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Patterns of fish distribution in tropical rock pools at Príncipe Island, Gulf of Guinea

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Little is known about the ichthyofauna from intertidal rock pools of the west coast of Africa, especially in the Gulf of Guinea. Rock pools are characteristic habitats of the intertidal zone of structurally complex rocky shores, adding important niche space to coastal fish species. In this study, rock pools of three similar rocky shores of Principe Island were sampled to describe the composition, abundance and distribution of fish assemblages and their relation to parameters of pool structure (volume, depth), water mass (temperature, salinity and pH) and biology (algal and coral cover, and biological species richness). A total of 18 fish species and one leptocephalus larva of unknown species, representing 13 families, were observed during sampling. In decreasing order, the five-most-abundant species were the goby Bathygobius burtoni, night sergeant Abudefduf taurus, West African rockhopper Entomacrodus cadenati, sailfin blenny Microlipophrys velifer and Biafra doctorfish Prionurus biafraensis, which together represented 81% of the total number of fish recorded during this study. The four-most-abundant species also proved to be the better adapted to the range of conditions found in rock pools. Overall, larger rock pools with minimal biological cover and higher salinity were found to support higher fish abundance and species richness. Most species individually preferred rock pools with larger volumes, but some presented a degree of habitat specificity, such as the absence or presence of biological cover. Species that were more-active swimmers preferred deeper pools.

Keywords: behavioural ecology, eastern tropical Atlantic, fish assemblage, habitat specificity, intertidal zone, rock pool characteristics, rocky shores, São Tomé and Príncipe

Online supplementary material: The Supplementary Information, available at https://doi.org/10.2989/1814232X.2022.2143423, contains plots of water parameters (temperature, pH and salinity) as a function of the volume of each rock pool on the three sampled shores.

Introduction

Owing to their accessibility, intertidal zones have been one of the most intensively studied marine environments across the globe, and many of these studies have included ichthyofauna. However, tropical rock pools have received little attention (Gibson 1982; Mahon and Mahon 1994; Martins et al. 2007), particularly on the west coast of Africa and adjacent islands (Zander et al. 1999). In this region, fish families such as Clinidae, Tripterygiidae and Blenniidae were the most commonly reported in intertidal habitats in past studies (Wirtz 1980; John and Lawson 1991; Zander et al. 1999), but recent work, particularly focusing on whole assemblages, is non-existent and very little is known about intertidal fishes of other families. Therefore, there is a lack of scientific knowledge on intertidal fishes of the eastern tropical Atlantic, and particularly of the Gulf of Guinea.

Although the marine ichthyofauna of the Gulf of Guinea is one of the least-studied in the world, marine fish in São Tomé and Príncipe have recently attracted scientific interest

(Tuya et al. 2018). Previous studies on the marine fishes of São Tomé and Príncipe have focused mainly on the open and coastal sea, and recently on mangrove ecosystems (Herrero-Barrencua et al. 2017; Cravo et al. 2021). Afonso et al. (1999) and Wirtz et al. (2007) documented limited sightings of fish in intertidal rocky pools, but with no detailed information. Of these, it is known that the blenniids West African rockhopper *Entomacrodus cadenati*, sailfin blenny *Microlipophrys velifer*, horseface blenny *Ophioblennius atlanticus* and molly miller *Scartella cristata* are resident species of the intertidal zone and widely distributed along the west coast of Africa (Zander et al. 1999).

Apart from the intrinsic scientific interest of intertidal fishes and their physiological behaviour, the intertidal and adjacent subtidal zones are also nursery areas for numerous fish species that eventually recruit to coastal fisheries (Gibson 1999a). Any degradation and drastic modification of such areas, therefore, have consequences

for both the economy and quality of life of many coastal and island countries (Gibson 1999a), such as São Tomé and Príncipe, where small-scale coastal fisheries are crucial to domestic trade and as coastal food-suppliers (Horemans et al. 1994; Abreu 2013; Tous 2015). Global climate change, in particular ocean warming, puts further pressure on the environmental conditions of rocky shores and their biological communities (Horn et al. 1999). Projections of climate change in São Tomé and Príncipe show an increase in temperature that could exceed 3 °C by the middle of the 21st century, as well as a heavier precipitation rate (Chou et al. 2020). Impacts of increased temperature on biological communities in tropical waters are expected to be significant because the species are stenothermic, and hence increases in water temperature can drive changes above their lethal limit (Raffaelli and Hawkins 1999). Rock pools constitute good models for assessing these impacts (Vinagre et al. 2018).

Rock pools are characteristic habitats found in the intertidal zone of rocky shores, adding important niche space to coastal habitats (Firth et al. 2014). During low tide, water is retained in holes and depressions that serve as refugia for many invertebrates and fishes (Zander et al. 1999; Martins et al. 2007). This renders rock pools as microhabitats that attract a high diversity and abundance of various organisms (White et al. 2015). Nonetheless, rock pool organisms are subject to stressful environmental conditions during the low-water tidal period. When isolated from the sea, rock pools become prone to large and rapid fluctuations in the physicochemical properties of the water, such as temperature, salinity, oxygen concentration, carbon dioxide concentration and pH (Huggett and Griffiths 1986; Horn et al. 1999; Martins et al. 2007). Additionally, rock pools exist in numerous shapes and volumes, are randomly distributed along the vertical and horizontal gradients of rocky shores, and are highly variable over time (i.e. tidally, diurnally and with seasonally induced fluctuations) and space (from geographic to local scales) (Martins et al. 2007; White et al. 2015). They also become more exposed to marine and terrestrial predators, such as fishes, octopuses and birds, compared with in the subtidal environment (Gibson 1986; White et al. 2015; Vinagre et al. 2018). Consequently, several fish species have developed behavioural, physiological and morphological adaptations to better endure the extreme environmental fluctuations of these habitats (Zander et al. 1999).

