Diel feeding activity of *Abudefduf saxatilis* (Perciformes: Pomacentridae) on southwestern Atlantic reefs

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Feeding ecology studies are crucial for understanding energy flow in reef ecosystems. In this study, we used an integrative approach to investigate the diel-feeding ecology of the sergeant-major *Abudefduf saxatilis*. To examine the possibility of diel-periodicity and size-class differences in foraging behaviour, we tracked fish individuals until their first bite on two subtropical reefs. During each observation, we recorded the substratum that was bitten and estimated the individual's total length. To assess the diet, we analysed the stomach contents of five individuals from each location. In total, we observed 2,703 individuals biting seven substrates. Our results showed no significant differences in substrate use for diel-periodicity. However, we found significant differences between two size classes. Despite this, both populations tended to forage near the surface in the water column in the morning and on the benthos in the afternoon, although this tendency was not statistically significant. Smaller individuals fed mostly in the water column, while larger individuals foraged on all substrates, likely due to their different energetic demands. Our findings indicate this species has an omnivorous, generalist diet, comprising 12 items from both benthos and plankton. The lack of differences in diel-periodicity is likely due to the sergeant-major's opportunistic behaviour.

Keywords: Fish behaviour, Reef fish, Rocky reef, Trophic ecology.

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Estudos de ecologia alimentar são cruciais para entender o fluxo de energia em ecossistemas recifais. Neste estudo, usamos uma abordagem integrativa para investigar a ecologia alimentar do sargentinho *Abudefduf saxatilis*. Para responder se há periodicidade ou diferenças relacionadas a classes de tamanho no substrato forrageado, acompanhamos indivíduos deste peixe até a primeira mordida, em dois recifes subtropicais. Durante cada observação, registramos o substrato mordido e estimamos o comprimento total do indivíduo. Para estudar a sua dieta, analisamos o conteúdo estomacal de cinco indivíduos em cada recife. No total, observamos 2.703 indivíduos mordendo em sete substratos diferentes. Nossos resultados não mostraram diferenças significativas no uso de substrato para a periodicidade diária. No entanto, encontramos diferenças significativas entre duas classes de tamanho. Apesar disso, ambas as populações tenderam a forragear próximo à superfície na coluna d'água pela manhã e no substrato bentônico à tarde, embora essa tendência não tenha sido estatisticamente significativa. Indivíduos menores forragearam principalmente na coluna d'água, enquanto os indivíduos maiores forragearam em todos os tipos de substratos, provavelmente devido às suas diferentes demandas energéticas. Nossos resultados corroboram que o sargentinho tem uma dieta onívora e generalista, composta por 12 itens de ambos os compartimentos, bentônico e planctônico. A falta de diferenças na periodicidade diária é provavelmente devido ao comportamento oportunista do sargentinho.

Palavras-chave: Comportamento de peixes, Ecologia trófica, Peixe recifal, Recifes rochosos.

INTRODUCTION

The energetic balance between food intake and energy requirements for growth and reproduction is a key factor of any animal life cycle (*e.g.*, Charnov, 1976; Manning *et al.*, 2019). Animals are able to exploit efficiently their food resources by developing different behavioural strategies, thereby minimising energy costs to obtain their nourishment (Charnov, 1976; Pyke *et al.*, 1977). According to the optimal foraging theory, animals make decisions to maximise their foraging efficiency based on key factors such as body mass/size and diet nutritional quality (MacArthur, Pianka, 1966). Body mass has a well-known effect on animal metabolism – smaller individuals have a higher bite rate compared to larger ones (Barneche *et al.*, 2009; Nunes *et al.*, 2021). Additionally, the diet's nutritional quality can be directly influenced by the period of the day in which the animal is foraging (Taborsky, Limberger, 1980; Zemke-White *et al.*, 2002; Dabrowski, Portella, 2005; Raubenheimer *et al.*, 2005; Mendes *et al.*, 2009). Benthic producers change their nutritional quality throughout the day, influencing photosynthesis and glucose production (Taborsky, Limberger, 1980). Consequently, this differentiated sugar production rate throughout the day can influence the feeding activity/behaviour of herbivorous and omnivorous fishes (Taborsky, Limberger, 1980; Zemke-White *et al.*, 2002).

Besides benthic producers, zooplankton is a diverse community recognised as one of the most important sources of energy sustaining fish biomass on reefs (Heidelberg *et al.*, 2004; Yahel *et al.*, 2005; Truong *et al.*, 2017). Zooplankton abundance and community composition varies in space and time and have complex diel changes with increase in the abundance close to reef bottom (< 1 m) during the night and depletion during the day (Heidelberg *et al.*, 2004; Yahel *et al.*, 2005). This depletion in zooplankton close to reef bottom, during daytime, is attributed to an intense predation by primary and secondary consumers, such as reef fishes, which is greater in areas up to 1.5 m above reef (Motro *et al.*, 2005; Heidelberg *et al.*, 2010).

