UNIVERSIDADE FEDERAL DE SANTA CATARINA

CENTRO DE CIÊNCIAS BIOLÓGICAS

DEPARTAMENTO DE ECOLOGIA E ZOOLOGIA

PROGRAMA DE PÓS-GRADUAÇÃO EM ECOLOGIA

Angela Marina Canterle

Nicho ecológico de duas espécies congenéricas de peixes criptobênticos

sintópicos no Sul do Brasil

Florianópolis

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O presente trabalho em nível de mestrado foi avaliado e aprovado por banca examinadora composta pelos seguintes membros:

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Certificamos que esta é a **versão original e final** do trabalho de conclusão que foi julgado adequado para obtenção do título de mestre em Ecologia.

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AGRADECIMENTOS

RESUMO

O nicho ecológico das espécies depende de fatores ecológicos e evolutivos. Espécies filogeneticamente próximas podem apresentar conservatismo de nicho, mantendo suas características ecológicas ancestrais. Alternativamente, em uma situação de recursos limitados, as espécies podem se diferenciar por meio de mudanças em suas características ecológicas e morfológicas para reduzir a sobreposição de nicho e facilitar a coexistência. Neste estudo, investigamos o nicho ecológico de duas espécies filogeneticamente próximas de peixes recifais criptobentônicos co-ocorrendo no sul do Brasil, *Parablennius pilicornis* e *P. marmoreus*. Nós investigamos a sobreposição de nicho das espécies em três dimensões (térmico, espacial e trófico) para verificar se elas apresentam conservatismo de nicho filogenético ou apresentam partição em alguma dimensão de nicho. Para isso, determinamos a densidade, verificamos a seletividade do microhabitat e fizemos análises da dieta de ambas as espécies em quatro recifes rochosos do Sul do Brasil. As espécies apresentaram pequenas diferenças na distribuição térmica, distribuição em profundidade, seletividade de microhabitats e ambas apresentaram dieta onívora generalista. Ambos apresentaram sobreposição de nicho de Pianka igual ou superior ao esperado ao acaso em todas as dimensões de nicho analisadas. Esses resultados sugerem que este par de espécies está coexistindo apesar da considerável sobreposição de nicho. Assim, a coexistência de espécies dentro desta linhagem pode não depender da evolução de padrões divergentes de uso de recursos, e sim da história evolutiva das espécies.

Palavras-chave: Blenniidae. *Parablennius pilicornis*. *Parablennius marmoreus*. Simpatria.

ABSTRACT

Species ecological niches depend 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 they hold phylogenetic niche conservatism or are partitioning some niche dimension. For that, we studied their densities, microhabitat affinities and diets in four rocky reefs of southern Brazil. The two species presented little differences in thermal and depth distributions, microhabitat preferences, and both presented a similar omnivorous diet. The Pianka niche overlap was equal to or higher than expected by chance in all analysed niche dimensions. These results suggest this species-pair is successfully coexisting despite considerable niche overlap. Thus, the coexistence of species within this lineage may not depend on the evolution of divergent patterns of resource use, but on the evolutionary history of the species.

Keywords: Blenniidae. *Parablennius pilicornis*. *Parablennius marmoreus*. Sympatry.

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1 INTRODUÇÃO GERAL

O primeiro pesquisador a propor o conceito de nicho ecológico no ambiente acadêmico foi o americano Joseph Grinnell, e desde então o termo tem sido amplamente discutido e utilizado (PATTEN; AUBLE, 1981). O primeiro uso do conceito na ciência foi em 1917, no artigo "*The niche relationships of the California thrasher*" (GRINNELL, 1917). O conceito de nicho Grinnelliano incorpora a ideia de que o nicho de uma espécie é determinado pela sua distribuição geográfica. Portanto, o nicho era considerado uma soma das propriedades abióticas do ambiente (*i.e.* temperatura, umidade, pluviosidade, salinidade, entre outros) que permitiam que uma espécie ocorresse. Porém, essa definição ignorava as interações ecológicas com outras espécies e seu efeito sobre a presença e ausência na distribuição (VANDERMEER, 1972).

Em 1927, o ecólogo britânico Charles Elton definiu o nicho ecológico como "o lugar de um animal no meio biótico, suas relações com o recurso e os inimigos" (ELTON, 1927). Ele classificou os nichos de acordo com os hábitos alimentares das espécies (CHASE; LEIBOLD, 2003). Elton forneceu exemplos de organismos que ocupam nichos semelhantes, como a raposa do Ártico que se alimenta de ovos de aves marinhas e restos de focas mortas por ursos, e a hiena malhada que se alimenta de ovos de avestruzes e restos de zebras mortas por leões (ELTON, 1927; SCHOENER, 1989). O nicho foi assim definido principalmente pelas interações bióticas, dinâmica de consumo dos recursos e posição dos animais em cadeias tróficas, como carnívoros, herbívoros, entre outros, além das suas relações com os fatores abióticos que a cercam (SOBERÓN, 2007).

Em 1957, George Hutchinson proporcionou mais uma mudança ao formalizar o conceito de nicho como um atributo da espécie, e não do ambiente (HUTCHINSON, 1957). O nicho foi descrito por Hutchinson um "espaço multidimensional" resultante de inúmeras características que condicionam a existência de uma determinada espécie (Figura 1). Ou seja, um espaço de variáveis ambientais (bióticas e abióticas) as quais representam os limites da viabilidade das espécies.
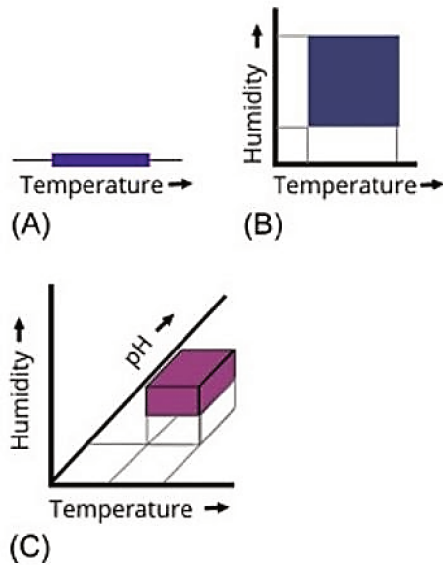
Figura 1 - Três variáveis ambientais ("condições": temperatura, umidade e pH) mapeadas em (A) uma, (B) duas, e (C) três dimensões no espaço (adaptada de FARMER, 2018).

