ORIGINAL PAPER

Syntopic cryptobenthic fishes can coexist with overlapping niches

Angela M. Canterle[1] · Lucas T. Nunes[1] · Luiz G. R. Oliveira-Santos[2] · Sergio R. Floeter[1]

Abstract
Species' niche depends on several ecological and evolutionary factors. Phylogenetically close species may present niche conservatism, retaining their ancestral ecological characteristics. Alternatively, in a situation of limited resources, species can differentiate themselves through changes in their ecological and morphological characteristics to reduce niche overlap, thus facilitating coexistence. In this study, we investigated the ecological niche of two phylogenetically closely related cryptobenthic reef fish species that co-occur in the southern Brazilian coast, *Parablennius pilicornis* and *P. marmoreus*. We examined possible overlap in three niche dimensions (thermal, spatial and trophic) to verify if species hold phylogenetic niche conservatism or are partitioning some niche dimension. For this, we studied their densities, microhabitat affinities and diets among four rocky reefs of southern Brazil. The two species presented differences in thermal distribution, and their abundance differed according to depth strata, but no differences were found for microhabitat preferences. They also presented a similar omnivorous diet, with crustaceans and algae as main prey types. The Pianka's niche overlap values did not differ from the values expected in the null model for thermal and depth, and it was higher than expected by chance for microhabitat and diet. Considering all the niche dimensions analysed together, the total niche overlap was greater than expected at random. These results suggest that the two species are successfully coexisting despite considerable niche overlap. Thus, their coexistence may not depend on the evolution of divergent patterns of resource use, but on the evolutionary history of the species.

Introduction

An ecological niche is defined as the space encompassing abiotic and biotic variables which limit the conditions for population growth, survival and persistence (Hutchinson 1957). Several dimensions compose a species niche, of these trophic and spatial niches are widely studied resource dimensions, as they are imperative for the presence or absence of species in certain locations (Pianka 1973; Winemiller et al. 2015). In addition to these two dimensions, the environmental temperature may be another critically important abiotic variable, due to its influence over species distribution

Responsible Editor: K.D. Clements.

✉ Angela M. Canterle
angelacanterle@hotmail.com

1   Marine Macroecology and Biogeography Lab, Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC, Brazil

2   Lab of Movement and Population Ecology, Universidade Federal do Mato Grosso do Sul, Campo Grande, MS, Brazil

(Pinksy et al. 2020), food processing efficiency (Knight et al. 2021), metabolic rates (Brown et al. 2004; Barneche et al. 2014), growth and reproduction (Magnuson et al. 1979; Tracy and Christian 1986).

The niche approach has allowed other important ecological concepts to emerge, such as niche overlap and niche partitioning (Colwell and Futuyma 1971; Cornell 2011). Niche overlap refers to the use of the same resources or conditions by two or more co-occurring species. The greater the number of resources shared, the greater the niche overlap and smaller the partitioning (Abrams 1980). Niche partitioning refers to the process by which natural selection drives competing species into different patterns of resource use or different niches (MacArthur 1958; Hector and Hooper 2002). Based on the "Limiting similarity theory", there is a maximum level of overlap allowing two or more competing species to coexist (Abrams 1983). In order to avoid competitive pressures, the "Character displacement theory" predicts syntopic species might differ ecologically or morphologically to minimise competitive pressures, thus coexisting in the same space and time (Brown and Wilson 1956; Slatkin 1980; Abrams 1983).

Otherwise, the stronger competitor shall lead the weaker to local extinction (competitive exclusion principle; Gause 1934; Hardin 1960).

A mechanism that competes with the ecological divergence of species is phylogenetic niche conservatism (Kraft et al. 2007), where species' niches can be conserved over evolutionary time by maintaining their fundamental niche aspects, such as feeding and habitat preferences (Peterson et al. 1999). This mechanism explains the sharing of ancestral patterns among species as the result of an evolutionary factor that constrains the differentiation of traits and contributes to trait homogenization (Munkemuller et al. 2015). According to Darwin's naturalization conundrum, the chance of species being in a certain location is higher when phylogenetic close relatives are present (Darwin 1859; Diez et al. 2008; Thuiller et al. 2010). Thus, one can expect closely related species to be distributed in similar ways of the niches, showing phylogenetic niche conservatism (Peterson et al. 1999; Peterson 2011). To better understand how ecological and evolutionary factors affect species' niche, it is important to investigate the niche conservatism across different species (Pianka et al. 2017).

Besides the above-mentioned mechanisms explaining species coexistence, the lottery hypothesis (Sale 1978) rises as a contradictory possible explanation for coexistence by considering no ecological differentiation between species. This hypothesis proposes the priority of arrival in recruitment (by chance)—instead of adults' competitive skills—as the main determinant of species presence/absence in a certain environment. A study on the coexistence of two goby species (*Gobiodon histrio* and *G. erythrospilus*) showed similar competitive ability and no difference in habitat use during the recruitment stage. This indicates both species can coexist by virtue of a competitive lottery, where vacant habitat is colonized by the first available recruit (Munday 2004).

Small cryptobenthic reef fishes are excellent models for testing hypothesis related to niche theory, as they live in a wide variety of reef habitats and have small home ranges, syntopic distributions, and short lifespan with consequent high turnover that may result in faster evolutionary splits (Wong and Buston 2013; Ahmadia et al. 2018; Brandl et al. 2018, 2020). Cryptobenthic fishes have a close association with the benthos and provide crucial energetic links in reef trophic chains, as they have exceptional growth rates and suffer high predation rates (Depczynski and Bellwood 2003; Brandl et al. 2018). These fishes are important for energy flow on reefs due to their high energy demands and functional roles (Brandl et al. 2019). Despite the abundance and importance of cryptobenthic fishes for reef environments, most studies have focused almost exclusively on the most "visible" members of the reef community (Sale 2006), providing little information on cryptobenthic species.