Omnivores are secondary consumers feeding on more than one trophic level (Pimm, 1982; Gerking, 1994). Usually, omnivorous marine fish species feed on a variety of resources including algae and animals (Gerking, 1994). As such, the diet of omnivorous species is shaped by resource availability, foraging behaviour and diel foraging patterns (Lawton, Pratchett, 2012). Omnivorous fish are one of the most abundant trophic groups on subtropical Brazilian reefs (Ferreira *et al.*, 2004; Morais *et al.*, 2017). Their behaviour plasticity makes them capable to explore different resources including benthic and plankton components (Gerking, 1994), while promptly filling vacant niches in depauperate reefs (Mendes *et al.*, 2019).

Among omnivorous reef fishes, the sergeant-major *Abudefduf saxatilis* (Linnaeus, 1758) is one of the most common and abundant species on tropical and subtropical reefs of the Atlantic Ocean (Krajewski, Floeter, 2011; Anderson *et al.*, 2015; Piñeros, Gutiérrez-Rodríguez, 2017; Fig. 1). This species belongs in the Pomacentridae (Damselfishes), which is a key family for studies on feeding ecology due to its importance as primary and secondary consumers on reef ecosystems worldwide (Barneche *et al.*, 2009). The populations of this species are genetically linked throughout the Brazilian Biogeographic Marine Province. However, genetic divergence was detected between the Caribbean and Brazilian populations, which is attributed to the influence of the Amazon-Orinoco River Plume (Piñeros, Gutiérrez-Rodríguez, 2017). Despite its vast distribution in the Atlantic Ocean, few studies have explored the trophic ecology of *A. saxatilis*. These studies report a diet composed mainly of invertebrates and algae (Randall, 1967; Dubiaski-Silva, Masunari, 2008), besides egg cannibalism (Foster, 1987; Hoelzer, 1995; Cheney, 2008), plus acting as a cleaner fish, feeding on ectoparasites, epibionts, and dead tissue from fishes and sea turtles (Sazima, 1986; Grossman *et al.*, 2006; Sazima *et al.*, 2010; Quimbayo *et al.*, 2018). This damselfish usually forages in the water column or on benthic substrates, and its peak feeding activity occurs between 10:00 and 13:00h (Fishelson, 1970). *Abudefduf saxatilis* commonly attains 15 cm as mean body size and has a bluish body colour (sometimes with yellowish back) and five darker vertical stripes (Fig. 1). Males display sexual dimorphism (deep blue colour) during parental care (Fishelson, 1970).

In this study, we quantify the diel foraging patterns of *A. saxatilis* on two Brazilian reefs to answer three questions: 1) Does this species forage more in the benthic or planktonic compartment throughout the day? We expected that this damselfish will forage mostly on zooplankton independent of the period of the day; 2) Do different size classes forage on different substrates? We expected that smaller individuals will forage mostly on the planktonic compartment, while larger individuals would primarily forage on the benthic compartment; 3) Can the species' diet be associated with foraging substrate selection? We expected that the diet would mainly comprise zooplankton,
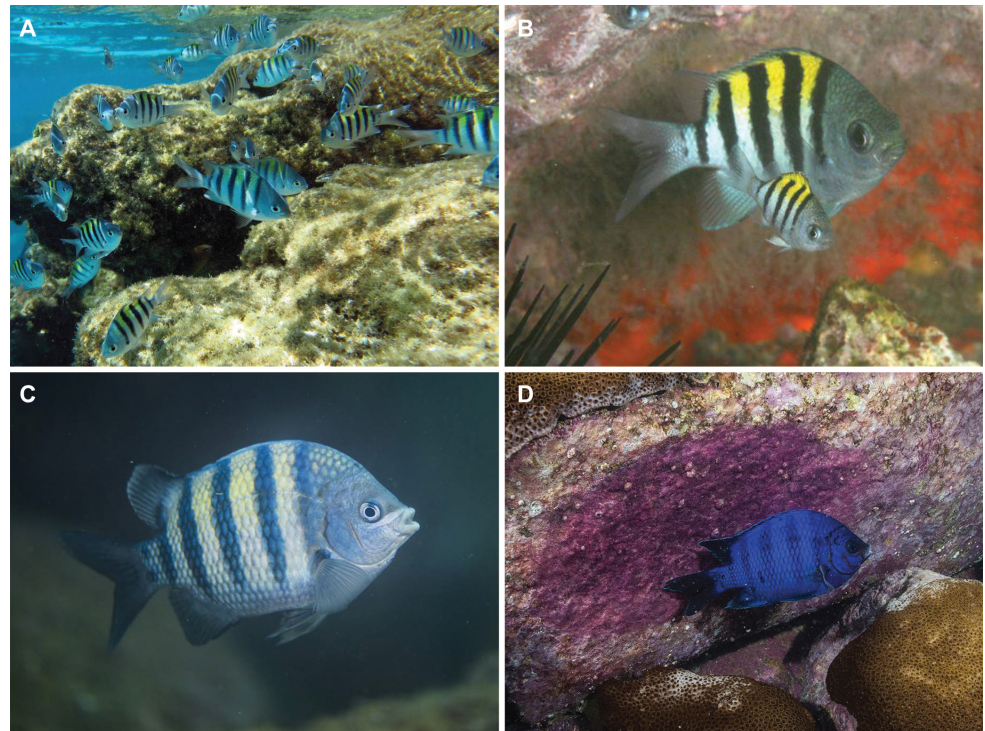
FIGURE 1 | *Abudefduf saxatilis* (sergeant major) displays different colours and development phases on different Brazilian reefs. **A.** Shoal of sub adults at Rocas Atoll (photo: Lucas Nunes); **B.** Adult and juvenile at Laje de Santos (photo: Osmar Luiz); **C.** Adult in Santa Catarina (photo: Thiago Fiuza); **D.** Male protecting its nest (purple blotch) on rock surface in Santa Catarina (photo: Thiago Fiuza).