Baseadas no conceito de nicho, outras importantes teorias ecológicas surgiram, como por exemplo o conceito de sobreposição de nicho (COLWELL; FUTUYMA, 1971; CARVALHO; FERNANDEZ; NESSIMIAN, 2005), que já havia sido considerada por Grinnell e Hutchinson em seus estudos. A sobreposição de nicho se refere ao compartilhamento de recursos ou outros fatores ecológicos por duas ou mais espécies (CORNELL, 2011). Por exemplo, os peixes em um recife podem se alimentar de invertebrados, e, assim, se sobrepor em suas dietas; e as plantas de uma floresta podem se sobrepor em sua necessidade de luz solar. A sobreposição de nicho é um conceito importante na ecologia de comunidades, pois com ele é possível determinar quantas e quais espécies podem coexistir em uma comunidade (CORNELL, 2011).

Um desfecho possível para quando os nichos estão sobrepostos e os recursos são limitantes pode ser a diferenciação de nicho, processo pelo qual espécies competidoras utilizam o ambiente de maneira distinta, de uma forma que possam coexistir (ARMSTRONG; MCGEHEE, 1980). Um exemplo de diferenciação de nicho pode ser visto nos lagartos do gênero *Anolis* nas ilhas do Caribe (WILLIAMS, 1983). Onze espécies compartilham requisitos alimentares, principalmente insetos. Entretanto, cada espécie vive em seu habitat preferencial, que é definido pela fitofisionomia, intensidade luminosa, umidade, entre outros fatores, evitando assim a competição (Figura 2). Sem essa diferenciação, o competidor mais

forte pode levar o competidor mais fraco a extinção local caso o recurso se torne escasso (princípio da exclusão competitiva) (GAUSE, 1934).
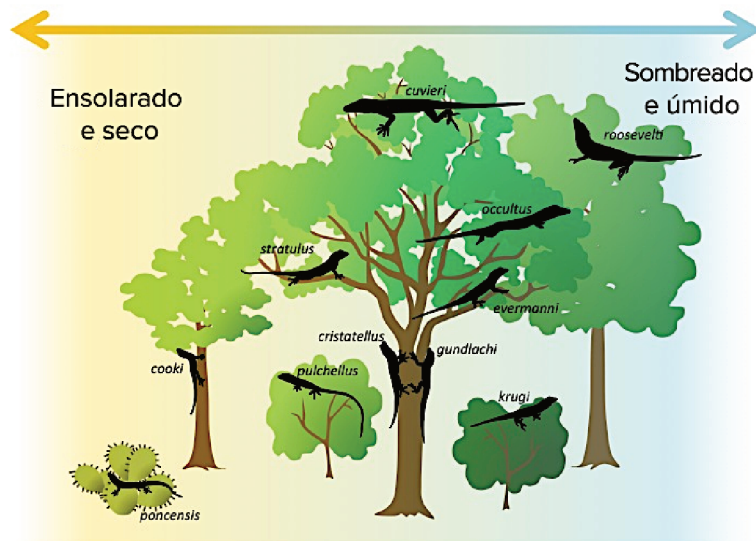
Figura 2 - Diferenciação de nicho em 11 espécies de lagartos do gênero *Anolis* (adaptada de WILLIAMS 1983).

Um mecanismo que contrasta com a diferenciação ecológica das espécies é o conservatismo de nicho filogenético. De acordo com o enigma da naturalização de Darwin, a chance de as espécies estarem em um determinado local é maior quando parentes próximos estão presentes, já que as espécies do mesmo gênero geralmente têm hábitos semelhantes (DARWIN, 1859; DIEZ et al., 2008; THUILLER et al., 2010). Peterson et al. (1999) demonstraram que nichos podem ser conservados ao longo do tempo, ou seja, espécies tendem a reter aspectos de seu nicho fundamental ao longo do tempo evolutivo. Dentro desse contexto, espera-se que espécies intimamente relacionadas estejam distribuídas em partes semelhantes do espaço de nicho, ou seja, apresentem conservatismo de nicho filogenético (PETERSON; SOBERÓN; SÁNCHEZ-CORDERO, 1999; PETERSON, 2011).

É importante destacar que, assim como o seu conceito, o nicho ecológico não é uma medida estática, e sim dinâmica. Em estudos ecológicos retratamos o nicho em algum momento do tempo, entretanto ele não é sempre igual em qualquer ocasião ou ambiente (BEGON; HARPER; TOWNSEND, 2006). Ele pode ser alterado ao longo das fases da vida, estações e ainda decorrente de perturbações ambientais (RICKLEFS; RELYEA, 2016). As alterações de características do ambiente, como a perda de habitats, podem afetar o nicho das espécies (COLWELL; FUTUYMA, 1971). Além disso, dificilmente conseguiremos quantificar todas as dimensões do nicho ecológico de algum organismo ou espécie. Contudo, considerando a dinamicidade do nicho, pode-se reconhecer a importância científica de descrever dimensões do

nicho, uso de habitats, características dos hábitos e a história das espécies no campo de estudo da ecologia.

Um modelo potencial para estudar a sobreposição de nicho é o grupo de peixes criptobentônicos da família Blenniidae, pois apresentam baixa dispersão, áreas de vida pequenas e são amplamente distribuídos nos habitats que ocupam (BRANDL et al., 2018; BRANDL; CASEY; MEYER, 2020; WONG; BUSTON, 2013). Os peixes criptobentônicos têm uma forte associação com o bentos (*i.e.* comunidade de organismos que vive associada ao substrato) e fornecem ligações energéticas cruciais nas cadeias tróficas dos recifes, pois apresentam taxas de crescimento populacional excepcionais e são altamente predados (DEPCZYNSKI; BELLWOOD, 2003; BRANDL et al., 2018). O gênero *Parablennius* pertence a este grupo e é composto por 26 espécies, das quais duas ocorrem no Brasil: *Parablennius pilicornis* (Cuvier, 1829) e *Parablennius marmoreus* (Poey, 1876).

