

# Chapter 2

## Biogeographic Patterns of Brazilian Rocky Reef Fauna



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**Abstract** Rocky shores are prominent features of the Brazilian SE-S coast that define the coastal contour in the region and are interspersed by sand beaches. The intertidal and subtidal zones are discussed here as a continuous along the depth gradient, where large rocky formations plunge into the sea and are bordered by a soft sediment basin. The SE-S rocky shore range overlaps climatic and oceanographic domains, with NE currents and winds, and cold fronts coming from S-SW during the dry season. The SE-S shores represent a gradual change in species composition from tropical to subtropical-temperate provinces, where some taxonomic groups peak in species richness along the Rio de Janeiro and São Paulo shores associated with less heterogeneous climatic and oceanographic domains. Fish, mollusk, ascidian, and sponge species richness decrease southward, while corals decrease in subtropical areas mostly because of their clear association with tropical waters. Although some rocky shores are within marine and coastal protected areas, the total area covered and the real enforcement applied to those protected areas are below desirable levels. These habitats are among the most impacted on the Brazilian coast because of their proximity of large cities and should be prioritized in sustainable development initiatives and coastal management planning.

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## Geographical and Climatic Context

Rocky shores are a conspicuous feature of the landscape on the Brazilian SE-S coast (Ab'Sáber 2000). Much of the rocky shores in this region delimit the coastal contour being interspersed by sand beaches that spread to the infralittoral in the enlarged siliciclastic shelf of this region (Knoppers et al. 1999). In this chapter, rocky shores included intertidal and subtidal zones because, with a few exceptions, both zones form a continuous along the depth gradient. Usually, large rocky formations plunge into the sea and are delimited by a soft sediment basin. Reef formations were considered only as those permanently immersed and detached from the coast. Rocky formations can be found predominantly from Vitória/ES (20.29 S, 40.28 W) to Laguna/SC (28.61 S, 48.82 W), with the more complex and continuous coastal formations located between Mangaratiba/RJ (22.98 S, 44.04 W) and São Sebastião/SP (23.77 S, 45.80 W), and the southernmost coastal crystalline rocky shore is located in Torres/RS (29.36 S, 49.73 W). Coastal rocky formations found on tropical domains from the northeast Brazilian coast are sparse (Coutinho 2004), punctually found from Ceará to Bahia (e.g., Baía de Todos os Santos—Paz et al. 2012; Nunes et al. 2013; Ilhéus and Itacaré—Santos 2020), and will not be treated here. Submerged rocky reefs are found scattered on shallow waters, and also form large patches of mesophotic habitats that are critical for many endemic and threatened species. These reefs are poorly mapped and were also not included in this chapter. Finally, most of the oceanic islands inside Brazilian territorial waters (São Pedro and São Paulo Archipelago, Fernando de Noronha Archipelago, and Trindade Island) are also dominated by rocky formations and will be briefly debated in a separate section in this chapter.

Climatic and oceanographic domains overlap in this SE-S rocky shore range, which means a unique overlap of biodiversity components. The Brazilian Current and NE winds prevail in the SE-S Brazilian shores, and local climate is classified as a tropical monsoon regime with dry “winters” (Alvares et al. 2013). Cold fronts coming from S-SW are especially influential during “winter” months in the region (Mazzuco et al. 2018). The coastal orientation deflected to the east at this portion of Brazil favors particular conditions that are associated with the shelf geomorphology, eddies formation and wind regimes that build up conditions to upwelling events to occur locally (Calado et al. 2010). The colder waters from the Southern Atlantic Central Water (SACW) mass influences directly the whole shelf and often reaches the surface, especially during September to March at the Cabo Frio/RJ region (Valentin 2001) and at Cabo de Santa Marta/SC (Campos et al. 2013). Upwelling events in Southeastern Brazil influences the local biota by, for instance, affecting larval abundance, recruitment, and productivity as a whole (Mazzuco et al. 2018). Coastal geomorphology and associated oceanographic characteristics create complex gradients of wave exposition, temperature and depth, increasing habitat diversity and harboring species-rich communities (Coutinho 2004; Pardal et al. 2021, 2023).

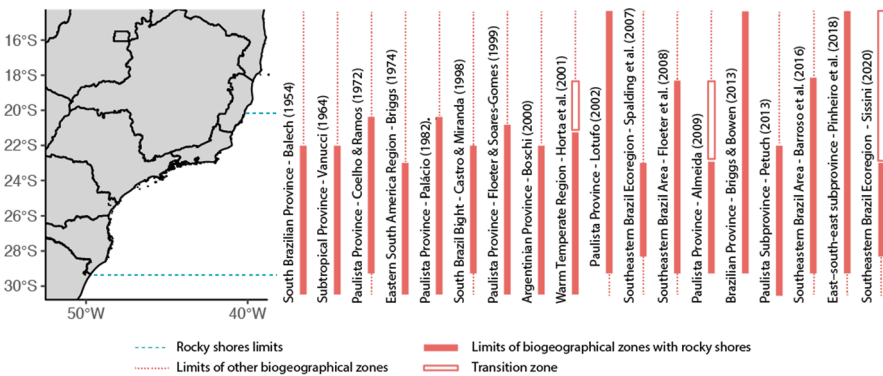
Biogeographical patterns associated with regional climatic and oceanographic phenomena will be detailed in the next sections.