reflecting the foraging behaviour of this species. To address these questions, we used an integrative approach (*i.e.*, foraging behaviour and stomach content analysis) to investigate the diel-feeding ecology of *A. saxatilis* on the two sampled reefs.

MATERIAL AND METHODS

Study area. Sampling was done on two coastal rocky reefs in South-eastern Brazil (Fig.2) distanced about 800 km. The Brazilian south and southeast coast are rocky and mainly covered with macroalgae, epilithic algal matrix and sessile animals such as corals and sponges (Aued *et al.*, 2018). Arraial do Cabo in the Rio de Janeiro State (22°58'0.69"S 42°0'39.20"W) has unique oceanographic characteristics that enable the occurrence of two different reef habitats in the same location. A sheltered bay with warmer sea surface temperature (Mean SST ~22 °C) harbours a tropical-related reef community. Outside the bay, there is a warm-temperate reef with colder waters (~18 °C) due to the direct effect of seasonal upwelling events (Valentin, 1984). The upwelling events directly favour the primary production and zooplankton biomass in both areas (Valentin, Monteiro-Ribas, 1993). Foraging behaviour data was obtained in a sheltered rocky reef inside the bay (Fig. 2). The coast of Santa Catarina state (between latitudes 27°08'26.83"S 48°28'44.33"W and 27°45'23.08"S 48°29'35.25"W) is a zone

of convergence between the warm tropical waters from the Brazil Current and cold waters from the South Atlantic Central Waters (SACW). Sea surface temperature ranges seasonally from 14 to 29 °C (Faria-Junior, Lindner, 2019).

Sampling. On each reef, underwater observations of *A. saxatilis* foraging behaviour were conducted while snorkelling in shallow areas of the reef slope (< 3 m deep). The foraging behaviour was quantified during the daytime using an adaptation of the focal animal method (see Lehner, 1996), from 8:00 to 17:00h. For each observation we followed a fish individual until the event of the first bite, then we attributed a size class by visually estimating the individual total length (cm), recorded the time-interval (*i.e.*, one-hour intervals throughout the day) when the bite occurred and the type of bitten substrate (see below). The sampling occurred following a linear path by haphazardly choosing fish individuals and thus avoiding individual resampling. If the chosen individual did not bite any substrate during a one-minute interval, it was discarded from the sampling.
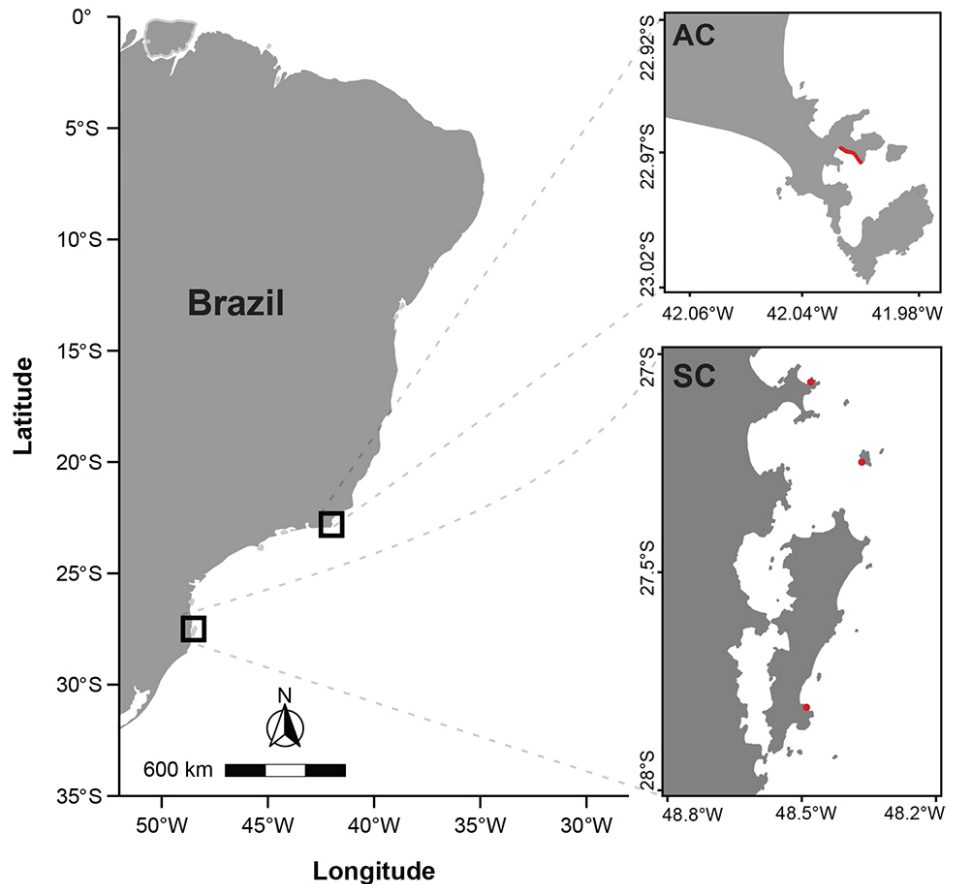

FIGURE 2 | Location of the sampled reefs in south-eastern Brazil. Red line is the site Praia do Forno in Arraial do Cabo (AC). Red dots are the sites Bombinhas, Arvoredo Island, and Praia do Matadeiro in Santa Catarina (SC).

