000 stereomicroscope and MITUTOYO 0,01-150 mm digital pachymeter. Specimens were deposited in the Cnidaria Collection at the Zoology Museum of Universidade Federal da Bahia (Table 1).

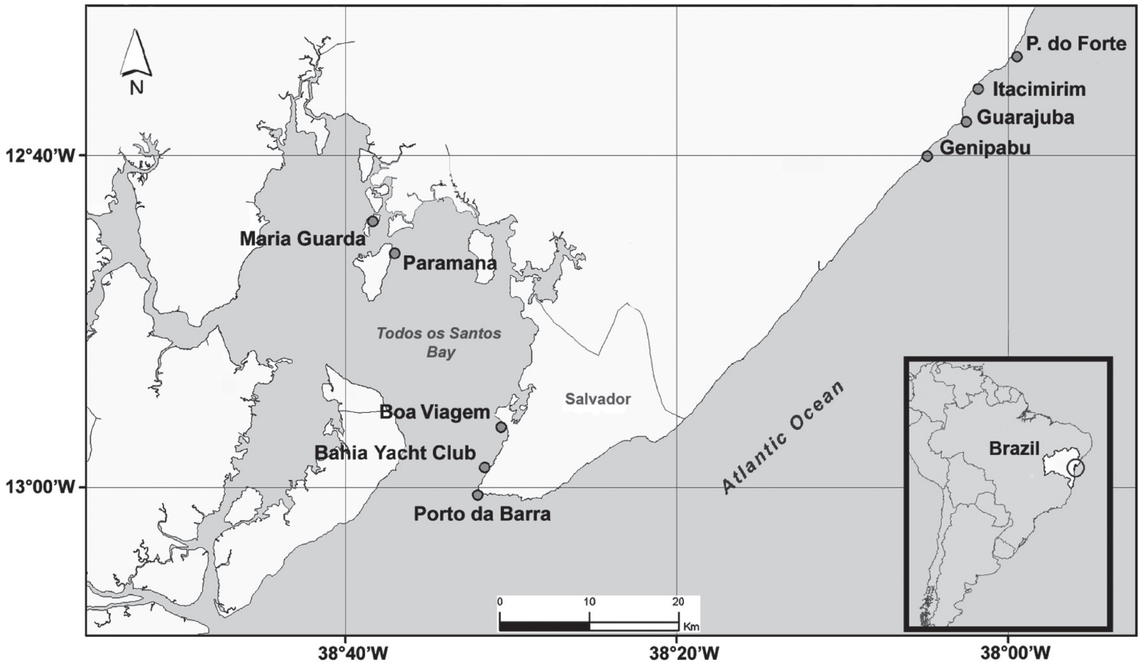

FIGURE 1: Map indicating study area and localities selected for sampling of *Siderastrea* colonies. Todos os Santos Bay (TSB) = Maria Guarda, Paramana Boa Viagem, Bahia Yacht Club and Porto da Barra; North Shore (NS) = Genipabu, Guarajuba, Itacimirim, and Praia do Forte.

Only mature corallites were examined ('old polyps' sensu Soong & Lang, 1992), *i.e.,* those with, at least, the third septal cycle well formed. Fifteen corallites for each colony were selected from three regions: top; middle; and edge. The top zone was defined as the upper surface of the colony distal from the base, a flattened or dome-like area 1 to 3 cm in diameter. The edge was defined as the marginal area in contact with the substratum, including three and/or four corallite upper lines (the first of which was frequently buried in the sand). The middle was defined as the large area between the inner limits of the two previous zones. For small colonies (aprox. 3 cm), were considered only 3 corallites in each region. Based on previously published studies (Milne Edwards & Haime, 1849; Verrill, 1868; Vaughan, 1919; Vaughan & Wells, 1943; Laborel, 1967, 1969/70; Budd & Gúzman, 1994; Neves, 2004; Foster, 1977, 1979, 1980, 1985; Budd, 1990), six morphological characters were selected: corallite diameter (based on the mean of two greater diameters – corD); collumela diameter (based on the mean of two greater diameters – colD); septal number (sepN); theca thickness (tecThick); columellar depth (depth); and the distance among corallites (corDist). Septal number is a count and not a measure variable as the other characteristics. However, this data shows assumptions postulated by the Central Limit Theorem, which include a large number of independent random variables with finite mean and variance, not Bimodal and Poisson distribution, and absence of zeros (Underwood, 1997). As such, we considered the septal number a continuous characteristic.

To evaluate morphological differences between species and among localities where colonies where sampled, we performed a Hierarchical Permanova Analysis based in a Euclidian distance matrix and 9999 permutations. It is a multivariate analysis that uses permutation to test differences among discrete groups. To identify the most important traits that determinate de morphological variation between species and among localities, and better understand *Siderastrea* morphotypes, we performed a Discriminant Canonical Analysis (DCA). It is a multivariate analysis that can be used to discriminate a set of independent variables that better describe *a priori* defined groups (Hair *et al.,* 2009; McCune & Grace, 2002). The relation of variables with canonical axis is represented on results by Pearson correlation analysis (Table 3). Significance adopted was 0,05, but it was changed to 0,025 by Bonferroni correction. Considering the absence of intracolonial influence in the variation of studied species (Menezes *et al.,* 2013), these analysis were based in the average corallites of each colony because of the difficulty in observe the great number of data on graph. Data were homocedastic, presented normal distribution and, consequently, were not transformed. Additionally, a descriptive analysis was carried out with mean, standard deviation and data amplitude. The programs used were Statistica 7 (StatSoft®), Primer 6 and Excel 2007 (Microsoft©).