## Biogeographical Patterns

### Subtidal Zone

Earlier delimitations of biogeographic regions within the Brazilian coast varied in setting boundaries according to the availability of information for each studied group (see Barroso et al. 2016), but the southeastern coast is usually considered as a transition region of intermediate characteristics from tropical and subtropical domains (Fig. 2.1). Briggs (1974) included the rocky shore domains within the Paulista province (limits between 21° and 30° S) based on endemism values and oceanographic and geological characteristics. Palácio (1982) compiled information about biogeographical patterns of several taxa (e.g., macroalgae, Porifera, Mollusca, Ascidiacea, Echinodermata, and fishes) on the Brazilian coast, and also discussed previous authors that described general patterns of distinct taxa, maintaining the classification proposed by Briggs (1974). Floeter and Soares-Gomes (1999) supported a similar division by Briggs (1974) but set the northern border around Maratázes/ES, although the highest Gastropoda species richness was found in Campos Basin and Cabo Frio, with most of the species showing tropical affinities within the Paulista Province. Later, Martínez and del Río (2002) extended further the province limits considering the whole Brazilian coast as a single province based on fossil records (Miocene) and extant mollusk fauna composition. Lotufo (2002) also defined wider limits to the Paulista Province: from northern Bahia until Santa Catarina based on gastropod species. Although there was a higher similarity in composition between the faunas from São Paulo, Rio de Janeiro, Santa Catarina, and Paraná, when compared to Bahia, the author set the northern limit of the Paulista Province based on the large dissimilarity in species composition when compared to the Brazilian and Patagonic provinces.

Considering algal groups, Horta et al. (2001) indicated the Espírito Santo coast as a transition zone between the Tropical (Piauí to Bahia coasts) and a Warm



**Fig. 2.1** Coastal area dominated by crystalline rocky shores and proposed biogeographic divisions for the Brazilian coast

Temperate Region (Rio de Janeiro to Rio Grande do Sul) due to its richness and mixed composition of species. Recently, the evaluation of coralline red algae richness patterns also indicated a hotspot of species diversity between Bahia and the north of Rio de Janeiro, reinforcing that region as a diversity center and transition zone for coralline red algae on the Brazilian coast (Sissini et al. 2021). Barroso et al. (2016) applied similar boundaries for Gastropods to those indicated by Lotufo (2002) but limiting the northern boundary of the E-SE province to southern Bahia, with the region from Rio de Janeiro to Santa Catarina as one unit and Espírito Santo more similar to NE region. The study conducted by Pinheiro et al. (2018) based on reef fishes found higher similarities between neighboring sites with a closer association between Rio de Janeiro and São Paulo in relation to Santa Catarina and Espírito Santo, the latter being more similar to Bahia. Lotufo (2002) based on the ascidian fauna considered the whole region from northern Bahia to southern Santa Catarina as one unit. It is worth noting that most biogeographic classifications were based on taxonomic groups occupying different habitats, which also usually include nonconsolidated substrates and ecotones (e.g., estuaries). Lotufo (2002), Horta (2000), Floeter et al. (2001, 2008), and Pinheiro et al. (2018) focused their studies on reef-associated species and agreed with other biogeographic studies classifying the rocky reef-dominated region as a transitional and species-rich region on the Brazilian coast.

Despite some disagreement about the northern and southern limits, there is a consensus that throughout the SE-S shores there is a gradual (rather than an abrupt) change in species composition from tropical to subtropical-temperate provinces. Habitat and oceanographic conditions have imposed different filters on marine groups, which directly influenced their geographical distribution limits causing the large frequency of overlap between Espírito Santo and Rio de Janeiro, especially in the north of Rio de Janeiro where upwelling influence is greater (Mazzuco et al. 2015). Some taxonomic groups show a peak in species richness along the Rio de Janeiro and São Paulo shores, reflecting an accumulation of species that gradually decreases to the north and south (Pinheiro et al. 2018) where climatic and oceanographic domains are less heterogeneous (Castro et al. 2006).

### ***Richness Gradients, Processes, and Species Origins***

The main pattern observed for fish, mollusk, ascidian, and sponge species richness (Table 2.1) does not follow the expected latitudinal gradient, i.e., a regular decrease in the number of species from lower to higher latitudes. Instead, species richness patterns on the Brazilian coast mostly show a hump-shaped profile with its center located in the SW region over the transition zone between tropical and subtropical regions, which match where rocky shores are dominant (Barroso et al. 2016; Pinheiro et al. 2018; Cruz-Motta et al. 2020). Corals, on the other hand, do decrease in species richness when considering rocky shore domains (Table 2.1), mostly because of their clear association with tropical waters (Leão et al. 2003).

**Table 2.1** Species richness of selected taxa along the crystalline rocky shores of southeastern coast and oceanic islands in Brazil

Taxa	ES	RJ	SP	PR	SC	SPSP	FN	TMV
<i>Reef fish</i>								
Chondrichthyes <sup>a</sup>	43	40	46	7	27	23	30	17
Actinopterygii <sup>a</sup>	424	395	427	131	301	202	201	172
<i>Mollusca</i>								
Prosobranchia <sup>b</sup>	288	316	252	154	170	17	126	156
Gastropoda, Bivalvia, Cephalopoda <sup>c, d, e</sup>						48	229	140
<i>Macroalgae</i> <sup>f, g, h</sup>	249	341	258	67	144	36	168	221
<i>Cnidaria</i>								
Scleractinia and Hydrozoa <sup>i, j, k</sup>	13	10	7	25	2	3	11	3
Zoantharia <sup>l, m, n</sup>	9	11	11	3	6		34	37
<i>Porifera</i> <sup>k, o, p, q</sup>	59	102	84	23	45	32	59	28
<i>Ascidiacea</i> <sup>k, n, s, t</sup>	28	32	66	25	34			

ES Espírito Santo, RJ Rio de Janeiro, SP São Paulo, PR Paraná, SC Santa Catarina, SPSP São Pedro and São Paulo Archipelago, FN Fernando de Noronha Archipelago, TMV Trindade and Martin Vaz Islands

<sup>a</sup>Pinheiro et al. (2018)

<sup>b</sup>Barroso et al. (2016)

<sup>c</sup>Oliveira et al. (2009)

<sup>d</sup>Gomes et al. (2006)

<sup>e</sup>Gomes et al. (2017)

<sup>f</sup>Horta et al. (2001)

<sup>g</sup>Villaça et al. (2006)

<sup>h</sup>Sissini et al. (2017)

<sup>i</sup>Leão et al. (2016)

<sup>j</sup>Capel et al. (2012)

<sup>k</sup>Amaral et al. (2009)

<sup>l</sup>Bumbeer et al. (2016)

<sup>m</sup>Santos et al. (2016)

<sup>n</sup>Santos et al. (2020)