Benthic substrates were grouped into five major categories: Epilithic Algal Matrix (EAM); *Sargassum* sp.; Calcareous Algae; *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860); and Demersal eggs. We divided the water column into two depth strata according to the distance (visually estimated) between the fish and the reef bottom: less than 50 cm from the bottom (water column < 50 cm) and more than 50 cm from the bottom (water column > 50 cm). This was necessary due to zooplankton stratification in the water column (Alldredge, King, 2009; Heidelberg *et al*., 2010), which may influence fish foraging close to the bottom or near the water surface. Individuals' were categorized into four classes, three of these classes were based on their total length: TL smaller than 5 cm (Size Class 1; SC), between 5.1 and 12 cm (SC2), and larger than 12 cm (SC3). Additionally, males in parental care (> 12 cm) were placed in a distinct category (referred to as 'SC4') due to behavioural differences (see Fishelson, 1970 for further details).

Diet. For diet analysis, we sampled five adult-fish individuals in each location using a hand-spear. We intentionally limited our sampling to a small number of individuals to minimize any potential impact on the population. All individuals were immediately frozen to avoid enzymatic digestion of the gut content. To avoid bias on stomach content due to different behaviour strategies we did not sample adult males during parental care. In the laboratory, the individuals were measured (total length and mass) and dissected. Stomachs were removed and individually stored in tubes with formaldehyde for three days. After fixation, the stomachs were dissected in a Petri dish and the content was identified under a stereomicroscope to the most detailed taxonomic category possible. Organic material mass that seemed unidentifiable was analysed under a microscope to search for features such as spicules and nematocysts. Amorphous material with the presence of different cellular structures (*i.e*., different taxonomic groups) was classified as "digested organic matter". Stomach contents that had no cellular structure were classified as "undetermined" (Nunes *et al*., 2019).

The volume of each food item was individually measured using a millimetre petri dish, with the item positioned between two 1 mm thick coverslips and kneaded with a microscope slide, and then the number of 1 mm^3 grids were counted (Liedke *et al*., 2016; Nunes *et al*., 2019). Diet composition was analysed by the volume (%VO) of each food item as a percentage of the total volume consumed by each individual fish, and the frequency of occurrence (%FO) is the frequency of stomachs containing a given item (Liedke *et al*., 2016; Nunes *et al*., 2019). Those parameters were combined to calculate the Feeding Index (%IAi), which quantifies the importance of feeding items in the diet (Kawakami, Vazzoler, 1980; Liedke *et al*., 2016; Nunes *et al*., 2019), through the equation:

$$\%IAi = ((FOi * VOi) / \textstyle\sum_{i=1}^{n}(FOi * VOi)) * 100;$$

where *IAi* is the feeding index (%) of item "i" in the diet, *FOi* is the frequency of occurrence of item "i" in the diet, *VOi* is the volume of the item "i" in the diet.

Statistical analyses. To answer if species forage differently on benthic or planktonic compartment throughout the day, we used descriptive analyses (*i.e.*, stacked barplots) and performed two Friedman tests using the number of bites on the substrates as

dependent variable. The first Friedman test was performed by using the one-hour intervals throughout the day as independent variable; for the second test we grouped the one-hour intervals in three blocks: Morning (between 8:00 to 10:00h), Midday (11:00 to 13:00h) and Evening (14:00 to 16:00h). We also grouped all the benthic substrates into one category, namely "benthos". To answer if the four size classes forage on different substrates at each location, we performed a Friedman test using size (TL cm) as the independent variable, and the number of bites on each substrate as the dependent variable. In the case of significant differences, we used a post-hoc test through the function "friedman.test.with.post.hoc". To investigate the association between the species' diet and its foraging substrate selection, we conducted a Principal Coordinate Analysis (PCoA) and a Permutation Multivariate Analysis of Variance (PERMANOVA). For both analyses, we employed a Euclidean distance matrix transformed by "standardization" to decrease data dispersion. Considering that both populations of *A. saxatilis* are isotropic super-generalist in terms of feed resource use (Gotelli *et al.*, 2015), we performed a null model to test whether the observed Pianka overlap index is expected over 999 resamplings. For this, we choose the "ra1" algorithm in the "niche_null_model" function of the EcosimR package (Gotelli *et al.*, 2015). We did all analyses in R software (R Development Core Team, 2020). All data and R code can be downloaded from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.8113695

