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Diversity and turnover in a rocky shore intertidal community of an upwelling region (Arraial do Cabo, Brazil)

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Abstract: The present study describes the community diversity and gives a seasonal distribution of an intertidal macroalgal assemblage at Prainha Beach, Arraial do Cabo City in Rio de Janeiro state, Brazil. Sampling was performed during four seasons of a 1-year period. Organisms were sampled and photographed using photoquadrats to quantify relative coverage. Ninety-six taxa of macroalgae were registered, including 23 chlorophytes, 19 ochrophytes, and 54 rhodophytes, while three barnacles, seven mollusks, one isopod, and one polychaete were recorded among the zoobenthos. In the upper intertidal zone, the coverage was frequently dominated by invertebrates. Macroalgae always dominated the middle and lower zones, covering almost 100 % in both zones. The highest values of species diversity (H'), richness (S), and turnover rates were found during the transition from spring to summer, which coincided with the upwelling period. A comparison with the 1980's flora revealed that the major changes in the macroalgal assemblage were among species belonging to the same genera, unless new additions were provided. The combination of photoquadrats and minimally destructive sampling allowed a detailed description of the composition and structural characteristics of the intertidal zone, a methodology that should be applied to study protected marine areas.

Key words: intertidal benthic communities, macroalgae, southwestern atlantic ocean, seasonal variability, upwelling system.

INTRODUCTION

Rocky shores are dynamic coastal environments that are considered to be zones of transition between aquatic and terrestrial ecosystems and are inhabited predominantly by specially adapted marine organisms (Ros et al. 1985). The diversity and productivity of rocky shores are associated with the presence of marine macroalgae, which are the main primary producers and serve as substrate, shelter, and reproduction sites for many vertebrates and marine invertebrates (Széchy et al. 2001, Tano et al. 2016). Besides, the presence of a variety of organisms there may serve as indicators of environmental conditions (Murray et al. 2006, Pinedo et al. 2007, Borja et al. 2012). For instance, Ulvophyceae may present higher coverage or be favored in anthropogenic disturbed sites (Faveri et al. 2010, Teichberg et al. 2010, Scherner et al. 2013), while the coverage of Phaeophyceae is reduced or locally absent under these conditions (Oliveira & Qi 2003, Menconi et al. 2012, Széchy et al. 2017). Zonation patterns and natural fluctuations are also broadly investigated concepts at different rocky shores worldwide (Masi et al. 2009, Goméz & Huovinen 2011, Stevčić et al. 2017, Vinagre et al. 2017, Little et al. 2018).

The coast of Brazil's Rio de Janeiro state is on the eastern coast of South America and is at the edge of two marine provinces: the Tropical Southwestern Atlantic and the Warm Temperate Southwestern Atlantic (Spalding et al. 2007). The region of Arraial do Cabo within this state is often treated as part of the border between these provinces, and because of this, Prainha Beach (within this region) can be considered an ecotone area. This area is seasonally under the influence of upwelling by the South Atlantic Central Water (SACW), which constitutes a discontinuous biogeographic barrier for marine fauna and flora in the Southwestern Atlantic and is thus recorded as the northern or southern limit of many species' distributions (Yoneshigue 1985, Guimaraens & Coutinho 1996, Floeter & Soares-Gomes 1999). The fisherman population of Arraial do Cabo demanded the establishment of a marine reserve to protect the integrity of the marine biodiversity in this area, which is a locally important economic resource (Mendonça et al. 2013). Thus, the Reserva Extrativista Marinha do Arraial do Cabo (RESEX) was established in 1997 to assure the sustainable utilization of marine resources by the traditional fishermen populations and the recreational and other activities under management norms (Silva 2004, ICMBIO 2017). These particular conditions support the high biodiversity of species with tropical and temperate affinities in the region, leading to the establishment of several lists and spatiotemporal comparisons of macroalgae in this area, particularly those of Yoneshigue (1985), Guimaraens & Coutinho (1996), and Brasileiro et al. (2009).

Several methodologies have been used to track the diversity of the marine organisms (Gomèz & Huovinen 2011, Trivedi et al. 2016, Perera-Valderrama et al. 2017, Rohde et al. 2017), however, the use of photographic sampling has arisen recently as a particularly quick and non-destructive alternative method to traditional destructive sampling techniques (Solan et al. 2003, Durden et al. 2016, Beisiegel et al. 2018). This method, allied to a new generation of software, facilitates statistical analyses and reporting of the occurrence of species in several habitats (Tanner et al. 2015, Arefin 2016, Gomes-Pereira et al. 2016, Romero-Ramirez et al. 2016).

Combining evidence from the RESEX implemented in Arraial do Cabo, including its oligotrophic status (Guimaraens & Coutinho 2000, Jara et al. 2006, Coelho-Souza et al. 2017) and the concept of natural fluctuations induced by environmental and biological factors (Hoek 1982, Ives & Carpenter 2007, Nascimento et al. 2014), we hypothesized that the species of marine flora at Prainha has changed over the years by its ecological equivalent (i.e. species with similar ecological function) and, consequently, there has been a large turnover of the species in this area. Thus, the aims of the present study were to (I.) analyze the diversity of an intertidal community of a rocky shore at Prainha and the turnover of its macroalgae assemblage throughout all four seasons, (II.) assess the change in the macroalgal composition of this community over an interval of almost 30 years, and (III.) evaluate the efficiency of different combinations of destructive and photographic approaches to characterize the species coverage and diversity of this rocky shore benthic community.

MATERIALS AND METHODS

Sampling was performed seasonally between 2011 and 2012 at Prainha Beach, Arraial do Cabo city, Rio de Janeiro state, Brazil (22°57'22.1"S, 42°01'36.5"W). It was an integrative approach of a non-destructive method with a minor destructive method and always performed at low tide on the left side of the rocky shore located outside the beach. The area sampled was approximately 10 m in length, which was horizontally delimitated with a line transect above the intertidal region and divided into three vertical zones (upper, middle, and lower) based on the typically predominant organisms found in each zone. At each vertical zone, five 900 cm² quadrats were randomly placed for photographic sampling. IIn addition, we manually collected macroalgae specimens from the transect area and those living around the rocky shore (outside the transect area) within a 40 min period to assist identification of local biodiversity, none marine invertebrates were collected. These collections were done to obtain estimates of the species richness and turnover while also sustaining the photoquadratic identifications. Specimens were collected, separated according to their intertidal zone, and preserved in a solution of 4 % formalin diluted in seawater for later identification.