RESULTS

The results of Hierarchical Permanova showed intraspecific and interspecific significant differences on morphology of *S. stellata* and *S. radians* (Sp: p = 0,0019; Lo(Sp): p = 0,0001) (Table 2).The Canonical Discriminate Analysis also allows discriminate distinct morphological patterns within and between species. The characteristics that show differences among groups were septal number (Wilks' Lambda = 0,160695, F (13, 137) = 21,15763, p < 0.0001), corallite diameter (Wilks' Lambda = 0,089802, F (13, 137) = 7,17432, p < 0.0001), and columellar depth (Wilks' Lambda = 0,081197, F (13, 137) = 5, 47718, p < 0.0001). Wilks' Lambda and F are components of DCA that indicate the ability of each variable in discriminate the *a priori* defined groups. The CV1 axis explained 50% of the variation founded, and was primarily related to septal number (R = 0,89), while the CV2 axis explained 32% of the variation and was mainly linked to corallites diameter (R = 0,72) and columellar depth (R = 0,70) (Fig. 2, Table 3).

From DCA graphic, it was possible to observe a wide variation within localities where each species were sampled. However, variation among localities was larger. The association of these results with descriptive data permits to infer the formation of different morphotypes for each species. *Siderastrea stellata* has basically three morphotypes: (1) corallites with small diameters (< 3.5 mm), reduced septal number (< 35), and shallow columellar depth (≤ 1.0 mm) – regular pattern of Paramana and Maria Guarda; (2) small corallites (< 3.5 mm), numerous septa (> 40), and deep columellar depth (> 1.0 mm) – typical pattern of Boa Viagem and Yacht Club; (3) large corallites (≥ 3.5 mm), reduced septal number (≤ 40), and deep columellar depth (> 1.0 mm) – pattern prevalent in Guarajuba, Itacimirim, Praia do Forte, Genipabu. Colonies from Porto da Barra showed a more intermediate morphotype.

S. radians also showed interesting morphotypes, despite the small number of colonies analyzed: (1) corallites with small diameter (< 3.0 mm) and shallow columella (< 1.1 mm) in Paramana and Ma-

TABLE 2: Results of Hierarchical Permanova. Sp = factor species; Lo (Sp) = factor localities nested to species; df = dregree of freedom, SS = sum of square, MS = mean square; (*) = p < 0.025.

Source	df	SS	MS	Pseudo-F	*P*
Sp	1	1288.5	1288.5	16.756	0.0019
Lo (Sp)	12	2019.6	168.3	13.391	0.0001*
Residual	142	1784.7	12.568		
Total	155	5520.1			

TABLE 3: Results of Discriminate Canonical Analysis for *S. stellata* and *S. radians.* CV1 and CV2 point to about 50% and 32% of the variation, respectively. CV = canonical variable; * = the most heavily weighted characters.

Character	CV1	CV2
Dcor	0,077541	0,722184*
Dcol	-0,157773	0,147833
Nsep	0,894014*	0,295482
Esptec	-0,117490	0,186949
Prof	0,182310	0,704478*
Distcor	-0,080194	0,172569
Eigenvalue	*2,44*	*1,58*
Cumulative prop.	*0,50*	*0,82*

ria Guarda; and (2) corallites with large diameter (< 3.2 mm) and deep columella (< 3.5 mm) in Praia do Forte, Itacimirim and Guarajuba. Septal number was always small for this species. Probably, the improving of our sampling should help us to better describe these morphotypes.

Our results also shows that, in average, *S. stellata* had larger values of corallite diameter, columellar depth and, mainly, septal number than *S. radians.* This result is also supported by descriptive data on Tables 4 and 5. However, some overlap can be observed between the two species, particularly among colonies of *S. stellata* from Maria Guarda and Paramana and colonies of *S. radians* (Fig. 2, Table 3). In this case, the specific identification of these species is a more difficult task.

DISCUSSION

Most studies on morphological variation of the 'Atlantic *Siderastrea* Complex' were realized with *S. siderea* (Foster, 1979, 1980). In Brazil, a few studies focus in describe morphological variation of siderastreids (Werner, 1996; Neves, 2004; Santos *et al.,* 2004; Neves *et al.,* 2010; Menezes *et al.,* 2013).