Ambas as espécies são filogeneticamente aparentadas (Figura 3; LEVY et al., 2013) e encontradas em habitats como fendas ou cracas vazias ao longo de costões rochosos, porém diferem em sua distribuição (RANGEL; GUIMARÃES, 2010; PINHEIRO et al., 2018). A espécie *P. pilicornis* comumente habita recifes de águas mais frias do mar Mediterrâneo e Atlântico Sul, enquanto *P. marmoreus* é registrada em recifes com água em geral mais quente (PINHEIRO et al., 2018). Em uma escala menor, foram identificadas diferenças na preferência de profundidade quando as espécies estão co-ocorrendo (DALBEN; FLOETER, 2012). Os hábitos alimentares dessas espécies são mal compreendidos, embora dados empíricos apontem uma dieta onívora diversificada para *P. pilicornis* (NIEDER, 1997) e uma dieta onívora à base de algas para *P. marmoreus* (RANDALL, 1996).
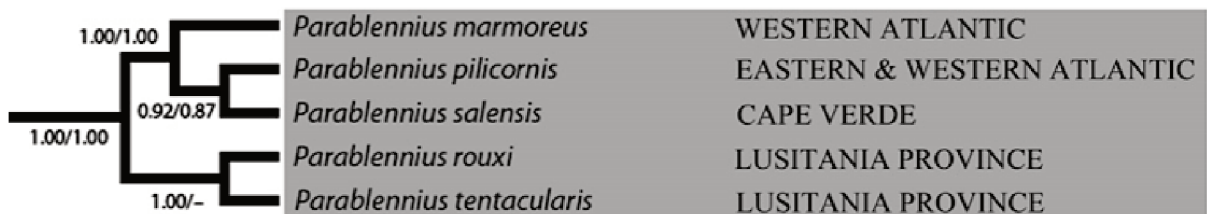

Figura 3 - Relação filogenética das espécies *P. pilicornis* e *P. marmoreus* (adaptada de LEVY et al., 2013).

Devido às suas altas demandas energéticas e seu potencial como presas, peixes criptobentônicos podem desempenhar papéis importantes na cadeia trófica recifal (BRANDL et al., 2019). Apesar dessa importância, os estudos com a assembleia de peixes se concentraram

quase que exclusivamente nos membros mais visíveis da comunidade recifal (SALE, 2006), fornecendo poucas informações sobre as espécies criptobentônicas. A co-ocorrência das duas espécies de *Parablennius*—uma característica exclusiva do Sul e Sudeste do Brasil—permite um estudo acerca da sobreposição de nicho ecológico, além de proporcionar uma oportunidade de melhor entendimento da ecologia deste grupo.

Assim, o presente estudo tem como objetivo determinar se existe partição em alguma dimensão de nicho (térmico, espacial ou trófico) das duas espécies de peixes do gênero *Parablennius* que co-ocorrem exclusivamente no litoral Sul e Sudeste brasileiro. Para tanto, determinamos a densidade de *P. pilicornis* e *P. marmoreus* em quatro recifes rochosos de Santa Catarina; registramos em quais profundidades e microhabitats as duas espécies ocorrem; e realizamos uma análise comparativa de suas dietas.

Como as duas espécies são morfologicamente similares e possuem história de vida semelhantes (LEVY et al., 2013), podemos postular dois cenários possíveis:

Cenário 1) Como as espécies são filogeneticamente próximas, apresentarão nichos semelhantes e sobrepostos, devido ao conservatismo filogenético de nicho;

Cenário 2) Considerando recursos limitantes, haverá algum tipo de diferenciação de nicho permitindo a coexistência (ABRAMS, 1983). No cenário 2 podemos propor as seguintes hipóteses: Nicho térmico: a espécie *P. pilicornis* está presente com maior abundância relativa nas águas mais frias do Sul da Ilha de Santa Catarina, enquanto *P. marmoreus* é mais abundante nas águas mais quentes do Norte da Ilha de Santa Catarina; Nicho espacial, ambas as espécies apresentação partição no uso de microhabitats e profundidades; Nicho trófico, itens alimentares mais energéticos (por exemplo, invertebrados) terão uma maior importância na dieta da espécie que habita águas mais frias (*i.e. P. pilicornis*), enquanto a espécie com afinidade tropical (*i.e. P. marmoreus*) apresentará um hábito mais herbívoro.

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2 CAPÍTULO ÚNICO: ECOLOGICAL NICHE OF TWO CONGENERIC CRYPTOBENTHIC REEF FISHES COEXISTING IN SOUTH BRAZIL

Para ser submetido ao periódico Marine Biology

Ecological niche of two congeneric cryptobenthic reef fishes coexisting in south Brazil

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ABSTRACT

Species ecological niches depend 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 close cryptobenthic reef fish species that co-occur in the southern Brazilian coast, *Parablennius pilicornis* and *P. marmoreus*. We examined possible species overlap in three niche dimensions (thermal, spatial and trophic) to verify if they hold phylogenetic niche conservatism or are partitioning some niche dimension. For that, we studied their densities, microhabitat affinities and diets in four rocky reefs of southern Brazil. The two species presented little differences in thermal and depth distributions, microhabitat preferences, and both presented a similar omnivorous diet. The Pianka niche overlap was equal to or higher than expected by chance in all analysed niche dimensions. These results suggest this species-pair is successfully coexisting despite considerable niche overlap. Thus, the coexistence of species within this lineage may not depend on the evolution of divergent patterns of resource use, but on the evolutionary history of the species.