<sup>o</sup>Muricy et al. (2011)

<sup>p</sup>Moraes et al. (2009)

<sup>q</sup>Moraes and Muricy (2017)

<sup>r</sup>Lotufo (2002)

<sup>s</sup>Rocha et al. (2011)

<sup>t</sup>Rocha et al. (2005)

Jacques Labrel seminal work (1970) (also see Labrel-Degen et al. (2019) for a commented version) described the Abrolhos region as the richest in coral species, decreasing southward, indicating the Cabo Frio region as the limiting zone of distribution for several species of gorgonians and fire corals, and the northern shore of São Paulo as the southern limit of occurrence of scleractinian corals. The steady decline in coral (17 species in Bahia) and hydrocoral species in the granitic shores of SE Brazil is usually associated with the lower water temperature, salinity, and turbidity, as main controls to coral development in higher latitudes (Leão et al. 2016). Further work has shown that Santa Catarina is the true limit for scleractinian

coral, with the presence of only *Madracis decactis* and *Astrangia rathbuni*, species known to be resistant to temperature and turbidity variation (Leão et al. 2003; Capel et al. 2012).

Algal groups sum up more than 250 infrageneric taxa in Espírito Santo, but the highest algal richness is found in Rio de Janeiro (341 taxa), decreasing toward southern Brazil (Horta et al. 2001). Fishes account for 515 species (464 Actinopterygii and 81 Chondrichthyes) within the rocky shore domain and show a decrease in species richness southward. However, reef fish assemblages show a high similarity in composition among sites between Bahia and Santa Catarina (Floeter et al. 2001; Pinheiro et al. 2018). Prosobranch mollusks also show higher species richness closer to the northern limits of Brazilian rocky shores with 359 species recorded from south of Bahia to Rio de Janeiro, decreasing to 170 species at the southern limit of rocky shores in Santa Catarina (Barroso et al. 2016).

Following the hypothesis of latitudinal gradients associated with decreasing water temperatures (Floeter et al. 2004, 2005; Brayard et al. 2005), the northern limit of the Brazilian rocky shores is coincident with higher species richness and higher mean temperature, despite the cold-water intrusions (Campos et al. 2000). Also, the southern limit has lower species richness (Horta et al. 2001; Floeter et al. 2008) and lower (and more variable) water temperatures (Campos et al. 1999). Such impoverished fauna at the southern sites of the Brazilian coast is usually attributed to the diminishing numbers of reef-associated species with tropical affinity. Most of these tropical lineages have evolutionary origins in the Caribbean (e.g., sea urchins—Lessios et al. (1999) and McCartney et al. (2000); corals—Nunes et al. (2011), and other groups already cited here). For reef fishes, most species have relatively recent Caribbean origins (Floeter et al. 2008), but for some taxa (e.g., some Blenniidae, Sparidae, Serranidae) other routes of species' origins are also known (Araújo et al. 2020). However, some taxa do not follow this trend such as brown algae (Horta et al. 2001), corals (Fukami et al. 2004), and sponges (van Soest and Hajdu 1997), which have phylogenetic histories prior to the Tethys closure, probably occupying the Southern Atlantic region before the connection with the Caribbean. This pattern indicates a southern route between Atlantic and Indo-Pacific (Horta et al. 2001), but also exporting species to the Caribbean region (Rocha et al. 2008).

The transitional role of the rocky reefs in the Brazilian coast is also supported by the low connectivity separating many populations from tropical to subtropical waters, including genetic evidence for corals (*Siderastrea stellata*—Neves et al. 2007; *Mussismilia hispida*—Picciani et al. 2016; Peluso et al. 2018) and reef fishes (Santos et al. 2006; Affonso and Galetti 2007; Machado et al. 2017). The Espírito Santo coast is evidently a transitional zone within the Brazilian Province, bearing a mix of habitats with rocky shores, rhodolite beds, arenitic and algal reefs overlapping, which slowly changes to rocky shore dominance in the central-southern coasts, roughly south of the Doce River (19° S) (Moura et al. 1999; Mazzuco et al. 2020). Temperature differences can act as barriers to species, as long as differences between close regions exceed the natural variability within them because of physiological constraints of species (Kocsis et al. 2018). Thus, summed to the change in habitat homogeneity, the upwelling area at São Tomé (Palóczy et al. 2014) and Cabo

Frio (Valentin 2001) together with coastal circulation patterns, create filters to species dispersion and establishment further south (Peluso et al. 2018). Turbidity was also indicated as an importance factor associated with changes in benthic cover composition along the Brazilian coast, where southeast Brazil rocky reefs were included as turbid, and the oceanic islands as clear water reefs (Santana et al. 2023). This composition split was also shown by multiple taxa, including macroalgae, corals, crustaceans, mollusks, elasmobranchs, and reef fish, indicating that those sub-provinces (southeastern and south) are consistently different from the rest of the Brazilian coast (Cord et al. 2022).

At the community level, few studies have evaluated changes in composition along Brazilian rocky shores (Floeter et al. 2001; Ferreira et al. 2004; Anderson et al. 2020a). Morais et al. (2017) and Aued et al. (2018) analyzed patterns of fish assemblages and benthic communities, revealing very similar patterns to those indicated previously, where rocky shore assemblages and communities presented homogeneity and larger within-site similarity when compared with tropical areas along the coast. Macroecological analyses of reef fishes revealed that they were more influenced by regional and local factors than large-scale processes, especially in rocky reefs (Morais et al. 2017). Bender et al. (2013) indicated the role of habitat differences (i.e., rocky reefs) in community assembly for the southwestern Atlantic, where either functional or taxonomic attributes applied to analyses indicated a high similarity in composition of reef fish communities in southeastern areas of the Brazilian coast, reinforcing the clustering of areas between Espírito Santo and Santa Catarina. A similar pattern in clustering of rocky reefs was found for benthic communities with large dominance of algal groups and a gradual decrease in coral species richness toward southern shores on the Brazilian coast (Aued et al. 2018). The local analysis also indicated a steady decline in fish species at higher latitudes (Pinheiro et al. 2018) and a turnover in composition to subtropical invertebrate species (Lotufo 2002; Barroso et al. 2016). Some subtropical to temperate reef fish species can also be found at lower latitudes but related to deep reefs or upwelling zones (e.g., *Pinguipes brasilianus*, *Dules auriga*—Anderson et al. 2015; *Serranus aliceae*—Carvalho-Filho and Ferreira 2013), associated with intrusion of the SACW. Finally, Luza et al. (2023) evaluated the functional patterns of reef fish, coral, and algae, and they observed that sea surface temperature, species richness, and region were the main factors determining spatially congruent functional diversity patterns across Brazilian reefs, irrespective of their evolutionary histories. Main differences between southern rocky reefs, northern reefs, and oceanic islands indicated a lower reef fish functional richness, but higher algal functional richness along southern rocky reefs (Luza et al. 2023), which follows the same patterns indicated for species richness along this chapter.