Intraspecific variation

As expected, we observed different results depending of morphological variation category. The most important traits that determined the founded morphological variation was diameter of corallites, number of septa, and columellar depth, while colu-

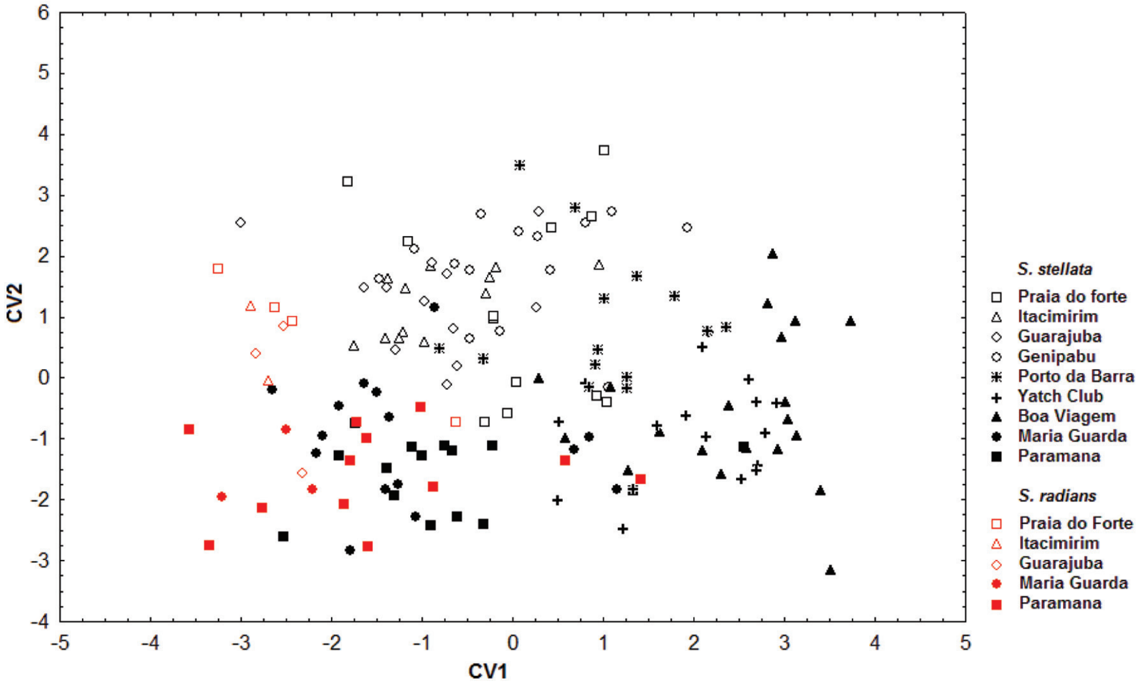

FIGURE 2: Graph of Discriminate Canonical Analysis for morphological comparison between *S. radians* and *S. stellata.* CV = canonical variable.

TABLE 4: Descriptive statistics: mean (μ), standard deviation (*s*) and range of morphological variables analyzed for *S. stellata* and *S. radians* localities. Metric values in millimeters.

Localities	Character	*S. stellata*		*S. radians*	
		μ ± *s*	range	μ ± *s*	range
Paramana	**Dcor**	3,2 ± 0,3	2,4-4,4	3,0 ± 0,3	2,3-3,7
	Dcol	0,5 ± 0,2	0,3-0,7	0,5 ± 0,1	0,3-0,8
	Nsep	35 ± 5,9	26-52	31 ± 6,5	24-46
	Esptec	0,6 ± 0,2	0,3-0,8	0,5 ± 0,1	0,2-0,7
	Prof	1,0 ± 0,2	0,6-1,4	1,0 ± 0,2	0,6-1,5
	Distcor	1,1 ± 0,2	0,6-1,5	1,0 ± 0,1	0,7-1,2
Maria Guarda	**Dcor**	3,2 ± 0,3	2,3-4,2	2,9 ± 0,2	2,4-3,7
	Dcol	0,4 ± 0,1	0,3-0,7	0,5 ± 0,1	0,3-0,7
	Nsep	33 ± 5,6	22-48	27 ± 3,1	22-34
	Esptec	0,6 ± 0,1	0,4-0,9	0,5 ± 0,1	0,3-0,7
	Prof	1,0 ± 0,2	0,5-1,7	1,1 ± 0,2	0,6-1,5
	Distcor	1,2 ± 0,2	0,6-1,6	1,0 ± 0,1	0,8-1,3
Boa Viagem	**Dcor**	3,4 ± 0,4	2,4-4,9		
	Dcol	0,4 ± 0,1	0,2-0,7		
	Nsep	45 ± 5,0	34-64		
	Esptec	0,5 ± 0,1	0,3-0,8		
	Prof	1,2 ± 0,3	0,3-3,2		
	Distcor	1,0 ± 0,2	0,6-1,6		
Bahia Yatch Club	**Dcor**	3,1 ± 0,4	2,4-4,3		
	Dcol	0,4 ± 0,1	0,2-0,7		
	Nsep	43 ± 4,4	28-54		
	Esptec	0,5 ± 0,1	0,3-0,8		
	Prof	1,3 ± 0,2	0,4-1,7		
	Distcor	1,0 ± 0,2	0,5-1,6		
Porto da Barra	**Dcor**	3,6 ± 0,4	2,4-5,1		
	Dcol	0,5 ± 0,1	0,2-0,9		
	Nsep	42 ± 5,1	28-54		
	Esptec	0,5 ± 0,1	0,4-0,9		
	Prof	1,4 ± 0,3	0,8-2,0		
	Distcor	1,1 ± 0,2	0,6-1,7		
Genipabu	**Dcor**	3,8 ± 0,4	2.3-4,6		
	Dcol	0,5 ± 0,1	0,3-0,8		
	Nsep	40 ± 5,1	26-50		
	Esptec	0,6 ± 0,1	0,3-0,8		
	Prof	1,4 ± 0,3	0,5-2,0		
	Distcor	1,2 ± 0,2	0,8-1,6		
Guarajuba	**Dcor**	3,5 ± 0,5	2,3-4,6	3,2 ± 0,3	2,7-3,8
	Dcol	0,5 ± 0,1	0,3-0,8	0,5 ± 0,1	0,3-0,7
	Nsep	36 ± 4,4	24-54	29 ± 2,9	24-38
	Esptec	0,6 ± 0,1	0,3-0,8	0,5 ± 0,1	0,4-0,7
	Prof	1,4 ± 0,3	0,5-2,1	1,2 ± 0,4	0,6-1,8
	Distcor	1,1 ± 0,2	0,7-1,8	1,1 ± 0,2	0,7-1,6
Itacimirim	**Dcor**	3,6 ± 0,4	2,5-4,6	3,4 ± 0,4	3,0-4,3
	Dcol	0,5 ± 0,1	0,3-0,7	0,4 ± 0,1	0,3-0,5
	Nsep	37 ± 4,5	24-48	30 ± 3,0	24-36
	Esptec	0,6 ± 0,1	0,3-0,8	0,6 ± 0,1	0,4-0,8
	Prof	1,4 ± 0,2	0,4-1,9	1,2 ± 0,3	0,7-1,6
	Distcor	1,1 ± 0,2	0,6-2,1	1,2 ± 0,1	0,9-1,4
Praia do Forte	**Dcor**	3,6 ± 0,5	2,7-4,8	3,4 ± 0,5	2,4-4,4
	Dcol	0,4 ± 0,1	0,2-0,7	0,6 ± 0,1	0,3-0,8
	Nsep	39 ± 4,9	28-50	31 ± 5,1	24-46
	Esptec	0,6 ± 0,1	0,3-0,8	0,5 ± 0,1	0,3-0,8
	Prof	1,3 ± 0,3	0,5-2,2	1,4 ± 0,3	0,8-2,0
	Distcor	1,2 ± 0,2	0,7-1,8	1,0 ± 0,2	0,7-1,6