RESULTS

We sampled 1,035 *Abudefduf saxatilis* individuals in Arraial do Cabo and 1,668 individuals in Santa Catarina. In Arraial do Cabo, the water column (> 50 cm) (*i.e.*, close to the surface) was the substrate predominantly used in the morning, with subsequent change to the water column < 50 cm (*i.e.*, close to the bottom) in the midday (Fig. 3). In Santa Catarina, we found a more similar pattern between the substrates foraged along the day (Fig. 3). Nevertheless, during the morning we observed an increased foraging in the water column close to the surface. Additionally, from midday onwards we observed an increase in foraging on the benthic substrate in both locations. Despite these observed tendencies, we found no statistically significant differences on foraging substrates considering the three blocks: Morning, Midday, Evening (Friedman test – Arraial do Cabo: X^2 = 0.67; df = 2; p = 0.72; Santa Catarina: X^2 = 2; df = 2; p = 0.37).

In Arraial do Cabo, more than 90% of bites occurred in the water column, 60% of which were near the surface (water column > 50 cm). Between 8:00 and 11:00h we observed *A. saxatilis* foraging exclusively near the surface. From midday onwards, the fishes foraged mainly in the water column close to the bottom (*i.e.*, water column < 50 cm) and on benthic substrates (Fig. 4). The most foraged benthic substrates were the Epilithic Algal Matrix (EAM) and the anthozoan *Palythoa* sp. No significant differences of foraged substrates were detected among the one-hour intervals (X^2 = 11.9; df = 8; p = 0.15).

In Santa Catarina, 70% of bites occurred in the water column, 40% of which occurred near the bottom (water column < 50 cm). The number of bites on the benthic substrate increased during the afternoon adding up to 35% of the bites (Fig. 4). The most foraged
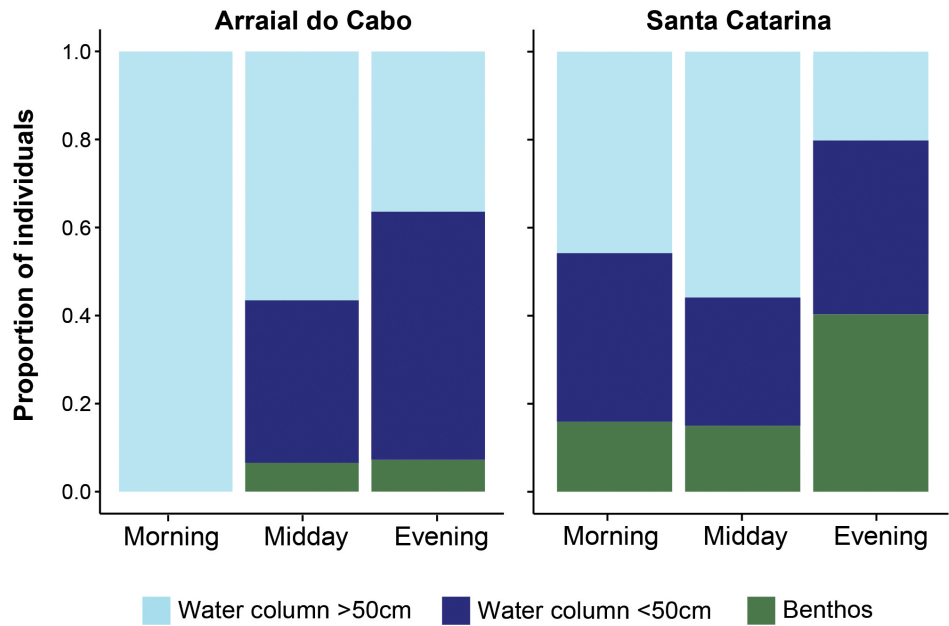
FIGURE 3 | Proportional foraging activity of *Abudefduf saxatilis* on Arraial do Cabo and Santa Catarina reefs. Substrates: Water column > 50 cm (close to water surface), Water column < 50 cm (close to bottom) and Benthos. Periods of the day: Morning (between 8:00 to 10:00h), Midday (11:00 to 13:00h) and Evening (14:00 to 16:00h).
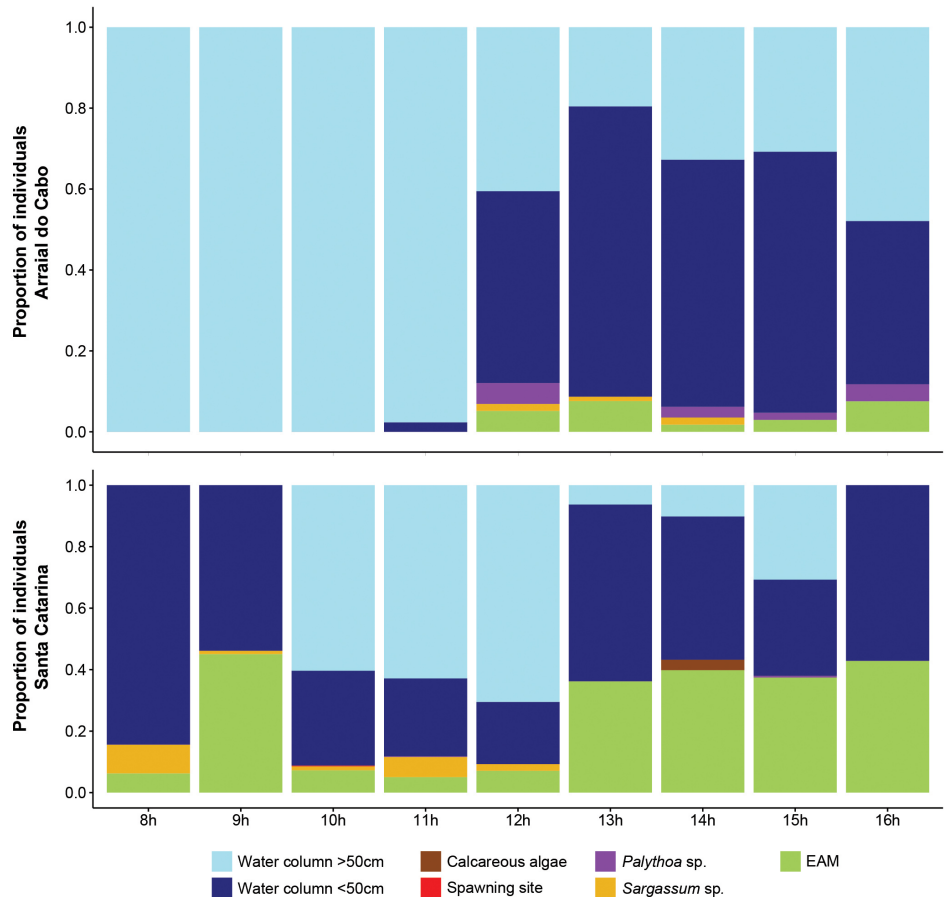

