PANAMJAS
Pan-American Journal of Aquatic Sciences

Multivariate morphological analyses in continental and island populations of *Abudefduf saxatilis* (Linnaeus) (Pomacentridae, Perciformes) of Western Atlantic

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Abstract. The reef species *Abudefduf saxatilis* (Linnaeus, 1758) is usually considered as a single large Western Atlantic population distributed in reef habitats from northern United States (Rhode Island) to Uruguay. However, principal components and canonical variables analyses of samples distributed along the Brazilian coast (Rio Grande do Norte, Ceará, Bahia, Rio de Janeiro and Santa Catarina states), and oceanic islands of Atol das Rocas and St. Paul's Rocks, showed morphological variation, which could suggest subdivisions among different populations. Clinal variations of meristic traits along the north-south direction seem to have temperature as their main causative factor. Also, there was a greater similarity among contiguous populations that become more differentiated with distance. In this context, the Brazilian Current flowing, in north-south direction, seems to play an important dispersive role. There were differences between insular and continental populations, which suggest the occurrence of self-recruitment either by a possible existence of circular currents, an active larval role and/or a possible selection for an optimal egg-laying period leading to restrictions in their dispersion. Thus, phenetic divergences seem to suggest restrictions to the genetic flow in the South Atlantic *A. saxatilis* population.

Key words: morphological analyses; canonical variable; population structure; geographical barriers; cline.

Resumo. Análises morfológicas multivariadas em populações continentais e insulares de *Abudefduf saxatilis* (Linnaeus) (Pomacentridae, Perciformes) do Atlântico Ocidental. A espécie de peixe recifal, *Abudefduf saxatilis*, tem sido considerada como uma única grande população Atlântica Ocidental distribuída em habitats recifais do norte dos Estados Unidos (Rhode Island) ao Uruguai. Contudo, análises por componentes principais e variáveis canônicas em amostras distribuídas ao longo da costa Brasileira (Estados do Rio Grande do Norte, Ceará, Bahia, Rio de Janeiro e Santa Catarina), e das ilhas oceânicas do Atol das Rocas e Rochedos de São Paulo, mostraram modificações morfológicas que podem sugerir subdivisões entre diferentes populações. Alguns padrões gerais podem ser observados quanto à distribuição de *Abudefduf saxatilis*. Variações clinais de características merísticas, na direção norte-sul, indicam a temperatura como o principal fator causal. Além disso, há uma maior similaridade entre populações contíguas que se tornam mais diferenciadas com a distância. Neste contexto, a Corrente do Brasil que flui na direção norte-sul parece desempenhar um importante papel dispersivo. Existem diferenças entre populações insulares e continentais, que sugerem a ocorrência de auto-recrutamento pela possível existência de correntes circulares, um papel ativo de larvas e/ou seleção para um período ótimo de desova levando a restrições a sua dispersão. Tais divergências fenéticas sugerem restrições ao fluxo genético entre populações de *A. saxatilis*.

Palavras Chave: análises morfológicas; variáveis canônicas; estrutura populacional; barreiras geográficas; clina.

Introduction

In spite of its physical continuity, the marine environment shows regional, oceanographic and ecological peculiarities. Reef fish populations living in distinct environmental conditions across wide geographic areas may present subtle color differentiation (Planes & Doherty 1997) or significant modifications in their body shape (Bell *et al*. 1982).

Pomacentridae family stands out as important reef fishes because of its abundance in Western Atlantic reefs. It has great species diversity but because their morphological similarities (cryptic species) and pigmentation patterns that vary ontogenetically (Novelli *et al.* 2000) it is difficult to differentiate among species. They are spread over vast areas (Allen 1975), whereas distribution of some species is restricted to oceanic islands (Emery 1972, Edwards & Lubbock 1983; Gasparini *et al.*, 1999). Others are found spread over vast areas (Allen, 1975, 1991).

Among widely distributed groups, the genus *Abudefduf* represents a good example of dispersive capacity, especially *A. saxatilis*. This species is distributed in reef and rocky environments from the northern USA to the border with Uruguay (Menezes & Figueiredo 1985). Disagreement about time period and number of species divergences within this genus has triggered molecular phylogenetic studies (Lessios *et al*. 1995, Bermingham *et al*. 1997).