TABLE 5: Descriptive statistics: mean (μ), standard deviation (*s*) and range of morphological variables analyzed for *S. stellata* and *S. radians.* General values including all localities. Metric values in millimeters

	S. stellata		*S. radians*	
Character	μ ± *s*	range	μ ± *s*	range
Dcor	3,4 ± 0,5	2,3 – 5,1	3,1 ± 0,4	2,4 – 4,3
Dcol	0,5 ± 0,1	0,2 – 0,9	0,5 ± 0,1	0,3 – 0,8
Nsep	40 ± 6,2	24 – 64	30 ± 4,8	24 – 46
Esptec	0,6 ± 0,1	0,3 – 0,9	0,5 ± 0,1	0,2 – 0,8
Prof	1,3 ± 0,3	0,3 – 2,2	1,1 ± 0,3	0,5 – 2,4
Distcor	1,1 ± 0,2	0,5 – 2,1	1 ± 0,2	0,7 – 1,6

mellar diameter, theca thickness and distance between corallites remained more homogeneous (Fig. 2, Table 3).

Within each point, both species vary considerably when colony *per* colony is compared (Fig. 2, Table 3). In literature, variations in this level have been attributed to genetic factors. Studying species of *Porites* from the Caribbean region, Brakel (1977) attributed discrepant morphological patterns occurred in similar environmental conditions (subtracts with the same slope and exposure to light) to genetic differences. Similarly, Foster (1979), evaluating colonies of *S. siderea* from the same region, suggested that the variation within populations could be genetic because when colonies were transplanted between different environments, some of them show morphological variation, but others, not.

Variations among localities were also founded, although it was wider for *S. stellata.* Neves & Silveira (2003) and Neves *et al.* (2008) suggested that the tendency of lecithotrophic and philopatric recruitment pattern restrict the spread of this species, sustaining a high variation among populations for both species. Less variation in *S. radians* is contradictory, since this specie is treated in the literature as a highly variable coral (Lewis, 1989). It can be attributed to the small number of samples per location. Based on this and other studies (Neves, 2004; Neves *et al.,* 2006b), populations of *S. radians* are, probably, less representative in the environment than *S. stellata,* which explains the low number of colonies collected. Other possibility is a major susceptibility of this specie to diseases, once sick colonies were not collected in this study. The limitation in colonies recognition in the field is a challenge that must be solved in future projects.