FIGURE 4 | Proportional foraging activity of *Abudefduf saxatilis* biting different substrates (colours) in Arraial do Cabo and Santa Catarina. Proportion refers to each time range 8h (8:00 to 9:00h), 9h (9:00 to 10:00h), 10h (10:00 to 11:00h), 11h (11:00 to 12:00h), 12h (12:00 to 13:00h), 13h (13:00 to 14:00h), 14h (14:00 to 15:00h), 15h (15:00 to 16:00h), 16h (16:00 to 17:00h).

benthic substrates were the Epilithic Algal Matrix (EAM) and the algae *Sargassum* sp. Significant differences on the foraged substrates were detected only between the intervals 11:00 and 16:00h (X^2 = 18.6; df = 8; p = 0.02).

In Arraial do Cabo, all individuals of SC1 were recorded foraging in the water column, most of which were near the surface; while SC2 and SC3 foraged both in water column and on benthos (Fig. 5). No bite of SC4 (reproductive male) was recorded at this site. Additionally, we found no significant differences among size classes as to the foraged substrates (X^2 = 5.2; df = 2; p = 0.07). In Santa Catarina, all size classes foraged in the water column and on the benthic substrates, with SC4 foraging on eggs. We found significant differences between the SC2 and SC4 regarding foraged substrates (X^2 = 8.2; df = 3; p = 0.04).
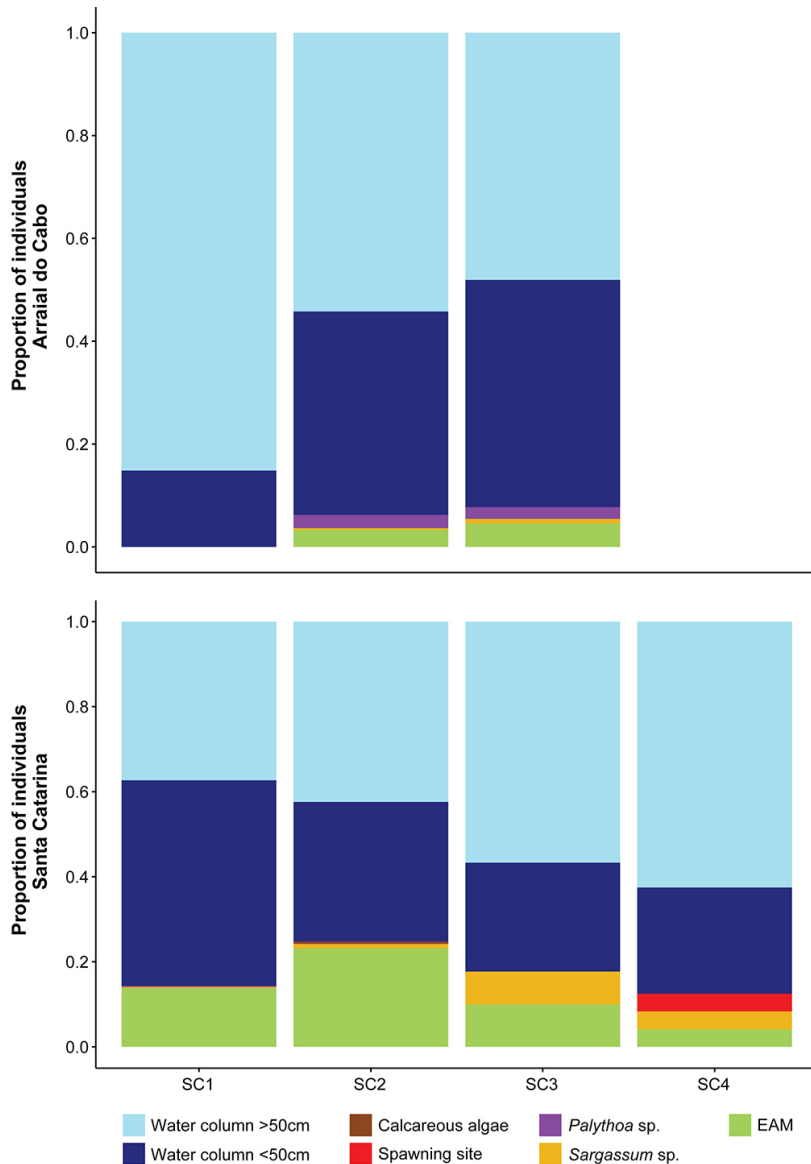