Human-induced biological invasions are also a key process gradually shaping the composition of reef communities, especially in regions with intense ship traffic such as the Santos and Guanabara bays. Fouling and ballast water serve as long-lasting occurring vectors (Carlton 1996; de Messano et al. 2019; Oricchio et al. 2019). Harbor areas on the Brazilian coast, especially in the southwestern region, are typically alien species-enriched habitats (Teixeira and Creed 2020). Consequently, non-native macroalgae, ascidians, corals, and soft corals have been found with more



frequency, many being reported as invasive (Ferreira et al. 2006; Lages et al. 2006; Silva et al. 2014; Menezes et al. 2022). However, negative effects of alien species over the benthic elements were detected only for invasive corals (e.g., *Chromonephthea braziliensis* vs. *Phyllogorgida dilatata*—Lages et al. (2006); *Tubastraea* spp. vs. *Mussismia hispida*—Creed (2006); *Tubastraea* spp. and vs. *Palythoa caribaeorum*—Guilhem et al. (2020); turf-forming algae following vs. *Latissimia ningalooensis*—Carvalho-Junior et al. (2023)), while a large-scale view of impacts over benthic communities is still to be revealed.

Natural invasions are much more difficult to register and a few have been indicated; for instance, the population expansion of the non-native damselfish *Chromis limbata* (Anderson et al. 2020b) has been increasing in densities, although non-negative impacts have been reported. A potential harmful threat to southern rocky reef communities is the lionfish *Pterois* spp. that was observed in Brazilian waters in 2015 which was probably a released vector from aquarium trade (Ferreira et al. 2015). The invasion initiated only in 2018 in Fernando de Noronha and North of Brazilian coast (Luiz et al. 2021). Then, lion fish populations have expanded their ranges along northeastern reefs (Soares et al. 2022), and it is just a matter of time for they reach the rocky reefs with potentially profound impacts (Bumbeer et al. 2018).

## Intertidal Zone

Intertidal areas have usually lower species richness compared to subtidal habitats in the same region because of the wide range of environmental stressors (e.g., hydrodynamics, temperature, and UV exposure) acting over the biota living between tides (Menge 2002; Twist et al. 2020). Those stressors act at different levels across the vertical relief creating zones dominated by species best adapted to such levels, and this marked vertical distribution has been debated as a global pattern irrespective of the marine region (Schiel 2004). The vertical zonation is also considered a true pattern for Brazilian intertidal rocky shores (Coutinho 1995), and, such changes in structuring species can also influence richness patterns in rocky shores where there is a negative correlation between tidal height and species richness (Coutinho 2004), i.e., the closer to the water, higher the richness.

Larger scale analysis of alpha and beta diversity of the intertidal communities indicated the Cabo Frio region as an inflexion point for both indicators with decreasing values toward higher latitudes on the Brazilian coast (Cruz-Motta et al. 2020), as observed for subtidal groups in the previous section. Beta diversity was predominantly associated with species turnover at the local scale, indicating small-scale variations as general drivers of assemblages' differentiation (Cruz-Motta et al. 2020). Also, barriers for species dispersion are congruent with those observed for subtidal taxa (Floeter et al. 2008), including the Rio Doce/ES at the north, and the Plata River-Lagoa dos Patos complex at the south, both with generous freshwater inputs to coastal waters that might work as filters for stenohaline species. Another crucial limiting factor to intertidal communities is the substrate availability, which is scarce at the southern border in Santa Catarina (Coutinho 2004). On the other



**Table 2.2** Number of species per Phyla, according to state provinces and tidal height, found on intertidal rocky shores reported by Cruz-Motta et al. (2020) supplemented with species registered by Pardal et al. (2023)

Taxonomic group	Espírito Santo			Rio de Janeiro			São Paulo			Paraná			Santa Catarina		
	HT	MT	LT	HT	MT	LT	HT	MT	LT	HT	MT	LT	HT	MT	LT
Cyanobacteria	1	–	–	–	1	1	–	1	1	–	–	–	–	–	13
Chlorophyta	4	–	19	–	3	5	2	9	12	2	–	9	9	–	6
Ochrophyta	4	–	12	–	2	4	–	3	8	–	–	12	2	–	23
Rhodophyta	7	–	53	–	7	10	4	15	28	6	–	31	5	–	–
Tracheophyta	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
Porifera	–	–	2	–	–	1	–	1	2	–	–	–	–	–	2
Cnidaria	1	–	3	–	–	1	–	–	2	–	–	–	–	–	5
Mollusca	10	–	7	2	10	9	7	18	19	3	–	6	6	–	1
Annelida	1	–	1	–	1	1	–	1	1	–	–	–	1	–	3
Arthropoda	2	–	1	1	2	3	2	4	4	1	–	3	2	–	–
Echinodermata	1	–	2	–	–	2	–	1	1	–	–	2	–	–	–
Bryozoa	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1
Chordata	–	–	–	–	–	1	–	1	1	–	–	–	–	–	–
Total	31	–	101	3	26	38	15	54	80	12	–	63	25	–	55

*HT* high-tide, *MT* mid-tide, *LT* low-tide

hand, many intertidal species can tolerate a wide range of environmental changes, making those species widely dispersed beyond the limits of the crystalline shores of the S-SE Brazilian coast, ranging up to Maranhão, and reappearing in the south of USA (Klôh et al. 2013; Nunes et al. 2016; Wares 2019).