At the laboratory, macroalgal taxa were identified to the lowest level possible with Olympus CX40 optical microscopy and Olympus SZ51 stereoscopic microscope, following Taylor (1972), Littler & Littler (2000) and Dawes & Mathieson (2008). Nomenclatural updates followed Flora 2020 (http://floradobrasil.jbrj.gov.br) and AlgaeBase (Guiry & Guiry 2019). The resulting list of macroalgae was compared to the data provided by Yoneshigue (1985) (Table I) to the same locality. Species that were considered as new occurrences for the area were deposited in the Herbarium Jorge Pedro Pereira Carauta (HUNI). The turnovers between seasons in the present study and between the species list from the current study and that proposed by Yoneshigue (1985), were calculated based on the concept of extinction (absence of species) and immigration (appearance of species) of all species along the shore throughout time as suggested in Brown & Kodrick-Brown (1977) and Magurran (2006).

The coverage of the community by each taxon was analyzed using Coral Point Count with Excel extensions (CPCe) (Kohler & Gill 2006) via an adapted database containing the names of the organisms in the studied region. When possible, identification of organisms from the photoquadrats was performed to the species level. However, it was not possible to identify small organisms to the species level using photographic analysis, in which case they were identified to the morphological or order level. In the coverage analysis, all taxa identified were treated as Community Components (CCs) based on their taxonomic or morphological level. Thirty points were randomly placed on each photograph for coverage analysis. The number of points needed to adequately represent the coverage of the community was established according to Silva et al. (2015). Afterwards, Shannon-Wiener (H') and Evenness (J) diversity indices were calculated based on the coverage of each and all species (Magurran 2006).

RESULTS

Coverage analysis

The upper zone of the rocky shore was dominated by invertebrates, which made up more than half of the CCs in all seasons, and the invertebrate cover was higher during winter, summer, and autumn, whereas algae had a higher coverage than invertebrates in the spring (Figure 1). For instance, *Tetraclita stalactifera* Lamarck 1818 (TET) was the most abundant species during the winter, spring, and summer and *Mytilaster solisianus* d'Orbigny 1842 (MYT) in autumn, winter and summer. In autumn, however, the crustose non-coralline rhodophyte *Hildenbrandia rubra* (Sommerfelt) Meneghini (HIL) was the most abundant species. Community components with less percentage coverages were identified during the year and included taxa such as TET, *Amphibalanus amphitrite* Darwin 1854 (AMA), *Perna perna* Linnaeus 1758

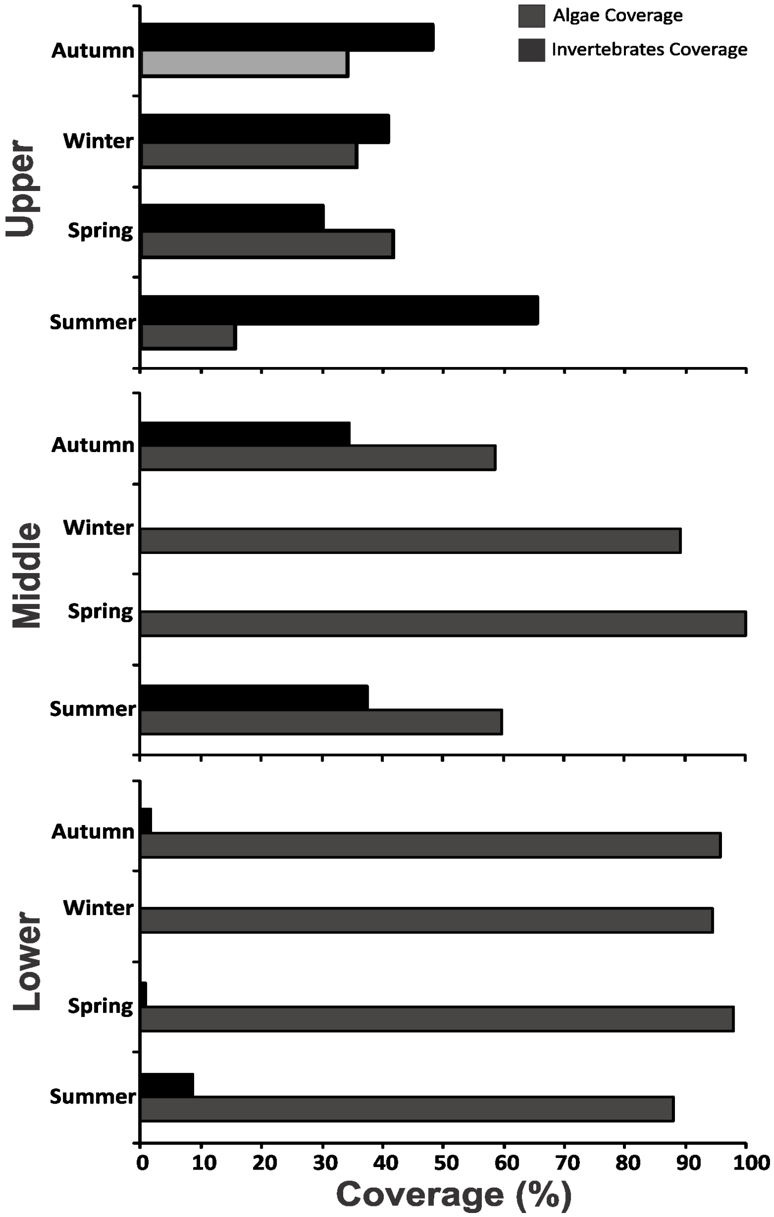

Figure 1. Sum of coverage Mean of Macroalgae and Invertebrate in each intertidal zone.

(PER), *Chthamalus bisinuatus* Pilsbry 1916 (CHT), crustose Corallinales and laminar forms of *Ulva* spp. (including *Ulva fasciata* Delile and *Ulva rigida* C. Agardh). Spring was the season with the highest diversity (16 CCs), while autumn had the lowest (10 CCs) (Figure 2).

In the middle and lower zones, macroalgae were the dominant organisms on the substrate throughout the year (Figure 1). The most important CC with the highest coverage was the group of articulated Corallinales (ACO), however, other algae were also found in both zones, *e.g.*, laminar forms of *Ulva* spp., crustose Corallinales (CCO), *Padina* spp. (PAD), *Colpomenia sinuosa* (Mertens ex Roth) Derbès & Solier (COL), and *Hypnea* spp. (HYP). Some invertebrates that were characteristic of the upper zone, such as TET, AMA and PER were also observed in the middle zone during the summer (Figure 2).