Pomacentridae shows great fidelity to their microhabitats, and can live in certain reefs for months or years (Reese 1973). This ecological characteristic indicates little or no influence of migration in their distribution, suggesting that it is conditioned basically by larval dispersion. Despite to its reduced pelagic larval stage (18-27 days), *A. saxatilis* shows homogeneous populations through Caribbean because its post larval, pelagic stage, may extend up to 55 days (Shulman & Bermingham 1995).

It is known that modifications in body shape of populations and species usually reflect an association of environmental conditions and adaptive genetic changes (Shaklee, 1984; Lessios *et al*. 1995). Considering the current assumption of a single large *A. saxatilis* population in the Atlantic Ocean, the present study aimed to compare geographically distant samples from the Brazilian coast and oceanic islands. We used principal components and canonical variables to analyze meristic and multivariate morphometry data in order to identify possible morphological variations suggesting population subdivisions.

Materials and Methods

Samples of different sizes (juveniles and adults) of *A. saxatilis* were collected in reef and rocky bottoms in the Brazilian offshore Islands - St Paul’s Rocks (0°55' N; 29°21' W), Atol das Rocas (3°50' S; 33°49' W), respectively 960 km and 270 km in front to northern coast, and along Brazil coast - Natal (05°52'43" S; 35°10'23" W) (Rio Grande do Norte state), Tinharé Island (13º28' S; 39º02' W), Cairu (Bahia state) and Bombinhas (27º07'54" S; 48º31'40" W), Penha (Santa Catarina state), and Fortaleza (03º41'15" S; 38º29' W) (Ceará state; only juveniles) (Fig.1). Samples were fixed in formaldehyde at 10% and stored in 70% ethyl alcohol. Body measurements were taken head to tail using a caliper precision 0.05mm using the truss networks method (Strauss & Bookstein 1982). The samples for each geographic area are showed in the Table I.

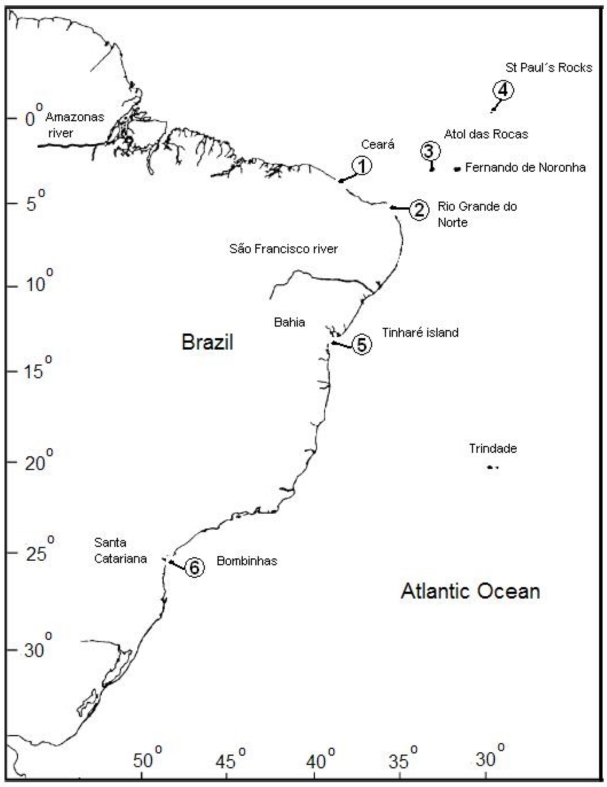

Figure 1. Map of the sampling locations. (1) Ceará, (2) Rio Grande do Norte, (3) Atol das Rocas, (4) St Paul’s Rocks, (5) Ilha de Tinhare, Bahia, (6) Bombinhas, Santa Catarina.

Twenty-two quantitative traits were measured for each specimen. The following morphological measurements of the distances of landmarks (Fig. 2) in the comparative analysis of *Abudefduf saxatilis* populations were used: 1. Pre-dorsal distance, 2. Dorsal pectoral distance,

Table I. Variation in meristic traits among *Abudefduf saxatilis* populations on the coast and oceanic islands of Western Atlantic.