Several species found on intertidal rocky environments have a wide distribution, such as Chthamalidae (Wares 2019) and Tetraclidae barnacles, besides Mytilidae mussels (Trovant et al. 2013), which are the structuring species of Brazilian rocky shores (Coutinho 1995). Because of the high dominance of few species and wide distribution, there is a large uniformity in the composition of intertidal communities of the Brazilian Province (Cruz-Motta et al. 2020). The next section deals with richness patterns of the dominant and most common species in the intertidal zone. However, as indicated above, most of these species are widespread along SE rocky shores, and richness patterns are more variable locally than between subregions (Pardal et al. 2023) (Table 2.2).

### Richness Gradients, Processes, and Species Origins

General richness of species in the intertidal zone indicated a higher number of species in São Paulo except for macroalgae that were more diverse in Espírito Santo shores, as observed for the same group in the subtidal zone. No clear pattern can be observed considering tide height maybe because of lack of data from mid-tide in Cruz-Motta et al. (2020), but richness of species was always higher at the low-tide

zone, as expected (Coutinho 1995). Nine species of barnacles are found on the Brazilian coast, and two native species (*Chthamalus bisinuatus* and *Tetraclita stalactifera*) dominate the upper and middle intertidal zones all over the south and southeastern Brazilian shores (Coutinho 2004). The highest richness of barnacle species ( $n = 5$ ) was found in Paraná, at Ilha do Mel, close to Port of Paranaguá, but with a large proportion of alien species ( $n = 4$ ) (Klôh et al. 2013). In the upper intertidal zone, *Chthamalus bisinuatus* can be found in sympatry with the native *Chthamalus proteus*. Both barnacle species are externally indistinguishable (Masi et al. 2009), but *C. proteus* is more associated with euryhaline environments, such as estuaries (Young 1993). Despite not being dominant, nonindigenous species are common elements on Brazilian rocky shores, especially next to harbors. The mobile fauna found at the upper intertidal zone is also poor in species number, where *Echinolittorina lineolata* is the most abundant species, also slightly overlapping in vertical occupation with *Littorina flava* (Rios 1994). Highly mobile isopods (*Lygia exotica*) also live associated with crevices in that zone but foraging all along the intertidal region (Christofolletti et al. 2011). The green crab *Pachygrapsus transversus* is also found occupying the intertidal zone, usually in larger densities at the mid-intertidal region (Flores & Negreiros-Fransozo 1999). These common mobile invertebrates from the upper intertidal are grazers and constitute a crucial part of trophic control of the few algal species (e.g., *Centroceras*, *Enteromorpha*, *Ulva*, and *Cladophora*) occupying this region susceptible to larger periods of air exposition (Coutinho 2004, Christofolletti et al. 2010).

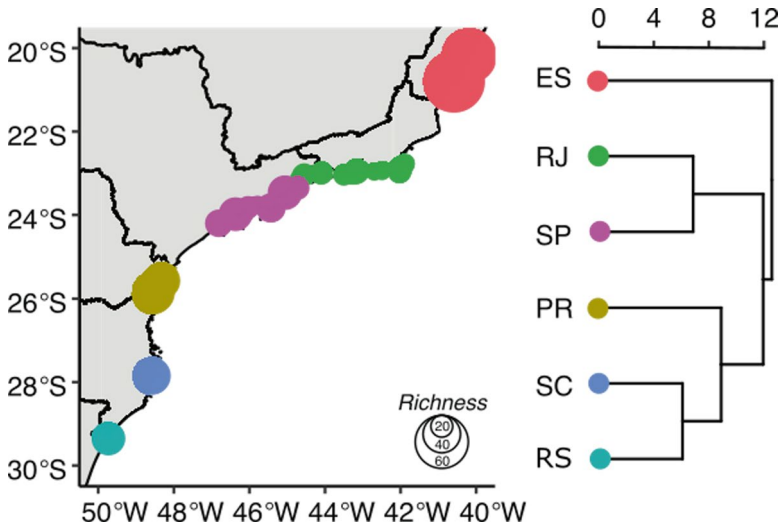
The species *Mytilaster solisianus* can be dominant in the upper portion of the mid-intertidal rocky zones in some sites, and *Brachidontes darwinianus* may occur in sympatry in estuaries (Trovant et al. 2016), following a similar trend of the Chthamalid species cited above. However, at a few shores, *M. solisianus* is absent from the middle intertidal zone, with examples from north of São Paulo and south of Rio de Janeiro shores influencing negatively local richness patterns (Pardal et al. 2023). The absence or low dominance of bivalves in Brazilian rocky shores, in opposition to what is observed worldwide (Schiel 2004; Murray et al. 2006), is mainly associated with recruitment patterns (Mazzuco et al. 2015, 2018) and herbivory pressure (Christofolletti et al. 2011). Still, the mid-intertidal zone is mostly dominated by *Tetraclita stalactifera*, often sharing space with other less frequent barnacle species (Klôh et al. 2013), and some previous (*Perna perna*—Souza et al. 2010) and recent invasive bivalves (*Isognomon bicolor*—López et al. 2014). Although considered as a nonindigenous species, *P. perna* has been established in the Brazilian Province for 2000 years (Souza et al. 2010; Calazans et al. 2021), and developed mussel beds can increase local structural complexity and aggregate considerable diversity of encrusting and vagile species (Jacobi 1987; Borthagaray and Carranza 2007). Algal groups are more diverse in this zone in comparison to the upper intertidal, with the genera *Chaetomorpha*, *Dictyota*, *Gracilaria*, *Acanthophora*, *Hypnea*, *Jania-Amphiroa* complex and other canopy-forming species being common (Brasileiro et al. 2009; Faveri et al. 2020). Mobile fauna is also more diverse in this zone, with grazers dominated by limpets (*Lottia subrugosa*, *Fissurella rosea*, and *Fissurella clenchi*) (Magalhães and Coutinho 1995), as well as secondary

consumers such as whelks (*Stramonita brasiliensis*, *Leucozonia nassa*, and *Claremontiella nodulosa*) and crabs (*Menippe nodifrons* and *Eriphia gonagra*).