Many coastal fishes use rock pools at some point in their life cycle to forage, take refuge from predators or as nursery areas (Horn et al. 1999), and thus rock pools represent a key habitat for supporting coastal fish species diversity (White et al. 2015). Such fishes can be grouped into three categories based on how they use rock pools and the proportion of their life cycle spent within them (Mahon and Mahon 1994; Griffiths 2003; White et al. 2015), namely residents or primary residents, secondary residents and transients. Residents spend almost their entire juvenile and adult lives in the intertidal zone. They are generally small, benthic fishes that are physiologically, morphologically and behaviourally adapted for intertidal life (White and Brown 2013). Secondary residents use the intertidal primarily as a nursery area, after which they migrate into the subtidal and

offshore habitats as they mature (Norton and Cook 1999; White and Brown 2013). A third group, transients, usually comprise a small fraction of the species in rock pools (Mahon and Mahon 1994), occupying them on only certain occasions to forage or by accident, when trapped at low tide (Horn et al. 1999; Griffiths 2003; White et al. 2015).

Throughout the tidal cycle, intertidal fishes need to find and occupy a favourable rock pool during emersion time to increase their chance of survival. Thus, many behavioural patterns of fishes found in rock pools can be interpreted as adaptations for protecting either the individual or its offspring from unfavourable conditions during low tide (Gibson 1986). Consequently, the different gradients of biotic and abiotic factors can produce consistent patterns in the structure, distribution and abundance of fish assemblages (Gibson 1982; Norton and Cook 1999; Zander et al. 1999). Thus, an important part of the study of intertidal fishes is to find the relationships between their distribution, physiology and behaviour and the environmental variables of the rock pools (Gibson 1999b).

In this study, we investigated rock pool fish assemblages at Príncipe Island, in the eastern tropical Atlantic, with the objective of describing the species composition and abundance in relation to abiotic and biotic factors. We aimed to: (i) determine the importance of rock pool dimensions (depth, surface area and volume), within-pool water conditions (temperature, salinity and pH), and algal, coral and total biological community cover in controlling fish assemblage structure; (ii) assess the variables that contributed most to the abundance of each species; and (iii) describe species distribution depending on the water properties.

We defined a priori our hypotheses as: (1) environmental variables drive fish assemblage structure; (2) fish species assemblages differ among sites; (3) environmental variables drive species richness; and (4) environmental variables drive species abundance.

Materials and methods

Ethical statement

Ethical review and approval were not required for the animal study since there are currently no institutional ethical guidelines in São Tomé and Príncipe, but only commonsense practices. The work was conducted entirely in the field at São Tomé and Príncipe under the jurisdiction and approval of the Príncipe Biosphere Reserve and did not involve animal experimentation or compromised animal welfare. The census of fish populations in this study consisted of direct observations. On rare occasions, to ensure better identification, specimens were captured, photographed and returned alive and undamaged to the environment with extreme care, following best practices.

Study sites and rock pool sampling

Sampling took place on Príncipe Island (part of São Tomé and Príncipe), a small oceanic island of volcanic formation located in the Gulf of Guinea (Figure 1). The island is part of the eastern tropical Atlantic, which is characterised by heavy and seasonal rainfall that is sufficient to reduce considerably the surface salinity levels to 30, increasing

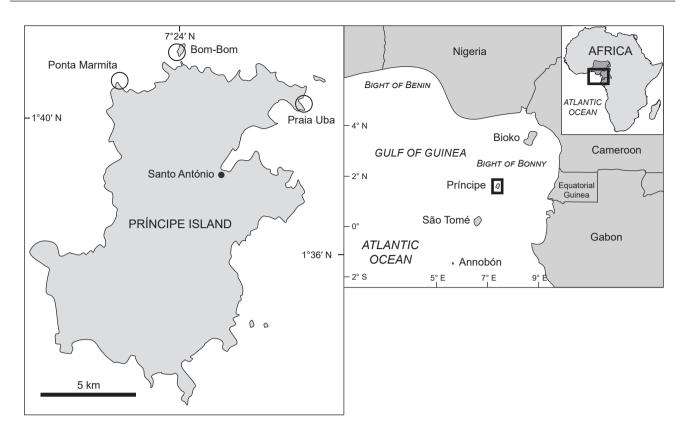


Figure 1: Location of the three rocky shore sampling sites at Príncipe Island: Bom-Bom Islet, Ponta Marmita and Praia Uba

turbidity over extensive areas, particularly around the mouths of the Niger and Congo rivers, but also affecting more-distant islands such as Príncipe Island (Reid 2011). The island has an equatorial humid tropical climate that can be divided into four seasons which alternate between wetter and drier periods, with an average annual rainfall of ~2 000–3 000 mm (NBSAP II 2015; Chou et al. 2020). The rainy seasons include the two main precipitation peaks, with the highest occurring between October and November and a secondary peak around April and May (Chou et al. 2020). These are interspersed by the dry seasons, with the more pronounced one (termed *gravana*) occurring between June and September, and the lesser dry season between January and March (Chou et al. 2020; Cravo et al. 2021).

Tidal ranges are relatively small at Príncipe Island, with a maximum of 1.9 m during extreme spring tides (0.2–2.1 m from hydrographic zero) and 0.4 m during neap tides (1.0–1.4 m from hydrographic zero) (Instituto Hidrográfico 2019).

Sampling occurred at three locations, Bom-Bom Islet, Ponta Marmita and Praia Uba, located on the north coast of Príncipe Island (Gulf of Guinea) (Figure 1). These locations were chosen for their similar geomorphological conditions and exposure to the sea, extensive rocky shores, numerous rock pools and relative ease of access.

A total of 20 permanent rock pools were sampled at each of the three locations between January and February 2020. Only rock pools in the eulittoral zone (mid-zone) were sampled to allow comparison between the different rocky shores. The lower limit of the eulittoral zone was delimited by a noticeable and abrupt absence of the encrusting

coralline alga *Lithophyllum incrustans* and the white encrusting zoanthid *Palythoa caribaeorum* on the freely draining open rock surface, followed by its replacement by black lichen *Verrucaria* sp. and hooded oyster *Saccostrea cucullata*, which defined the upper limit of the eulittoral.

Sampling was performed only close to peak low tide so that splashes from waves would not influence the water conditions of the rock pools. Pools with freshwater drainage from land or pools connected to other adjacent pools were avoided to ensure relatively uniform conditions. Therefore, only saltwater rock pools isolated during emersion were sampled. Salinity, temperature and pH were registered in each pool using a YSI Multi 350i handheld meter.