Area	N	Dorsal rays			Pectoral rays			Anal rays			Lateral line scales		
		min/ max	Mode	Mean	min/ max	Mode	Mean	min/ max	Mode	Mean	min/ max	Mode	Mean
Atol das Rocas	16	14-15	14 (87%)	14.1	19	19 (100%)	19.0	13-14	13 (75%)	13.2	21-22	22 (56%)	21.6
St Paul's Rocks	11	13-14	13 (63%)	13.4	18-19	19 (72%)	18.7	12-14	13 (63%)	12.8	21-22	21 (63%)	21.4
Ceará	09	13	13 (100%)	13.0	18-19	19 (89%)	18.9	11-13	12 (66%)	12.1	21-22	21 (55%)	21.4
R.io Grande do Norte	17	13-14	13 (94%)	13.0	17-19	18-19 (94%)	18.2	12	12 (100%)	12.0	21-22	21 (58%)	21.4
Bahia	13	13-14	13 (92%)	13.1	18-19	19 (77%)	18.8	11-13	12 (54%)	12.3	21-22	21 (77%)	21.2
Santa Catarina	10	12-13	13 (90%)	12.9	16-18	17 (50%)	17.3	12-14	12 (60%)	12.5	21-22	21 (50%)	21.5

3. Pectoral ventral distance, 4. Ventral-anal distance, 5. Pectoral anal distance, 6. Diagonal between the 1st ray on the dorsal fin and 1st ray on the anal fin, 7. Diagonal between the pectoral fin and the last ray on the dorsal fin, 8. Diagonal of the 1st ray of the anal fin to the start of the 3rd lateral bar, 9. Distance between the 1st ray of the dorsal fin to the start of the 3rd lateral bar, 10. Length of the 1st ray of the anal fin, 11. Distance between the start of the 3rd lateral bar and the last dorsal fin ray, 12. Diagonal between the 1st anal ray to the last dorsal ray, 13. Length from the base of the dorsal fin, 14. Diagonal between the 1st ray of the dorsal fin to the last anal ray, 15. Length of the base of the anal fin, 16. Diagonal between the last ray of the dorsal fin to the last ray of the anal fin, 17. Diagonal from the last ray of the dorsal fin to the lower base of the tail, 18. Dorsal fin to upper tail base distance, 19. Distance anal fin to lower base of the tail, 20. Diagonal from the last ray of the anal fin to the upper base of the tail, 21. Height of the tail peduncle, 22. Interorbital distance.

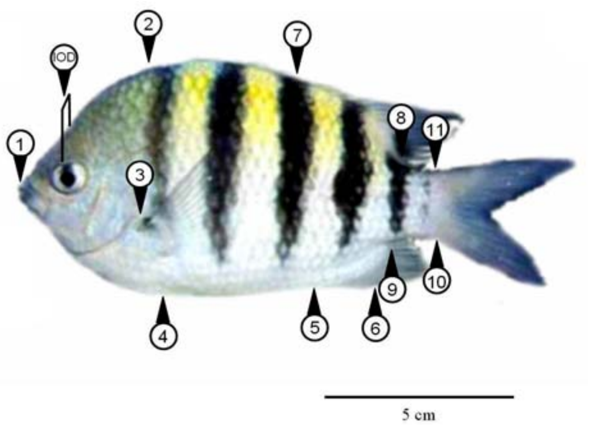

Figure 2. *Abudefduf saxatilis* (Linnaeus, 1758) specimen. Landmarks used in this study (1-11 and interorbital distance - IOD). (1) snout, (2) anterior base of dorsal fin. (3) anterior base of pectoral fin (leading edge). (4) anterior base of pelvic fin. (5) anterior base of anal fin. (6) length of first anal ray. (7) upper edge of third lateral strip. (8) posterior base of dorsal fin. (9) posterior base of anal fin. (10) ventral base of caudal fin. (11) dorsal base of caudal fin. Scale bars = 5 cm.

