Temporal and spatial variations in tidepool fish assemblages of the northeast coast of Brazil

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Abstract

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Temporal and spatial variations and environmental factors influencing the structure of tidepool fish assemblages were quantitatively investigated at Iparana beach, northeast Brazilian coast. The majority of the tidepool fishes sampled were suprabenthic juvenile individuals of great mobility. We recorded during monthly diurnal underwater visual censuses a total of 4,750 fish from 26 species, represented mainly by partial residents from the families Scaridae, Haemulidae, Gerreidae and Pomacentridae. The number of species and individuals showed significant variability among tidepools as a response to variations in their volume and type of substrate cover. The greatest species abundance and richness associated with rocks covered with algae suggested that substrate complexity is one of the main factors defining the spatial structure of the tidepool ichthyofauna. Temporal variability in species abundance and richness was associated with changes in salinity levels due to seasonal rainfalls. A higher number of juvenile fishes from December to May in our samples corroborate the hypothesis that the tidepools act as nursery sites. Therefore, the species associations found in this study and their relation to seasonal and spatial discontinuities may be partly explained according to their habitat requirements and reproductive cycles.

Keywords: tidepool fishes, environmental factors, seasonality, diversity, abundance.

Resumo

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Investigamos quantitativamente variações espaciais e temporais, assim como os fatores ambientais que podem influenciar a estrutura da fauna de peixes em poças de maré da praia de Iparana, nordeste do Brasil. A maioria dos peixes registrados eram indivíduos suprabênticos jovens de grande mobilidade. Registramos, através de censos visuais subaquáticos diurnos mensais, um total de 4.750 peixes pertencentes a 26 espécies, representados principalmente por residentes parciais das famílias Scaridae, Haemulidae, Gerreidae e Pomacentridae. Os números de espécies e indivíduos mostraram variação significativa entre as poças amostradas com relação ao seu volume e tipo de cobertura do substrato. As maiores abundância e riqueza de espécies foram associadas à presença de rochas cobertas com algas, sugerindo que a complexidade estrutural do substrato é um dos principais fatores que define a estrutura espacial da ictiofauna em poças de marés. A variabilidade temporal em abundância e riqueza de espécies foi associada com variações de salinidade devido à sazonalidade das chuvas. Um maior número de peixes jovens registrados entre dezembro e maio corrobora a hipótese de que as poças de maré funcionam como berçários. Portanto, as associações de espécies encontradas neste estudo, assim como suas relações de descontinuidades sazonais e espaciais podem ser explicadas parcialmente de acordo com as exigências de hábitat e ciclos reprodutivos.

Palavras-chave: peixes de poças de maré, fatores ambientais; sazonalidade, diversidade, abundância.

Introduction

Coastal intertidal reefs and their tidepools are important habitats, especially for young-of-the-year of both coastal and oceanic fish species, many of which of special economic interest (Caddy & Sharp 1986, Griffiths et al. 2003). Coastal reefs in northeast Brazil often become uncovered at low tides, forming several tidepools, some of them entirely or partly isolated from the adjacent sea. Wind, solar radiation, and rainfall are factors that affect the water temperature, salinity, and dissolved oxygen, turning the tidepools into highly variable habitats both in time and space (Vasconcelos & Rocha 1986, Bridges 1994, Little & Kitching 1996).

Tidepools may serve as nursery habitats for larvae and juveniles of several marine organisms coming from the adjacent areas (Beckley 1985, Bennett 1987, Horn et al. 1999), also providing refuges for many other organisms during the low tides (Mahon & Mahon 1994). Fishes inhabiting tidepools can be categorized as: (1) true residents, represented by small-sized species, including benthic fishes of the families Gobiidae and Blenniidae (Horn et al. 1999); (2) partial residents, which are mainly juveniles from several families such as Scaridae, Pomacentridae, Acanthuridae, Pomacanthidae, and Chaetodontidae, also including some of economic interest as Lutjanidae, Serranidae, and Haemulidae (Gibson 1982, Mahon & Mahon 1994); and (3) transient or occasional species, which may be sporadically retained in tidepools at the low tides (e.g. Carangidae, Scianidae, Scombridae) (Mahon & Mahon 1994).

Most of the information on the composition, diversity, distribution, and abundance of tidepool fishes originated from studies conducted in North America (Thompson & Jones 1978, Yoshiyama 1981, Moring 1986, Yoshiyama et al. 1986), Caribbean (Mahon & Mahon 1994), Taiwan (Chang et al. 1977, Lee 1980), and South Africa (Christensen & Winterbottom 1981, Bennett & Griffiths 1984, Beckley 1985, Bennett 1987). In South America, Quijada & Cáceres (2000) studied the tidepool ichthyofauna in the temperate zone of Chile. In the northeastern tropical areas of Brazil Rosa et al. (1997, at the state of Paraíba) and Araújo et al. (2000, at the state of Ceará) studied species composition and biodiversity, but they did not investigate temporal and spatial patterns of the fish assemblages.