To determine the area of the rock pools, a scaled photograph was taken from directly above each pool, as parallel to the pool surface (i.e. horizontally) as possible. Rock pools were only considered if they fitted into the full frame of the camera (GoPro Hero7 Black in linear mode). The area was then calculated using ImageJ software. To calculate the water volume, the average depth was calculated from 10 random depth measures. Maximum depth was also recorded.

Fish and biological community sampling

An absence of obstructions such as large macroalgae with considerable canopy meant that fish were clearly visible in the rock pools, and thus direct observations were deemed adequate to census the fish populations (Gibson 1999b). Sampling consisted of first identifying the visible fish species in the rock pool and their respective abundance, with minimal

disturbance so the fish would not hide in crevices. Besides ichthyofauna, the different macroalgae and animal species other than fish in the pools were quantified simply in terms of presence or absence by visually identifying the species. The percentage cover of macroalgae and coral was recorded and estimated by eye for the whole rock pool to the nearest 10%. If necessary, boulders were occasionally moved to account for possible hidden fish and other organisms. To ensure correct species identification, the bottom, ledges and holes of the rock pool were filmed using a waterproof camera, for later examination.

Observations in the field were carried out by trained observers. Species identifications were confirmed *in situ*, on recorded videos and in the laboratory using existing taxonomic references for the region (i.e. Afonso et al. 1999; Wirtz et al. 2007; Carpenter and De Angelis 2016a, 2016b; Vasco-Rodrigues et al. 2018). The taxonomy is according to Nelson (2006).

Data treatment

Draftsman plots using Pearson correlations were made between the environmental variables to determine highly correlated pairs (p > 0.9) to eliminate any possible redundant variables. The remaining variables were average depth (cm), volume (I), pH, salinity, water temperature (°C), coral cover (%), macroalgae cover (%), total biological cover (%), macroalgae species richness and metazoan species richness. These variables were normalised, and a resemblance matrix was constructed using Euclidean distances. Rock pool variables were then compared among the three study sites using principal coordinates analysis (PCoA).

Fish assemblage data were log-transformed, and a resemblance matrix was constructed using the zero-adjusted Bray-Curtis similarity coefficient. This was done to generate the distance matrix among samples because the sampled rock pools did not have all species in common (Clarke et al. 2006). Rock pool fish assemblages were also compared among the three study sites using PCoA. In this PCoA of the fish data, the vectors of the environmental variables that were correlated as >0.3 and the main fish species that were correlated as >0.4 were overlapped for comparison.

Based on the resemblance matrix of fish samples, a distance-based linear model (DISTLM) was used in combination with a distance-based redundancy analysis (dbRDA) for visualising the results (Anderson et al. 2008), to identify which of the environmental variables accounted for the most significant part of the variation in fish assemblage composition, while also assessing the relationship of all variables individually with marginal tests. The selection criterion and procedure were, respectively, the Akaike information criterion for small sample sizes (AICc) and the BEST routine, which selects the best possible model. The resulting variables of the DISTLM model were used in a permutational multivariate analysis of variance (PERMANOVA) as covariates in the order of the proportion of squared differences (Prop.) in the marginal tests. The sequential (Type I) sum of squares (SS) was used, with Location as the last fixed factor. This allowed for the evaluation of the effect of location over and

above the combined effect of all the covariates selected using the BEST routine. One-way analysis of variance (ANOVA) was also used to compare the mean species richness and total abundance among sampling locations.

The effect of rock pool environmental variables (excluding pH and temperature) on the abundance of individual species was analysed using multiple linear regressions with stepwise variable selection. These *post hoc* regressions were conducted only for species that occurred in more than three pools and were represented by more than 10 individuals.

All analyses were performed using the software PRIMER-E 6.1.11, PERMANOVA+ 1.0.1 and IBM SPSS Statistics 26.0.

Results

Fish assemblages

A total of 746 fish from 18 species and a leptocephalus of an unknown species, together representing 13 families, were observed during sampling in the three study locations (Table 1). In decreasing order, the five-mostabundant species were the goby *Bathygobius burtoni*, night sergeant *Abudefduf taurus*, *E. cadenati*, *M. velifer* and Biafra doctorfish *Prionurus biafraensis*, which together represented 81% of the total number of fish recorded during this study.

Sampled fish abundance and composition varied between the three locations (Figure 2). Some species appeared in all three locations, such as A. taurus, Guinean damselfish Microspathodon frontatus, Cape Verde gregory Stegastes imbricatus, E. cadenati, M. velifer, L. nuchipinnis, B. burtoni and P. biafraensis (Figure 2). Other species were found in only two locations, like the silverside Atherina lopeziana found at Bom-Bom and Praia Uba, and spotted soapfish Rypticus subbifrenatus, sergeant major Abudefduf saxatilis and Monrovia doctorfish Acanthurus monroviae found at Bom-Bom and Ponta Marmita (Figure 2). Lastly, some were found at only one rocky shore site: cardinal fish Apogon imberbis, crevalle jack Caranx hippos and orangespotted filefish Cantherhines pullus were found in Bom-Bom, and the leptocephalus (Anguilliformes non-determined [nd]), pebbletooth moray Echidna peli, Niger hind Cephalopholis nigri and Newton's wrasse Thalassoma newtoni in Ponta Marmita (Figure 2).

Sampled rock pools were occupied predominantly by resident fishes, which represented 64% of total individuals but only 16% of total species (Table 1). In contrast, secondary residents represented 34% of total individuals but 58% of total species (Table 1). Finally, transient fishes represented only 2% of total abundance but 26% of total species (Table 1).

Ten additional species were sighted during field observations outside the sampling period in the eulittoral zone of the same rocky shores and at similar shore sites around the island, adding five more families (Table 2). These were the honeycomb moray *Muraena melanotis*, round sardinella *Sardinella* cf. aurita, white mullet *Mugil curema*, rock hind *Epinephelus adscensionis*, grey snapper *Lutjanus griseus*, blacktail picarel *Spicara nigricauda*, West African hawkfish *Cirrhitus atlanticus*, *Hypleurochilus aequipinnis*, *O. atlanticus* and *S. cristata*.