The Blenniidae represents a taxonomically diverse family, highly abundant in many marine ecosystems. The genus *Parablennius* comprises 26 species (Patzner et al. 2009), of which the following two phylogenetically close species occur in Brazil: the Ringneck blenny *Parablennius pilicornis* (Cuvier, 1829) and the Seaweed blenny *Parablennius marmoreus* (Poey, 1876) (Levy et al. 2013). Both are found in habitats such as crevices or empty barnacles along reefs; however, they differ in their distribution (Rangel and Guimarães 2010; Pinheiro et al. 2018). While *P. pilicornis* commonly inhabits colder waters on the Atlantic Ocean, *P. marmoreus* is mostly found on warmer waters of the Western Atlantic (Fig. 1). According to literature, the recorded depth range for *P. marmoreus* is 0–15 m (Dalben and Floeter 2012), but in our study we found individuals below 15 m (please refer to the results section). While *P. pilicornis* occurs between 0 and 25 m deep (Froese and Pauly 2021). On a smaller spatial scale, some differences

Fig. 1 Distribution of *Parablennius pilicornis* (blue, **a**) and *Parablennius marmoreus* (pink, **b**) in the Atlantic Ocean. Blue-pink dashed area indicates the Southeast Brazilian coast where species distribution overlap. Photos: João Paulo Krajewski
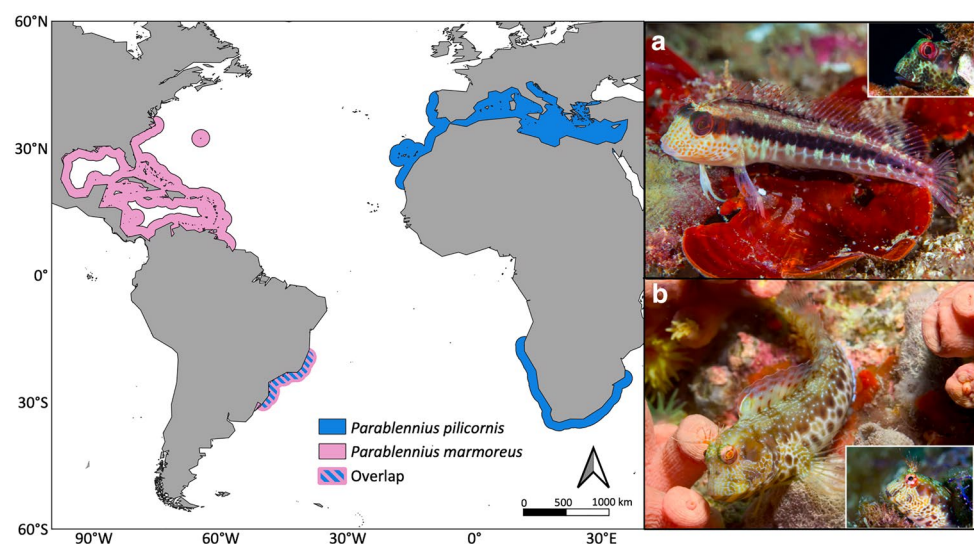
in depth preference have been suggested when species co-occur in South-eastern Brazil, with *P. marmoreus* having its distribution pushed to deeper waters (> 10 m deep) in the presence of its congeneric (Dalben and Floeter 2012). The dietary habits of these species are poorly understood, although empirical data suggest a diversified omnivorous diet for both species (Nieder 1997; Lindquist and Dillaman 1986). The co-occurrence of the two syntopic *Parablennius* species is a good opportunity to investigate niche overlap, and also to expand the knowledge of the ecology of this group.

The present study aims to test if *Parablennius* species are partitioning three important niche dimensions (thermal, spatial or trophic). As the two species are phylogenetically related and also have similar life histories (Levy et al. 2013), we postulate the following scenarios: 1) the two species will hold similar niches over evolutionary time, due to phylogenetic niche conservatism; 2) there will be some level of niche differentiation allowing coexistence (Abrams 1983). Considering the second scenario, we tested three hypothesis each related to a different niche dimension: Thermal—*P. pilicornis* is present in a higher relative abundance in locally cooler waters, while *P. marmoreus* is more abundant in the warmer waters; Spatial—both species will differ in microhabitat use and differ in density according to depth; Trophic—a more energetic diet for *P. pilicornis* and a more herbivorous diet for *P. marmoreus*.

Materials and methods

Study sites

Sampling occurred during the austral summer, from 2016 to 2020, on coastal sites of south Brazil as follows: Galés Island (site location: 27°10′59"S|48°24′41"W), Arvoredo Island (27°16′39"S|48°22′31"W), Xavier Island (27°36′33"S|48°23′13"W), and Pântano do Sul (27°47′12"S|48°30′28"W). These sites present different thermal characteristics, due to an increased frequency of water temperature below 16 °C during the austral winter as the latitude increases among the studied sites (Fig. 2; Faria-Junior and Lindner 2019).

Thermal niche

In each site, we performed underwater visual censuses (UVCs) to estimate the density (individuals/m^2) of both *Parablennius* species. Each census consisted of a belt transect in which a SCUBA diver swam at a constant velocity and identified, counted and estimated the total length of fishes within a 40-m^2 area (20 × 2 m; see details in Morais et al. 2017). Water temperature data for Santa Catarina coast
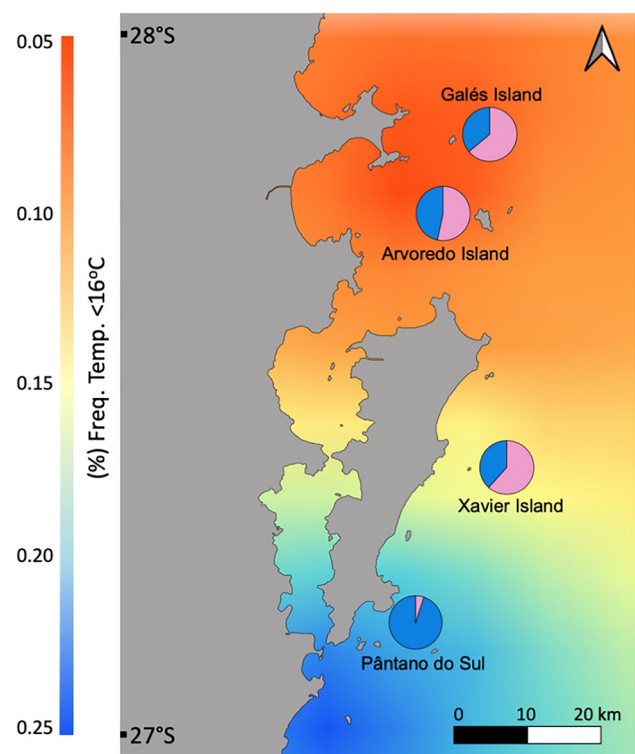

Fig. 2 Relative abundance of *Parablennius pilicornis* (blue) and *Parablennius marmoreus* (pink) across the following four sampled reefs in South Brazil: Galés Island, Arvoredo Island, Xavier Island and Pântano do Sul (Data from the years 2016–2020). Temperature range expressed as the frequency of temperature below 16 °C during the austral winter in Santa Catarina Coast

were retrieved from an online underwater temperature dataset from coastal islands in Santa Catarina (see details in Faria-Junior and Lindner 2019). For the thermal niche, the abundance of both species within sites was summed across transects and compared using Chi-squared test of independence, followed by post-hoc test, through the packages "MASS" (Venables and Ripley 2002) and "chisq.posthoc. test" (Ebbert 2019) of R software (R core team 2018).