Much concern has been raised about the health of coastal ecosystems in Ceará, due to intense degradation of the coastal reefs by tourism, fisheries and coastal development (Campos et al. 2003). Nevertheless, the baseline studies to determine benchmarks for monitoring the health coastal reefs and tidepools are lacking. Following Meador & Matthews (1992), without the baseline spatial and temporal data on the inherent variability in sampling of aquatic biological communities, the detection of the effects of human-induced or natural perturbation becomes difficult. The present study aimed to investigate changes in tidepool fish assemblages structure on coastal reefs of Iparana, state of Ceará, NE Brazil, by (1) describing their taxonomic composition; (2) quantitatively assessing the patterns of variation across a range of spatial and temporal scales; (3) identifying which environmental variables may be important in influencing their structure; and (4) evaluating the importance of the tidepools as nursery areas for marine fishes.

Material and Methods

The tidepools here studied are located at Iparana beach (3° 40' 18" S and 38° 36' 42" W), on the coast of Ceará (Figure 1). This area is located at the Brazilian northeastern coast, Western South Atlantic. Local Calcium Carbonate and Iron Oxide shore reefs are often elongated and discontinuous, extending from the beach face to nearly two hundred meters seaward (Morais 1969, Maida & Ferreira 1997, Leão & Dominguez 2000). These structures become partly
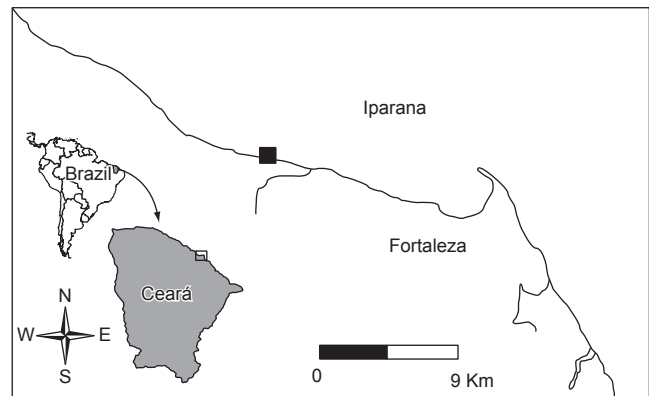
Figure 1. Iparana beach, state of Ceará, NE Brazil.
Figura 1. Praia de Iparana, Estado Ceará, Nordeste do Brasil.

exposed during low tides, isolating tidepools of several sizes and depths within the reef extension. The five tidepools monitored in this study were located and randomly distributed in the lower intertidal zone. Tidepool selection was based on three assumptions: a) to be exposed only at very low tides; b) to have the appropriate size and depth for conducting visual census; c) to become nearly isolated from neighboring tidepools.

Diurnal and monthly visual censuses were conducted at syzygy low tides lower than or equal to 0.1 m. Censuses consisted of an intensive species search, by snorkelling around the internal rim of the tidepools, using the methods suggested by Christensen & Winterbottom (1981) in respect to observation time. Each search lasted less than 25 minutes to avoid repetitive counts. A total of 55 samplings and approximately 23 hours of visual censuses were conducted between June 1998 and May 1999. Water visibility was always greater than the largest pool length.

Tidepools bottom cover was measured by using a square frame (0.5 x 0.5 m) placed over the substrate, and percent cover was categorized into 1) sand-rubble - SR; 2) bare rock - BR; and 3) rock covered with algae - RA. The surface area (A) of each tidepool was estimated by measuring and adding up triangular areas (m^2) to match the approximate surface area of the tidepool. Average depth (D) in meters was estimated from three measurements taken at random locations along a longitudinal transect in order to estimate the pool volume (PV = A x D).

The salinity (SA), temperature (TE,°C), pH, and dissolved oxygen (DO, mg.L^{-1}) of the seawater were recorded by using a multiparameter probe (Hydrolab). Data of rainfall (RF, mm yr^{-1}) and wind velocity (WV, ms^{-1}) during the studied period were obtained from the Fundação Cearense de Meteorologia (FUNCEME).

A full factorial two-way ANOVA was utilized for evaluating the tidepools (1 to 5) along the four trimesters (I – June to August, II – September to November, III – December to February, and IV – March to May), and also to analyse their interactions with the environmental variables, total species abundance, and species richness. Student-Newman-Keuls, a posteriori test, was applied for multiple comparisons. Variables were transformed as required by applying a logarithmic transformation of the type $Y = \log_{10}(x + 1)$ (Boesch 1977, Zar 1996).