At the subtidal fringe, frondose macroalgae beds (e.g., *Sargassum* spp.) and sabellariid reefs (*Phragmatopoma caudata*) can congregate a substantial number of associated taxa. Crustacean and Gastropoda species are the most studied group associated with algal fronds in the intertidal, with richness of Decapoda and Peracarida summing up to 23 (Széchy et al. 2001; Barros-Alves et al. 2017), and 42 (Jacobucci et al. 2018) species, respectively, and, Gastropoda groups ranging from 14 to 68 species (Longo et al. 2019; Colares et al. 2021). Sabellariid reefs can be found throughout the Brazilian coast but are scattered along SW rocky shores, depending on specific conditions of wave exposure and sedimentation (Nunes et al. 2016). Several groups can be found in association with these gregarious polychaetes, such as Decapoda crustaceans (five species in Micheletti-Flores and Negreiros-Fransozo (1999), and eight species in Bosa and Masunari (2002)). Unfortunately, the available information showed great variation in sampling effort and methodology, which is insufficient to depict general patterns about associated fauna with either macroalgae, mussel beds, or sabellariid reefs.

Looking at evolutionary time, processes influencing the biogeographic past of intertidal species seem to be coherent with those observed for subtidal species. The phylogeography and distributional patterns of intertidal organisms are congruent with those observed for subtidal species, where the principal barriers found along the Atlantic helped shape the actual diversity and endemism patterns. Considering the scale of dispersal as the main vicariant process, the width of the Atlantic Ocean, the Amazon outflow, and the closing of the Isthmus of Panama were the three major barriers that have contributed to the speciation of many species in the western Atlantic (Rocha 2003; Floeter et al. 2008; Reid 2009; Pinheiro et al. 2018), including those occupying the intertidal habitats. Despite the wide distribution along the Brazilian coast, some of the dominant and structuring species in the intertidal are endemic to the Southwestern Atlantic and have a recent past. For instance, the scorched mussel *M. solisianus* also appears to have an ancestor dispersed from the Caribbean region by crossing the Amazon filter, ca. 2.6 Ma (Trovant et al. 2016), and the same is hypothesized for *P. transversus* (Schubart et al. 2005) despite occurring on both sides of the Atlantic. The *E. lineolata*, endemic to the Brazilian province, seems to have originated in the Thethyan period, but its basal position makes speculation about the taxon's origin difficult. The same is not true for the oceanic island endemic *Echinolittorina vermeiji* found only in Brazilian oceanic islands, which have a Caribbean sister species, and apparently diverge from it after the Amazon drainage established in the Atlantic in the Late Miocene (Reid 2009).

Recent patterns of communities' composition are usually reported for restricted scales on Brazilian rocky shores (Paula et al. 2020). However, based on the surveying of 62 rocky shores ranging from north of Rio de Janeiro (Armação dos Búzios/RJ) to south of São Paulo (Itanhaém/SP), Pardal et al. (2023) and Cordeiro et al. (2024) sampled the relative cover of sessile taxa and density of mobile invertebrates in a large gradient encompassing >50% of the rocky shore domains in SE Brazilian coast. The analysis of the presence and absence of species along sampled shores



**Fig. 2.2** Patterns of similarity and species richness of intertidal communities based on Cruz-Motta et al. (2020) and Pardal et al. (2023). The hierarchical clustering was based on Jaccard coefficient applied to sites ( $n = 83$ ) community species' composition (presence and absence) using the average linkage method

indicated higher similarity between close sites and no evidence of richness gradients from north to south. Clusters obtained from a classification of environmental and biotic indicators (sea surface temperature [SST], wave exposure, average depth, and chlorophyll-a [Chl-a]) for the studied region also support higher similarities among neighbor shores (Fig. 2.2). Sites at north of Guanabara Bay (RJ) were clustered together and associated with higher Chl-a concentration and low SST, indicating effects of the upwelling (Coelho-Souza et al. 2012). Sites south from Rio de Janeiro and north from São Paulo (from Mangaratiba/RJ to São Sebastião/SP) were similar especially because of their variable wave exposure associated with the complex coastal contour forming small inlets either facing or protected from prevailing swells (Pardal et al. 2021). Finally, sites close to Santos and Guanabara bays had large similarities concerning Chl-a concentration, which is associated with the large productivity of those eutrophic populated regions (Miyashita et al. 2009; Villac and Tenenbaum 2010). The spatial dependency of sampled sites indicates that local factors may overcome the influence of regional processes at the scale investigated. The general forcing factors of recent patterns and the local-scale influence cited here are just to better frame dominant processes acting on rocky shore communities but will be better developed and discussed in the following publications (Pardal et al. 2021, 2023; Cordeiro et al. 2024).

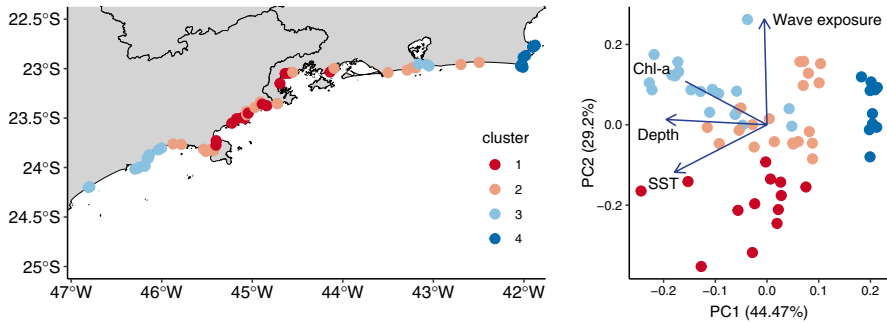
Benthic-pelagic coupling is especially critical for intertidal taxa, while oceanographic phenomena modulate recruitment and settlement patterns of structuring species (Menge 1991; Connolly and Roughgarden 1998), helping to shape communities and regulating richness patterns (Burrows et al. 2008). Oceanographic and

meteorological conditions on the SE coast of Brazil were described in another chapter of this book and will be only briefly discussed here. As indicated previously, currents, eddies, and the coastal morphology have a greater influence on regional processes shaping communities in Brazilian rocky shores. In the SE-S coast, the effects of the cold-enriched waters from SACW are spread throughout but are more intense in northern Rio de Janeiro (Fig. 2.2) because of Cabo de São Tomé and Cabo Frio upwellings. These nutrients boost local productivity, enhancing phytoplankton growth and the productivity of communities on these rocky shores (Guimaraens and Coutinho 1996; Coelho-Souza et al. 2012), but in the present evaluation, there were no elements to directly link productivity to species richness.