Spatial niche

To assess the spatial niche, we used two approaches regarding vertical distribution in the reef and microhabitat preferences. To assess if *Parablennius* species differ in their density across three depth strata (0–5 m, 5.1–10 m, and 10.1–16 m; see Online Resource 1 for information on the number of samples in each strata) recorded from the UVCs, we performed a Kruskal–Wallis analysis and *post-hoc* Dunn test, through the package "dunn.test" (Dinno 2017) of R software (R Core Team 2018).

To determine microhabitat preferences, we adapted the focal animal method (Lehner 1996), in which the diver followed a straight line on the reef haphazardly registering

adult individuals of *Parablennius*. When a fish individual was sighted, we recorded the species and the substratum immediately below the individual. A total of 14 individuals of *P. pilicornis* and 46 individuals of *P. marmoreus* were recorded on Arvoredo Island; 16 *P. pilicornis* and 59 *P. marmoreus* on Xavier Island; and 70 *P. pilicornis* and 9 *P. marmoreus* on Pântano do Sul. This sampling occurred between 4 and 6 m deep in Arvoredo and Xavier Island, due to both species occurring in a similar density (see Fig. 3). In Pântano do Sul sampling occurred between 0 and 2 m depth, because it is a shallower reef compared to the other studied site.

Benthic assessments at each studied site were conducted to compare the frequency of use, by the fishes, with the relative cover availability of each substratum type. The availability of each substratum type was visually estimated by using PVC quadrats (30 × 30 cm). On each site the diver followed a straight line on the reef—between 4 and 6 m deep for Arvoredo and Xavier Island, and 2 m for Pântano do Sul—haphazardly placing the quadrats on the substrate and estimating the percentage cover of each substratum type inside the quadrat. A total of 20 quadrats were performed on each site. The substrates were categorized as: epilithic algal matrix (sensu Wilson et al. 2003), macroalgae, crustose calcareous algae, rock, sand, sea urchins and Zoantharia (please see Online Resource 2 for details on each site).

The selection of microhabitats by each species was analysed using a Resource Selection Function (RSF; Manly et al. 1993; Manly 1993, 1997). The RSF was built using a Conditional Logistic Regression (CLR) approach due to our data consisting of direct observations of substrates on which different individuals inhabited (scored as 1) among a variety of available substrates (random sampling of substrates, scored as 0). Resource availability was assessed by generating 100 random substrate points for each observed individual, which were taken from the relative substrate availability measured in the entire reef site where each species was

observed. The CLR was conditioned to individual identity. Fish species and substratum type were used as categorical variables in the model. Our CLR model was thus represented by the following log-linear form of the logistic regression for each i substrate and j species as follows:

$$\text{logit}(w_{ij}) = \beta_{1i} \cdot FS + \beta_{2ij} \cdot FS \cdot species,$$

in which w depicts the selection strength based on the use/availability ratio and βs are model coefficients that indicate the odds ratio of each i substrate, inhabited by j species, to be used in a different proportion of its availability. The CLR was solved using the "clogit" function in the "survival" package (Therneau 2015). We fitted the CLR, clustering the observations within individuals to control pseudo replication of correlated samples, and to allow us to calculate robust standard errors of the estimated coefficients in a very conservative way (Craiu et al. 2008). This analysis was performed using the packages "car" (Fox and Weisberg 2019) and "plotrix" (Lemon 2006) of R software (R core team 2018).

Trophic niche

For diet analysis, we sampled a total of 20 individuals—Arvoredo Island (*P. pilicornis* $N = 3$; *P. marmoreus* $= 10$) and Pântano do Sul (*P. pilicornis* $N = 7$; *P. marmoreus* $= 0$). All individuals were sampled using hand nets, immediately frozen and sent to the laboratory where they were measured and had the guts removed and fixed on a formaldehyde solution of 10%. Individual guts were dissected in Petri dishes under a stereomicroscope and all its food items were identified to the lowest taxonomic level possible. Amorphous organic matter was analysed with an optical microscope to identify diagnostic structures, such as nematocysts and spicules (Liedke et al. 2018; Nunes et al. 2020). The Digested Organic Matter (DOM) category was assigned

Fig. 3 Species density (individuals/m²) of both species (blue triangle—*Parablennius pilicornis*, pink circle: *Parablennius marmoreus*) in the sampled sites in three different depth strata. Pink circles and blue triangles represent each transect. White circles indicate the mean, and the black lines indicate standard error. *p* values according to Kruskal–Wallis test and letters represent Dunn's post hoc pairwise comparisons (treatments with the same letter are not significantly different ($p > 0.05$)
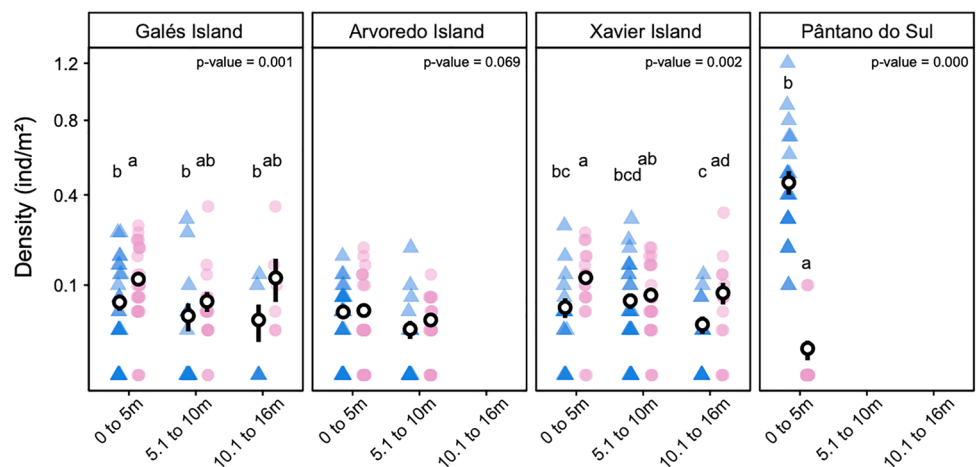
when taxonomic identification was not possible. Diet was quantified using the frequency of occurrence (%FO, i.e. how often a food item is present in the sampled guts) and volumetric index (%V, i.e. summed volume of each item pooled across individuals divided by the total volume of the sampled guts; Nunes et al. 2020). The volume of each food item, in each gut, was measured by using a Petri dish on a millimetre paper. Each feeding item was placed on the Petri dish 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. 2018; Nunes et al. 2020). To evaluate the importance of each feeding item for each species, we used the Feeding index equation, calculated as follows:

$$\%IA_i = \frac{(F_i \cdot V_i)}{\sum_{x=1}^{n}(F_i \cdot V_i)},$$

in which F_i is the number of guts with a given prey type i in relation to the total number of guts and V_i is the volume of prey item i in relation to the total volume of all of the items in the diet of each species (Kawakami and Vazzoler 1980; Nunes et al. 2020). To compare the diet between the two species, we used a Principal Coordinates Analysis (PCoA) with a subsequent PERMANOVA to test the null-hypothesis of different diets between species. We generated sample-based accumulation curves to check the sampling effort adequacy (Online Resource 3). These analyses and graphics were performed using the packages "vegan" (Oksanen et al. 2019) and "ggplot2" (Wickham 2016) of R software (R core team 2018).