Cluster analysis was used for organizing species (R-mode), trimesters or tidepools (Q-Mode), into nearly homogeneous groups based on a species vs. samples abundance matrix. Cluster analyses were performed by using the Euclidean Distance and Group Average (UPGMA) linkage methods (Boesch 1977, Valentin 1995). To minimize the effects of artificial groups and facilitate cluster interpretation,

normal and inverse classifications were related to each other using nodal analysis, which determines species-collections coincidences. This was done using the concepts of Constancy and Fidelity as defined by Boesch (1977). Analyses were performed in SPSS for Windows (v.11) and Microsoft Excel 2000 Softwares.

Stepwise multiple linear regression was used to analyze the effects of the environmental variables recorded (i.e. tidepool volume, substrate type, salinity, temperature, pH, dissolved oxygen of the sea water, rainfall, and wind velocity) on total species abundance and richness (Draper & Smith 1981). When species determination was uncertain in the field, specimens were captured for laboratory identification. These specimens were not included in the statistical analysis. The collected material was identified, photographed, preserved and deposited at the Aquatic Biology Collection of the Department of Fisheries Engineering at the Federal University of Ceará.

Results

The 16 fish families recorded were represented by at least 26 species. Haemulidae was the richest family represented by six species. The most abundant families were Scaridae, Haemulidae, Gerreidae, and Pomacentridae, in a decreasing order. Of the total 4,750 fishes counted, 10 taxa amounted to about 98% of the total abundance, and the six most abundant species (*Sparisoma* cf. *axillare*, *Haemulon parra*, *Eucinostomus* spp., *Abudefduf saxatilis*, *Lutjanus apodus*, and *Acanthurus chirurgus*) represented about 94% of this

total. With respect to the frequency of occurrence, individuals of *Sparisoma* cf. *axillare* were present in 96% of the censuses, followed by *Eucinostomus* spp. (95%); *Abudefduf saxatilis* and *Lutjanus apodus* (both in 87%), and *Haemulon parra* (85%) (Table 1).

Two-way ANOVA did not show any significant results between the tidepools and the trimesters ($F_{12.0} = 1.28$, $p > 0.05$ and $F_{12.0} = 0.78$, $p > 0.05$), considering the total species abundance and richness.

The isolated effect of tidepools was significant ($F_{4.0} = 23.02$, $p < 0.01$) on species abundance but not for species richness ($F_{4.0} = 2.15$, $p = 0.88$). Average total abundance was significantly higher on tidepools 1 and 4 in relation to tidepools 2, 3, and 5 (Newman-Keuls, $p < 0.01$, $1 = 4 > 2 = 3 = 5$) (Figure 2).

Both species abundance ($F_{3.0} = 16.15$, $p < 0.01$) and richness ($F_{3.0} = 8.14$, $p < 0.01$) varied significantly in relation to the sampling trimester. Total abundance was low on trimester I, high on III and IV, and intermediate on trimester II, showing a positive trend from the beginning to the end of the study period (Newman-Keuls, $p < 0.05$, $I < II < III = IV$). Average number of species was low on trimesters I and II and high on III and IV (Newman-Keuls, $p < 0.05$, $I = II < III = IV$) (Figure 3).

Multiple regression analysis significantly explained about 78% of the variation in abundance and 57% of the species richness as a function of the environmental variables considered. Species abundance was positively correlated with the tidepools volume and the presence of rock covered with algae, and negatively correlated with

Table 1. Iparana tidepools fish abundance expressed in number (N), percentage (%N) and accumulation (%A); and fish frequency expressed in number (F), and percentage (%F) from June 1998 to May 1999.

Tabela 1. Abundância de peixes em poças de maré na praia de Iparana expressa em Número (N), percentual (%N) e Acumulada (%A); e Freqüência de ocorrência numérica (F) e percentual (%F) de junho de 1998 a maio de 1999.