Keywords: Blenniidae, Diet, *Parablennius pilicornis*, *Parablennius marmoreus*, Sympatry

INTRODUCTION

The ecological niche is defined as the space encompassing abiotic and biotic variables which limit the conditions for populations growth, survival and persistence (Hutchinson 1957). Several dimensions compose a species niche, among which 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). Besides these two dimensions, one can consider the environmental temperature the most important abiotic variable, due to its influence over species distribution (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 allowed other important ecological concepts to emerge, such as the 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 the 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 that allows 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). 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). Species' niche can be conserved over evolutionary time by maintaining their fundamental niche aspects (Peterson et al. 1999). Thus, one can expect closely related species are distributed in similar ways of the niche, showing phylogenetic niche conservatism (Peterson et al. 1999; Peterson 2011). It is important to investigate this concept in different taxa, to better understand the influence of ecological and evolutionary factors in ecological niches (Pianka et al. 2017).

Small cryptobenthic reef fishes are excellent models for testing hypothesis related to niche, as they present low dispersal abilities, wide distribution in reef habitats, small home ranges, syntopic distributions, and high turnover (resulting 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 are highly predated (Depczynski and Bellwood 2003; Brandl et al. 2018). These fishes are important for the energy flow of reefs trophic chains due to their high energy demands and functional roles (Brandl et al. 2019). Despite its abundance and importance for the dynamics of marine ecosystems, most studies have focused almost exclusively on the most visible members of the reef community (Sale 2006), providing little information on cryptobenthic species.

Among the cryptobenthics, the genus *Parablennius* comprises 26 species, of which 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). At the smaller scale, some differences in depth preference have been suggested when species co-occur in Southeastern Brazil, with *P. marmoreus* having its distribution pushed to deeper waters in the presence of its congeneric (Dalben and Floeter 2012). The dietary habits of these species are poorly understood, although empirical data point to a diversified omnivorous diet for *P. pilicornis* (Nieder 1997) and an omnivorous algae-based diet for *P. marmoreus* (Randall 1996). 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.
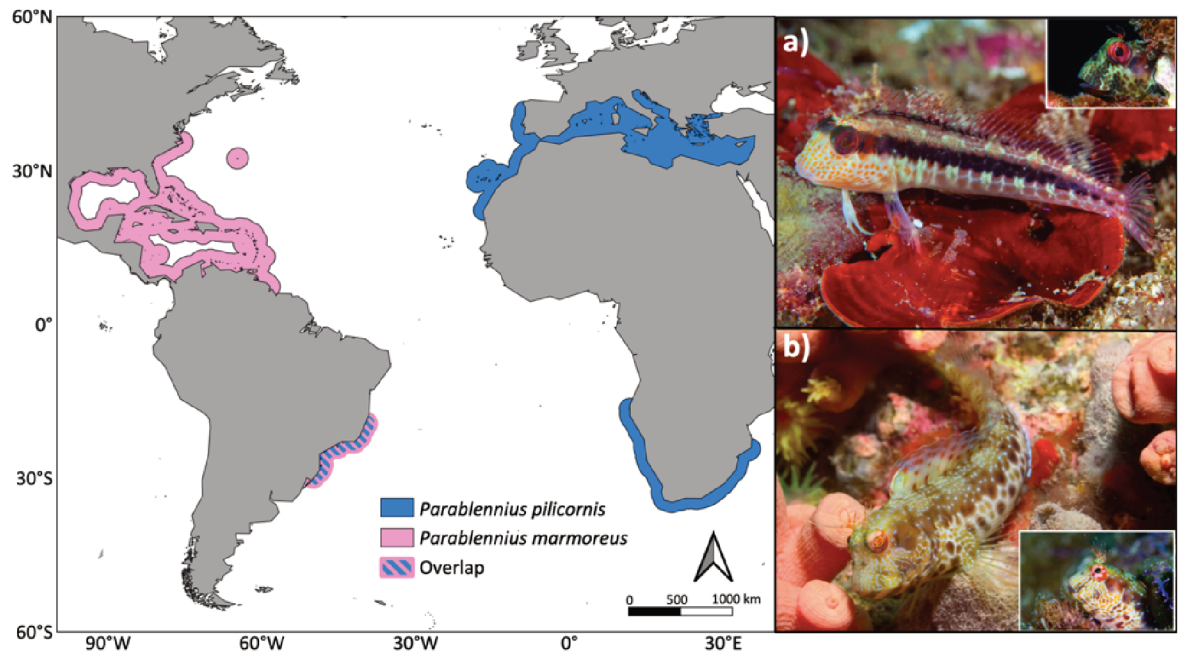
Fig. 1 Distribution of *Parablennius pilicornis* (blue, photo a) and *Parablennius marmoreus* (pink, photo b) in the Atlantic Ocean. Blue-pink dashed area indicates the Southeast Brazilian coast where species distribution overlap. Photos: João Paulo Krajewski

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) they will hold similar niche 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 herbivore 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: Galés Island (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 in 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 in a constant velocity and identified, counted, and estimated the total length of fishes within a 40m² area (20 x 2 m; see details in Morais et al. 2017). Censuses data were used for thermal and spatial niche dimensions. The relative abundance of both species across sites was compared using the Log likelihood ratio (G-test) test of independence (Goodman 1964).

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, 5.1-10m, and 10.1-16m; please 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.

To determine microhabitat preferences, we recorded 100 individuals of *P. pilicornis* and 114 individuals of *P. marmoreus* by haphazardly searching the reef in Arvoredo Island, Xavier Island and Pântano do Sul. When a fish individual was sighted, we recorded the species and the substratum immediately below the individual. Benthic assessments were conducted to compare the frequency of use by the fishes with the relative cover availability of each substrate type at the study sites. To characterize the benthic community, the percentage cover of each substratum type was visually estimated using 30x30 cm quadrats. Twenty quadrats were haphazardly distributed on each sampled site. The substrata were visually categorized in: epilithic algal matrix (sensu Wilson et al. 2003), macroalgae, crustose calcareous algae, rock, sand, sea urchins and Zoantharia. Non-representative substrates (i.e. benthic cover <5%) were discarded from the analyses.

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). We used 100 random substrate points (scored as 0) 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:

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

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).