Table I: Comparison of intertidal species list from Prainha by Yoneshigue (1985) and the current study. Species that were listed only in the present study are highlighted with **bold**, species registered within Prainha by Yoneshigue (1985) and by the present study are also marked with "*" and species listed only by Yoneshigue (1985) are not in bold. The species recognized by CPCe received the classification codes as follow: "ACO" – Articulated Corallinales; "CEG" – *Centroceras gasparrinii*; "FRH" – Filamentous Rhodophyta; "GEL" – Gelidiales; "GYM" – *Gymnogongrus griffthsiae*; "HIL" – *Hildenbrandia rubra*; "HYP" – *Hypnea* spp.; "LAU" – *Laurencia* spp.; "TRH" – Turfs of Rhodophyta; "CAN" – *Canistrocarpus cervicornis*; "COL" – *Colpomenia sinuosa*; "FOC" – Filamentous Ochrophyta; "CHA" – *Chaetomorpha antennina*; "ENT"- Tubular Ulva; "ULV" – Foliose Ulva; "FCH" – Filamentous Chlorophyta; "TCH" – Turfs of Chlorophyta; "COE" – Erect Codium; "COC" – Crustose Codium"; "AMA" – *Amphibalanus amphitrite*; "CHT" – *Chthamalus bisinuatus*; "FIS" – *Fissurella clenchi*; "ISO" – *Isognomon bicolor*; "LOT – *Lottia subrugosa*; "MYT" – *Mytilaster solisianus*; "OST" – Ostreidae; "PER" – *Perna perna*; "PHR" – *Phragmatopoma caudata*; "STA" – *Stramonita haemastoma*; "-" Not Identified in the Photography; "ND" No data, i.e., not found during this study.

	Community Components
Rhodophyta	
Stylonemataceae	
***Bangiopsis dumontioides* (P.L.Crouan & H.M.Crouan) V.Krishnmurthy**	-
***Stylonema alsidii* (Zanardini) K.M.Drew ***	-
Erythrotrichiaceae	
***Erythrotrichia carnea* (Dillwyn) J.Agardh ***	-
Sahlingia subintegra* (Rosenvinge) Kornmann	-
Bangiaceae	
Bangia fuscopurpurea (Mertens ex Roth) C.Agardh	ND
***Porphyra pujalsiae* Coll & E.C.Oliveira ***	-
Pyropia acanthophora (E.C.Oliveira & Coll) M.C.Oliveira, D.Milstein & E.C.Oliveira	ND
Colaconemataceae	
***Colaconema codicola* (Børgesen) Stegenga, J.J.Bolton & R.J.Anderson**	-
Acrochaetiaceae	
Acrochaetium crassipes (Børgesen) Børgesen	ND
Acrochaetium flexuosum Vickers	ND
Acrochaetium globosum Børgesen	ND
***Acrochaetium microscopicum* (Nägeli ex Kützing) Nägeli in Nägeli & Cramer**	-
Gelidiellaceae	
Millerella pannosa (Feldmann) G.H.Boo & L.Le Gall	ND
Gelidiaceae	
***Gelidium pusillum* (Stackhouse) Le Jolis ***	GEL
Pterocladiaceae	
***Pterocladiella capillacea* (S.G.Gmelin) Santelices & Hommersand ***	TRH
***Pterocladiella caerulescens* (Kützing) Santelices & Hommersand**	TRH
Bonnemaisoniaceae	
***Asparagopsis taxiformis* (Delile) Trevisan**	FRH

Table I (continuation)

Plocamiaceae	
Plocamium brasiliense (Greville) M. Howe & W.R.Taylor	ND
Lomentariaceae	
Ceratodictyon variabile (J.Agardh) R.E.Norris	ND
Lomentaria rawitscheri A.B.Joly	ND
Gracilariaceae	
Gracilaria cervicornis (Turner) J. Agardh	ND
Gracilaria mammillaris (Montagne) M.A.Howe	-
Cystocloniaceae	
Hypnea cervicornis J. Agardh*	HYP
Hypnea pseudomusciformis Nauer, Cassano & M.C.Oliveira *[1]	HYP
Hypnea spinella (C. Agardh) Kützing *	HYP
Phyllophoraceae	
Gymnogongrus griffthsiae (Turner) C. Martius*	GYM
Gigartinaceae	
Chondracanthus acicularis (Roth) Fredericq	CHO
Chondracanthus saundersii C.W.Schneider & C.E.Lane	CHO
Chondracanthus teedei (Mertens ex Roth) Kützing *	CHO
Corallinaceae	
Amphiroa beauvoisii J.V.Lamouroux *	ACO
Amphiroa brasiliana Decaisne	ACO
Amphiroa fragilissima (Linnaeus) J.V. Lamouroux	ND
Arthrocardia flabellata (Kützing) Manza	ND
Arthrocardia variabilis (Harvey) Weber-van Bosse	ACO
Corallina officinalis Linnaeus	ND
Jania adhaerens J.V. Lamouroux *	ACO
Jania capillacea Harvey *	ACO
Jania rubens (Linnaeus) J.V. Lamouroux	ACO
Pneophyllum fragile Kützing	ND
Hildenbrandiaceae	
Hildenbrandia rubra (Sommerfelt) Meneghini *	HIL
Champiaceae	
Champia parvula (C.Agardh) Harvey	TRH
Champia vieillardii Kützing	TRH
Gastroclonium parvum (Hollenberg) C.F.Chang & B.M.Xia	TRH
Rhodymeniaceae	
Rhodymenia Pseudopalmata (Lamouroux) Silva	ND

Table I (continuation)