| Species	Families	N	%N	%A	F	%F
Sparisoma cf. *axillare*	Scaridae	1728	36.38	36.38	53	96.36
Haemulon parra	Haemulidae	972	20.46	56.84	47	85.45
Eucinostomus spp.	Gerreidae	609	12.82	69.66	52	94.55
Abudefduf saxatilis	Pomacentridae	490	10.32	79.98	48	87.27
Lutjanus apodus	Lutjanidae	346	7.28	87.26	48	87.27
Acanthurus chirurgus	Acanthuridae	308	6.48	93.75	29	52.73
Lutjanus jocu	Lutjanidae	78	1.64	95.39	22	40.00
Engraulidae	Engraulidae	76	1.60	96.99	15	27.27
Anisotremus virginicus	Haemulidae	30	0.63	97.62	15	27.27
Pomacanthus paru	Pomacanthidae	25	0.53	98.15	18	32.73
Labrisomus nuchipinnis	Labrisomidae	22	0.46	98.61	18	32.73
Mugil curema	Mugilidae	15	0.32	98.93	3	5.45
Haemulon plumieri	Haemulidae	13	0.27		5	9.09
Stegastes variabilis	Pomacentridae	6	0.13		6	10.91
Gymnothorax vicinus	Muraenidae	6	0.13		5	9.09
Haemulon steindachneri	Haemulidae	5	0.11		2	3.64
Anisotremus surinamensis	Haemulidae	5	0.11		2	3.64
Anisotremus moricandi	Haemulidae	3	< 0.1		2	3.64
Acanthurus coeruleus	Acanthuridae	3	< 0.1		2	3.64
Sphoeroides testudineus	Tetraodontidae	2	< 0.1		2	3.64
Epinephelus adscensionis	Serranidae	2	< 0.1		2	3.64
Chaetodipterus faber	Ephippididae	2	< 0.1		1	1.82
Scorpaena plumieri	Scorpaenidae	1	< 0.1		1	1.82
Halichoeres brasiliensis	Labridae	1	< 0.1		1	1.82
Gymnothorax funebris	Muraenidae	1	< 0.1		1	1.82
Alphestes afer	Serranidae	1	< 0.1		1	1.82
Total: 26 species	16 families	4,750 individuals			55 censuses	

the wind velocity, bare rock and salinity. Species richness was also directly related to tidepools volume, but it was negatively related to the salinity (Table 2).

Q-mode cluster analysis resulted in groups which represented spatial and temporal discontinuities (Figure 4a). Tidepools 1 and 4 grouped together and represented the type 1 environment characterized by large volume (mean 187.4 m³) when compared with type 2 environment (average 49.3 m³ in volume; $F_{(1)} = 428.03$, $p < 0.01$). The type 1 environment is also marked by a predominance of rock covered with algae ($F_{(1)} = 110.82$, $p < 0.01$).
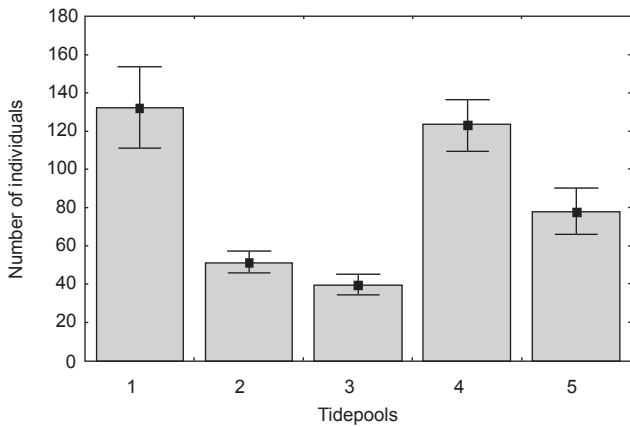
Figure 2. Mean (+/- standard error) of the total number of individuals per tidepools sampled at Iparana, from June 1998 to May 1999.

Figura 2. Média (+/- erro padrão) do número total de indivíduos por poças de maré amostradas em Iparana, de junho de 1998 a maio de 1999.
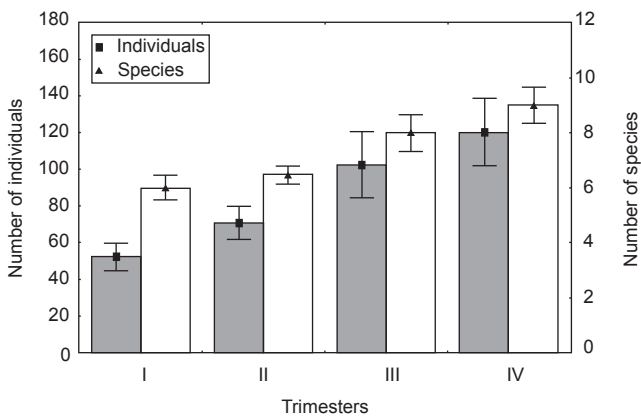
Figure 3. Mean (+/- standard error) of the total number of individuals and species per trimester in tidepools sampled at Iparana from June 1998 to May 1999.

Figura 3. Média (+/- erro padrão) do número total de indivíduos e espécies por trimestre em poças de maré amostradas em Iparana de junho de 1998 a maio de 1999.