Body shapes were studied by morphometric analysis of the canonical variables independent of size (Reis *et al*. 1990). This analysis allows visualization of morphological similarities among individuals by projecting individual scores on canonical axes of a bidimensional graph. It also allows discrimination of traits obtained for each group of individuals and related to collection points. Principal components analysis (PCA) (Morrison 1976) was used to identify shape and size variation among *A. saxatilis* individuals (n=76, using the SAS®-PC (SAS Institute In. 1988) statistical program. Meristic counts of the soft ray of dorsal, pectoral and anal fins, and lateral line scales were obtained for all samples. The geographic sites and analyzed individuals per sample are showed in the Table I.

Results

Meristic characters

There were indications of a clinal reduction in number of segments across the north-south direction along the Brazilian coast (Table I). Atol das Rocas samples showed highest values for almost all traits analyzed, including samples from St Paul's Rocks, located further north. Clinal values were more evident through analyses of structures means. The lowest counts were detected at Bombinhas (Santa Catarina state) in the southern portion of the Brazilian coast. Number of lateral line scales hardly varied among samples analyzed. However, a higher modal value was observed in the Atol das Rocas samples.

Table II. Coefficients of variables on the first (PC1) and second (PC2) principal component of traits studied in the *Abudefduf saxatilis* populations.

Character	PC1	PC2
L1	0.2002	-0.0457
L2	0.2175	0.0898
L3	0.2404	0.0372
L4	0.2159	-0.3635
L5	0.2313	-0.3458
L6	0.2285	0.0084
L7	0.2188	-0.1659
L8	0.2272	0.0380
L9	0.2259	-0.0229
L10	0.1755	0.4615
L11	0.2198	-0.2884
L12	0.2147	0.0941
L13	0.2217	-0.0466
L14	0.2210	-0.0450.
L15	0.2128	0.1860
L16	0.2151	0.0039
L17	0.2007	0.0251
L18	0.1833	0.1429
L19	0.1751	-0.2299
L20	0.1973	-0.0754
L21	0.2159	0.1085
L22	0.2161	0.5212
% variation	98.78	0.2100

Principal Component Analysis (PCA)

Two eigenvectors extracted from the variance-covariance matrix accounted for 98.78% and 0.21% of the observed variation, respectively (Table II). All coefficients of the first eigenvector were positive, suggesting it may be interpreted as a multivariate measurement of size. The second eigenvector had positive and negative values and could be interpreted as a shape axis.

Individual scores of *A. saxatilis* populations plotted in PC1 and PC2 space (Fig. 3) revealed an extensive overlap among samples distributed on PC2 axis. There were no precise differentiations among island and continental samples, but samples from Atol das Rocas and St Paul’s Rocks could be discriminated from each other. Also, samples from Atol das Rocas and Santa Catarina differentiated in form. Individuals from Ceará formed a well defined group by PC1, possibly reflecting the lower sizes of these individuals.

Canonical Variables Analysis (CVA)

Canonical variables 1, 2 and 3 explained 51.41%, 25.43% and 11.73% of the observed variation, respectively. Both axes had positive and negative values showing interaction between shape and size. The dispersion scores graphic of canonical variable CV1, CV2 and CV3, plotted in bidimensional space, indicate that point distances are proportional to dissimilarity degree among populations. The most important morphometric traits in the discrimination of each variable (p = 0.001) were the measurements 10, 7, 3 and 21 for the negative side of the first axis. In contrast, variables that most influenced the discrimination on the second axis were 7, 5, 14 and 11 on the positive side and 22, 12, 2 and 21 on the negative side.