Table 1: Fish species documented in 60 rock pools from three locations at Príncipe Island: Bom-Bom Islet (BB), Ponta Marmita (PM) and Praia Uba (PU). R = resident; SR = secondary resident; T = transient

Family	Species	Local common name	Residency status	No. observed	Location	Rock pool ID no.
Anguilliformes nd	Leptocephalus larva	_	Т	1	PM	32
Muraenidae	Echidna peli (Kaup, 1856)	Moreia-salpicada	SR	1	PM	32
Atherinidae	Atherina lopeziana (Rossignol and Blache, 1961)	-	Т	12	BB, PU	6, 60
Serranidae	Rypticus subbifrenatus (Bloch and Schneider, 1801)	Peixe-sabão	SR	2	BB, PM	16, 32
Epinephelidae	Cephalopholis nigri (Günther, 1859)	Cota-uê	Т	1	PM	30
Apogonidae	Apogon imberbis (Linnaeus, 1758)	Cardinal	Т	1	BB	10
Carangidae	Caranx hippos (Linnaeus, 1766)	Corcovado	SR	3	BB	17, 19
Pomacentridae	Abudefduf saxatilis (Linnaeus, 1758)	Txim-txim	SR	29	BB, PM	15, 32
Pomacentridae	Abudefduf taurus (Müller and Troschel, 1848)	Txim-txim-preto	SR	129	BB, PM, PU	5, 6, 8, 9, 11, 15, 17, 18, 19, 23, 28, 31, 32, 33, 34, 36, 39, 44, 45, 46, 48, 49, 50, 58, 59
Pomacentridae	Microspathodon frontatus Emery, 1970	Txim-txim	SR	27	BB, PM, PU	5, 6, 15, 19, 28, 29, 60
Pomacentridae	Stegastes imbricatus Jenyns, 1840	Txim-txim	SR	39	BB, PM, PU	5, 6, 9, 15, 17, 18, 19, 27, 28, 29, 31, 34, 50, 60
Labridae	Thalassoma newtoni (Osório, 1891)	Dodongo	SR	1	PM	29
Blenniidae	Entomacrodus cadenati Springer, 1967	-	R	97	BB, PM, PU	1, 2, 3, 4, 5, 6, 8, 9, 11, 12, 15, 18, 23, 28, 29, 31, 35, 37, 41, 42, 43, 45, 46, 50, 51, 52, 53, 54, 56, 57, 58, 59, 60
Blenniidae	Microlipophrys velifer (Norman, 1935)	-	R	86	BB, PM, PU	4, 10, 16, 17, 19, 20, 21, 23, 24, 28, 29, 31, 32, 36, 38, 39, 40, 41, 42, 43, 45, 49, 51, 52, 53, 55, 57, 58, 59
Labrisomidae	Labrisomus nuchipinnis (Quoy and Gaimard, 1824)	-	SR	20	BB, PM, PU	6, 9, 11, 12, 17, 19, 35, 37, 49, 56, 60
Gobiidae	Bathygobius burtoni (O'Shaughnessy, 1875)	Xarroco/Batu	R	245	BB, PM, PU	,
Acanthuridae	Acanthurus monroviae Steindachner, 1876	Lâmina	SR	3	BB, PM	5, 15, 32
Acanthuridae	Prionurus biafraensis (Blache and Rossignol, 1962)	Cabo-verde	SR	48	BB, PM, PU	15, 17, 19, 28, 29, 30, 32, 36, 45, 49, 56, 60
Monacanthidae	Cantherhines pullus (Ranzani, 1842)	Peixe-asno-magro	Т	1	ВВ	5

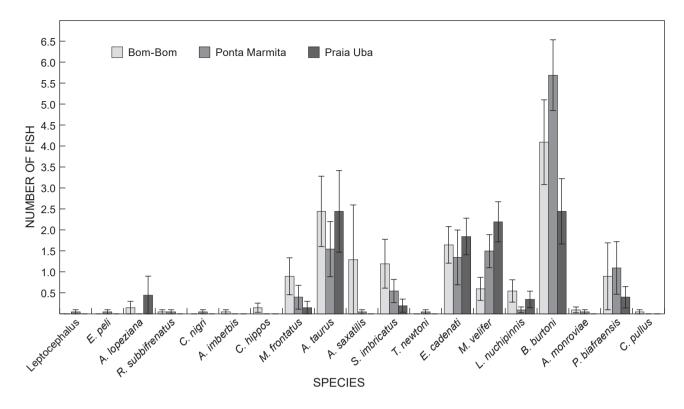


Figure 2: Average number of fish per rock pool of each species observed in rock pools of the eulittoral zone of three locations at Príncipe Island: Bom-Bom, Ponta Marmita and Praia Uba. Error bars represent SE. For full species names see Table 1

Table 2: Additional fish species observed outside the sampling period in rock pools of the eulittoral zone of several rocky shores around Príncipe Island. R = resident; SR = secondary resident T = transient

Family	Species	Local common name	Residency status
Muraenidae	Muraena melanotis (Kaup, 1859)	Moreia-mapinta	SR
Clupeidae	Sardinella cf. aurita (Valenciennes, 1847)	Sardinha/Longo	Т
Mugilidae	Mugil curema (Valenciennes, 1836)	Tainha	SR
Epinephelidae	Epinephelus adscensionis (Osbeck, 1765)	Garoupa	SR
Lutjanidae	Lutjanus griseus (Duméril, 1861)	Corvina	SR
Sparidae	Spicara nigricauda (Norman, 1931)	_	Т
Cirrhitidae	Cirrhitus atlanticus Osório, 1893	Cazebudo	SR
Blenniidae	Hypleurochilus aequipinnis (Günther, 1861)	_	R
Blenniidae	Ophioblennius atlanticus (Valenciennes, 1836)	_	SR
Blenniidae	Scartella cristata (Linnaeus, 1758)	_	R

Relationship between rock pool characteristics and fish assemblages

Sixty permanent rock pools were sampled, having a range of area (0.08–~8 m²), volume (9.8–~3 180 l), and depth (10–75 cm). The physicochemical properties of the water in the rock pools (temperature, pH and salinity) fluctuated more in smaller volumes and oscillated somewhat less as volume increased (Supplementary Figure S1).