Niche overlap

Species niche overlap for temperature, depth, diet, microhabitat and all dimensions together were calculated using Pianka's index (Pianka 1973) that varies in a scale from 0 (no common resource) to 1 (complete overlap). Values greater than 0.6 suggest a strong overlap between species (Pianka 1973). To evaluate thermal niche, we used the relative abundance data of both species in distinct sites. For spatial niche (regarding depth), we used the relative abundance data of both species among depth strata. For spatial niche (regarding microhabitats), we used the relative abundance data of both species in each microhabitat category. For the trophic niche, we used the feeding index (%IA$_i$) of each feeding item for both species. To analyse all unified dimensions, we normalized the data for each dimension through the "decostand" function of the "vegan" package (Oksanen et al. 2019). The niche overlap values were statistically tested against null models through the "EcoSimR" package (Gotelli et al. 2015) using the algorithm RA3. We performed 999 MonteCarlo randomizations to create pseudo-communities for each niche dimension and all dimensions together, and

then statistically compared the patterns (mean niche overlap) in these randomized communities with those in the real data matrix. Interspecific partitioning might be occurring when the observed mean overlap values are significantly lower than those expected by chance, whereas similar patterns lead values higher or equal than those expected by chance (Albrecht and Gotelli 2001).

Results

Thermal niche

We performed a total of 195 underwater visual censuses: 54 transects in Galés Island, 54 in Arvoredo Island, 64 in Xavier Island, and 23 in Pântano do Sul. The relative abundance of *P. marmoreus* was higher than *P. pilicornis* in the warmest sites (Fig. 2), but no significant differences between species were found for Galés Island, Arvoredo Island and Xavier Island. We found significant differences ($X^2 = 10.53$, $df = 3$, $p = 0.01$, Fig. 2) only in the Pântano do Sul, where *P. marmoreus* was less abundant (residuals $= -3.22$, $p = 0.01$) while *P. pilicornis* was highly abundant (residuals $= 3.22$, $p = 0.01$).

Spatial niche

Both species were found in all depth strata (0–5 m, 5.1–10 m, 10.1–16 m). At the sites Galés Island, Xavier Island, and Pântano do Sul, we found a difference on species density according to depth strata (Fig. 3). At Arvoredo Island, there was no difference in density of both species across depths. At Galés Island, the density of *P. marmoreus* was higher than *P. pilicornis* among all depth strata. At the Xavier Island, the density of *P. marmoreus* was higher than the density of *P. pilicornis* in two depth strata (1–5 m and 10.1–16 m), and there was no difference between their densities in the 5.1–10 m stratum. At the Pântano do Sul, the density of both species differed with *P. pilicornis* showing higher abundance than *P. marmoreus* in 0–5 m depth stratum.

The RSF indicated small differences in microhabitat selection between *P. pilicornis* and *P. marmoreus* (Fig. 4). Both species selected epilithic algal matrix (EAM), and rejected the sea urchin (URCH) microhabitat (Fig. 4). The crustose calcareous algae (CCA) microhabitat was selected by *P. pilicornis*, but used in accordance with its availability in the reef by *P. marmoreus* (Fig. 4). The Zoantharia (ZOAN) microhabitat was selected by *P. marmoreus*, but used in accordance with its availability by *P. pilicornis* (Fig. 4). Sand and rock microhabitats were used according to their availability by both species (Fig. 4). The estimated coefficients from the RSF
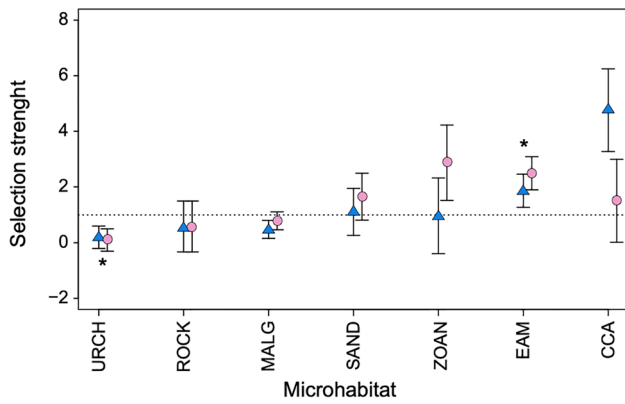
Fig. 4 Selection strength of microhabitat by *P. pilicornis* (blue triangle) and *P. marmoreus* (pink circle). Microhabitats with values crossing the dashed lines were used according to their availability (use/availability = 1); positive and negative values indicate selection and rejection, respectively. Asterisk indicate substrates which were selected or rejected for both species. Acronyms for microhabitats are as follows: *URCH* sea urchins, *CCA* crustose calcareous algae, *ZOAN* Zoantharia, *EAM* epilithic algal matrix, *MALG* macroalgae

and their respective 95% confidence intervals are provided in Online Resource 4.

Trophic niche

Both species exhibited an omnivorous diet, presenting items of different trophic levels (ranging from algae to fishes) in their gut content (Fig. 5a) and there was no significant difference between their diets (PERMANOVA: $F = 1.59$; $R^2 = 0.08$, $p = 0.07$; Fig. 5b). The PCoA ordination also reflected an overlap between both species diets (Fig. 5b), with the two first axes explaining 43.2% of the observed variation. Both species have crustaceans and algae as main prey types Fig. 5a), followed by mollusks (for *P. pilicornis*) and eggs (for *P. marmoreus*).

Niche overlap

Niche overlap values did not differ from the values expected in the null model for thermal and depth (Table 1). For microhabitat and diet, the niche overlap was higher than the value expected by chance in the null model (Table 1). Considering all the dimensions analysed together, the total niche overlap was significantly greater than expected at random. This suggests a high niche overlap between species in all dimensions analysed.