Trophic niche

For diet analysis, we sampled a total of 20 individuals (10 of each species) on Arvoredo Island and Pântano do Sul. All individuals were sampled using hand nets, immediately frozen and sent to the laboratory where they were measured and had the stomachs removed and fixed in formaldehid 10%. Individual stomachs 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 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 stomachs) and volumetric index (%V, i.e. summed volume of

each item pooled across individuals divided by the total volume of the sampled stomachs; Nunes et al. 2020). The volume of each food item, in each stomach, was measured through a millimetre Petri dish where each item was placed between two 1-mm-thick coverslips and kneaded with a microscope slide, and then the number of 1mm³ 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 it follows:

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

in which *Fi* is the number of stomachs with a given prey type *i* in relation to the total number of stomachs and *Vi* 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 2).

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). The niche overlap values were statistically tested against null models through EcoSimR using the algorithm RA3 (Gotelli et al. 2015). We performed 999 MonteCarlo randomizations to create pseudo-communities, 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).

All analyses were performed in R software, through the packages "car" (Fox and Weisberg 2019), "ggplot2" (Wickham 2016), "EcoSimR" (Gotelli et al. 2015), "scales"

(Wickham 2018), "survival" (Therneau 2015) and "vegan" (Oksanen et al. 2019) (R core team 2018).

RESULTS

Thermal niche

We performed a total of 195 underwater visual censuses, being 54 transects in Galés Island, 54 in Arvoredo Island, 64 in Xavier Island, and 23 in Pântano do Sul. The relative abundance of *Parablennius marmoreus* was higher than the abundance of *P. pilicornis* in Galés Island (64.1% *P. marmoreus*; 35.9% *P. pilicornis*), Arvoredo Island (53.5% *P. marmoreus*; 46.5% *P. pilicornis*) and Xavier Island (61.9 % *P. marmoreus*; 38.1 *P. pilicornis*) (Fig. 2). At Pântano do Sul, the relative abundance of *P. pilicornis* was higher (1.9% *P. marmoreus*; 98.1% *P. pilicornis*) (Fig. 2). When comparing the proportion of *P.marmoreus* and *P. pilicornis* across sites, no significant differences were found (G = 1.3091, X-squared df = 3, p-value = 0.72).

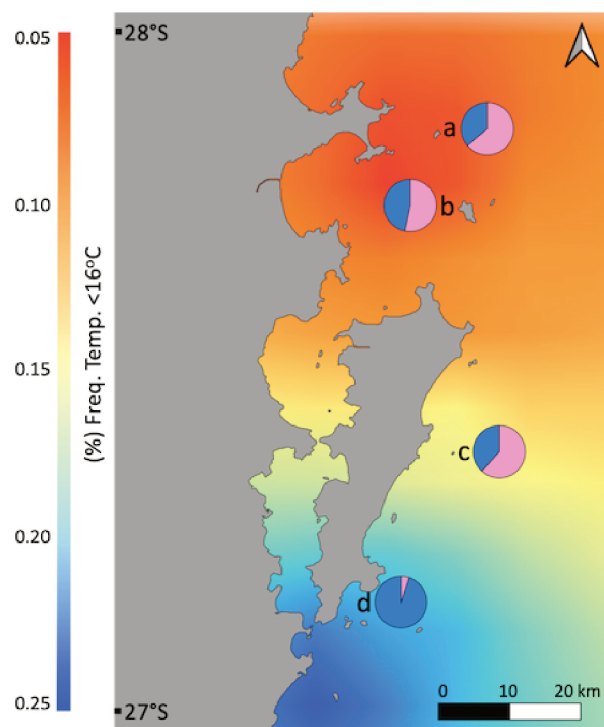**Fig. 2** Relative abundance of *Parablennius pilicornis* (blue) and *Parablennius marmoreus* (pink) across the four sampled reefs in South Brazil (Data from the years 2016 to 2020). Letters indicate Galés Island (a), Arvoredo Island (b), Xavier Island (c) and Pântano do Sul (d). Temperature range expressed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

Spatial niche

Both species were found in all depth strata (0 to 5 meters, 5.1 to 10 meters, 10.1 to 16 meters). 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 the Arvoredo Island, there was no difference on density of both species across depths. At the Galés Island, the density of *P. marmoreus* was higher than *P. pilicornis* in 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 to 5 meters and 10.1 to 16 meters), and there was no difference between their densities in the 5.1 to 10 meters stratum. At the Pântano do Sul, the density of both species differed with *P. pilicornis* showing higher abundance than *P. marmoreus* in 0 to 5 meters depth stratum.
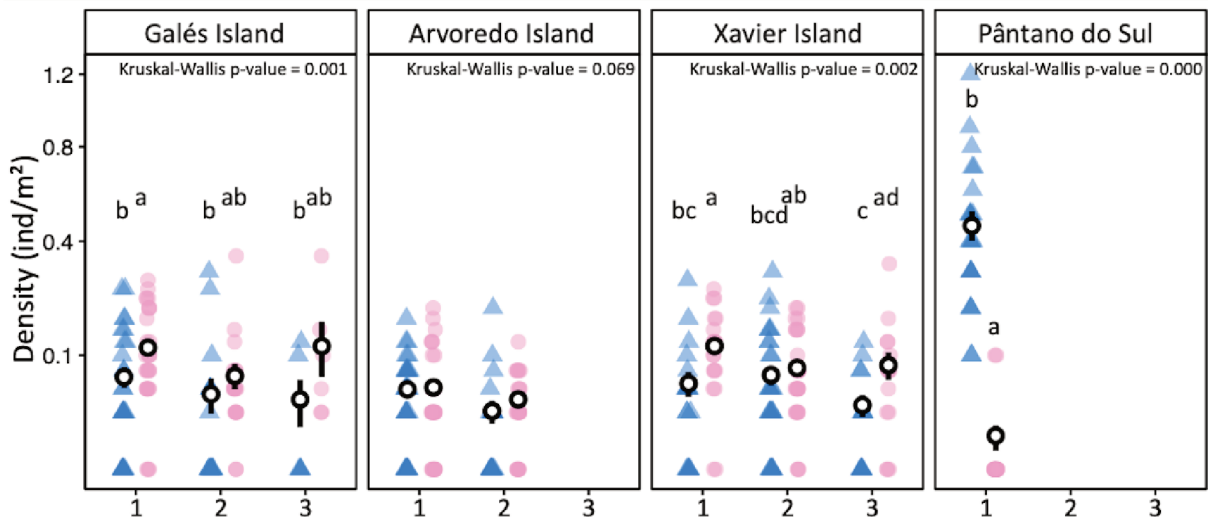
Fig. 3 Species density (individuals / m²) of both species (Blue triangle - *Parablennius pilicornis*, Pink circle: *Parablennius marmoreus*) in the sampled sites in three different depth strata (1 - 0 to 5 meters, 2 - 5.1 to 10 meters, and 3 - 10.1 to 16 meters). Pink circles and blue triangles represent each transect. White circles indicate the mean, and the black lines indicate standard error. Treatments with the same letter are not significantly different (P > 0.05) by Dunn's post hoc pairwise comparisons