Algal cover varied from 0% to 90% and was mainly composed of encrusting coralline pink macroalgae, with some other small red and brown macroalgae present. Coral cover likewise varied from 0% to 90% and predominantly comprised the zoanthid *P. caribaeorum*. Other sessile organisms that were somewhat abundant included sponges, anemones, tubeworms (Serpullidae nd), the

oyster *Striostrea denticulate* and mussel *Mytilus* sp., but these rarely exceeded 10% cover. In terms of mobile organisms, the most frequent and abundant were the rock-boring urchin *Echinometra lucunter*, a hermit crab (Diogenidae nd), and the sea snail *Nerita senegalensis*. Crabs of the family Grapsidae and other small crabs, sea slugs of the genus *Dolabrifera*, and a limpet *Fissurella* sp. were also common, but not as abundant.

The PCoA of the fish data (Figure 3a) shows the overlap of rock pools from the three locations and how environmental variables can explain the distribution of pools in the multivariate space. Macroalgal, coral and total percentage cover appear to be indirectly correlated with the abundance and richness of species in most rock pools, except for some pools that coincided with a

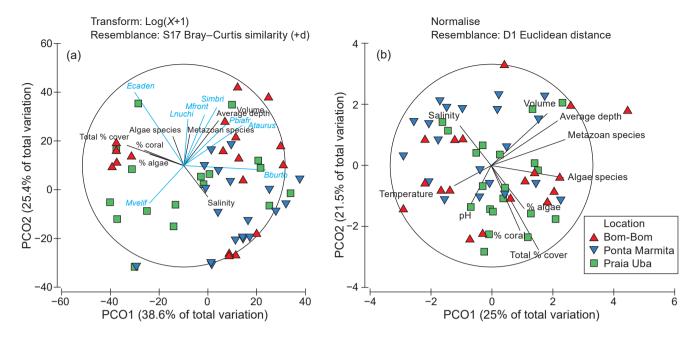


Figure 3: (a) Principal coordinates ordination (PCoA) plot based on zero-adjusted Bray–Curtis dissimilarities of the species composition matrix. Environmental biotic and abiotic vectors inside the circle represent their effect on fish assemblages, and the fish species vectors show in which pools these species tended to be found. (b) PCoA based on Euclidean distances of normalised environmental variables in rock pools at three locations at Príncipe Island. Vectors represent the effect on the characteristics of the rock pools; the longer the line, the more influential is the variable. The name codes for fish species correspond to the following: Ataurus – Abudefduf taurus; Mfront – Microspathodon frontatus; Simbri – Stegastes imbricatus; Ecaden – Entomacrodus cadenati; Mvelif – Microlipophrys velifer; Lnuchi – Labrisomus nuchipinnis; Bburto – Bathygobius burtoni; Pbiafr – Prionurus biafraensis

greater correlation with the presence of the two blenniids, *E. cadenati* and *M. velifer*. This indicates that these species prefer rock pools with greater biological cover. The remaining species were more closely correlated with rock pools with greater volume and depth and more metazoan species present. Both *M. velifer* and *B. burtoni* appear to be moderately tolerant to more saline pools.

Overall, the PCoA of the environmental variables data (Figure 3b) shows only a slight clumping of pools from the same location, with a considerable overall mix of rock pools from different locations. However, salinity appears to be more closely correlated with rock pools from Ponta Marmita. This can be explained primarily by the fact that these rock pools were sampled on two consecutive days when there was low precipitation and high solar radiation, conditions which characterise the peak of the dry season.

According to the DISTLM, the variation in the fish assemblages was better explained by the combination of three environmental variables: volume, total biological community percentage cover and salinity, in descending order of most influential (Table 3). Of these significant variables, volume and salinity had a more positive influence on fish assemblage, whereas the total percentage cover had a more negative one. Of the remaining variables, the average depth, pH, coral percentage cover and macroalgae percentage cover also had a significant impact on fish assemblage (Table 3). The presence of other metazoans was marginally significant.

The PERMANOVA with the resulting variables of the best DISTLM model, and with location as the last fixed factor.

showed that the effect of location did not contribute to explain additional variation (p = 0.160), accounting for only 4% of the variation in the analysis (Location SS/Total SS) (Table 4). Furthermore, according to the ANOVA analysis, there were no significant differences among the three study locations in species richness (F = 0.392, p = 0.677) and total abundance (F = 0.348, p = 0.707).

The dbRDA, using only the three variables selected by the DISTLM (Figure 4), accounted for 32.8% of the total variation in the data, of which 89.1% could be explained by the first two axes. Rock pools with more fish tended to be positioned farther to the left in the ordination plot and those with less fish more to the right. There were a few pools with large numbers of fish that were somewhat smaller in volume and had a high total percentage cover (i.e. rock pools nos. 6, 28, 29). These pools grouped towards the bottom right corner of the ordination plot (Figure 4). Pools with smaller volumes closely grouped along a strong gradient, parallel to the vectors of total % cover and salinity (Figure 4).

The values at which the highest species richness and abundance were observed (Figure 5) were, respectively, at maximum depths of 35 cm and 65 cm; salinities of 32.4 and 31.9; temperatures of 31.2 °C and 31.6 °C; and pH values of 7.996 and 7.964.

The observed patterns of distribution of the richness and abundance of fish species are suggested to be linked to their physiological tolerances (White et al. 2015). Given their distribution along the different gradients, the species that showed the greatest flexibility regarding available

Table 3: The influence of rock pool environmental variables on the variation in fish assemblages at Príncipe Island, as revealed by the distance-based linear model (DISTLM) analysis. The best predictive model (with the lowest Akaike information criterion for small sample sizes [AICc]) achieved when testing all possible combinations (BEST routine) was composed of three variables: volume, salinity and total % cover (shown in bold font), and it explained 32.8% of the variance. Prop. = proportion of squared differences; RSS = root sum squared; SS = sum of squares