Discussion

We demonstrated both *Parablennius* species have spatial and trophic niche overlap, suggesting syntopic species can coexist with overlapping niches. Thus, the coexistence of
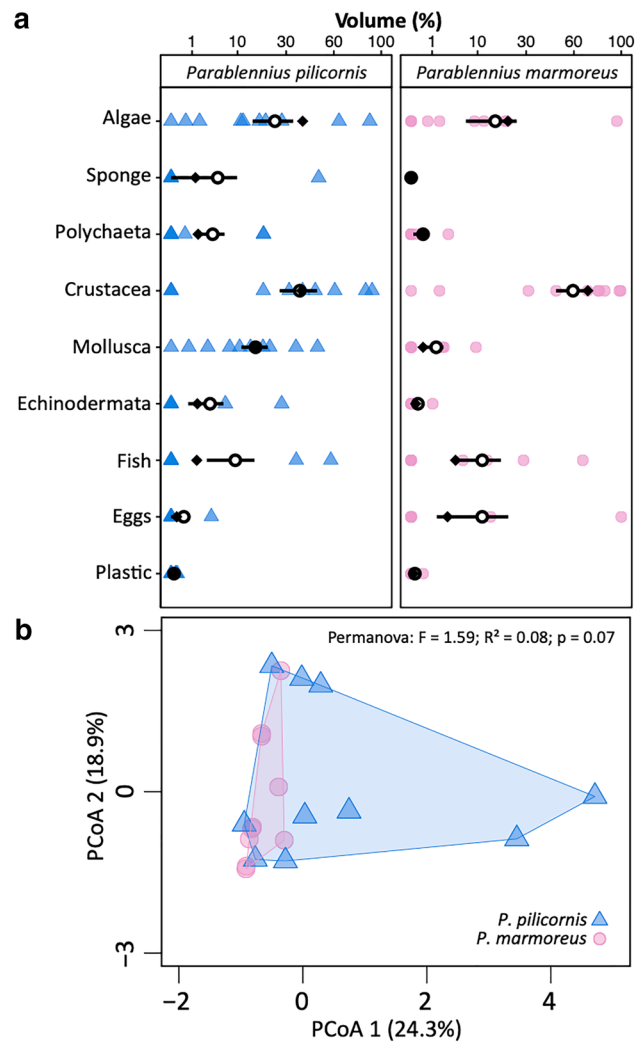

Fig. 5 a Scatterplot for diet composition of *Parablennius pilicornis* and *P. marmoreus* in Santa Catarina. Coloured points represent the volume (%) of each feeding item for each individual. Black and white circles and black lines represent the mean feeding items volume and its standard error, respectively. Black diamonds represent the importance (%IAi) of each feeding item for the species diet. **b** Principal coordinate analysis (PCoA) showing ordination of samples according to the volume of feeding items

species may not depend only on the evolution of divergent resource use patterns, but on the evolutionary history of the species. Phylogenetically close lineages have a tendency to retain their ancestral ecological characteristics over time (Peterson 1999). As the congeners *P. pilicornis* and *P. marmoreus* share a recent evolutionary history, they are prone to present similar resource use patterns, consequently presenting high niche overlap (Pianka et al. 2017). Alternatively, both species may have their populations regulated via intra-specific competition (McPeek and Gomulkiewicz 2005). However, we do not have experimental data

Table 1 Observed and expected thermal, spatial and trophic niche overlap (Pianka's index) and the one-tailed *p* value based on 999 randomizations for *P. pilicornis* and *P. marmoreus*

Niche dimension	Observed overlap	Expected overlap	*P* value
Thermal niche (sites)	0.456	0.682	0.774
Spatial niche (depth)	0.935	0.640	0.163
Spatial niche (microhabitat)	0.937	0.395	**0.033**
Trophic niche (diet)	0.840	0.270	**0.019**
All dimensions	0.794	0.431	**0.001**

The *p* values represent the significance of the niche overlap when it was higher than that expected by chance

Statistically significant *P* values ($P < 0.05$) are highlighted in bold

on species interactions, nor recruitment data over time available to test this hypothesis.

Our results suggest that the most likely scenario is the ongoing phylogenetic niche conservatism between both *Parablennius* species. This genus probably diverged in the Macaronesia region, with subsequent dispersal and occupation of the Northeast Atlantic by *P. pilicornis* and the Northwest Atlantic by *P. marmoreus* (Levy et al. 2013). This allopatric distribution possibly reduced any need for morphological or ecological divergence (Bowen et al. 2001; Santos et al. 2006), thus conserving their ecological niches. Both species were geographically reunited in the Southwestern Atlantic, where they have successfully coexisted for at least 400,000 years (Dias 2019). The high niche overlap found between the species in Southern Brazil can be explained by an absence of local drivers to separate them ecologically, after their secondary contact. This region presents low species richness and high primary productivity (Segal et al. 2017), characteristics that may provide ecological opportunities for species to establish themselves with minimal or no competition (Wellborn and Langerhans 2015). This implies that effects from local processes are minimal, not justifying niche partitioning (scenario 2; Ahmadia et al. 2018). In contrast, studies in intertidal reef pools, that are highly resource-limited environments, have demonstrated competition and resource partitioning between cryptobenthic reef fish species (Quimbayo et al. 2018; Andrades et al. 2021).

The successful colonizers of new areas are often those that emigrate from areas with similar environmental conditions (Wiens et al. 2009). Other cases of eastern Atlantic species and lineages successfully established in this region have already been recorded, such as the Azorean chromis *Chromis limbata* (Anderson et al. 2020), the Dusky grouper *Epinephelus marginatus* (Luiz et al. 2004), the Comb-tooth blenny *Scartella cristata* (Araújo et al. 2020) and the Trumpetfish *Aulostomus strigosus* (Bowen et al. 2001). In addition, some species' characteristics may influence the possible lack of competition, such as their feeding habits.

The two *Parablennius* species presented a generalist diet consisting of items from various taxonomic groups, ranging from algae to fish. In the Mediterranean, *P.*

pilicornis responds to food shifts in its habitat, using a broad spectrum of food resources (Nieder 1997). Generalist feeders usually present physical and behavioural characteristics that are intermediate between those of herbivores and carnivores, and these traits should allow species to switch among food items (Garvey and Whiles 2016). This generalist and opportunistic habit may strongly reduce the potential for competition, and therefore, favour trophic niche overlap (Schoener 1971). It is important to consider that niche overlap among species can decrease as the resolution of the gut content analysis increases (Brandl et al. 2020). However, even a high resolution that could be provided by metabarcoding analyses, for example, would not be ideal since this method hampers quantitative comparisons between diets, and therefore to infer trophic niche differences (Nielsen et al. 2018).

We believe the low relative abundance of *P. marmoreus* in Pântano do Sul (Fig. 2) could be associated with the low temperature limiting this species distribution. A similar pattern was observed in a local comparison between *P. pilicornis* and *P. marmoreus* densities in Arraial do Cabo (RJ), where *P. pilicornis* was more abundant in a colder area (less than 18 °C) under strong influence of seasonal upwelling, while *P. marmoreus* was abundant in the warmer area (~ 22 °C; Rangel 2007).