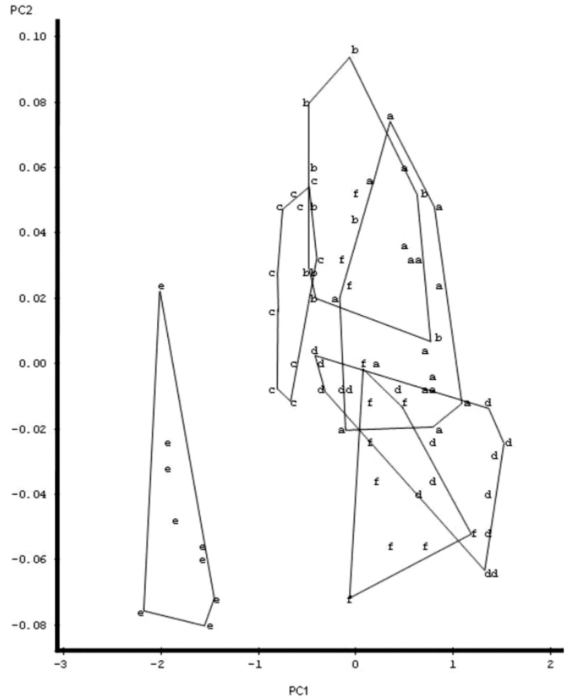

Figure 3. Dispersion diagram of individual scores in different *Abudefduf saxatilis* populations in the space defined by PC1 and PC2. (a) Rio Grande do Norte, (b) Santa Catarina, (c) St Paul’s Rocks (d) Atol das Rocas, (e) Ceará and (f) Bahia.

Similarly to PCA, the diagram of canonical variable 1 (CV1) and canonical variable 2 (CV2) (Fig. 4) showed that *A. saxatilis* from Ceará state was different from other samples. Dispersion of individual scores demonstrated overlapping among samples of Bahia and Atol das Rocas, forming a distinct cluster in the second canonical axis compared to one composed by St Paul’s Rocks, Santa Catarina and Rio Grande do Norte samples. This analysis showed that samples from both oceanic islands were different in shape and size.

Scores plotted in CV1 and CV3 spaces (Fig. 5) discriminated island samples from those of continent along CV3 axis. Continental samples showed greater overlapping, except for Ceará samples, which formed an isolated cluster along CV1. Specimens from Atol das Rocas and St Paul’s Rocks were also discriminated between each other by the size component.

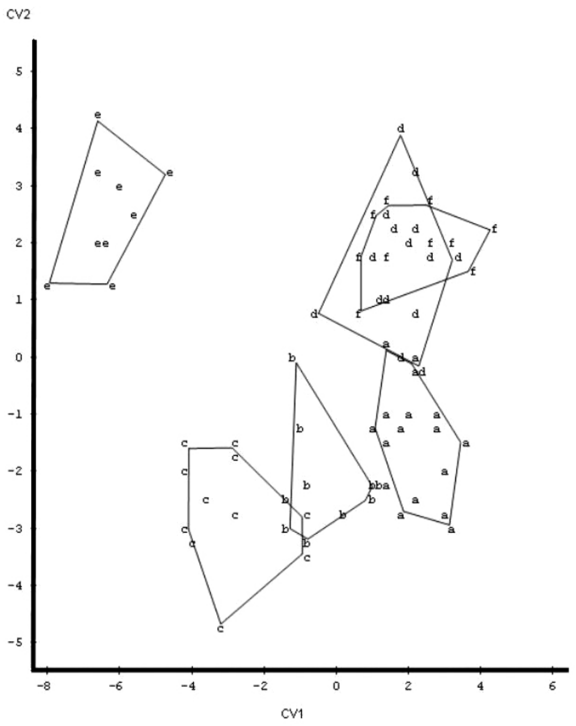

Figure 4. Dispersion of individual scores of *Abudefduf saxatilis* populations in the space defined by CV1 and CV2. (a) Rio Grande do Norte, (b) Santa Catarina, (c) St Paul's Rocks, (d) Atol das Rocas, (e) Ceará and (f) Bahia.