Some relation of morphological variation and environment characteristics can be proposed in this study. The morphotype 1 of *S. stellata* and *S. radians* occurred in Paramana and Maria Guarda, a place of muddy substrate; the morphotype 2 of *S. stellata* were observed in Boa Viagem Beach and Yacht Club, both areas of sandy substrate; and the morphotypes 3 and 2 of *S. stellata* and *S. radians,* respectively, were taken from the sandy bottom pools located on the plateau of the NS reefs (Guarajuba, Itacimirim, Praia do Forte and Genipabu). The place Porto da Barra, a region of sandy substrate presented colonies with intermediate morphology. Curiously, this region is located in a transition between the Todos-os-Santos Bay and the open sea region. Only two morphotypes were previously described by Laborel (1969/70): one, similar to *S. radians* (corallites 2-3 mm in diameter, incomplete fourth cycle of septa) and another similar to *S. siderea* (corallites with 5 mm, presence of the fifth cycle of septa), which seem to fit the patterns founded in the present study. But the change was considered 'progressive' by the author, particularly associated with the depth.

No experimental analysis in our study was made to validate a parallel between morphotypes and environment. However, some inferences based in the literature can be done. In general, zooxantellate scleractinian corals are extremely sensitive to sediment and turbidity. The influence of sediment on coral morphology is immense because it involves both, increasing energy costs with the removal of sediment (usually by complex mucociliary process – reference) and the maintenance of tolerable levels of energy for metabolic activities. In addition, layer of sediment deposited on the oral disk hinders light penetration in tissues and therefore reduces the zooxanthellae photosynthetic production (Rogers, 1990). According to Stafford-Smith (1993), in places with high sediment deposition, corallites with small diameter and more septa are more efficient cleaners, but, the effect may vary to different species. Some data on *S. radians* show that it tolerates short periods of burial with minimal physiological effects. Senescence and death were documented for periods longer than 48 hours (Lirman & Manzello, 2009). About the sediment removing, this specie is also capable to rid the surface in just one hour (Lirman & Manzello, 2009). As such, changes in of sediment size and water energy in the points of TSB and NS studied may have caused the formation of the founded morphotypes.

Moreover, as previously mentioned, genetic factors cannot be overlooked. According to Neves *et al.* (2008), *S. stellata* and *S. radians* have moderate genetic structure along the Brazilian coast, which could also explain the fact that nearby localities have colonies with higher morphological affinity than those more distant. But these are still speculation. Responses to morphological variation may reside in single or joint action of genetic mechanisms and environment. For TSB and LN, the speculation is greater because the results of Neves *et al.* (2008) did not extend to the coast of Bahia. In fact, molecular and morphological data for *S. stellata* and *S. radians* are still a gap for many sectors of the coast.

Interespecific variation

One of the main goal of this study was to provide additional data for the recognition of the interspecific limits between *S. stellata* and *S. radians.* In agreement with the arguments exposed primarily by Neves (2004), significant differences were obtained between these congeners. According to the results, within the morphological characters analyzed, the number of septa was the most informative to distinguish these species. It was possible to observe that there are two groups of *S. stellata* that are totally distinct from *S. radians* and, also, one group that overlap morphological groups (Fig. 2, Table 3). In the latter, it becomes practically impossible to differentiate the species through the used characters. For these morphotypes, only presence of the fourth complete cycle of septa, characteristic indisputably relevant to the identification of *S. stellata,* can be used for differentiation.

The complete fourth cycle of septa for *S. stellata* has been cited by diverse authors such as Verrill (1868, 1901), Gravier (1909), Vaughan (1919), Yonge (1935), and posteriorly by (Neves, 2004; Neves *et al.,* 2010 and Menezes *et al.,* 2013). However, it is important to highlight a common confused interpretation. *Siderastrea stellata* colonies can also include some corallites with an incomplete fourth cycle. It is distinctly different from *S. radians,* in which a complete 4th cycle never occurs. Thus, *S. stellata* and *S. radians* cannot be confused because of the presence of an incomplete S4 in both species, but should be distinguished by the absence of a complete S4 in *S. radians.*

Morphological overlays between *S. stellata* and *S. radians* were also observed by other authors. Comparing morphological characteristics of *Siderastrea,* Santos *et al.* (2004) found that the average diameter of the corallites and septa number of *S. stellata* from Pernambuco (dcor = 3.43; Nsep = 36.84) are similar to values found for *S. radians* from Panama (dcor = 3.42; Nsep = 35.19). In addition, these sites were very close in a grouping statistical analysis. One important factor probably influenced this result: the author doesn't consider the occurrence of *S. radians* in the Brazilian coast. Indeed, Neves (2004) founds more than 60% of

S. radians on the Pernambuco samples and records the species for reefs from Formoso, Santo Aleixo, Porto de Galinhas, and São José da Coroa Grande. Thus, noise may have been assimilated to the results. Unlike Santos *et al.* (2004), who didn't question the taxonomic status of *S. stellata,* Werner (1996) tried to synonymize the congeners based in a morphometric statistical analysis. However, the author doesn't realize a wide taxonomical review of these species and doesn't consider the occurrence of *S. radians* for the Brazilian coast.

Finally, despite the feasible morphological differentiation of species, its identification cannot be performed *in situ.* Diameter of the corallites is the only trait easy to see in the field. However, this characteristic is one of the most variable morphological traits, with great potential for overlap among species. Currently, many scleractinian visual identification guides have been published (*e.g.,* Humman, 2002). But the margin of error for species complexes, without the scrutiny coral and corallites structures is considerable. Observation of diagnostic characters is essential to scleractinian coral identification. Therefore, the use of '*Siderastrea* spp.' (see Cruz *et al.,* 2008; Leão *et al.,* 2008) has gained a degree of acceptance as a secure practice for reporting findings of the genus by those other than expert taxonomists.