It is important to highlight that, as its concept, the ecological niche is not a static measure, but a dynamic one. In ecological studies we portray the niche at some point in time, however it is not always the same in distinct occasions or environments (Begon 2006). It can be changed throughout life stages, seasons and also due to environmental disturbances (Ricklefs and Relyea 2018). Changes in environmental characteristics, such as habitat loss, can affect the species' niche (Colwell and Futuyma 1971). Furthermore, as the ecological niche has several dimensions, and they are not static in space and time, it is hard to isolate and measure all of them in one study. Since a niche dimension might influence other dimensions, the partition of resources between closely related species can be subtle and difficult to identify in natural communities (Pianka 2017). However, considering the dynamics of ecological niches, we must recognize the

scientific importance of describing its dimensions in eco-logical studies.

Only few studies on reef fishes have integrated dietary and spatial information to examine the interplay between them (see Liedke et al. 2016; Brandl et al. 2020). Furthermore, ecologists do not generally incorporate historical biogeography knowledge, even when it is crucial for addressing some of their central questions (Wiens and Donohgue 2004). This integration offers a line of inference concerning eco-evolutionary dynamics of species (Wiens and Donohgue 2004). Here, we analysed ecological aspects of species and linked their ecological niches to evolutionary history and biogeography, presenting the case of two syntopic reef fish species exhibiting high niche overlap and well-defined niche conservatism.

Declarations

References

Abrams P (1980) Some comments on measuring niche overlap. Ecology 61:44–49. https://doi.org/10.2307/1937153

Abrams P (1983) The theory of limiting similarity. Annu Rev Ecol Syst 14:359–376. https://doi.org/10.1146/annurev.es.14.110183.002043

Ahmadia G, Tornabene L, Smith D, Pezold F (2018) The relative importance of regional, local, and evolutionary factors structuring cryptobenthic coral-reef assemblages. Coral Reefs 37:279–293. https://doi.org/10.1007/s00338-018-1657-2

Albrecht M, Gotelli NJ (2001) Spatial and temporal niche partitioning in grassland ants. Oecologia 126:134–141. https://doi.org/10.1007/s004420000494

Anderson AB, Silva JP, Sorvilo R, Francini CLB, Floeter SR, Barreiros JP (2020) Population expansion of the invasive Pomacentridae *Chromis limbata* (Valenciennes, 1833) in southern Brazilian coast: long-term monitoring, fundamental niche availability and new records. J Fish Biol 97:362–373. https://doi.org/10.1111/jfb.14365

Andrades R, Joyeux JC, Macieira RM, Godoy BS, Reis-Filho JA, Jackson AL, Giarrizzo T (2021) Niche-relationships within and among intertidal reef fish species. Front Mar Sci 8:574. https://doi.org/10.3389/fmars.2021.659579

Araújo GS, Vilasboa A, Britto MR, Bernardi G, Von der Heyden S, Levy A, Floeter SR (2020) Phylogeny of the comb-tooth blenny genus *Scartella* (Blenniiformes: Blenniidae) reveals several cryptic lineages and a trans-Atlantic relationship. Zool J Linnean Soc 190:54–64. https://doi.org/10.1093/zoolinnean/zlz142

Barneche DR, Kulbicki M, Floeter SR, Friedlander AM, Maina J, Allen AP (2014) Scaling metabolism from individuals to reef-fish communities at broad spatial 494 scales. Ecol Lett 17:1067–1076. https://doi.org/10.1111/ele.12309

Bax NJ (1998) The significance and prediction of predation in marine fisheries. ICES J Mar Sci 55:997–1030. https://doi.org/10.1006/jmsc.1998.0350

Begon M, Townsend CR, Harper JL (2006) Ecology: from individuals to ecosystems. Blackwell Publishing, Oxford

Bowen W, Bass AL, Rocha LA, Grant WS, Robertson DR (2001) Phylogeography of the trumpetfishes (*Aulostomus*): ring species complex on a global scale. Evolution 55:1029–1039. https://doi.org/10.1554/0014-3820(2001)055[1029:pottar]2.0.co;2

Brandl SJ, Goatley C, Bellwood D, Tornabene L (2018) The hidden half: ecology and evolution of cryptobenthic fishes on coral reefs: cryptobenthic reef fishes. Biol Rev 93:1846–1873. https://doi.org/10.1111/brv.12423

Brandl SJ, Tornabene LM, Goatley CHR, Casey JM, Morais RA, Baldwin CC, Côté IM, Parravicini V, Schiettekatte NMD, Bellwood DR (2019) Demographic dynamics of the smallest marine vertebrates fuel coral reef ecosystem functioning. Science 364:1189–1192. https://doi.org/10.1126/science.aav3384

Brandl SJ, Casey JM, Meyer CP (2020) Dietary and habitat niche partitioning in congeneric cryptobenthic reef fish species. Coral Reefs 39:305–317. https://doi.org/10.1007/s00338-020-01892-z

Brown WL, Wilson EO (1956) Character displacement. Syst Zool 5:49–64. https://doi.org/10.2307/2411924

Brown JH, Gillooly JF, Allen AP, Savage VM, West GB (2004) Toward a metabolic theory of ecology. Ecology 85:1771–1789. https://doi.org/10.1890/03-9000

Colwell RK, Futuyma DJ (1971) On the measurement of niche breadth and overlap. Ecology 52:567–576. https://doi.org/10.2307/1934144

Cornell HV (2011) Niche overlap. In: Hastings A, Gross LJ (eds) Encyclopedia of theoretical ecology. University of California Press, Berkeley, pp 489–497

Craiu RV, Duchesne T, Fortin D (2008) Inference methods for the conditional logistic regression model with longitudinal data. Biom J 50:97–109

Dalben A, Floeter SR (2012) Cryptobenthic reef fishes: depth distribution and correlations with habitat complexity and sea urchins. J Fish Biol 80:852–865. https://doi.org/10.1111/j.1095-8649.2012.03231.x

Darwin C (1859) On the origin of species. John Murray, London

Depczynski M, Bellwood D (2003) The role of cryptobenthic reef fishes in coral reef trophodynamics. Mar Ecol Prog Ser 256:183–191. https://doi.org/10.3354/meps256183

Dias RM (2019) Evolução e biodiversidade de peixes recifais criptobentônicos do Oceano Atlântico. PhD thesis, Universidade Federal do Rio de Janeiro, Brazil

Diez JM, Sullivan JJ, Hulme PE, Edwards G, Duncan RP (2008) Darwin's naturalization conundrum: dissecting taxonomic patterns of species invasions. Ecol Lett 11:674–681. https://doi.org/10.1111/j.1461-0248.2008.01178.x

Dinno A (2017) dunn.test: Dunn's test of multiple comparisons using rank sums. R package version 1.3.5. https://CRAN.R-project.org/package=dunn.test

Ebbert D (2019) chisq.posthoc.test: a post hoc analysis for pearson's chi-squared test for count data. R package version 0.1.2. https://CRAN.R-project.org/package=chisq.posthoc.test

Faria-Junior E, Lindner A (2019) An underwater temperature dataset from coastal islands in Santa Catarina, southern Brazil: high accuracy data from different depths. SEANOE. https://doi.org/10.17882/62120

Fox J, Weisberg S (2019) An r companion to applied regression. Sage, Thousand Oaks

Froese R, Pauly D (2021) FishBase. World Wide Web electronic publication. www.fishbase.org, version (08/2021).