Marginal tests				
Variable	SS (trace)	Pseudo-F	<i>p</i> -value	Prop.
(1) Average depth	8 378.6	6.5381	0.002	0.10455
(2) Volume	12 565.0	10.412	0.001	0.15678
(3) pH	2 995.6	2.1745	0.042	0.037379
(4) Salinity	5 077.0	3.7875	0.007	0.063349
(5) Temperature	929.0	0.65674	0.615	0.011592
(6) % Coral	5 147.3	3.8435	0.007	0.064226
(7) % Macroalgae	4 275.2	3.1557	0.022	0.053345
(8) Total % cover	11 426	9.3117	0.001	0.14257
(9) Algae species	2 847.1	2.0627	0.091	0.035525
(10) Metazoan species	3 282.2	2.3914	0.057	0.040954
Overall best solution –				
AICc	R ²	RSS	No. of variables	Selections
405.09	0.32814	53 845	3	2; 4; 8

Table 4: Assessment of the effect of location over and above the combined effect of all the covariants selected by the BEST routine using a distance-based linear model (DISTLM) analysis (volume, total % cover, salinity). These were introduced in a permutational multivariate analysis of variance (PERMANOVA) in order of the proportion of squared differences (Prop.) on the DISTLM marginal tests, using a sequential (Type I) sum of squares (SS). MS = mean squares

PERMANOVA table of results						
Variable	df	SS	MS	Pseudo-F	<i>p</i> -value	Unique perms
Volume	1	12 565	12 565	12.838	0.001	999
Total % cover	1	10 526	10 526	10.755	0.001	998
Salinity	1	3 206.7	3 206.7	3.2765	0.014	998
Location	2	2 952.7	1 476.3	1.5085	0.16	999
Res	52	50 892	978.7			
Total	57	80 143				

vertical space and fluctuations in physicochemical properties were the residents *B. burtoni*, *E. cadenati* and *M. velifer* and the secondary resident *A. taurus*, which were the four-most-abundant species.

The stepwise regression analysis was restricted to the eight species for which there were sufficient data (Table 5). The presence of *A. taurus*, *M. frontatus* and *S. imbricatus* was higher in rock pools with larger volumes. *Entomacrodus cadenati* was more significantly correlated with pools with higher macroalgae cover and the presence of other organisms. A presence model was not produced for *M. velifer* since no variables could significantly predict its abundance. *Labrisomus nuchipinnis* was found more often in pools with larger volumes and more total cover of the bottom by the biological community. *Bathygobius burtoni* and *P. biafraensis* were more significantly correlated with rock pools with larger volumes and minimal biological cover. These results can also be observed in the PCoA of fish assemblages (Figure 3a).

Discussion

Fish assemblage composition and abundance seemed to be influenced mostly by the volume of rock pools, total coverage by flora and fauna, and water salinity. Rock pools with larger volumes generally supported a higher abundance and richness of fish species. The volume of a tidepool is often a good predictor of the number of fish it contains (Prochazka and Griffiths 1992; Mahon and Mahon 1994; Gibson 1999b), as larger volumes allow for more space (and thus more biomass) and also decrease the fluctuation of the physicochemical properties of the water (temperature, salinity, pH and oxygen saturation) throughout tidal and diurnal cycles and variations in climate conditions (Raffaelli and Hawkins 1999). This provides more-stable conditions that a higher number of fish species can tolerate. This becomes particularly important in rock pools of tropical rocky shores, as extreme exposure to the heat and sun during the drier seasons can

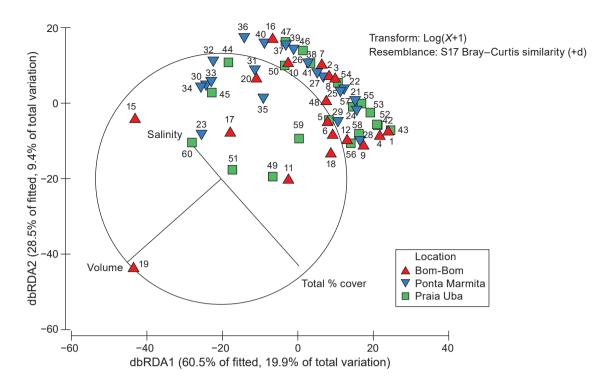


Figure 4: Distance-based redundancy analysis (dbRDA) ordination plot of the best DISTLM model based on the species composition matrix using zero-adjusted Bray–Curtis dissimilarities, displaying the relationship between rock pool variables that best explain the variation of fish assemblages among pools at three locations at Príncipe Island. Numbers refer to the ID no. of each rock pool. Vectors represent the correlation of variables with both axes

cause dangerous rises in water temperatures (Vinagre et al. 2018), and both rainfall, which is heavy in the region (Herrero-Barrencua et al. 2017; Chou et al. 2020), and freshwater runoff can considerably decrease the salinity of rock pools (Evans et al. 1999; Raffaelli and Hawkins 1999).

The average salinity in rock pools was somewhat lower than expected for the dry season, despite the rising temperatures during the day that could lead to high evaporation in the pools (Evans et al. 1999). This may be due to the salinity of the surrounding sea being reduced by the influence of the plume of the Congo and Niger rivers throughout the Gulf of Guinea at this time of year (Measey et al. 2007; Reid 2011). Any salinity variation in pools with similar volumes was most likely caused by local weather conditions, such as occasional rainfall before the sampling period. Across the recorded salinity range, rock pools with higher salinity offered a better environment for marine animals and attracted more fishes, although some fish species showed tolerance to lower salinities. However, the recorded salinity range is only representative of the weaker dry season in which this study took place. Thus, it is likely that salinity may play a more critical role in determining fish assemblage variations throughout the seasons (Horn et al. 1999).

The amount of biological cover on the bottoms of the pools was the second-most-influential variable and it tended to be negatively correlated to fish composition and abundance, especially in smaller-volume pools. It possibly reflects the effect on the pH of the water, as pH is affected by the amounts of dissolved carbon dioxide and

oxygen in the water (Martin and Bridges 1999; Raffaelli and Hawkins 1999), which in turn depend largely on the conjunction of the tidal and diurnal cycles at emersion time, and the presence of animals and plants (Truchot and Duhamel-Jouve 1980). During the day, pools with coral and macroalgae produce oxygen which overrides carbon dioxide released from respiration, and hence the water becomes alkaline during emersion time (Truchot and Duhamel-Jouve 1980; Martin and Bridges 1999; Raffaelli and Hawkins 1999), as was observed in this study. At night during emersion, the pH decreases as more carbon dioxide is solubilised and there is no oxygen production, rendering the pools more acidic (Truchot and Duhamel-Jouve 1980; Raffaelli and Hawkins 1999). Thus, rock pools with relatively more macroalgae and/or coral cover will be more susceptible to large and rapid fluctuations in oxygen and carbon dioxide, and consequently will have very variable pH values. This occurs especially in small and shallow pools that can change by several pH units over the course of a few hours (Bridges 1993a, 1993b; Martin and Bridges 1999). Thus, only the fish species that are well-adapted for respiratory stress are capable of surviving in such pools, and these tend to be mostly residents and juveniles of secondary residents. Additionally, oxygen consumption by residents can exacerbate aquatic hypoxia in tidepools, especially in the absence of algae by day, or at night in pools with numerous plants and animals (Truchot and Duhamel-Jouve 1980; Martin and Bridges 1999; Richards 2011). Hypoxic conditions further reduce the possibility of other fish species settling. In contrast, large rock pools