Callithamniaceae	
Aglaothamnion uruguayense (W.R.Taylor) N.E.Aponte, D.L.Ballantine & J.N.Norris	ND
Ceramiaceae	
Centroceras clavulatum (C. Agardh) Montagne	ND
***Centroceras gasparrinii* (Meneghini) Kützing**	CEG
***Centrocerocolax ubatubensis* A.B. Joly ***	-
***Ceramium brasiliense* A.B. Joly ***	TRH
***Ceramium brevizonatum* var. *caraibicum* H.E.Petersen & Børgesen in Børgesen**	TRH
***Ceramium clarionense* Setchell & N.L.Gardner**	TRH
Ceramium codii (H. Richards) Mazoyer	ND
***Ceramium dawsonii* A.B. Joly *** [2]	TRH
Ceramium lutzelburgii O.C. Schmidt	ND
***Ceramium tenerrimum* (G. Martens) Okamura ***	TRH
***Ceramium vagans* P.C.Silva in P.C. Silva, Meñez & Moe**	TRH
Gayliella mazoyerae T.O.Cho, Fredericq & Hommersand [3]	ND
Gayliella sp. [4]	ND
Wrangeliaceae	
Anotrichium tenue (C.Agardh) Nägeli	ND
***Wrangelia argus* (Montagne) Montagne**	-
Spyridiaceae	
***Spyridia hypnoides* (Bory) Papenfuss ***	TRH
Delesseriaceae	
Cryptopleura ramosa (Hudson) Kylin ex Newton	ND
***Taenioma perpusillum* (J.Agardh) J.Agardh**	-
Dasyaceae	
Dasya brasiliensis E.C.Oliveira Filho & Y.Y.Braga	ND
Dasya corymbifera J. Agardh	ND
***Dasya ocellata* (Grateloup) Harvey in Hooker**	FRH
***Dasya rigidula* (Kützing) Ardissone**	TRH
Rhodomelaceae	
Bostrychia binderi Harvey	ND
Bryocladia thyrsigera* (J.Agardh) F.Schmitz in Falkenberg	TRH
***Chondria atropurpurea* Harvey**	TRH
***Herposiphonia bipinnata* M. Howe**	-
***Herposiphonia delicatula* Hollenberg**	-
***Herposiphonia nuda* Hollenberg**	-
***Herposiphonia parca* Setchell**	-

Table I (continuation)

Herposiphonia secunda (C Agardh) Ambronn	ND
Herposiphonia secunda var. tenella (C. Agardh) M.J. Wynne	ND
***Laurencia aldingensis* Saito & Womersley**	LAU
***Laurencia dendroidea* J.Agardh**	LAU
Melanothamnus ferulaceus (Suhr ex J.Agardh) Díaz-Tapia & Maggs	ND
***Melanothamnus gorgoniae* (Harvey) Díaz-Tapia & Maggs**	-
***Melanothamnus sphaerocarpus* (Børgesen) Díaz-Tapia & Maggs**	-
Murrayella periclados (C. Agardh) F. Schmitz	ND
***Polysiphonia scopulorum* Harvey**	-
Polysiphonia villum J.Agardh	ND
***Xiphosiphonia pennata* (C.Agardh) Savoie & G.W.Saunders ***	-
Ochrophyta	
Acinetosporaceae	
***Feldmannia indica* (Sonder) Womersley & A.Bailey**	-
***Feldmannia irregularis* (Kützing) G.Hamel ***	-
***Feldmannia mitchelliae* (Harvey) H.-S.Kim ***	-
Bachelotiaceae	
***Bachelotia antillarum* (Grunow) Gerloff**	-
Asteronemataceae	
***Asteronema breviarticulatum* (J.Agardh) Ouriques & Bouzon ***	FOC
Ectocarpaceae	
***Ectocarpus fasciculatus* Harvey**	FOC
Ectocarpus rallsiae Vickers	ND
Chordariaceae	
***Levringia brasiliensis* (Montagne) A.B.Joly ***	FOC
Neoralfsiaceae	
Neoralfsia expansa (J.Agardh) P.-E.Lim & H.Kawai ex Cormaci & G.Furnari	ND
Scytosiphonaceae	
***Chnoospora minima* (Hering) Papenfuss**	FOC
***Colpomenia sinuosa* (Mertens ex Roth) Derbès & Solier ***	COL
***Rosenvingea orientalis* (J.Agardh) Børgesen**	FOC
Rosenvingea sanctae-crucis Børgesen *	FOC
Sphacelariaceae	
Sphacelaria brachygonia Montagne	ND
***Sphacelaria novae-hollandiae* Sonder**	-
***Sphacelaria tribuloides* Meneghini**	-
Dictyotaceae	
***Canistrocarpus cervicornis* (Kützing) De Paula & De Clerck**	CAN

Table I (continuation)

***Dictyopteris delicatula* Lamouroux**	-
Dictyota menstrualis (Hoyt) Schnetter, Hörning & Weber-Peukert[5]	ND
***Padina antillarum* (Kützing) Piccone**	PAD
***Padina gymnospora* (Kützing) Sonder ***	PAD
Sargassaceae	
***Sargassum furcatum* Kützing ***	-
***Sargassum vulgare* C.Agardh**	-
Chlorophyta	
Ulvaceae	
***Ulva compressa* Linnaeus ***	ENT
Ulva fasciata Delile	ND
***Ulva flexuosa* Wulfen ***	ENT
***Ulva lactuca* Linnaeus**	ULV
***Ulva linza* Linnaeus**	ENT
***Ulva prolifera* O.F.Müller**	ENT
***Ulva rigida* C. Agardh ***	ULV
Ulvellaceae	
Ulvella viridis (Reinke) R.Nielsen, C.J.O'Kelly & B.Wysor	ND
Kornmanniaceae	
Pseudendoclonium marinum (Reinke) Aleem & E. Schulz	ND
Cladophoraceae	
***Chaetomorpha aerea* (Dillwyn) Kützing**	-
***Chaetomorpha antennina* (Bory) Kützing ***	CHA
***Chaetomorpha brachygona* Harvey ***	-
Cladophora rupestris (Linnaeus) Kützing	ND
***Cladophora sericea* (Hudson) Kützing**	FCH
***Cladophora vagabunda* (Linnaeus) Hoek ***	FCH
***Rhizoclonium riparium* (Roth) Harvey**	FCH
***Willeella brachyclados* (Montagne) M.J.Wynne ***	FCH
Valoniaceae	
Valonia macrophysa Kützing	ND
Boodleaceae	
***Cladophoropsis macromeres* W.R.Taylor**	TCH
***Phyllodictyon anastomosans* (Harvey) Kraft & M.J.Wynne**	TCH
Bryopsidaceae	
Bryopsis corymbosa J. Agardh	ND
***Bryopsis pennata* Lamouroux**	FCH

Table I (continuation)

***Bryopsis plumosa* (Hudson) C. Agardh**	FCH
***Bryopsis ramulosa* Montagne**	FCH
Derbesiaceae	
Derbesia marina (Lyngbye) Solier	ND
Derbesia tenuissima (Moris & De Notaris) P.Crouan & H.Crouan	ND
Codiaceae	
***Codium decorticatum* (Woodward) M. Howe ***	COE
***Codium intertextum* Collins & Hervey ***	COE
Codium isthmocladum Vickers	ND
***Codium spongiosum* Harvey ***	COC
***Codium taylorii* P.C.Silva ***	COE
Caulerpaceae	
***Caulerpa racemosa* (Forsskål) J.Agardh**	-

[1] reported as *Hypnea musciformis* (Wulfen) J.V. Lamouroux by Yoneshigue (1985)

[2] reported as *Ceramium taylorii* E.Y. Dawson by Yoneshigue (1985)

[3] reported as *Ceramium gracillimum* var. *byssoideum* Mazoyer by Yoneshigue (1985)

[4] following Wynne (2017), *Ceramium flaccidum* in Brazil must be considered a non-identified ***Gayliella*** species.