Garvey JE, Whiles MR (2016) Trophic Ecology. Taylor and Francis, Boca Raton. https://doi.org/10.1201/9781315367804

Gause GF (1934) The struggle for existence. Williams and Wilkins, Baltimore

Gotelli NJ, Hart EM, Ellison AM (2015) EcoSimR: null model analysis for ecological data. https://doi.org/10.5281/zenodo.16522

Hardin G (1960) The competitive exclusion principle. Science 131:1292–1297. https://doi.org/10.1126/science.131.3409.1292

Hector A, Hooper R (2002) Darwin and the first ecological experiment. Science 295:639–640. https://doi.org/10.1126/science.1064815

Hixon M, Jones G (2005) Competition, predation, and density-dependent mortality in demersal marine fishes. Ecology 86:2847–2859. https://doi.org/10.1890/04-1455

Hutchinson GE (1957) Concluding Remarks. Cold Spring Harb Symp Quant Biol 22:415–427. https://doi.org/10.1101/SQB.1957.022.01.039

Kawakami E, Vazzoler G (1980) Método gráfico e estimativa de índice alimentar aplicado no estudo de alimentação de peixes. Braz J Oceanogr 29:205–207. https://doi.org/10.1590/S0373-55241980000200043

Knight NS, Guichard F, Altieri AH (2021) A global meta-analysis of temperature effects on marine fishes' digestion across trophic groups. Glob Ecol Biogeogr 00:1–16. https://doi.org/10.1111/geb.13262

Kraft NJ, Cornwell WK, Webb CO, Ackerly DD (2007) Trait evolution, community assembly, and the phylogenetic structure of ecological communities. Am Nat 170:271–283. https://doi.org/10.1086/519400

Lehner PN (1996) Handbook of ethological methods. Cambridge University Press, Cambridge

Lemon J (2006) Plotrix: a package in the red-light district of R. R-News 6(4):8–12

Levy A, von der Heyden S, Floeter SR, Bernardi G, Almada VC (2013) Phylogeny of *Parablennius* Miranda Ribeiro, 1915 reveals aparaphyletic genus and recent Indo-Pacific diversification from an Atlantic ancestor. Mol Phylogenet Evol 67:1–8. https://doi.org/10.1016/j.ympev.2012.12.010

Liedke AMR, Barneche DR, Ferreira CEL, Segal B, Nunes LT, Burigo APC, Carvalho JA, Buck S, Bonaldo R, Floeter SR (2016) Abundance, diet, foraging and nutritional condition of the banded butterflyfish (*Chaetodon striatus*) along the western Atlantic. Mar Biol 163:6. https://doi.org/10.1007/s00227-015-2788-4

Liedke AMR, Bonaldo RM, Segal B, Ferreira CEL, Nunes LT, Burigo AP, Buck S, Oliveira-Santos LGR, Floeter SR (2018) Resource partitioning by two syntopic sister-species of butterflyfish (Chaetodontidae). J Mar Biolog Assoc UK 98:1767–1773. https://doi.org/10.1017/S0025315417001321

Lindquist DG, Dillaman RM (1986) Trophic morphology of four Western Atlantic Blennies (Pisces: Blenniidae). Copeia 1:207–2013. https://doi.org/10.2307/1444909

Luiz OJ, Floeter SR, Gasparini JL, Ferreira CEL, Wirtz P (2004) The occurrence of the African surgeonfish *Acanthurus monroviae* (Perciformes: Acanthuridae) in the southwestern Atlantic, with comments on other eastern Atlantic reef fishes occurring in Brazil. J Fish Biol 65:1173–1179. https://doi.org/10.1111/j.0022-1112.2004.00519.x

MacArthur RH (1958) Population ecology of some warblers of Northeastern coniferous forests. Ecology 39:599–619. https://doi.org/10.2307/1931600

Magnuson JJ, Crowder LB, Medvick PA (1979) Temperature as an ecological resource. Am Zool 19:331–343. https://doi.org/10.1093/icb/19.1.331

Manly BFJ (1993) A review of computer intensive multivariate methods in ecology. In: Patil GP, Rao CR (eds) Multivariate environmental statistics. Elsevier, Amsterdam, pp 307–346

Manly BFJ (1997) Randomization, bootstrap and Monte Carlo methods in biology. Chapman and Hall, London

Manly BFJ, McDonald LL, Thomas DL (1993) Resource selection by animals: statistical design and analysis for field studies. Chapman and Hall, London

McPeek M, Gomulkiewicz R (2005) Assembling and depleting species richness in metacommunities: insights from ecology, population genetics, and macroevolution. In: Holyoak M, Leibold MA, Holt RD (eds) Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, pp 355–373

Morais RA, Ferreira CEL, Floeter SR (2017) Spatial patterns of fish standing biomass across Brazilian reefs, Southwestern Atlantic. J Fish Biol 91:1642–1667. https://doi.org/10.1111/jfb.13482

Munday PL (2004) Competitive coexistence of coral-dwelling fishes: the lottery hypothesis revisited. Ecology 85:623–628. https://doi.org/10.1890/03-3100

Munkemuller T, Boucher FC, Thuiller W, Lavergne S (2015) Phylogenetic niche conservatism, common pitfall, and ways forward. Funct Ecol 29:627–639. https://doi.org/10.1111/1365-2435.12388

Nieder J (1997) Seasonal variation in feeding patterns and food niche overlap in the mediterranean blennies *Scartella cristata*, *Parablennius pilicornis* and *Lipophrys trigloides* (Pisces: Blenniidae). Mar Ecol 18:227–237. https://doi.org/10.1111/j.1439-0485.1997.tb00439.x

Nielsen JM, Clare EL, Hayden B, Brett MT, Kratina P (2018) Diet tracing in ecology: methods comparison and selection. Methods Ecol Evol 9:278–291. https://doi.org/10.1111/2041-210X.12869