Cold front events associated with winds from the south quadrant, with a higher frequency during the autumn and winter months, affect many of these rocky shores. This wind regime disables the coast upwelling system, being more intense on southernmost sites (Campos et al. 2013). Despite influencing the regional scale, the effects of cold fronts on structuring benthic communities on south-southeastern Brazilian rocky shores have yet to be investigated. Mazzuco et al. (2018) evaluated the impact of cold fronts on the settlement and larvae abundance in areas between Arraial do Cabo/RJ and São Sebastião/SP and observed a significant influence of the seasonal incursion of SW-S-SE winds altering coastal larval transport and affecting positively barnacles and mussels, which are foundation species of intertidal habitats (Coutinho 1995).

Regional-scale processes, such as ocean productivity and water temperature, are determinant to rocky shore communities in Brazil (Cruz-Motta et al. 2020) and elsewhere (e.g., Bosnan et al. 1987; Blanchette et al. 2006; Lathlean et al. 2015). However, local processes (e.g., shore structural complexity, wave exposure, and community composition) seem to be crucial to understand intertidal communities on Brazilian rocky shores (Flores et al. 2015). The evidence and data debated herein indicated an effect of local-scale features on richness patterns additionally to regional tendencies associated with the SACW influence. Low levels of wave exposure were related to higher densities of barnacles than bivalves (Christofoletti et al. 2011), and such determination of the foundation species possibly affects general patterns of species richness. At reduced wave exposure, *M. solisianus* may be absent (Christofoletti et al. 2011), being substituted by oysters in the middle intertidal zones or suppressed by competing species as *C. bisinuatus* in high wave exposure shores. On the other hand, the barnacle *T. stalactifera* may be replaced by *P. perna* mussels on highly exposed shores (Coutinho 2004).

As general patterns, rocky shores from the Cabo Frio region are more similar considering biological (community composition and Chl-a) and environmental variables in relation to other rocky shores. Rocky shores close to large bays (Santos and Guanabara) had similar communities and high Chl-a values associated with eutrophic conditions, while all other rocky shores formed a gradient associated with different wave exposure degree and water temperature (Fig. 2.3). All observations reinforce the importance of the oceanographic context shaping intertidal communities (Menge et al. 2003), with a regional gradient in SST associated with the Cabo Frio upwelling, besides wave exposition and productivity (Chl-a) influencing rocky



**Fig. 2.3** Rocky shores sampled ( $n = 62$ ) for intertidal community composition along the Southeast Brazilian coast by Cordeiro et al. (2024). Clusters were calculated using k-means over environmental data similarity matrix (Euclidean distance). PCA was made based on standardized values (i.e., mean equals to zero and variance to unit)

intertidal communities in the SE Brazilian coast. However, top-down processes acting in local scale may be determinant to species composition (O'Connor et al. 2011) on other population-level parameters (e.g., biomass and productivity) not discussed here.

### *Offshore Rocky Shores*

The Brazilian oceanic islands, namely, Fernando de Noronha Archipelago (FN), São Pedro and São Paulo Archipelago (SPSP), and Trindade and Martin Vaz Islands (TMV), are true rocky formations but differ from coastal rocky shores in their climatic domain, which are all located on tropical waters. Atol das Rocas is one of the Brazilian oceanic systems, but it consists of a biogenic reef consolidated by calcareous algae and vermetids (Soares et al. 2011) and will not be included in further discussions because of the great difference in its reef formation. FN and TMV have a volcanic origin and are composed of steep shores and rocky terraces (Castro 2009), while SPSP is a tiny ( $\sim 130 \text{ m}^2$ ) emerged tip of the Meso-Atlantic Ridge with steep shores and limited shallow areas (Campos et al. 2009).

Oceanic islands are unique biogeographic outposts, in general showing low species richness and higher endemism levels when compared to continental domains because of area and connectivity limitations (MacArthur and Wilson 1967). The Brazilian oceanic islands are no exception for these patterns, and several taxonomic groups have low species richness and several endemics (Hachich et al. 2015; Quimbayo et al. 2018). In general, each island has distinct faunal components and may be defined as independent subprovinces due to high endemism (Spalding et al. 2007; Floeter et al. 2008; Pinheiro et al. 2018). The endemism for reef fish species is below 10% (SPSP = 9%, FN = 4.5% and TMV = 6%—Pinheiro et al. 2018), but it goes beyond this level when adding other taxa, which conferred the status of

separate ecoregions in Spalding et al. (2007). Despite their singularities, some islands present higher similarity with continental areas, as in Barroso et al. (2016), where FN and TMV were close together near continental sites, while SPSP formed an isolated branch because of its low species richness ( $n = 17$ ) and restricted reef area. The TMV have higher connectivity with continental areas because of submarine mounts that act as stepping stones for species (Hachich et al. 2015; Pinheiro et al. 2017), while populations from SPSP and FN may rely mostly on larvae brought by currents. This argument is reinforced by the absence of long route larvae transportation for the TMV islands (Endo et al. 2019), which implies to some local populations (Sally Lightfoot crab *Grapsus grapsus*) to rely on self-recruitment (Freire et al. 2021). Curiously, population connectivity among coral species and crustaceans in the oceanic islands indicates gene exchanges among island populations (Teschima et al. 2016; Peluso et al. 2018; Freire et al. 2021) leaving open questions about their level of isolation. Despite their isolation, island communities are still more similar between them and share more species with the Brazilian coast than with other Atlantic oceanic islands (Floeter et al. 2001; Rocha 2003). However, the presence of Paleogene and Neogene species living together, as well as more recent species in the Brazilian oceanic islands, indicates that they can serve as evolutionary hotspots in the South Atlantic (Pinheiro et al. 2017, 2018).