[5] reported as *Dictyota dichotoma* (Hudson) J.V. Lamouroux by Yoneshigue (1985)

Invertebrates	
Arthropoda	
Tetraclitidae	
***Tetraclita stalactifera* (Lamarck, 1818)**	TET
Chthamalidae	
***Chthamalus bisinuatus* Pilsbry, 1916**	CHT
Balanidae	
***Amphibalanus amphitrite* (Darwin, 1854)**	AMA
Ligiidae	
***Ligia exotica* Roux, 1828**	LYG
Mollusca	
Muricidae	
***Stramonita haemastoma* (Linnaeus 1787)**	STA
Fissurellidae	
***Fissurella clenchi* Pérez Farfante, 1943**	FIS
***Lottia subrugosa* (d'Orbigny, 1846)**	LOT
Mytilidae	
***Mytilaster solisianus* (d'Orbigny, 1842) ***	MYT
***Perna perna* (Linnaeus, 1758) ***	PER

Table I (continuation)

Ostreidae	
***Cassostrea rhizophorae* (Guilding, 1828)**	OST
Pteriidae	
***Isognomon bicolor* (C.B. Adams, 1845)**	ISO
Annelida	
Sabellariidae	
***Phragmatopoma caudata* Krøyer in Mörch, 1863**	PHR

In comparison to other seasons and zones, the coverage of the middle zone during the summer presented the highest total number of CCs, making it the most diverse assemblage in terms of coverage found throughout the year (Figure 2). During winter and spring, the middle zone was dominated by articulated Corallinales (ACO, 36-54 % coverage), while invertebrates were absent. Afterwards, in summer and autumn, the dominance of articulated Corallinales was replaced by *Chaetomorpha antennina* (Bory) Kützing (CHA, 18.5 %) and HIL (25.7 %), and the invertebrates returned and made up for more than half of the CCs registered.

In the lower zone, macroalgae accounted for more than 87 % of the coverage (Figure 1). The ACO were the prevailing CC for the whole year. The principal component of this algal group was *Jania crassa* J. V. Lamouroux, but it also included *Amphiroa beauvoisii* J. V. Lamouroux to a lesser extent. The number of registered CCs in the lower zone went from eight during the winter up to 14 in autumn, with invertebrates accounting for two CCs or less during the entire period sampled (Figure 2).

Macroalgal assemblage richness, diversity, and turnover

The Shannon diversity index values obtained demonstrated that the richness and homogeneity of the species present decreased between summer and autumn in the upper zone (Figure 3). Between spring and summer, the richness in the middle zone increased considerably, although there was no concurrent change in the equitability (Figure 3). This change in the number of species was concomitant with the highest turnover rate for the whole year (Figure 4d). In the transition between spring and summer, six species were not observed, and eight new occurrences appeared in the macroalgal assemblage. This variation was greater than the annual turnover in the region, and thus this was the period out of the year with the largest replacement of organisms (Figure 4d).

In the lower zone, the richness and equitability exhibited little variation, which was reflected in the fact that the diversity of this zone was similar in all seasons of the year (Figure 3). Regarding the turnover rate between winter and spring, eight new species were recorded, while seven were not observed on the rocky shore after this period (Figure 4d).

In terms of the turnover of phyla, the turnover rate of Chlorophyta ranged from 0.27 to 0.42, with the largest change occurring between spring and summer (Figure 4a). Rhodophyta exhibited high turnover rates (> 0.50) for all seasons, indicating constant and major shifts in the composition of red macroalgal assemblages (Figure 4b). Comparing the present study and the former (Yoneshigue 1985) community compositions were compared, green algae were also found to have a lower turnover rate than