FIGURE 5 | Proportion of *Abudefduf saxatilis* individuals on size classes foraging on different substrates (colours). SC1) individuals smaller than 5 cm; SC2) individuals between 5 cm and 12 cm; SC3) individuals larger than 12 cm; and SC4) individuals larger than 12 cm displaying parental care.

We recorded 12 food items in the diet of *A. saxatilis* (10 food items in Arraial do Cabo and 11 in Santa Catarina; Fig. 6). The item Detritus was the most important food item for diet in both locations, with an importance of about 30%. Algae (*Codium* sp., *Sargassum* sp., calcareous algae and unidentified algae) had the predominant volume in the diet, with an importance of 37.22% in Arraial do Cabo and 53.18% in Santa Catarina. There were no significant differences in the diet of populations (PERMANOVA R^2 = 0.11; F = 0.98; p = 0.56; Fig. 6). This result was supported by the observed Pianka value, which showed high overlapping in the diet (equal to 0.83) between populations, and the Null–model Expected Pianka value (equal to 0.79), which was within the 95% confidence interval.
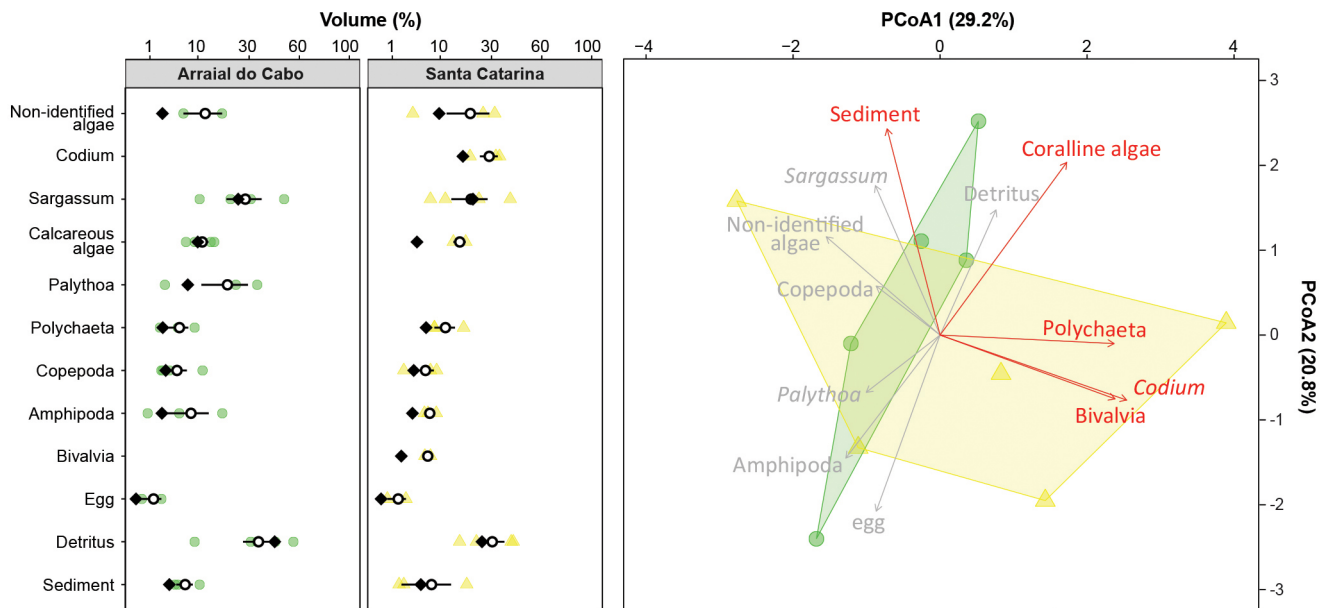

FIGURE 6 | Food items importance in the diet of two populations of *Abudefduf saxatilis*. Green and yellow dots represent the volume of each food item for each stomach and locality. Black diamonds represent the Feeding Index (%IAi). White circles and black bars show the mean volume percentage of each item and the standard error, respectively. Principal coordinate analysis (PCoA) demonstrates diet similarities between the two populations of *A. saxatilis*. Red lines indicate significant feeding items (p < 0.05) while grey lines are non-significant.