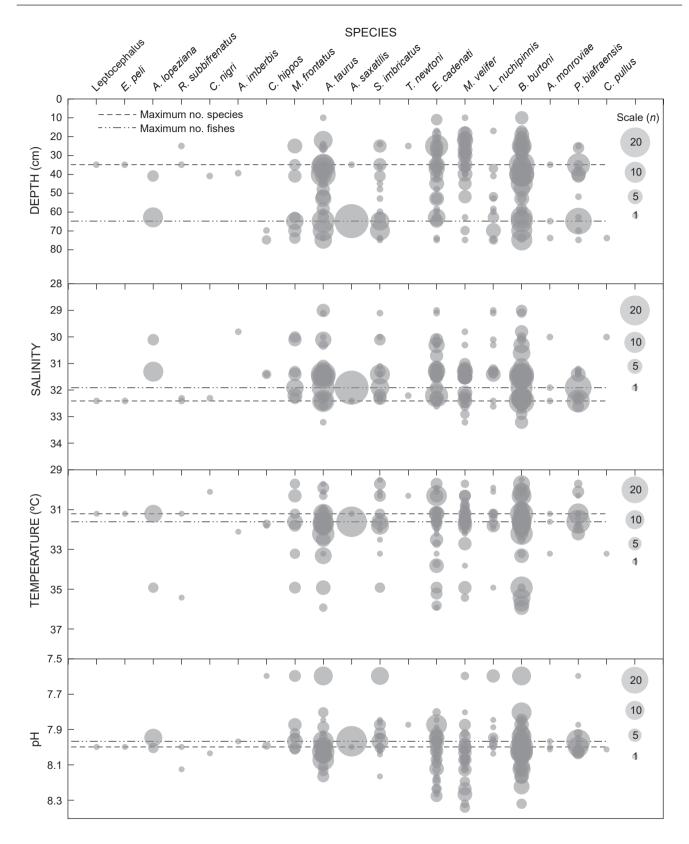


Figure 5: Distribution of fish species abundance and richness along the observed variation of depth, salinity, temperature and pH in rock pools at Príncipe Island. The lines across the plots represent the value at which the maximum numbers of fish and species were found. For full species names see Table 1

Table 5: Relationship between rock pool characteristics and abundance of individual fish species (stepwise regression results) at Príncipe Island. Variables are listed in order of addition in the forward-selection model. Only rock pool characteristics that had a significant effect on fish abundance are displayed

Species	Variables	R²	F	<i>p</i> -value		
Abudefduf taurus	Volume	0.377	35.032	<0.0001		
Microspathodon frontatus	Volume	0.204	14.876	0.0003		
Stegastes imbricatus	Volume	0.388	36.762	<0.0001		
Entomacrodus cadenati	% Algae	0.110	7.177	0.0100		
	Other metazoans	0.188	5.442	0.0230		
Microlipophrys velifer	No variables were entered into the equation					
Labrisomus nuchipinnis	Volume	0.431	45.671	<0.0001		
	Total % cover	0.506	7.606	0.0078		
Bathygobius burtoni	Total % cover	0.361	32.704	<0.0001		
	Volume	0.537	21.686	< 0.0001		
Prionurus biafraensis	Volume	0.132	8.847	0.0043		
	Total % cover	0.224	6.736	0.0120		

are less susceptible to these changes and will have less polarised pH values (Raffaelli and Hawkins 1999). Even those that had 80% or more of total biological cover still presented high fish abundance.

The location effect was not considered as one of the main causes of the differences in fish assemblages. This makes sense given that the three rocky shores are similar in geomorphology, exposure and orientation to the sea, and have a negligible geographic distance between them.

Depth had a considerable effect on the abundance and richness of fish species found in rock pools, being the third-most-influential variable for fish assemblages in this study (Table 3). In terms of water conditions, deeper pools offer more protection from the heat and sun and allow the formation of a vertical salinity gradient under rainfall, allowing fish to shelter at the bottom in higher salinity. In addition, deeper rock pools allow freer movement of fishes that are more active swimmers or that form schools (Lawson et al. 1999), and offer more protection from predatory birds, which were frequently seen around the pools preying on trapped fish. These included four species of herons, western reef heron Egretta gularis, little egret E. garzetta, cattle egret Bubulcus ibis and striated heron Butorides striatus, as well as the endemic Príncipe kingfisher Corythornis nais.

The structural complexity of the rock pools was not documented during sampling, but structures like rock ledges, caves, crevasses and loose rocks were seen sheltering fish in some rock pools. The presence of some of these structures appears to be very important in determining the abundance and choice of habitat of intertidal fish, which may be linked to predator avoidance behaviour (White et al. 2015). The greater the complexity, the greater the availability of cover for fish to hide. Based on field observations in this study of fish behaviour and the regular occurrence of predatory birds around rock pools, it is likely that structural complexity also plays an important role in determining fish preference of rock pools on the island, a hypothesis that requires further study.