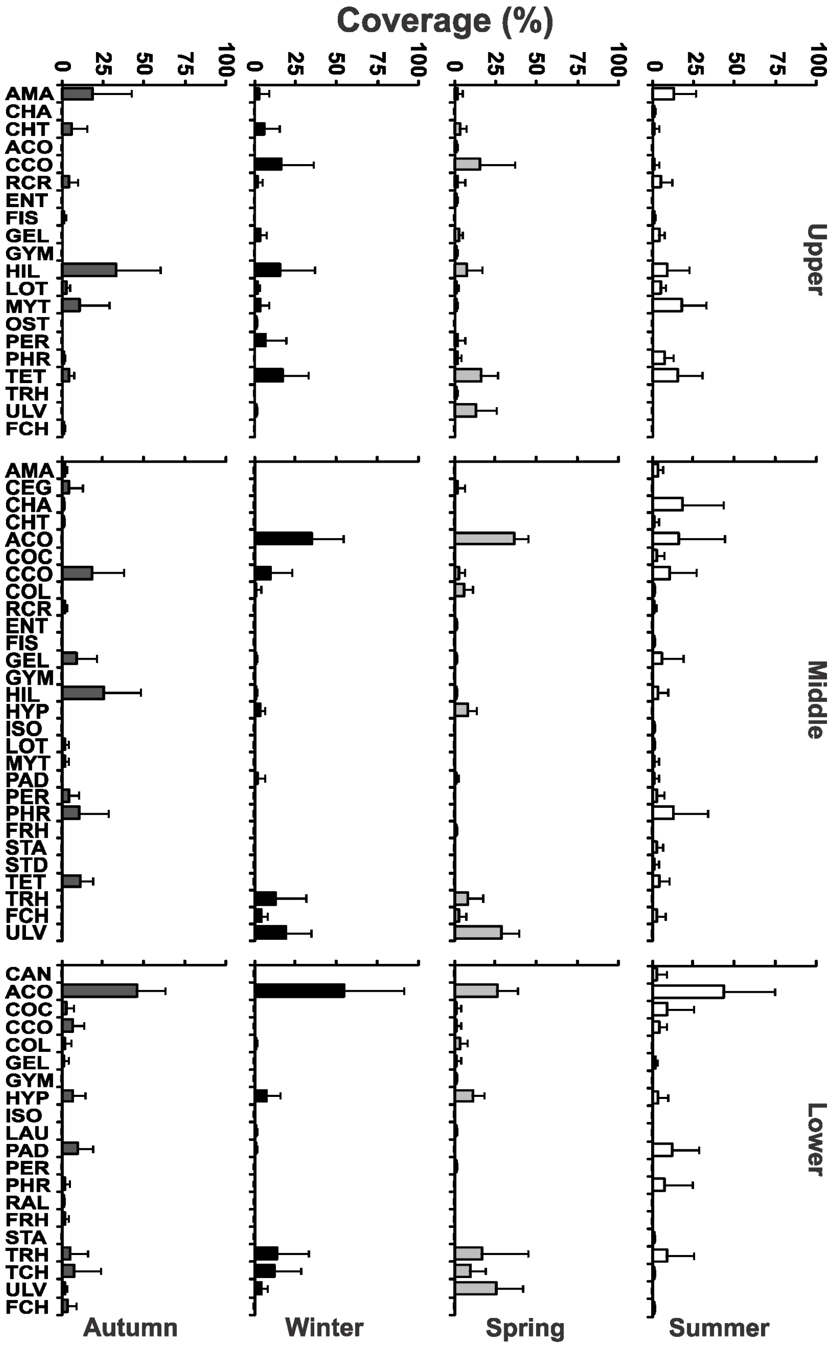

Figure 2. Percent cover of different community components (CC) in each zone. Values presented are means ± standard deviations. AMA = *Amphibalanus amphitrite;* CAN = *Canistrocarpus cervicornis;* CEG = *Centroceras gasparrinii;* CHA = *Chaetomorpha antennina;* CHT = *Chthamalus bisinuatus;* ACO = Articulated Corallinales; COC = *Codium spongiosum;* CCO = Crustose Corallinales; COL = *Colpomenia sinuosa;* RCR = Recruit Cirripedia; ENT = Tubular *Ulva* spp.; FCH = Filamentous Chlorophyta; FIS = *Fissurella clenchi;* FRH = Filamentous Rhodophyta; GEL = Gelidiales; GYM = *Gymnogongrus griffithsiae;* HIL = *Hildenbrandia rubra;* HYP = *Hypnea* spp.; ISO = *Isognomon bicolor;* LAU = *Laurencia* spp.; LOT = *Lottia subrugosa;* MYT = *Mytilaster solisianus;* OST = *Cassostrea rhizophorae;* PAD = *Padina* spp.; PER = *Perna perna;* PHR = *Phragmatopoma caudata;* RAL = *Neoralfsia expansa;* STA = *Stramonita haemastoma;* STD = *Stramonita haemastoma spawning;* TCH = Turfs of Chlorophyta; TET = *Tetraclita stalactifera;* TRH = Turfs of Rhodophyta; ULV = Laminar *Ulva* spp.

Rhodophyta (Figure 4e). However, Ochrophyta was a phylum that underwent lower annual variations than others (Figure 4c), nevertheless, it experienced a higher turnover during the transitions from spring to summer and winter to spring. Comparing to Yoneshigue (1985) dataset, Ochrophyta also showed the lowest turnover rate, with low exclusion and immigration rates compared to those of other phyla (Figure 4c).

Macroalgal comparison

Yoneshigue (1985) registered 85 species as occurring at Prainha Beach, of which 20 were species of Chlorophyta, 12 were Ochrophyta, and

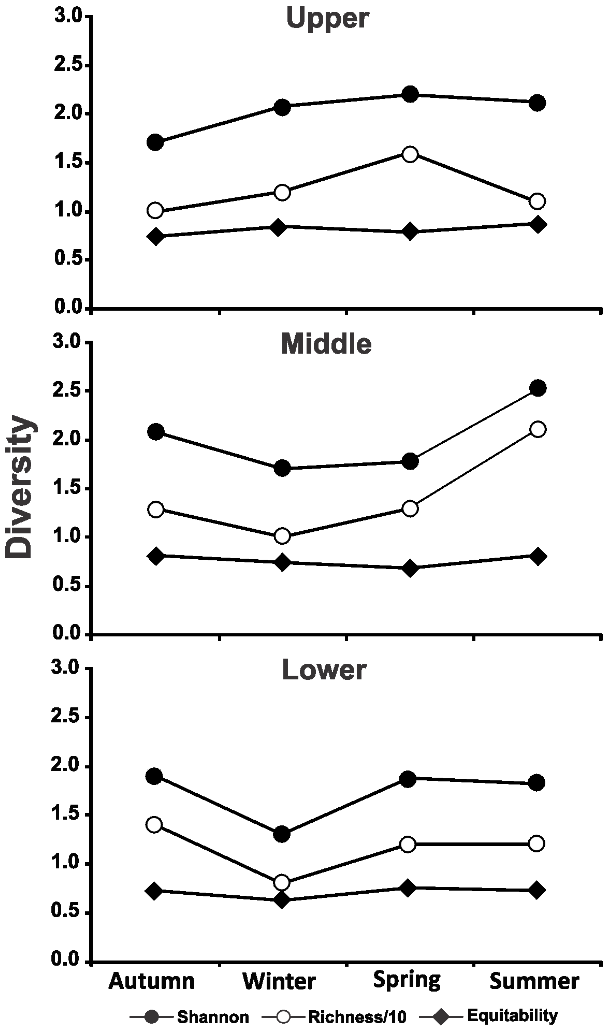

Figure 3. Diversity indices calculated for the upper, middle, and lower zones of the rocky shore at Prainha.

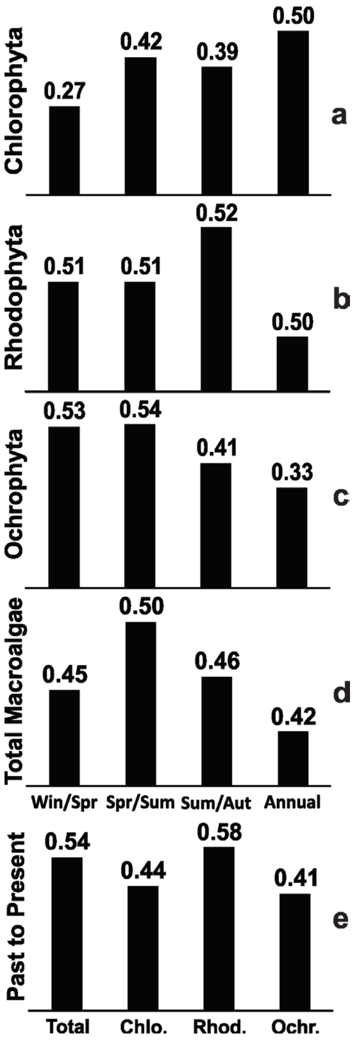

Figure 4. Turnover of taxa found on the rocky shore at Prainha. Turnover is shown for Chlorophyta, Rhodophyta, Ochrophyta, all taxa of macroalgae, and is compared between Yoneshigue (1985) and the present study.