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 in the reef 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 and their respective 95% confidence intervals are provided in Online Resource 3.
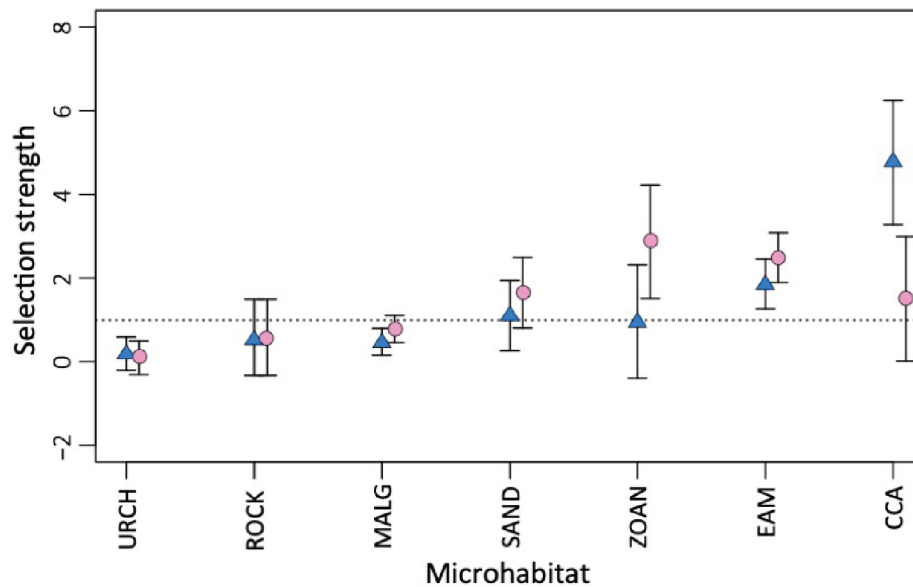

Fig. 4 Selection strength of microhabitat by *P. pilicornis* (blue triangle) and *P. marmoreus* (pink circle). Microhabitats with values crossing the dashed lines were used according to their availability (use/availability = 1); positive and negative values indicate selection and rejection, respectively. Acronyms for microhabitats are as follows: URCH, sea urchins; CCA, crustose calcareous algae; ZOAN, Zoantharia; EAM, epilithic algal matrix; MALG, macroalgae

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. Individuals of *P. pilicornis* presented crustaceans (IAI%: 36.3), algae (IAI%: 28.7), mollusks (IAI%: 11.9), sponges (IAI%: 8.9), echinoderms (IAI%: 5.1), fish (bones and scales) (IAI%: 4.9), polychaetes (IAI%: 3.6), eggs (IAI%: 0.5) and plastic (IAI%: 0.03) in their gut content. Individuals of *P. marmoreus* presented crustaceans (IAI%: 56.8), algae (IAI%: 21.9), eggs (IAI%: 10.8), fish (bones and scales) (IAI%: 8),

polychaetes (IAI%: 1), mollusks (IAI%: 0.7), echinoderms (IAI%: 0.3), and plastic (IAI%: 0.1) in their gut content, and did not presented sponges (Fig. 5a).
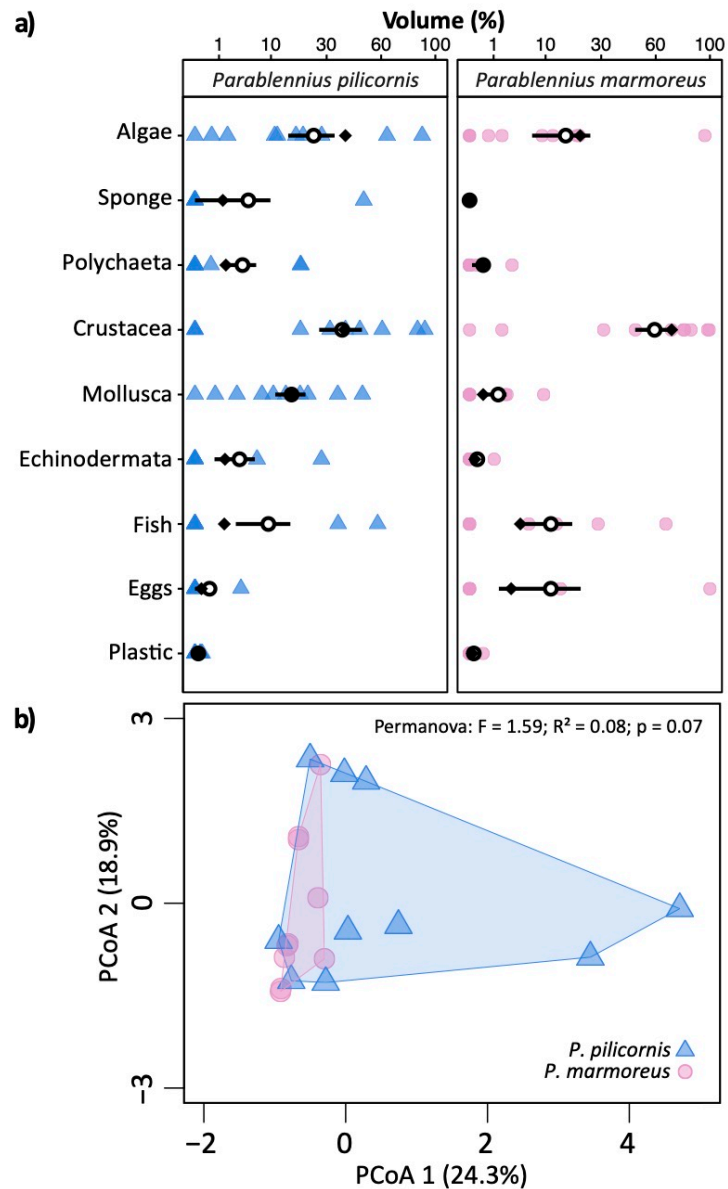
Fig. 5 a) Scatterplot for diet composition of *Parablennius pilicornis* and *P. marmoreus* in Santa Catarina. Coloured points represent the volume (%) of each feeding item for each individual. Black and white circles and black lines represent the mean feeding items volume and its standard error, respectively. 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