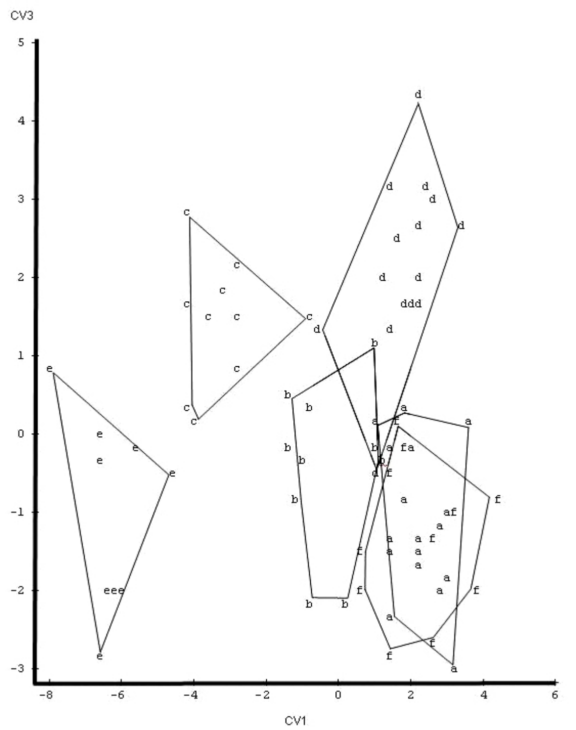

Figure 5. Dispersion of individual scores of *Abudefduf saxatilis* populations in the space defined by CV1 and CV3. (a) Rio Grande do Norte, (b) Santa Catarina, (c) St Paul's Rocks, (d) Atol das Rocas, (e) Ceará and (f) Bahia.

Discussion

Occurrence of physical barriers among marine fish populations is not always clear (Joyeux *et al.* 2001). However, geographic and/or ecological subdivisions allow the establishment of population's traits representing suitable models for biogeographic, taxonomic, ecological and genetic studies. In such cases, morphometric analyses can produce valuable information about phenotypic plasticity of species and possible effects of genetic changes on morphological variation (Hauser *et al*. 1995).

Abudefduf saxatilis populations along South America coast showed a clinal gradient in the north-south direction in relation to their meristic variables. Temperature may be a decisive factor explaining regional differences among these samples and it is not uncommon for meristic traits to have lower number of segments in colder waters at the southern coast, when compared to northern warmer waters. Usually, parameters delaying ontogenetic development, such as hypoxia, low temperatures, high salinity and reduced food sources, favor the development of greater number of body segments (Barlow 1961; Shaklee & Tamaru 1981). Notably, Atol das Rocas population had highest counts even compared with St Paul's Rocks located at the limit of the equatorial line. Higher mean temperatures in shallower waters of Atol das Rocas than those of St Paul's Rocks (environmental factor) or differences in the genetic pool of these populations (genetic factor) could account for this discrepancy.

In some cases, although temperature and salinity influenced some species regarding numbers of fins' rays, certain structures are not modified by different environmental conditions, suggesting a major genetic control in the establishment of serial elements (Barlow 1961).

Among various characteristics identified in species with wide geographic distribution, size is the most frequently observed. In Pomacentridae, clinal variations in color have been shown and it is related to the great variety of pigmentation patterns in this species (Doherty *et al*. 1994). Genetic analyses, carried out in populations with pigment variation, have shown divergences (*Amphiprion clarkii*, Bell *et al*. 1982, *Acanthochromis polyacanthus*, Planes & Doherty 1997) or even the existence of cryptic species in this group (*Chrysiptera cyanea*, Lacson 1994, *Stegastes nigricans* and *Chrysiptera glauca*, Lacson & Clark 1995). However, the level of genetic intraspecific variability is compatible with the one observed in species with no color variations (Lacson & Clark 1995). Although data suggesting between-populations, morphological and genetic differences are not necessarily correlated (Gorman & Kim 1977, Bell *et al*. 1982), genetic polymorphisms detected by RAPD (Random Amplification of Polymorphic DNA) markers or alozymes are associated with pronounced among-population morphometric variations in some marine species (Dahle *et al*. 1997; Mamuris *et al*. 1998). Thus, morphometric analyses can provide real data on species plasticity and possible effects of genetic changes on morphological traits.