53 were Rhodophyta. In addition, the review of Brasileiro et al. (2009) registered 207 taxa for Arraial do Cabo, of which Prainha had 98 species and was the second most diverse location in the region after Ponta da Cabeça (108 species). The present study found 96 taxa at Prainha, of which 23 belonged to the phylum Chlorophyta, 19 to Ochrophyta, and 54 to Rhodophyta, with the last phylum remaining the most well-represented at Prainha.

Rhodomelaceae and Ceramiaceae (Rhodophyta), were the families with the higher diversity at Prainha, with 12 species (22 % of the total) and eight species (15 %), respectively. The most well-represented families of Chlorophyta at the study site were Cladophoraceae and Ulvaceae, with seven and six species present, respectively. Comprising together 57 % of the total abundance of the phyla observed. Among Ochrophyta, two families comprised most of the composition: Dictyotaceae, which increased its representation from 15 to 21 % of the total (four species) over time; and Scytosiphonaceae, which increased its representation (two species) in the community in comparison to that in the early 1980s.

Altogether, compared to past surveys (Yoneshigue 1985, Brasileiro et al. 2009) 55 new occurrences were added for Prainha Beach and 27 for Arraial do Cabo. Considering these new occurrences, Prainha reached a total of 125 taxa, which would make it the most diverse area in Arraial do Cabo. These new records also increased the number of taxa present in Arraial do Cabo, enhancing it from 207 to 234 species.

DISCUSSION

Autumn and winter in this region are periods that are marked by the frequent occurrence of cold fronts and storms. As a result, the water column is mixed in these seasons, increasing the amount of organic and inorganic particles it contains (Coelho-Souza et al. 2017) and causing the senescence of a large part of the coastal flora (Riggs et al. 1998). In addition to these physical disturbances, the prevalence of south-southwest quadrant winds favors the proximity and residence of the Brazilian Current along the coast and prevents upwelling of the SACW. The proximity of the Brazilian Current could lead to inorganic nutrient stress and/or limitation, especially for organisms in the upper zone of the coast, resulting in the deceased abundance of several components of the community and increasing the turnover rates, as was observed during the present study. Under nutrient limitation, resistant macroalgae with shorter canopies are selected (Steneck & Dethier 1994). The same seasonal effects on the benthic community were observed at Ubatuba (state of São Paulo, Brazil), another upwelling region that is influenced by the SACW (Alves et al. 2014). On the other hand, during spring and summer, upwelling events increase in frequency and intensity at Arraial do Cabo. The water column stratifies more frequently and becomes enriched with inorganic nutrients, such as nitrate and phosphate (Coelho-Souza et al. 2012, 2017). The increased input of such inorganic nutrients could explain the rising number of macroalgal species in the middle and lower zones of the coast that we observed, as well their turnover rates during the beginnings of these periods.

The interactions between macroalgae and invertebrates over the three zones of the intertidal community of Prainha observed in the present study were similar to those described by Yoneshigue (1985), as well as to those in other upwelling regions of the world (Hosegood et al. 2017, Jiang & Wang 2018, Walter et al. 2018). However, some exceptions were observed, such as the differences in the species dominating the upper zone throughout all seasons, wherein *Chthamalus bisinuatus* Pilsbry, 1916 dominated community coverage in the early 1980s (Yoneshigue 1985), while *Tetraclita stalactifera* and *Hildenbrandia rubra* dominated in the present study. The results for the middle and lower zones agreed between this and past studies in relation to species dominance, with one exception during autumn; specifically, Yoneshigue (1985) recorded a large settlement of crustose Corallinales algae in the lower zone in the autumn, whereas our study observed that the complex thalli of articulated Corallinales dominated this season.

Previous studies emphasized the influence of upwelling on the megafaunistic composition of marine communities at other sites around the world (*e.g.*, Lavaleye et al. 2002, Kelaher & Castilla 2005, Carlier et al. 2015). At Cabo Frio, Brazil, in particular, most species have subtropical affinities and food resources are available in larger amounts for the entire food chain (Léo & Pires-Vanin 2006, Braga et al. 2018). Furthermore, in addition to the afore mentioned physicochemical and/or biological disturbances, invertebrates compete with macroalgae for available space, which is a potentially limiting resource in coastal habitats. This competition thus exerts an influence on the community and likely alters its species richness and diversity (Dayton 1971, Tlig-Zouari et al. 2010).

Changes in the macroalgal composition and relative occurrence of different algal families were observed at Prainha before and after an interval of almost 30 years. According to Yoneshigue (1985) and Brasileiro et al. (2009), among Chlorophyta families, Cladophoraceae and Codiaceae were the most diverse families, representing half of the green macroalgae found on the rocky shore. In the present study, Cladophoraceae and Ulvaceae were the most well-represented families. *Bryopsis corymbosa* J. Agardh and *Valonia macrophysa* Kützing, whose abundance characterized Prainha to Yonesigue (1985), were not recorded in the present study, which might indicate that significant alterations in the community have occurred. Furthermore, *B. corymbosa* was replaced by different species of the same genus at this site (*B. pennata* J. V. Lamouroux, *B. plumosa* (Hudson) C. Agardh, and *B. ramulosa* Montagne), increasing the representation of Bryopsidaceae; this change was considered a substitution of one species by its ecological equivalent(s). Nevertheless, other previously reported species were not recorded during the present study, such as *Derbesia marina* (Lyngbye) Solier, *Derbesia tenuinissima* (Moris & De Notaris) P. Crouan & H. Crouan and *Ulvella lens* P. Crouan & H. Crouan. When comparing the previous studies' lists of macroalgae, 12 species of Chlorophyta were added for Prainha, and six new occurrences were recorded for the larger region of Arraial do Cabo: *Bryopsis ramulosa*, *Cladophora sericea* (Hudson) Kützing, *Cladophoropsis macromeres* W. R. Taylor, *Phyllodictyon anastomosans* (Harvey) Kraft & M. J. Wynne, *Ulva prolifera* O. F. Müller, and *Willeella brachyclados* (Montagne) M. J. Wynne.