Trimesters I and II clustered together and formed a winter-spring group (semester I), whereas the trimester III and IV formed a summer-fall group (semester II). Semester I was characterized by low rainfall (mean 37.33 mm), high salinity (mean 36.7) and wind velocity (mean 4.8 m.s⁻¹), whereas semester II showed a higher precipitation (mean 198.1 mm), lower salinity (mean 35.2) and lower wind velocity (mean 3.5 m.s⁻¹). All of these differences were significant.

R-mode cluster analysis formed three to four species groups, in which *Sparisoma axillare* and *Haemulon parra* were grouped together or considered as single species groups, depending on whether a spatial or temporal analysis was performed. The second group included *Eucinostomus* spp., *Abudefduf saxatilis*, *Lutjanus apodus*, and *Acanthurus chirurgus*; whereas the third group was formed by less abundant and frequent species (e.g. *Lutjanus jocu*, *Labrisomus nuchipinnis* and *Pomacanthus paru*). All 19 remaining species were clustered in this group. Either the groups two and three were consistent regardless if a spatial or temporal analysis was performed (Figure 4b).

Species and sample groups were reorganized into nodal contingency tables, aiming to maximize constancy and fidelity within each cell (nodes). Figure 5 shows the formation of four sampling dimensions (semesters 1 and 2 within environments 1 and 2) and seven species groups with the following characteristics:

Group I – represented by the dominant and most abundant species, showed a very high constancy and low fidelity to all environmental dimensions analysed, and was composed by *Sparisom* cf. *axillare*, *Haemulon parra*, *Lutjanus apodus*, *Eucinostomus* spp., and *Abudefduf saxatilis*;

Group II – had a moderate to very high constancy, especially in the Semester II, but low fidelity to all sampling dimensions, and included frequent species such as *Acanthurus chirurgus*, *Lutjanus jocu*, *Anisotremus virginicus*, *Pomacanthus paru*, and *Labrisomus nuchipinni*s;

Group III - this group presented low to moderate constancy and fidelity, particularly associated to Semester II and environment 1, and included *Mugil curema*, *Haemulon plumieri*, *Stegastes variabilis*, and *Gymnothorax vicinus*;

Groups IV – VII – these groups included occasional species, showed moderate to low constancy, but high to very high fidelity. The groups IV (*Gymnothorax funebris*, *Epinephelus adscensionis*) and V (*Anisotremus moricandi*, *Acanthurus coeruleus*, *Sphoeroides testudineus*, *Chaetodipterus faber*) were strongly associated with the environment 1, whereas the groups VI (*Anisotremus surinamensis*) and VII (*Alphestes afer*, *Scorpaena plumieri*, *Halichoeres brasiliensis*, *Haemulon steindachneri*) were strongly associated with the environment 2.

Discussion

The majority of the fishes in tidepools at Iparana were suprabenthic juvenile individuals of great mobility. According to Gibson & Yoshiyama (1999), the structure of tidepool fish com-

Table 2. Multiple regression models for total abundance and species richness as a function of the following independent variables: wind velocity (WV), bare rock (BR), rock covered with algae (RA), tidepool volume (PV), and salinity (SA). Significance level: * = 0.01 < p < 0.05; ** = p < 0.01.

Tabela 2. Modelos de regressão múltipla para a abundância total e riqueza de espécies em função das seguintes variáveis independentes: velocidade dos ventos (WV), rocha nua (BR) , rocha coberta com alga (RA), volume da poça (PV), e salinidade (SA). Nível de significância: * = 0,01 < p < 0,05; ** = p < 0,01.