RESUMO

Siderastrea *é um pequeno gênero de corais escleractíneos zooxantelados composto por formas coloniais e maciças. Além de contribuir para a consolidação da estrutura dos recifes, representa um grupo com significativa resistência ao estresse ambiental. Até a década de 70, a sua taxonomia foi uma tarefa complicada, limitada pela dificuldade em identificar morfotipos. Mais recentemente, os limites interespecíficos foram redefinidos para as Siderastreas do Atlântico 'Complexo* Siderastrea *do Atlântico'. No entanto, apesar de novas perspectivas, incluindo a ocorrência de* S. radians *e* S. siderea *para o Brasil, os padrões morfológicos são ainda pouco estudados. A fim de caracterizar os níveis de variação intra e interespecífica em* S. stellata *e* S. radians, *análises morfométricas foram desenvolvidas em colônias da costa da Bahia. As amostras foram coletadas na Baía de Todos os Santos e Litoral Norte. Uma Análise Discriminante Canônica foi aplicada sobre seis caracteres para avaliar os diferentes níveis de variação. Os testes sugerem que o diâmetro dos coralitos, profundidade da columela e número de septos variam entre populações. Número de septos é o caracter mais importante para a diferenciação das espécies.* Siderastrea stellata, *com três diferentes padrões morfológicos, foi mais variável do que* S. radians.

Palavras-Chave: Sistemática; Organismos modulares; Morfotipos; Corais zooxantelados; Atlântico Sul.

ACKNOWLEDGEMENTS

The authors are grateful for the support of the LABIMAR team (IB, UFBA), to MSc Igor Cruz (IB, UFBA) for collecting samples and to Marcelle Badaró (IB, UFBA) for outstanding help in the field. Special thanks are given to Ricardo Acácio (IMA – Setor Geoprocessamento) for assistance in preparing the map and to the Prof. Dr. Francisco Barros (IB, UFBA) for help with statistical analysis. This study was supported by the 'Programa de Pesquisa e Pós-Graduação/ IGEO-UFBA' with a scholarship and grants from the 'Fundação de Amparo à Pesquisa da Bahia' (FAPESB) (BOL 1070/2005, APR0469/2005) to E. Neves, the 'Conselho Nacional de Desenvolvimento Científico e Tecnológico'(CNPq) (470336/2004-8 Edital Universal) to R. Johnsson, and the 'Programa Institucional de Bolsas de Iniciação Científica' (PIBIC/IB-UFBA 2006, 2007) to N.M. Menezes. The authors also would like to thanks the 'Programa de Pós-Graduação em Diversidade Animal – PPGDA at the Federal University of Bahia' and the 'American Journal Experts' for the English review.

REFERENCES

Amado-Filho, G.M.; Salgado, L.T.; Rebelo, M.F.; Rezend, C.E.; Karez, C.S. & Pfeiffer, W.C. 2008. Heavy metals in benthic organisms from Todos os Santos Bay, Brazil. *Brazilian Journal of Biology,* 68(1): 95-100.

Amaral, F.M.D.; Hudson, M.M.; Steiner, A.Q. & Ramos, C.A.C. 2007. New findings on corals and calcified hydroids of the Manuel Luiz Marine State Park (State of Maranhão, Northeast Brazil). *Biota Neotropica,* 7: 1-9.

Best, M.B.; Boekschoten, G.J. & Oosterbaan, A. 1983. Species concept and ecomorph variation in living and fossil Scleractinia. *Paleontografica Americana,* 54: 70-79.

Brakel, W.H. 1977. Corallite variation in Porites and the species problem in corals. *Proceedings of 3rd International Coral Reef Symposium,* 1: 457-462.

Budd, A.F. 1990. Long term patterns of morphological variation within and among species of reef-corals and their relationship to sexual reproduction. *Systematic Botany,* 15(1): 150-165.

Budd, A.F. & Gúzman, H.M. 1994. *Siderastrea glynni,* a new species of scleractinian coral (Cnidaria, Anthozoa) from the Eastern Pacific. *Proceedings of Biology Society of Washington,* 107(4): 591-599.

Celino, J.J. & Queiroz, A.F.S. 2006. Fonte e grau de contaminação por hidrocarbonetos policíclicos aromáticos (HPAs) de baixa massa molecular em sedimentos da Baía de Todos os Santos. *Revista Escola de Minas,* 59(3): 265-270.

Cirano, M. & Lessa, G.C. 2007. Oceanographic characteristics of Baía de Todos os Santos, Brazil. *Revista Brasileira de Geofisica,* 25(4): 363-387.

Costa, O.S.J.; Leão, Z.M.A.N.; Nimmo, M. & Attrill, M.J. 2000. Nutrification impacts on coral reefs from Northern Bahia, Brazil. *Hydrobiologia,* 440: 307-315.