The vertical position of a rock pool on the rocky shore is also known to affect fish community composition (Zander et al. 1999). Residents *E. cadenati*, *M. velifer* and *B. burtoni*

and secondary residents A. taurus and P. biafraensis were the most abundant in the eulittoral zone. However, field observations suggest that pools positioned higher in the tidal profile were more often occupied by these species, particularly A. taurus and B. burtoni. Pools lower on the shore were characterised by noticeably higher species richness and a more equitable proportion of residents, secondary residents and transients, likely because of the more stable water conditions. The age structure of fish assemblages is also affected by the vertical position of pools, as some studies have observed that smaller fishes are generally more abundant higher up in the intertidal zone (Zander et al. 1999), demonstrating greater tolerance to extreme physicochemical changes. Although no individual size measurements were taken in this study, the field observations and underwater video footage provided a general qualitative perception of fish sizes. In the eulittoral, residents appeared both as juveniles and adults, whereas secondary residents and transients were predominantly and distinctively juveniles, with occasional occurrences of subadults and adults of damselfishes, L. nuchipinnis, C. atlanticus and moray eels, for example. Pools higher on the shore were occupied largely by juveniles, with the exception of B. burtoni. Rock pools lower on the shore contained adult residents and noticeably more subadults and adults of secondary residents and transients, but still with an apparent dominance of juveniles. This suggests that the rocky shores of Príncipe Island act as a nursery area for a number of species, including some with local commercial interest, such as S. aurita, R. subbifrenatus, C. nigri, E. adscensionis, C. hippos, S. nigricauda, A. saxatilis, S. imbricatus, A. monroviae, P. biafraensis and C. pullus (Horemans et al. 1994; Afonso et al. 1999; Direção das Pescas 2015; Tous 2015). Lutjanus griseus is also commercially exploited elsewhere (Anderson 2002; Frédou and Ferreira 2005) but has not been recorded in the local markets of São Tomé and Príncipe.

Six out of the eight species with sufficient data for the regression analysis were more likely to be found in rock pools with larger volumes (i.e. *A. taurus*, *M. frontatus*, *S. imbricatus*, *L. nuchipinnis*, *B. burtoni* and *P. biafraensis*). Even though these species occupied a variety of pool

environments, including small and shallow ones, the larger pools are more stable and provide continuously favourable conditions. *Entomacrodus cadenati* and *M. velifer* were, apparently, equally likely to be found in smaller and larger volumes. This can be related to the utilisation of different habitats during different stages of their development as their size increases (White et al. 2015).

In addition to the above eight fish species, the other species observed in rock pools sampled in this study were either secondary residents (E. peli, R. subbifrenatus, C. hippos. A. saxatilis. T. newtoni and A. monroviae) or transients (the leptocephalus, A. lopeziana, C. nigri, Apogon imberbis and C. pullus). These occurred in low abundance and were mostly found in larger and deeper pools, possibly because they are mostly temporary or accidental inhabitants of the intertidal zone. They were found in a narrow range of temperature, salinity and pH values, in comparison to residents and the more-abundant secondary residents, suggesting that these species that thrive in open waters are more sensitive to fluctuations in water conditions. Furthermore, some of these species are pelagic and more-active swimmers (C. hippos, A. saxatilis, T. newtoni, A. monroviae, A. lopeziana), and many of them are gregarious, which creates large demands for space (Lawson et al. 1999; White et al. 2015). Various species. including P. biafraensis and A. taurus, were often seen shoaling within pools, maybe as a mechanism of defence against predators.

Predation by birds is a frequent cause of death in the rock pools of Príncipe Island. For primary and secondary resident fish species that spend a significant part of their life in tide pools, predator avoidance is essential to ensure survival. Two strategies are the use of cryptic colouration and cryptic behaviour (Gibson 1982). Fish species reliant on colouration may choose rock pools in which they can best camouflage themselves. In addition to B. burtoni and P. biafraensis being more abundant in larger pools, they were also more likely to be found in pools with more bare rock, possibly suitable for camouflage. Their cryptic colouration (Miller 2016; Rocha 2016) blended well with the rocky black and grey bottom. They also displayed cryptic behaviour. When approached by observers, these fishes often remained still, especially B. burtoni. Juveniles of P. biafraensis sometimes lay sideways against the rock and even adjusted their colour slightly between lighter and darker shades.

Entomacrodus cadenati, M. velifer and L. nuchipinnis also present cryptic colouration (Williams and Springer 2016a, 2016b), and in our study these fish were seen changing between darker and lighter colour patterns, allowing them to camouflage themselves against a wide range of surroundings (rocks, coral, oysters, coralline and other macroalgae, and sandy bottoms). Both E. cadenati and L. nuchipinnis were, in fact, significantly more likely to be found in pools with some cover of macroalgae, coral or both. The presence of M. velifer was not correlated with any type of environment since it was seen in rock pools of all descriptions.

Other species also have cryptic colouration in relation to a variety of backgrounds found in rock pools. *Abudefduf taurus*, which is yellowish with five vertical brown bars (Edwards 2016), is camouflaged against surfaces covered by the yellow coral *P. caribaeorum*, which is very common

in both the intertidal and sublittoral. Although *A. taurus* was not correlated with coral percentage cover in this study, several individuals were regularly sighted in lower intertidal rock pools completely covered with the yellow coral, as in shallow coastal waters. Eulittoral rock pools covered in coral may develop harsh water conditions, which could explain the absence of correlation with coral percentage cover in this study.

Overall, given the geographic and climate setting of Príncipe Island, fish assemblages tend to prefer rock pools with larger volumes, reduced presence of biological cover and higher salinity. However, other within-pool characteristics that were not sampled may also influence fish presence, in particular the availability of cover (i.e. rock ledges, caves, and loose rocks) which is likely to be representative of a preferred habitat (White et al. 2015).

Primary and secondary resident species contributed the most to the fish assemblage structure in our study, but the extent to which they do so is likely to vary vertically on the shore and seasonally owing to variations in rock pool conditions (Gibson and Yoshiyama 1999; Zander et al. 1999). Fish distribution may also change seasonally with the arrival of juveniles following the breeding season (White et al. 2015) and the migration of secondary residents to lower zones on the shore as they grow bigger (Norton and Cook 1999).

The conspicuously small size of many residents, but especially secondary residents and transients, indicates that these rocky shores play a role as a nursery area for many coastal fish species of Príncipe Island. Future studies should focus on the structural complexity of rock pools to assess the effect of certain structures on fish species abundance and composition. In addition, seasonal and vertical distribution patterns should be assessed in more detail, also taking into account the size/age structure of fish populations, to better understand the use of rock pools as fish nursery grounds throughout the year.

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