			Regression Model ($y = y_0 + ax_1 + bx_2 + cx_3 ...$)				
Dependent Variables	**R²**	**F**	**y_0**	**a**	**b**	**c**	**d**	**e**
Total abundance	0.775	15.157**	4.732	-0.128* WV	-0.259** BR	0.002* RA	0.003** PV	-0.045** SA
Species richness	0.570	5.844**	1.022	0.257* PV	-0.021** SA			
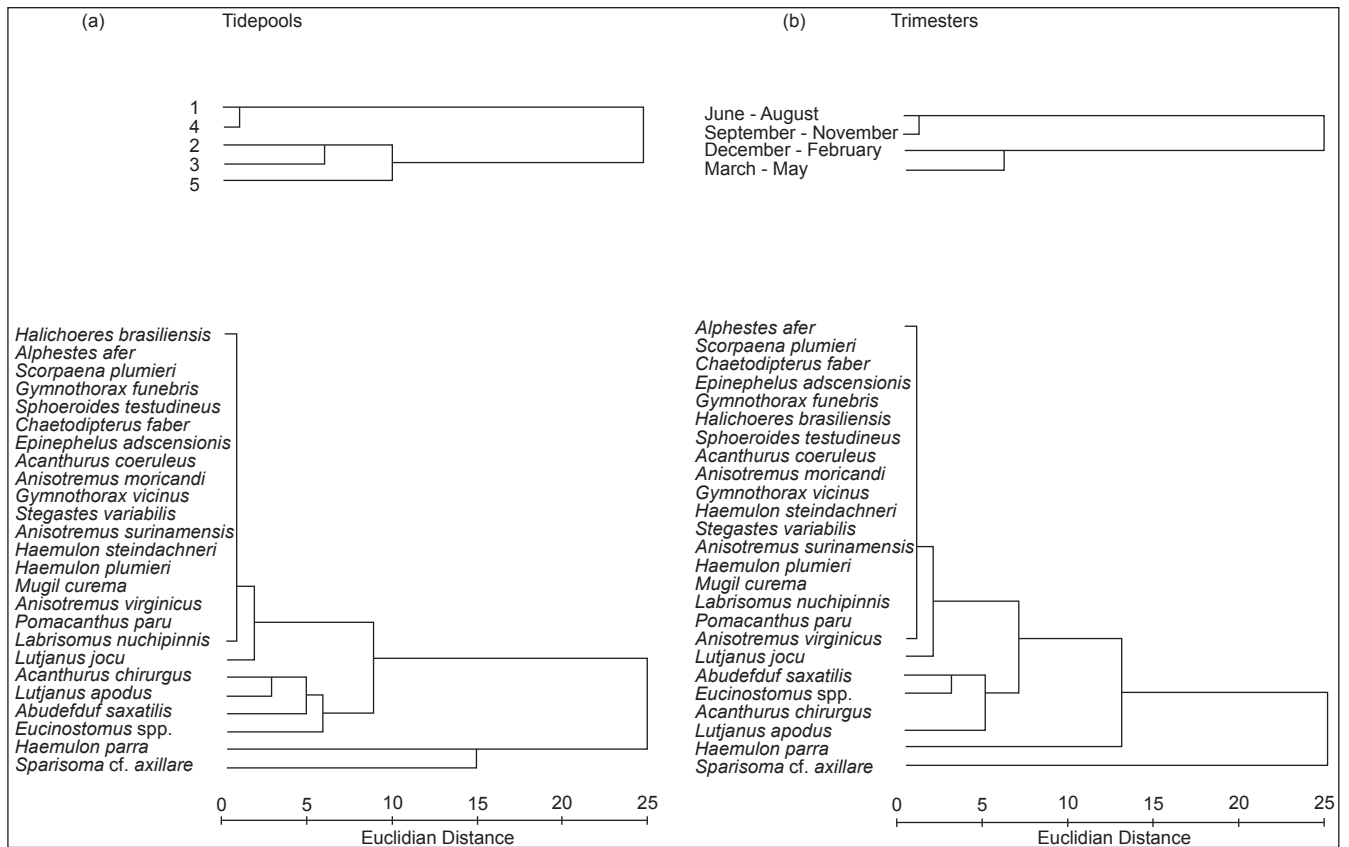
Figure 4. Dendrogram of results of cluster analysis (Euclidean distance, average linkage clustering method - UPGMA) of fish abundances by tidepools (a) and trimesters (b) at Iparana beach from June 1998 to May 1999. Trimesters: I (June - August), II (September - November), III (December - February), IV (March - May).

Figura 4. Dendrograma dos resultados da Análise de Agrupamento (Distância Euclidiana, método da ligação média não ponderada - UPGMA) da abundância de peixes por poças de maré (a) e trimestres (b) na praia de Iparana, de junho de 1998 a maio de 1999. Trimestres: I (Junho - Agosto), II (Setembro - Novembro), III (Dezembro - Fevereiro), IV (Março - Maio).

munities depends mostly on the size of the sampled area, the height of the pool within the intertidal zone, and the sample size. Mahon & Mahon (1994) stated that large tidepools close to the lowest intertidal zone, such the ones sampled in this study contained more species, and a higher proportion of transient species than tidepools located at the highest intertidal zone. These findings may explain why the tidepools at Iparana showed a greater proportion of transient and occasional species. Another consideration was the fact that visual census sub-samples cryptic species such gobies and blennies, often regarded as true residents in tidepools (Christensen & Winterbottom 1981, Brock 1982, Ackerman & Bellwood 2000, Ackerman & Bellwood 2002). Methods that adequately sample cryptic fishes often include ichthyocides, anaesthetics or empty the tidepools. Whereas these methods may yield accurate estimates of species richness, they may not be adequate to sample less isolated lower intertidal pools. Furthermore, such methods may be incompatible with conservation objectives and assessment of highly impacted areas (F.E.A. Cunha, unpublished data).