At the community scale, all islands showed similar patterns of benthic composition dominated by primary producers (turf and macroalgae) and with low complexity components (e.g., zoanths and massive corals—Aued et al. 2018). Reef fish assemblages are dominated by planktivores and omnivorous species (Morais et al. 2017), which is compatible with plankton-based trophic chains (Ferreira et al. 2004). Also, the density and biomass of fish species tend to be higher when compared to continental reefs, especially because of the contribution of pelagic species and lesser influence from fishing (Morais et al. 2017).

Data related to intertidal environments in the Brazilian oceanic islands is scarce, despite the easy access to the intertidal zone in most of them (Andrades et al. 2018). However, high swells and steep areas are additional risks to intertidal work in oceanic islands and may restrict research possibilities to some sites and certain seasons in each island. Despite the steepness of those rocky shores, tide pools are abundant on intertidal flats of some areas in all Brazilian oceanic islands and harbor a high number of endemic species, even higher than found for the same taxa in the subtidal region (Andrades et al. 2017). For instance, the endemism level of tidepool-resident fish species can reach 44% at FN ( $n = 8$  species) and 38% at Trindade Island ( $n = 5$ ), being dominated by herbivorous species that structure local assemblages (Andrades et al. 2018). In contrast, sessile and mobile organisms living on zones subject to air exposition during low tides show limited species richness, and some important groups can be monospecific in each island, such as limpets and littorinids (Eston et al. 1986; Simone 2008; Barroso et al. 2016). Encrusting calcareous algae are abundant in intertidal rocky shores with high inclination and walls of tide pools in TMV and SPSP, which may indicate a large grazing pressure (pers. obs.). Filter feeding species are rare as a probable reflex of the oligotrophic waters, with small mitylid patches found at FN (Eston et al. 1986, pers. obs.). It is also worth noting



that the most conspicuous intertidal taxa, i.e., barnacles, are virtually absent from the Brazilian oceanic islands, being found only at Trindade Island in very low densities (*Chthamalus* sp.—pers. obs.) and rarely in FN (*Megabalanus coccopoma*—Eston et al. 1986). Finally, the yellow crab *Grapsus grapsus* as a potential key species is worth mentioning. The yellow crab is a conspicuous and important component for intertidal communities of all Brazilian oceanic islands and a voracious omnivorous predator, which can feed from algae to conspecifics, imposing a high predation pressure to intertidal species (Freire et al. 2011).

## Final Remarks

Our understanding of ecological patterns of the communities inhabiting the rocky shores of the southeastern-south of Brazil indicated ecological drivers as more important than historical ones (Lotufo 2002), since there are no evident biogeographical barriers or filters within the region occupied by coastal rocky shores. Despite the upwelling area located in the Cabo Frio region could represent the geographical limit for some species, it acts as a turning point for most species by aggregating species from both tropical and subtropical-temperate domains. Warm temperate affinity reef fishes that are widely distributed along the subtropical shallow habitats of rocky reefs domain, where ACAS and BC merge, have their distribution limited to the north until the northeastern coast in some habitats of Bahia state (Carvalho-Filho 1999; Pinheiro et al. 2018). However, some temperate affinity fishes that inhabit mesophotic reefs along the SE-S coast [e.g. *Pronotogrammus martinicensis* (Carvalho et al. 2009) and *Halichoeres sazimai* (Luiz et al. 2009)] can be detected in shallow reefs in the Cabo Frio region, where upwelling processes take place. Thus, oceanographic and habitat characteristics overlap around the rocky shores of the Cabo Frio region, especially at Arraial do Cabo, but those limits are the confluence of wider environmental gradients. Still, habitat availability is limited for species associated with consolidated substrate with large gaps between stable environments: around 120 km of a long sand stretch between Santa Marta Cape/SC and Torres/RS, and >600 km between Torres/RS and La Coronilla (Uruguay). However, artificial structures, such as the breakwaters of Rio Grande/RS, may act as stepping stones (Steigleder et al. 2019) for species dispersion into new habitats on the Argentinean coast.

The number of intertidal species did not show the same decrease observed for subtidal taxa towards southern rocky shores. Indeed, for all rocky shore/reef-associated groups there is a sign of main oceanographic characteristics determining local communities' composition within the crystalline shores' domains. Sea surface temperature and productivity are the most prominent environmental factors acting at regional scale, but the similarity of spatially closest shores indicates the importance of local-scale processes, which may include biotic interactions. In order to confirm such larger influence of abiotic drivers, large experimental approach and

long-term monitoring focused on stratified sampling along natural gradients are potential next steps in rocky shore research.

In this chapter, contemporaneous pressures derived from anthropogenic causes were not discussed as drivers of species richness patterns. Ocean warming may also pose additional challenges to conservation actions along Brazilian subtropical shores. Tropicalization examples in the Southwestern Atlantic are rare (e.g., Araújo et al. 2018; Franco et al. 2020) and yet to be reported for rocky shores, but deserve deeper investigation with special attention to species occupying a wide depth range (Coelho et al. 2021) and to possible buffer effects of the upwelling on temperature rise (Inagaki et al. 2020). Finally, as observed for inter and subtidal taxa, the crystalline shores of the Brazilian coast are a hotspot of biodiversity and happen to be located on the most populated part of Brazil. Although some rocky shores are within marine and coastal protected areas, the total area covered and the real enforcement applied to those protected areas are still below desirable levels (Magris et al. 2020). Thus, these rich habitats are among the most impacted on the Brazilian coast because of the proximity of large cities (Lotufo 2002; Ferreira and Rosso 2009) and should be prioritized on sustainable development initiatives and coastal management planning.

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