Lessios *et al*. (1995) identified particular color patterns, in the lower suborbital margin (scale presence or absence) and in the pre-opercule, between *Abudefduf concolor* from eastern Pacific coast and *A. declivifrons* from Atlantic Ocean. Body depth, snout length and caudal peduncle depth play a discriminatory role among these species. These data, together with molecular differences in mtDNA and isoenzymes, confirmed they are distinct species. In spite of separation estimative of ca. 14 to 15 million years, they still show similar phenotypic characteristics. Long periods of time, in some cases, seem to be insufficient to overcome a conservative situation in the morphotype of certain species. Thus, isoenzymatic markers and multivariate morphometric analyses were able to discriminate two sympatric and cryptic species of the *Albula* genus in Hawaii waters. Even though they diverged around 20 to 30 million years ago, these two species seem to have extremely conservative morphology (Shaklee & Tamaru 1981).

Abudefduf saxatilis populations showed little morphological discrimination when analyzed by principal components analysis. This methodology is appropriated to access the morphological variability in shape and size in different populations. Much of the variation observed could be associated to a size component. However, the analysis showed good discrimination for shape between Atol das Rocas (270 km from the coast) and St Paul’s Rocks (960 km from the coast) populations. Atol das Rocas was also divergent in size and shape from Santa Catarina coastal sample. These data agree with meristic values showing that populations of these two localities were markedly different. Ceará sample, consisting of juvenile individuals, showed strong discrimination in size.

Canonical variable analysis showed differentiation among populations in distinct locations. Canonical variables 1 and 2 showed greater body similarity among samples from Atol das Rocas, Bahia and Ceará compared to those from St Paul’s Rocks, Rio Grande do Norte and Santa Catarina. Canonical variables 2 and 3 showed a similar tendency, with both clusters being clearly defined. This pattern could be explained by dispersive events caused by the Equatorial South Current that comes from East Atlantic, passes by St Paul’s Rocks and Atol das Rocas and divides at Rio Grande do Norte coast, with one branch following the north coast as the Guyana Current and the other flowing south as the Brazil Current. The South Equatorial Current seems to provide a contact zone among oceanic populations of the Atol das Rocas, and the populations of Ceará (north coast) and Bahia. Positioned between these two resulting currents, Rio Grande do Norte population has lower contact with these neighboring areas.

Abudefduf saxatilis population at St Paul’s Rocks, because of its distance from the South American coast, seems to form an isolated and self-maintaining population. The discontinuity caused by oceanic isolation was evident when canonical variables 1 and 2 were analyzed. Two clusters, diverging for shape, were discriminated; one oceanic representing Atol das Rocas and St Paul’s Rocks populations and another clustering coastal populations.

Isolated *A. saxatilis* populations collected on Ascension Island, southeast of St Paul’s Rocks in the mid Atlantic, showed mtDNA pattern different from those of Western Atlantic (Bermingham *et al*. 1997), also suggesting a probable genetic component associated to the morphological differences observed in the geographical isolated St Paul’s Rocks and Atol das Rocas populations.

Morphological and genetic differences in island populations arise from the impediment to genetic flow, caused by closed circulation currents in the reproduction areas where eggs and larvae tend to remain within their area of influence with few possibilities to disperse and to establish contact with populations from other areas. Clustering of coastal populations in one group on PC1 and PC3 seems to suggest an unidirectional dispersion system among them, capable of showing shared similarities. However, they had sufficient peculiar characteristics to be distinguished by PC1 and PC2 axes.

The analyzed data indicated structuring of morphologically distinct *A. saxatilis* populations in the Brazilian Province, whose effects were attributed to dispersion by dominant currents (e.g., Briggs 1974, Floeter *et al.* 2001). St Paul’s Rocks and Atol das Rocas populations were differentiated morphologically in all performed analyses.

Our study provided the first investigation using methods of multivariate morphometry in Atlantic populations of a reef fishes involving distances over 5,000 km. Lower morphological homogeneity than expected, emphasizes the importance of conservation of these populations, especially of the St Paul's Rocks. These results, complemented by future genetic marker analyses, could support effective conservation Pomacentridae species in South Atlantic.

Acknowledgments

The authors are grateful to P.R.A.M. Affonso for sample collections of Rio de Janeiro and F. Hostim for collection of individuals in Santa Catarina coast. This research received funding from CAPES (fellowship to WFM), CNPq and institutional support from UFRN and UFSCar.

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Received March 2006
Accepted June 2006
Published online June 2006