DISCUSSION

We studied the diel patterns on foraging behaviour and the diet of *Abudefduf saxatilis* on two Brazilian subtropical reefs. The results unequivocally demonstrate that this damselfish has an omnivorous generalist behaviour and feeding plasticity, despite a lack of a clear pattern in diel foraging, which can be influenced by various environmental characteristics (*e.g.*, temperature, currents, and plankton availability). The foraging substrates do not vary with size class, which suggests that feeding plasticity is retained through different sizes. Although we could not find statistically significant differences in diel foraging on the three main substrates, we observed a tendency to forage mostly in the water column during the morning and an increase of bites on the benthos during the afternoon. The food items we found in our diet analyses agree with previous studies on the feeding behaviour of *A. saxatilis*, as this species forages on multiple trophic levels (Fishelson, 1970; Dubiaski-Silva, Masunari, 2008).

The high foraging rate in the water column, compared to benthic substrates, can be explained by the presence of plankton (Pereira, Soares-Gomes, 2009). Zooplankton is abundant and relatively easy to obtain by planktivorous fishes on reefs (Heidelberg *et al.*, 2010), making for lower energy costs to obtain this food type, which substantiate the observed foraging patterns, as already suggested in previous studies (*e.g.*, Fishelson, 1970; Frédérich *et al.*, 2013). In Arraial do Cabo, upwelling events continuously enrich the local food web, while plankton production increases (Valentin, 1984; Fishelson, 1970), and fish as consumers profit from this condition on daily basis. The increase of bites on benthos during the afternoon is probably due to increase of nutritional quality of the algae throughout the day. Algae reach high values of starch along the morning and mid-day, which results in higher rates of foraging on this source (Taborski, Limberger, 1980; Zemke-White *et al.*, 2002; Raubenheimer *et al.*, 2005).

We observed that smaller *A. saxatilis* individuals display the tendency to forage close to the water surface, while larger individuals tend to forage more often on benthic substrates. These tendencies may be related to energetic demands of the different size classes (Barneche *et al.*, 2009), or a higher predation risk close to the bottom (Hay, 2009; Michel *et al.*, 2020). The difference between size classes SC2 and SC4 observed in Santa Catarina is probably related to the occurrence of nest sites as a foraging substrate for class SC4. Males that performed parental care, which tends to reduce their feeding activity while focusing on protection of spawn (Fishelson, 1970), represented this latter class. Despite the reduction of their feeding activity while on parental care, males did not stop feeding as expected. This is clearly an important way to supply energy costs or spoiled eggs removal, but they also can turn to cannibalism (Hoelzer, 1995). The diet of *A. saxatilis* clearly reflected its feeding behaviour, as we found food items from both benthos and plankton. On the Epilithic algal matrix (EAM) varied reef fishes find a variety of food items, such as invertebrates and detritus (Wilson *et al.*, 2001). Detritus is an important source of nutrition in different reef systems due to its high concentration of proteins and amino acids (Crossman *et al.*, 2001; Wilson *et al.*, 2001). Some feeding items had a high frequency of occurrence, but with low volume, which resulted in low values of the feeding index (*i.e.*, low importance in the diet). These items, such as eggs, are probably fed upon as supplementary energy resources for *A. saxatilis*. Nevertheless, items such as sediment could be accidentally ingested along with items of

greater importance, thus not accounting for great nutritional importance (Lobel, 1981; Jobling, 1994). The diet analysis we did herein confirms the designation of *A. saxatilis* as a generalist omnivorous fish that forages on different animal and algal sources.

Abudefduf saxatilis is a key species for trophic studies of reef fish communities, given their abundance in different shallow reef habitats along the Brazilian Province (Ferreira *et al.*, 2004; Morais *et al.*, 2017). Despite this, there is a lack of knowledge about different spatial (*e.g.*, reef habitats to localities) and time scales (daily cycle) of its diet, foraging behaviour, and general nutritional ecology. In this study, we emphasise the importance of studying both feeding behaviour and stomach content analysis to obtain a comprehensive information of the trophic ecology of this damselfish in two different subtropical reefs. This information is a key factor to understand the feeding ecology of this highly generalist omnivorous fish, while it also helps to clarify other ecological features, such as its cosmopolitan distribution and high abundance on most reefs in the Atlantic Ocean. These attributes seem directly related to the generalist feeding behaviour, which allows it to exploit multiple resources and persist under different environmental conditions. Lastly, we emphasise the importance of further studies on the trophic ecology of *A. saxatilis* using complementary approaches, such as isotopic analyses and bite rates, to understand its trophic importance and role in different reef systems. Additionally, DNA-metabarcoding analyses would reveal the quality and quantity of nutrients obtained from cleaning behaviour, as *A. saxatilis* eats ectoparasites, skin, and mucus (Sazima *et al.*, 2010; Quimbayo *et al.*, 2018). This method was recently used in a study of two mucus- and scale eating catfishes (Trichomycteridae), revealing varied assemblages of host fishes (Bonato *et al.*, 2018), and in a study of diet breadth of butterflyfishes (Chaetodontidae), discovering a significant overlap between corallivorous sympatric species (Coker *et al.*, 2022).

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