Niche overlap

Niche overlap values did not differ from the values expected in the null model for sites 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. Thus, *P. pilicornis* and *P. marmoreus* presented high niche overlap in all dimensions analysed.

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

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**

DISCUSSION

We demonstrated both *Parablennius* species have a high thermal, spatial and trophic niche overlap, suggesting syntopic species can coexist with overlapping niches if resources are not limited. Thus, the coexistence of 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).

Our results suggest that the most likely scenario is the ongoing phylogenetic niche conservatism between both *Parablennius* species. This genus probably diverged on 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 conditioned no need for morphological or ecological divergence at the time (Bowen et al. 2001; Santos et al. 2006), thus conserving their ecological niches. Both species were geographically reunited in the Southwestern Atlantic, where they are successfully coexisting 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 (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 habit.

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). Yet, the significantly

high costs associated with a molecular approach, such as metabarcoding, usually hinder this practice. Also, there are some problems associated with this kind of analysis, such as the difficulty of measuring volume and of identifying most of the items due to the lack of genetic sequences (Brandl et al. 2020).

Another factor that can limit the re-settling of the fishes and reduce competition is predation pressure (Shpigel 1982; Hixon and Jones 2005). Fish are a major predator of other fish, particularly of the smaller size classes, in marine ecosystems (Bax 1998). Cryptobenthic fishes present rapid growth and are highly predated in reef systems, being responsible for almost 60% of consumed reef fish biomass (Brandl 2019). This high mortality rate could cause a natural regulation of the populations by predation (Hixon and Jones 2005).

There are some coexistence theories that do not require species to be ecologically distinct, such as the lottery hypothesis (Sale 1978). Lottery hypothesis proposes that what determines the presence of species in the environment is the priority of arrival in recruitment, not the competitive skills of adults (Sale 1978). Species can coexist through demographic mechanisms, with no need of resource partitioning (Munday 2004). A study on the coexistence of two goby species (*Gobiodon histrio* and *G. erythrospilus*) demonstrated that, as recruits, they have similar competitive ability and no difference in habitat use (coral colonies). The colonies are a limiting resource and both species coexist by virtue of a competitive lottery, where vacant habitat is colonized by the first available recruit (Munday 2004).

Despite the lack of a strong thermal niche differentiation, we believe the low relative abundance of *P. marmoreus* in Pântano do Sul (Fig. 2) could be associated to 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).

Only few studies on cryptobenthic fishes have integrated dietary and spatial information to examine the interplay between them (see Brandl et al. 2020; Liedke et al. 2018). 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. This knowledge can offer a unique perspective on classical ecological concepts, such as niche conservatism, and also on elucidating factors that are structuring reef assemblages.

ACKNOWLEDGEMENTS

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ONLINE RESOURCES

ESM 1 Number of underwater visual censuses sampled per depth strata in each studied site

Site	1 to 5m	5.1 to 10m	10.1 to 16m	Total
Galés Island	29	19	6	54
Arvoredo Island	32	22	0	54
Xavier Island	19	30	15	64
Pântano do Sul	23	0	0	23
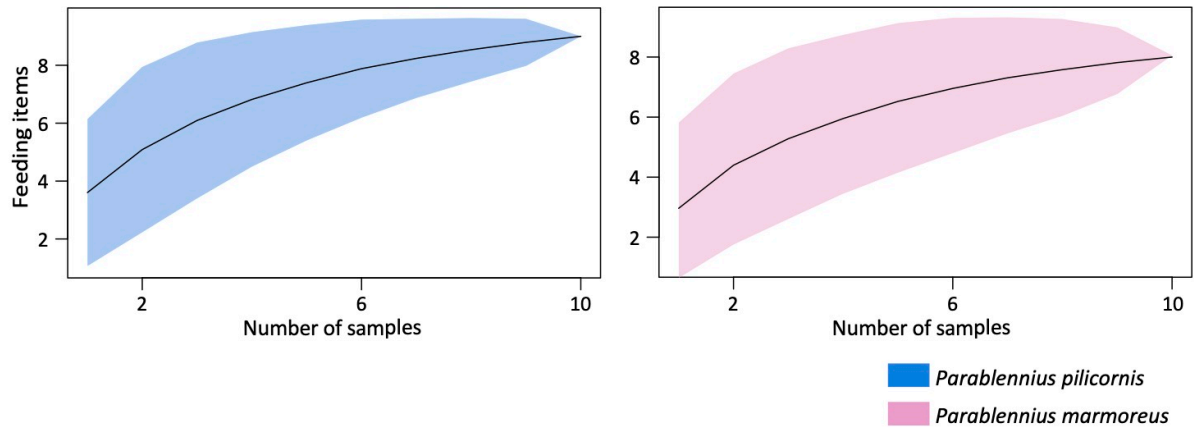
ESM 2 Sample based accumulation curves for *Parablennius pilicornis* and *Parablennius marmoreus*. The x-axis represents the number of samples (stomachs) and the y-axis represents the number of different food items

ESM 3 Coefficient estimates and their 95% confidence intervals of the Resource Selection Function. The reference level for species identity and microhabitat was *P. marmoreus* and MALG, respectively. Acronyms for microhabitat are as follows: URCH, sea urchins; CCA, crustose calcareous algae; ZOAN, Zoantharia; EAM, epilithic algal matrix; MALG, macroalgae; ROCK, rock; SAND, sand