The most representative Ochrophyta flora reported by Yoneshigue (1985) belonged to the families Acinetosporaceae, Dictyotaceae, and Scytosiphonaceae, with each family comprising 15 % of the Ochrophyta flora. In the present study, Acinetosporaceae, Dictyotaceae, Sargassaceae, and Scytosiphonaceae were the families with the highest coverage. The latter three families form complex thalli important to microhabitat formation. Some species that form less complex thalli were recorded by Yoneshigue (1985) and Brasileiro et al. (2009), but were not registered in the present study. Eleven species of Ochrophyta were added to the list of Yoneshigue (1985) for Prainha: *Bachelotia antillarum* (Grunow) Gerloff, *Canistrocarpus cervicornis* (Kützing) De Paula & De Clerck, *Chnoospora minima* (Hering) Papenfuss, *Sphacelaria novae-hollandiae* Sonder, *Sphacelaria tribuloides* Meneghini, *Ectocarpus fasciculatus* Harvey, *Dictyopteris delicatula* J. V. Lamouroux, *Feldmannia indica* (Sonder) Womersley & A. Bailey, *Padina antillarum* (Kützing) Piccone, *Rosenvingea orientalis* (J. Agardh) Børgesen, and *Sargassum vulgare* C. Agardh. However, only the last five of these algae represented new occurrences for the region of Arraial do Cabo.

The diversity of Rhodophyta families, unlike the other macroalgal phyla, did not change in the present study, comparing to the lists of Yoneshigue (1985) and Brasileiro et al. (2009). On the other hand, one species registered by Yoneshigue (1985), *Ceramium codii* (H. Richards) Mazoyer, was replaced by its ecological equivalent *C. vagans* P. C. Silva in P. C. Silva, Meñez & Moe. The families Callithamniaceae, Lomentariaceae, Gelidiellaceae, Plocamiaceae, and Rhodymeniaceae were recorded by Yoneshigue (1985) at Prainha but were not found in the present study. In relation to the review by Brasileiro et al. (2009), the present study added 18 rhodophyte species for Arraial do Cabo region: *Arthrocardia variabilis* (Harvey) Weber-van Bosse, *Amphiroa brasiliana* Decaisne, *Centroceras gasparrinii* (Meneghini) Kützing, *Ceramium clarionense* Setchell & N. L. Gardner, *Dasya ocellata* (Grateloup) Harvey in Hooker, *Taenioma perpusillum* (J. Agardh) J. Agardh, *Chondria atropurpurea* Harvey, *Herposiphonia delicatula* Hollenberg, *Herposiphonia nuda* Hollenberg, *Herposiphonia parca* Setchell, *Laurencia aldingensis* Saito & Womersley, *Laurencia dendroidea* J. Agardh, *Melanothamnus gorgoniae* (Harvey) Díaz-Tapia & Maggs, *Melanothamnus sphaerocarpus* (Børgesen) Díaz-Tapia & Maggs, *Pterocladiella caerulescens* (Kützing) Santelices & Hommersand, *Hypnea cervicornis* (J. Agardh), *Chondracanthus saundersii* C. W. Schneider & C. E. Lane, and *Gracilaria mammillaris* (Montagne) M. A. Howe.

The changes in the macroalgal composition observed may have been related to several factors acting over the intervening years. The RESEX was created in 1997, establishing a protection area for the marine resources in the area and at the same time implementing a plan for the sustainable utilization of these resources by the local community (Silva 2004). Additionally, the Companhia Nacional de Álcalis, which was established in 1960 at Prainha, used to constantly discharge warmer water and sodium carbonate (barrilha) into the seawater. This company ceased its operations in 2006 (FEEMA 1988, Pereira 2010). Thus, the absence of chemical material inputs and the creation of a protection policy for this area could have influenced the increases we observed in the number of species at Prainha and, consequently, the area's biodiversity.

The present study recorded a reduced turnover rate of brown algal species in relation to Yoneshigue's (1985) data. This group of algae is frequently referred to as one that is particularly ecologically susceptible to anthropogenic influences (Ballesteros et al. 2007, Pinedo et al. 2007, Martins et al. 2012). Therefore, this suggests that the results of this study present a favorable diagnosis to the water quality at Prainha. The presence of macroalgae with structurally complex thalli (such as *Canistrocarpus cervicornis*, *Laurencia* spp., and *Sargassum* spp.) is also an indicator of good water quality at the site because in polluted environments, opportunistic taxa (*i.e.* macroalgae with simple thalli) are favored and intensely compete with invertebrates for space on the rocky shore, which decreases the local diversity (Soares-Gomes et al. 2016).

A non-destructive sampling approach is widely used in ecological studies, including in Brazil, due to its ability to analyze rocky shore communities efficiently and cost-effectively without negatively impacting sensitive species (Masi et al. 2016, Beisiegel et al. 2017, Mantelatto et al. 2018). Despite having some limitations (*e.g.*, it can be difficult to visualize small organisms, and requires one to have previous knowledge of the occurrence of relevant species for the area to perform analyses), the photoquadrat technique is still recognized as an important tool for non-destructive environmental monitoring (Pech et al. 2004, Gomes-Pereira et al. 2016, Perkins et al. 2016).

The utilization of the methodology discussed above may similarly provide assistance to monitoring programs aiming to prevent new (invasive) organisms from settling in an area and control the behavior of exotic species that are already established. For instance, such programs detected and continuously monitoring the Caribbean mollusk *Isognomon bicolor* C. B. Adams, 1845, which has been detected at Prainha since the early 1990s (Domaneschi &

Martins 2002). This invasive species has been expanding its geographical distribution in the southwestern Atlantic since the 1980s, and is present from Rio Grande do Norte, Brazil to Uruguay (Domaneschi & Martins 2002, Breves et al. 2014). The monitoring of exotic species in benthic communities is important due to the threat they pose to native biota, and even entire ecosystems (Amaral & Jablonski 2005).

In conclusion, our analyses of the species coverage, richness, and diversity of a rocky shore community demonstrated that seasonal upwelling-downwelling events may lead to species turnover and changes in diversity between seasons (Weir & Schluter 2007). The studied rocky shore community at Prainha is therefore susceptible to alterations during upwelling periods, but the replacement of any lost species was basically driven by their ecological equivalents (*i.e.* species from the same families or genera), which we consider to be relatively natural and expected intra-annual changes. The comparison of the currently registered flora to those registered almost 30 years ago demonstrated (I.) new occurrences; (II.) high turnover, especially among red algae; and low turnover among brown algae. These temporal differences were smaller than our hypothesis had expected, which indicates good water quality at the site, perhaps related to the changes in coastal waste disposal between the previous and present studies. The present study used approaches that combined reduced sampling impacts (only carried out to obtain some specimens for identification) and photoquadrats, which allowed us to make a detailed description of the intertidal composition and structural characteristics of different zones on the rocky shore with minimal impact, and is recommended as a good methodology for the study of protected marine areas. The information obtained and techniques developed could assist in the management of the RESEX of Arraial do Cabo , for example to improve the supervision and protection of the benthic community that occupies the rocky shore of Prainha.

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