The fish dwellers at Iparana tidepools were mainly species recruited from surrounding subtidal areas. Gibson & Yoshiyama (1999) considered that tidepools may contain large number of juveniles representing predominant subtidal species, suggesting that, within the intertidal zone, tide pools may act as nursery habitats for such species. Their suggestion is based on the assumption that tidepools are spatial and temporal refuges from large-sized and numerous predators of the subtidal zone. Mahon & Mahon (1994) also observed that intertidal pools at Barbados (Caribbean) have many partial residents which are juveniles of reef species, and concluded that the intertidal habitats are natural juvenile stocks for many reef fish populations. A higher number of juvenile fishes from December to May (both in number of individuals and species) further support the hypothesis that these tidepools act as nursery sites.

Tidepools on rocky reefs at Iparana may also serve as refuges for opportunistic estuarine species. *Eucinostomus* spp., *Mugil curema*, and the species of Engraulidae were frequent on censuses, indicating that the studied area, which is located near the mouth of the Ceará river estuary, within large stretches of sandy beaches, uses to be visited by these species, probably seeking shelter and/or food during migrating periods to and from estuarine nursery grounds. The temporal structure of species communities in these areas is often the result of seasonal settlement or consecutive waves of migration by the juvenile stages. However, it is generally accepted that the movement of the juvenile fishes into the intertidal zone is related with feeding (Amara & Paul 2003). Another hypothesis focuses on the predation avoidance provided by the shallow intertidal waters (Gibson 1994).

Reproductive patterns in tropical latitudes are often linked with seasonal changes on wind strength and velocity, and also with the rainfall (Lowe-McConnell 1987). Similar correlations were found for fishes (Costa et al. 1995, Cunha et al. 2000) and lobsters (Fonteles-Filho 1986) on the coast of Ceará, in which the great-
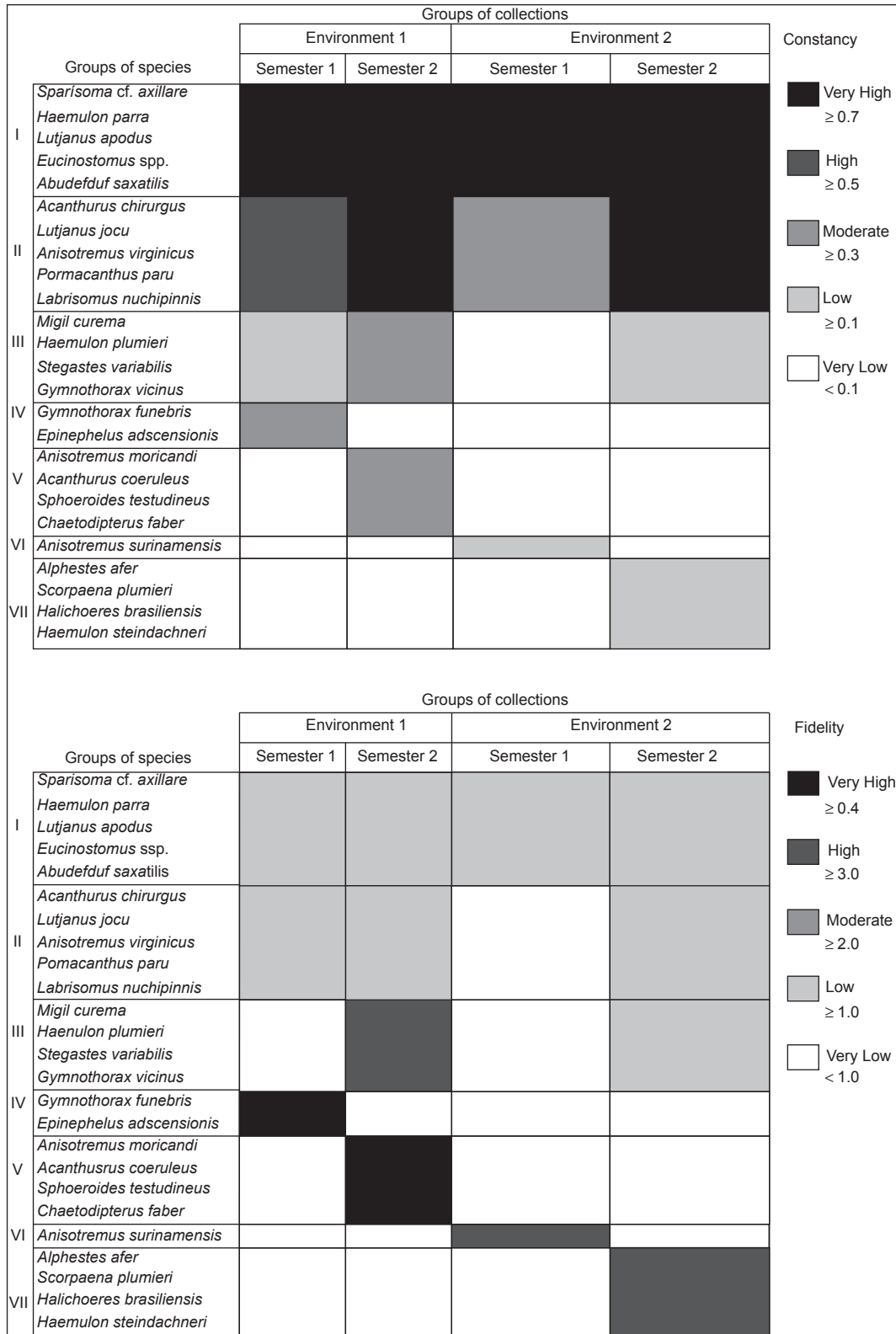
Figure 5. Nodal constancy (top) and fidelity (bottom) diagrams showing interrelations between seasonal (Semester 1: June - November; Semester 2: December - May) and spatial (Environment 1: tidepools 1, 4; Environment 2: tidepools 2, 3, 5), collections and groups of species (I-VII) at Iparana, from June 1998 to May 1999.