Cruz, I.C.S.; Kikuchi, R.K.P. & Leão, Z.M.A.N. 2008. Use of the video transect method for characterizing the Itacolomis reefs, Eastern Brazil. *Brazilian Journal of Oceanography,* 56: 271-280.

Davidson, B.; Jacobs, M.W. & Swalla, B.J. 2004.The individual as a module: solitary-to-colonial transistors in Metazoan evolution and development. *In:* Schlosser G. & Wagner, G.P. Modularity in development and evolution. Chicago Press, Chicago, 43-65p.

Eble, G.L. 2004. Morphological modularity and macroevolution: conceptual and empirical aspects. *In:* Callebaut, W. & Rasskin-Gutman, D. Modularity: Understanding the development and evolution of natural complexes systems. Vienna Series in Theoretical Biology, 221-238.

Felizzola, J.F.; Wagener, A.L.R.; Almeida, A.C. & Lin, W.O. 2008. Butyltin speciation in sediments from Todos os Santos Bay (Bahia, Brazil) by GC-PFPD. *Química Nova,* 31(1): 89-93.

Forsman, Z. 2003. Phylogeny and phylogeography of *Porites* & *Siderastrea* (Scleractinia: Cnidaria) Species in the Caribbean and Eastern Pacific; Based on the nuclear ribosomal ITS region. Univ. Houston, Houston, Ph.D. Thesis.

Foster, A.B. 1977. Patterns of small-scale variation of skeletal morphology within the Scleractinian corals, *Montastraea annularis* and *Siderastrea siderea. Proceedings of 3rd International Coral Reef Symposium,* 2: 409-415.

Foster, A.B. 1979. Phenotypic plasticity in the reef corals *Montastrea annularis* (Ellis & Solander) and *Siderastrea siderea* (Ellis & Solander). *Journal of Experiments in Marine Biology and Ecology,* 39: 25-54

Foster, A.B. 1980. Environmental variation in skeletal morphology within the Caribbean reef corals *Montastrea annularis* and *Siderastrea siderea. Bulletin of Marine Science,* 30(3): 678-709.

Foster, A.B. 1985. Variation within coral colonies and its importance for interpreting fossil species. *Journal of Paleontology,* 59(6): 1359-1381.

Gattuso, J.P.; Pichon, M. & Jaubert, J. 1991. Physiology and taxonomy of Scleractinian corals. A case study in the genus *Stylophora. Coral reefs,* 13: 49-56.

Gravier, C. 1909. Madréporaires des Îles San Thomé et du Prince (Golfe de Guinée). *Annales de l'Institut Océnographique,* 1(2): 17-28.

Hageman, S.J. 2003. Complexity generated by iteration of hierarchical modules in Bryozoa. *Integrative and Comparative Biology,* 43: 87-98.

Hair, J.F.; Black, W.C.; Babin, B.J.; Anderson, R.E. & Tatham, R.L. 2009. Análise Multivariada dos dados. Bookman, Porto Alegre, 688p.

Humann, P. & Deloach, N. 2006. Coral reef identification Florida Caribbean Bahamas. New World Publications, INC. Jacksonville, 288p.

Kikuchi, R.K.P. 2000. Evolução dos recifes e das comunidades de corais hermatípicos da plataforma continental no norte da Bahia durante o Holoceno. Universidade Federal da Bahia, Salvador, Ph.D. Thesis.

Laborel, J. 1967. Leus Peuplements de Madréporaires des Côtes Tropicales du Brésil. *Annales l' Universite d'Abidjan Ecologie,* 2(3): 1-261

Laborel, J. 1969/70. Madreporaires et hidrocoralliaires récifaux dês cotes brésiliennes: Systematique, écologie, réparttion verticale et géographique. Campagne de la Calypso au large dês cotes atlantiques de l'Amerique do Sud. *Annales de l'Institut Océnographique,* 47(9): 15-229.

Laborel, J. 1974. West African reef corals an hypothesis on their origin. *Proceedings of 2nd International Coral Reef Symposium,* 1: 425-443.

Leão, Z.M.A.N. 1986. Guia para identificação dos corais do Brasil. PPPG/UFBA, Salvador, 57p.

Leão, Z.M.A.N. & Kikuchi, R.K.P. 2005. A relic coral fauna threatened by global changes and human activities, Eastern Brazil. *Marine Pollution Bulletin,* 51: 599-611.

Leão, Z.M.A.N.; Kikuchi, R.K.P. & Oliveira, M.D.M. 2008. Branqueamento de corais nos recifes da Bahia e sua relação com eventos de anomalias térmicas nas águas superficiais do oceano. *Biota Neotropica,* 8: 69-82.

Lewis, J.B. 1989. Spherical growth in the Caribbean coral *Siderastrea radians* (Pallas) and its survival in disturbed habitats. *Coral Reefs,* 7(4): 161-167.

Lirman, D. & Manzello, D. 2009. Patterns of resistance and resilience of the stress-tolerant coral *Siderastrea radians* (Pallas) to sub-optimal salinity and sediment burial. *Journal of Experiments in Marine Biology and Ecology,* 369(1): 72-77.

Menezes, N.M.; Neves, E.G.; Barros, F.; Kikuchi, R.K.P. & Johnsson, R. 2013. Intracolonial variation in Siderastrea de Blainville, 1830 (Anthozoa, Scleractinia): taxonomy under challenging morphological constraints. *Biota Neotropica,* 13 108-116, 2013.