Nunes L, Siqueira AC, Cord I, Ford BM, Liedke AMR, Ferreira CEL, Floeter SR (2020) The influence of species abundance, diet and phylogenetic affinity on the co-occurrence of butterflyfishes. Mar Biol 167:107. https://doi.org/10.1007/s00227-020-03725-7

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens

MHH, Szoecs E, Wagner H (2019) vegan: community ecology package. R package version 2.5-5. https://CRAN.R-project.org/package=vegan

Patzner RA, Hastings PA, Springer VG, Wirtz P, Gonçalves EJ (2009) List of valid species of Blennies. In: Patzner RA, Gonçalves EJ, Kapoor BG (eds) The biology of Blennies. Science Publishers, New Hampshire, pp 443–473

Peterson AT (2011) Ecological niche conservatism: a time-structured review of evidence. J Biogeogr 38:817–827. https://doi.org/10.1111/j.1365-2699.2010.02456.x

Peterson AT, Soberón J, Sánchez-Cordero V (1999) Conservatism of ecological niches in evolutionary time. Science 285:1265–1267. https://doi.org/10.1126/science.285.5431.1265

Pianka ER (1973) The structure of lizard communities. Annu Rev Ecol Syst 4:53–74. https://doi.org/10.1146/annurev.es.04.110173.000413

Pianka ER, Vitt LJ, Pelegrin N, Fitzgerald DB, Winemiller KO (2017) Toward a periodic table of niches, or exploring the lizard niche hypervolume. Am Nat 190:601–616. https://doi.org/10.1086/693781

Pinheiro HT, Rocha LA, Macieira RM, Carvalho-Filho A, Anderson AB, Bender MG, Di Dario F, Ferreira CEL, Figueiredo-Filho J, Francini-Filho R, Gasparini JL, Joyeux JC, Luiz OJ, Mincarone MM, Moura RL, Nunes JACC, Quimbayo JP, Rosa RS, Sampaio CLS, Sazima I, Simon T, Vila-Nova DA, Floeter SR (2018) Southwestern Atlantic reef fishes: zoogeographic patterns and ecological drivers reveal a secondary biodiversity center in the Atlantic Ocean. Divers Distrib 24:951–965. https://doi.org/10.1111/ddi.12729

Pinksy ML, Selden RL, Kitchel ZJ (2020) Climate-driven shifts in marine species ranges: scaling from organisms to communities. Ann Rev Mar Sci 12:153–179. https://doi.org/10.1146/annurev-marine-010419-010916

Quimbayo JP, Giglio VJ, Ferreira CEL, Fraga A, Nunes JACC, Mendes TC (2020) Contrasting feeding and agonistic behaviour of two blenny species on a small and remote island in the equatorial Atlantic Ocean. J Fish Biol 96:74–82. https://doi.org/10.1111/jfb.14180

R Core Team (2018) R: a language and environment for statistical computingR Foundation for Statistical Computing, Vienna. https://www.R-project.org/

Rangel CA (2007) Peixes recifais criptobênticos de Arraial do Cabo, RJ: Composição, estrutura da comunidade e comparações biogeográficas. PhD thesis, Universidade Federal Fluminense, Brazil

Rangel CA, Guimarães RZP (2010) Taxonomia e distribuição da família Blenniidae (Teleostei: Blennioidei) na costa leste do Brasil. Revista Brasileira De Zoociências 12:17–41

Ricklefs RE, Relyea R (2018) Ecology: the economy of nature. W. H. Freeman and Company, New York

Sale PF (1978) Coexistence of coral reef fishes—a lottery for living space. Environ Biol Fish 3:85–102. https://doi.org/10.1007/BF00006310

Sale PF (2006) Coral reef fishes—dynamics and diversity in a complex ecosystem. Academic Press, San Diego

Santos S, Hrbek T, Farias IP, Schneider H, Sampaio I (2006) Population genetic structuring of the king weakfish, *Macrodon ancylodon* (Sciaenidae), in Atlantic coastal waters of South America: deep genetic divergence without morphological change. Mol Ecol 15:4361–4373. https://doi.org/10.1111/j.1365-294X.2006.03108.x

Schoener TW (1971) Theory of feeding strategies. Ann Rev Ecolog Sys 2:369–404

Segal B, Freire AS, Lindner A, Krajewski JP, Soldateli M (2017) MAArE - Monitoramento Ambiental da Reserva Biológica Marinha do Arvoredo e Entorno. Universidade Federal de Santa Catarina, Florianópolis

Shpigel M (1982) Niche overlap among two species of coral dwelling fishes of the genus *Dascyllus* (Pomacentridae). Environ Biol Fishes 7:65–68

Slatkin M (1980) Ecological character displacement. Ecology 61:163–177. https://doi.org/10.2307/1937166

Therneau T (2015) A package for survival analysis in R. https://CRAN.R-project.org/package=survival

Thuiller W, Gallien L, Boulangeat I, Bello FD, Münkemüller T, Roquet C, Lavergne S (2010) Resolving Darwin's naturalization conundrum: a quest for evidence. Divers Distrib 16:461–475. https://doi.org/10.1111/j.1472-4642.2010.00645.x

Tracy R, Christian K (1986) Ecological relations among space, time, and thermal niche axes. Ecology 67:609–615. https://doi.org/10.2307/1937684

Venables WN, Ripley BD (2002) Modern applied statistics with S, 4th edn. Springer, New York

Wellborn GA, Langerhans RB (2015) Ecological opportunity and the adaptive diversification of lineages. Ecol Evol 5:176–195. https://doi.org/10.1002/ece3.1347

Wickham H (2016) ggplot2: elegant graphics for data analysis. Springer, New York

Wiens JJ, Donoghue MJ (2004) Historical biogeography, ecology and species richness. Trends Ecol Evol 19:639–644. https://doi.org/10.1016/j.tree.2004.09.011

Wiens JA, Stralberg D, Jongsomjit D, Howell CA, Snyder MA (2009) Niches, models, and climate change: assessing the assumptions and uncertainties. Proc Natl Acad Sci USA 106:19729–19736. https://doi.org/10.1073/pnas.0901639106

Wilson SK, Bellwood DR, Choat JH, Furnas MJ (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol 41:279–309

Winemiller KO, Fitzgerald DB, Bower LM, Pianka ER (2015) Functional traits, convergent evolution, and periodic tables of niches. Ecol Lett 18:737–751. https://doi.org/10.1111/ele.12462

Wong MYL, Buston PM (2013) Social systems in habitat-specialist reef fishes: key concepts in evolutionary ecology. Bioscience 63:453–463