Microhabitat	Coefficient	Lower	Upper
CCA	0.64	-0.16	1.45
URCH	-2.08	-4.09	-0.06
ZOAN	1.29	0.37	2.2
SAND	0.74	-0.04	1.52
EAM	1.15	0.66	1.62
ROCK	-0.31	-2.31	1.70
MALG: sp *P. pilicornis*	-0.49	-1.15	0.16
CCA: sp *P. pilicornis*	1.15	0.36	1.94
URCH: sp *P. pilicornis*	0.69	-1.70	-3.09
ZOAN: sp *P. pilicornis*	-1.09	-2.70	0.51
SAND: sp *P. pilicornis*	-0.40	-1.44	-0.63
EAM: sp *P. pilicornis*	-0.29	-0.66	-0.07
ROCK: sp *P. pilicornis*	0.00	-2.77	2.77

3 CONCLUSÃO GERAL

Neste estudo, demonstramos que *Parablennius pilicornis* e *P. marmoreus* têm uma alta sobreposição de nicho ecológico quando em simpatria. Eles não demonstraram diferenciação clara de nicho térmico, espacial e trófico, apresentaram dieta onívora semelhante e pouca diferenciação no uso do habitat. Esses resultados sugerem que este par de espécies está coexistindo com sucesso, apesar da considerável sobreposição de nicho. Assim, a coexistência de espécies dentro desta linhagem pode não depender da evolução de padrões divergentes de uso de recursos, mas da história evolutiva das espécies.

Nossos resultados sugerem que o cenário 1 proposto (conservatismo filogenético do nicho ecológico) é bem estabelecido entre as duas espécies de *Parablennius*. Considerando esse conceito, linhagens filogeneticamente próximas têm uma tendência a reter suas características ecológicas ancestrais (e nichos) ao longo do tempo (PETERSON, 1999). Como os congêneres *P. pilicornis* e *P. marmoreus* compartilham uma história evolutiva recente, eles são propensos a apresentar padrões de uso de recursos semelhantes, consequentemente apresentando alta sobreposição de nicho (PIANKA et al., 2017). O grupo *Parablennius* provavelmente divergiu no centro de diversificação deste gênero, na Macaronésia (LEVY et al., 2013). Enquanto *P. pilicornis* ocupou o Atlântico Nordeste, *P. marmoreus* ocupou o Atlântico Noroeste (LEVY et al., 2013). Pelo fato de viverem em alopatria, as espécies não divergiram em suas características morfológicas ou ecológicas na época (BOWEN et al., 2001; SANTOS et al., 2006), portanto, ambas as espécies carregaram seus atributos conservando seus nichos ecológicos. Ambas as espécies de *Parablennius* foram geograficamente reunidas no Atlântico Sudoeste (Sul e Sudeste do Brasil), nossa área de estudo, e coexistem aqui há pelo menos 400 mil anos (DIAS, 2019).

Os altos valores de sobreposição de nicho encontrados entre as espécies em Santa Catarina podem ser possivelmente explicados pela ausência de forças locais para separá-los ecologicamente, após seu contato secundário no Atlântico Sudeste. Esta região apresenta baixa riqueza de espécies e alta produtividade primária (SEGAL et al., 2017), características que podem fornecer oportunidades ecológicas para as espécies se estabelecerem com mínima ou nenhuma competição (WELLBORN; LANGERHANS, 2015). Isso implica que os efeitos dos processos locais são mínimos, não justificando a ocorrência do cenário 2 proposto (partição de nicho ecológico) (AHMADIA et al., 2018).

Além disso, características das espécies podem influenciar a possível falta de competição, como seu hábito alimentar. Ambas as espécies apresentam dieta diversificada composta por itens de vários grupos biológicos, que vão desde algas até peixes. O fato de ambas as espécies de *Parablennius* consumirem uma grande variedade de recursos alimentares de forma generalista e oportunista pode reduzir fortemente o potencial de competição e, portanto, aumentar a sobreposição de nicho trófico (SCHOENER, 1971). Isso sugere uma ausência de competição interespecífica prevalente por recursos alimentares limitados em Santa Catarina. É importante considerar que a detecção da sobreposição de nicho entre as espécies pode diminuir à medida que a resolução da análise do conteúdo estomacal aumenta (BRANDL et al., 2020). Ainda assim, os custos significativamente altos associados a uma abordagem molecular, como metabarcoding do conteúdo estomacal, geralmente dificultam essa prática (BRANDL et al., 2020).

Outro fator que pode afetar a dinâmica populacional dos peixes e reduzir a competição é a pressão de predação (SHPIGEL, 1982; HIXON; JONES, 2005). Os peixes são grandes predadores de outros peixes em ecossistemas marinhos, particularmente das classes de tamanho menor (BAX, 1998). Peixes da família Blenniidae apresentam rápido crescimento e são altamente predados em sistemas recifais, sendo responsáveis por quase 60% da biomassa de peixes recifais consumidos (BRANDL, 2019). Esta alta taxa de mortalidade pode causar uma regulação natural das populações por predação (HIXON; JONES, 2005).

Apenas alguns estudos sobre peixes criptobênticos integraram informações tróficas e espaciais para examinar a interação entre elas (BRANDL et al., 2020). Além disso, ecólogos geralmente não incorporam o conhecimento da biogeografia histórica, mesmo quando é crucial para abordar algumas de suas questões centrais (WIENS; DONOHGUE, 2004). Esta integração oferece uma linha de inferência sobre a dinâmica eco-evolutiva das espécies (WIENS; DONOHGUE, 2004). Aqui, nós analisamos aspectos ecológicos das espécies e relacionamos seus nichos ecológicos à história evolutiva e biogeografia, apresentando o caso de duas espécies de peixes recifais sintópicos exibindo alta sobreposição de nicho e conservatismo de nicho bem definido. Esse conhecimento pode oferecer uma perspectiva única sobre conceitos ecológicos clássicos, como o conservatismo de nicho, e também sobre fatores que estão estruturando as assembleias recifais criptobênticas.

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