McCune, R. & Grace, J.B. 2002. Analysis of ecological communities. MJM Software Design, Oregon, 300p.

Miller, K.J. 1994. Morphological variation in the coral genus *Platygyra:* environmental influences and taxonomic implications. *Marine Ecology Progress Series,* 110: 19-28.

Milne Edwards, H. & Haime, J. 1857. Histoire naturelle des coralliaires, polypes propement dits. Librairie Encyclopédique de Roret, Paris, 326p.

Neves, E.G. & Silveira, F.L. 2003. Release of planula larvae, settlement and development of *Siderastrea stellata* Verrill, 1868 (Anthozoa: Scleractinia). *Hidrobiologia,* 132: 243-254.

Neves, E.G. 2004. Complexo *Siderastrea:* espécies distintas? Significado da variabilidade do gênero Siderastrea de Blainville, 1830 (Anthozoa: Scleractinia) no Brasil. Universidade de São Paulo, São Paulo, Ph.D. Thesis.

Neves, E.G.; Kikuchi, R.K.P.; Johnsson, R.; Soares, R.C.; Menezes, N.M. & Bispo, R. 2006b. Distribuição e preferências de habitat das espécies distribuição e preferências de habitat das espécies de *Siderastrea* (Anthozoa: Scleractinia) na Baía de Todos os Santos (Bahia). Resumo da 3ª Semana de Biologia da UFBA 1: 56.

Neves, E.G.; Andrade, S.C.S.; Lang, F.S. & Solferini, V.N. 2008. Genetic variation and population structuring in two brooding coral species (*Siderastrea stellata* and *Siderastrea radians*) from Brazil. *Genetica,* 132: 243-254.

Neves, E.G.; Silveira, F.L.; Pichon, M. & Johnsson, R. 2010. Cnidaria, Scleractinia, Siderastreidae, Siderastrea siderea (Ellis and Solander, 1786): Hartt Expedition and the first record of a Caribbean siderastreid in tropical Southwestern Atlantic. *Check List,* 6(4): 505-510.

Rogers, C.S. 1990. Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series,* 62: 185-202.

Santos, M.G.; Amaral, F.D.; Hernandez, M.I.M.; Knowlton, N. & Jara, J. 2004. Variação morfológica de *Favia gravida* Verrill, 1868 e *Siderastrea stellata* Verrill, 1868 (Cnidaria, Scleractinia): Aspectos esqueléticos. *Boletim do Museu Nacional de Zoologia,* 517: 1-9.

SOONG, K. & LANG, J.C. 1992. Reproductive integration in reef corals. *Biological Bulletin,* 183: 418-431.

STAFFORD-SMITH, M.G. 1993. Sediment rejection efficiency of 22 species of Australian scleractinian corals. *Marine Biology,* 115: 229-243.

TODD, P.A. 2008. Morphological plasticity in Scleractinians corals. *Biological Reviews,* 83: 315-337.

UNDERWOOD, A.J. 1997. Experiments in ecology: their logical design and interpretation using analysis of variance. Cambridge university press, Cambridge.

VAUGHAN, T.W. 1919. Fossil corals from Central America, Cuba, and Porto Rico, with an account of the American Tertiary, Pleistocene, and recent coral reefs. Contribution to geology and paleontology of the Canal Zone, Panama, and geologically related areas in Central America, and the West Indies. *Bulletin of Smithsonian Institute,* 103: 189-524.

VAUGHAN, T.W. & WELLS, J.W. 1943. Revision of the suborders, families, and genera of the Scleractinia. *Geological Society of Ameria Special Papers,* 44: 343.

VERON, J.E.N. 1995. Corals in space and time: The biogeography and evolution of the Scleractinia. UNSW Press, Sydney, 336p.

VERON, J.E.N. 2000. Coral of the world 3. Australian institute of marine science, Townsville, 489pp.

VERRILL, A.E. 1868. Notice of the corals and echinoderms colleted by prof. C.F. Hartt, at the Abrolhos Reefs, province of Bahia, Brazil, 1867. *Transactions Connecticut Academy of Arts and Sciences,* 1(2): 351-37.

VERRILL, A.E. 1901. Variations and nomenclature of Bermudas, West Indian and Brazilian reef corals, with notes on various Indo-Pacific corals. Part III. *Transactions Connecticut Academy of Arts and Sciences,* 11: 63-168.

WERNER, T.B. 1996. Recent Zooxanthellate Corals (Order: Scleractinia) from Ascension and St. Helena Is., South Atlantic, with a summary of their geographic distribution in the Atlantic Ocean. Univ. Maryland, Maryland, Ph.D. Thesis.

YONGE, C.M. 1935. Studies on the biology of Tortugas corals. II. Variation in the genus *Siderastrea. Carnegie Institution of Washington,* 452: 201-208.

Aceito em: 25/04/2014
Publicado em: 30/09/2014

**Publicado com o apoio financeiro do
Programa de Apoio às Publicações
Científicas Periódicas da USP**

Seção de Publicações do MZUSP