Figura 5. Diagramas dos índices de Constância (superior) e Fidelidade (inferior) Nodal mostrando as inter-relações entre grupos sazonais (Semestre 1: Junho - Novembro, Semestre 2: Dezembro - Maio), espaciais (Ambiente 1: poças de maré 1, 4; Ambiente 2: poças de maré 2, 3 e 5) e grupos de espécies (I-VII) em Iparana, de junho de 1998 a maio de 1999.

est abundance was observed during the rainy season. In fact, Alves & Lima (1978) observed that most of the fishes found off the coast of Ceará showed rest reproductive cycles during the dry windy season.

Multiple linear regression analysis was partly consistent with the environmental discontinuities indicated by Q-Mode cluster analysis. The positive correlation of both species abundance and richness and the presence of rock-algae substrate in environment 1 suggested that substrate structural complexity was probably one of the main factors defining spatial community structure. Bennett & Griffiths (1984) and Gibson & Yoshiyama (1999) reported that the area, volume, and rugosity of the tidepools are factors of great importance affecting the fish assemblage structure. Furthermore, the presence of holes and crevices of varied sizes in the rocky walls, and multiple sized boulders at the bottom further enhanced habitat complexity and, therefore, the abundance and diversity of the fish assemblages (Bennett 1987, Mahon & Mahon 1994, Núñez Lara & Arias González 1998). Ferreira et al. (2001) studying the rocky coastline in southern Brazil also observed that not only biotic factors (like abundance of sessile benthic invertebrates), but also the physical structure (like the surface area), explains the highest diversity and abundance of fishes.

The fact that the tidepools volume was a significant factor in this study corroborates the literature, and support the hypothesis that tidepools size also plays an important role at Iparana, mostly by controlling the habitat variability. For instance, Rosa & Moura (1997) suggested that large volume tidepools are less affected by temperature and salinity variations, which can reach critical levels in such micro-ecosystems. The positive correlation of species richness and tidepools volume, and its negative correlation with salinity, may be an important evidence of the buffering effect of large tidepools vs. the small ones at Iparana.

The species associations found in this study and their relation to seasonal and spatial discontinuities may be partly explained according to their habitat requirements and reproductive cycles. Species belonging to group I in our classification were considered by Alves & Lima (1978) as ubiquitous, abundant and nearly year round spawners in the coast of Ceará, whereas those of groups II and III often show reproduction peaks matching the semester II of our classification. Species groups II and III also showed a greater affinity with larger and more complex tidepools. Groups I and III give a substantial contribution in number of species and individuals to the fish community in the tidepools at Iparana, being considered as true and partial residents, according to the classification of Mahon & Mahon (1994). The species *Labrisomus nuchippinis* and *Gymnothorax vicinus* are true cryptic residents. The other species of Groups I and III are partial residents in the tidepools, occurring mainly as juveniles. Species belonging to Groups from IV to VII were classified as transient or occasional species.

In summary, we conclude that the tidepool fish fauna at Iparana presents complex seasonal and spatial relationships, dependent upon cyclic changes on physical environment and reproduction of its fish species. Connectivity and interdependence between the tidepools and the adjacent ecosystems such as the subtidal reefs, sandy shores and estuaries was also apparent in our study. However, despite our findings that some environmental and habitat variables appeared to influence the structure of the tidepool fish assemblages, it is necessary to investigate other mechanisms related within community structure and population size such as recruitment, predation, and competition patterns, assessing theirs effects on such fish assemblage structures.

Acknowledgments

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