

Population expansion of the invasive Pomacentridae *Chromis limbata* (Valenciennes, 1833) in southern Brazilian coast: long-term monitoring, fundamental niche availability and new records

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Abstract

Human-mediated species invasions are recognized as a leading cause of global biotic homogenization and extinction. Studies on colonization events since early stages, establishment of new populations and range extension are scarce because of their rarity, difficult detection and monitoring. *Chromis limbata* is a reef-associated and non-migratory marine fish from the family Pomacentridae found in depths ranging between 3 and 45 m. The original distribution of the species encompassed exclusively the eastern Atlantic, including the Azores, Madeira and the Canary Islands. It is also commonly reported from West Africa between Senegal and Pointe Noire, Congo. In 2008, vagrant individuals of *C. limbata* were recorded off the east coast of Santa Catarina Island, South Brazil ($27^{\circ} 41' 44''$ S, $48^{\circ} 27' 53''$ W). This study evaluated the increasing densities of *C. limbata* populations in Santa Catarina State shoreline. Two recent expansions, northwards to São Paulo State and southwards to Rio Grande do Sul State, are discussed, and a niche model of maximum entropy (MaxEnt) was performed to evaluate suitable *C. limbata* habitats. Brazilian populations are established and significantly increasing in most sites where the species has been detected. The distributional boundaries predicted by the model are clearly wider than their known range of occurrence, evidencing environmental suitability in both hemispheres from areas where the species still does not occur. Ecological processes such as competition, predation and specially habitat selectivity may regulate their populations and

overall distribution range. A long-term monitoring programme and population genetics studies are necessary for a better understanding of this invasion and its consequences to natural communities.

KEY WORDS

alien species, biological invasions, damselfishes, maximum entropy niche model, southwestern Atlantic

1 | INTRODUCTION

Human-mediated climate change is the main cause of irreversible changes in marine ecosystems, such as ocean warming and acidification, biodiversity loss, declines and distributional shifts in marine species populations (Booth *et al.*, 2017; Pecl *et al.*, 2017). Biological invasions mediated by anthropic activities are recognized as a leading cause of global biotic homogenization and extinction (Bailey *et al.*, 2011). Such phenomena, alongside factors such as habitat loss and overexploitation of natural resources, have been acting synergically as drivers of worldwide biodiversity loss (Butchart *et al.*, 2010). Therefore, much attention has been paid to a better understanding of processes and the mechanisms involved in each stage of human-mediated invasions (*i.e.*, transport, colonization, establishment and control) (Anderson *et al.*, 2017; Carlton, 1996).

In the Hawaiian Islands, from 1955 to 1961, 11 grouper, snapper and emperor fish species were intentionally released by the Hawaii Division of Fish and Game to enhance Hawaiian shallow-water game and food fisheries (Johnston & Purkis, 2016). Within 15 years, three of the introduced species established populations, whereas eight did not. Two species, *Lutjanus kasmira* (Forsskål, 1775) and *Cephalopholis argus* Schneider, 1801, are now considered invasive (Johnston & Purkis, 2016).

There are now over 1000 alien species inhabiting the Mediterranean Sea, and most of them are thermophilic (*i.e.*, can have their populations increased and established or have their distributional range increased by global warming) that have entered the eastern basin through the Suez Canal (Katsanevakis *et al.*, 2014; Kletou *et al.*, 2016). According to Kletou *et al.* (2016), Lessepsian invasions are increasing rapidly, and *ca.* 130 species of marine fish are now inhabiting the Mediterranean. For example, the blue spotted cornetfish *Fistularia commersonii* Rüppell, 1838, colonized nearly the entire Mediterranean in just 7 years, threatening over 41 taxa of native fish species (Kletou *et al.*, 2016). Another example is the pufferfish *Lagocephalus sceleratus* (Gmelin, 1789) which preys upon Mediterranean commercially important cephalopod species and is now classed as a fisheries pest (Kletou *et al.*, 2016). Despite all efforts to access, understand and control ecological invasion processes, studies about colonization events since early stages are scarce because of their difficult detection and complex and expensive monitoring (Anderson *et al.*, 2017).

The Azores chromis *Chromis limbata* (Valenciennes, 1833) is a marine reef-associated and non-migratory Pomacentrid fish, inhabiting rocky reefs at depths ranging from 3 to 45 m (Allen, 1991; Anderson *et al.*, 2017; Brito *et al.*, 2002). Its original distribution encompasses the eastern Atlantic, including the Azores, Madeira and Canary Islands, and West Africa between Senegal and Pointe Noire, Congo (Allen, 1991; Anderson *et al.*, 2017; Edwards, 1986) (Figure 1). Adults inhabit rocky reefs and sand-weed bottoms (Allen, 1991; Anderson *et al.*, 2017). They are oviparous and have distinct pairing during breeding. After spawning, their eggs adhere to the substrate where parental care by males includes vigilance and aeration (Anderson *et al.*, 2017; Breder & Rosen, 1966). During summer, nesting males defend territories and take care of the demersal eggs (Mapstone & Wood, 1975). *Chromis chromis* (Linnaeus, 1758), the most likely sister species of *C. limbata* (Edwards, 1986; Wood, 1977), after a pelagic larval phase of 18–19 days settles on adult grounds (Anderson *et al.*, 2017; Domingues *et al.*, 2006; Raventós & Macpherson, 2001). Immature specimens of *C. limbata* are more uniformly brownish, with silvery shining longitudinal bands. Juveniles and adults prey upon zooplankton (Allen, 1991; Anderson *et al.*, 2017). Wirtz (2012) observed *C. limbata* forming large plankton-feeding aggregations of more than 100 individuals and males defending rocky reef spawning areas in places deeper than 10 m.

Brazilian reef fishes have been studied and monitored by local marine scientists since the end of the past century (Floeter *et al.*, 2001; Moura *et al.*, 1999). In 2008, vagrant individuals of *C. limbata* were observed at Campeche Island, located 1.5 km on the east coast of Santa Catarina Island, southern Brazil (27° 41' 44" S, 48° 27' 53" W) (Leite *et al.*, 2009). Since then, Santa Catarina's populations of *C. limbata* have colonized most islands and islets in the vicinities of Santa Catarina Island (Florianópolis), with densities significantly increasing (Anderson *et al.*, 2017). Also, in 2008, vagrant individuals of *C. limbata* were reported in the vicinities of São Sebastião Island, São Paulo State, Brazil. After reports of recent new records from the São Sebastião Island, questions emerged among invasive species scientists: (a) Have the populations reached a growth asymptote (carrying capacity), or are they themselves fluctuating? (b) Are there more niches available for *C. limbata* along the Brazilian coast and elsewhere?

This study evaluated the increasing densities of *C. limbata* populations in Santa Catarina State. A niche model of maximum

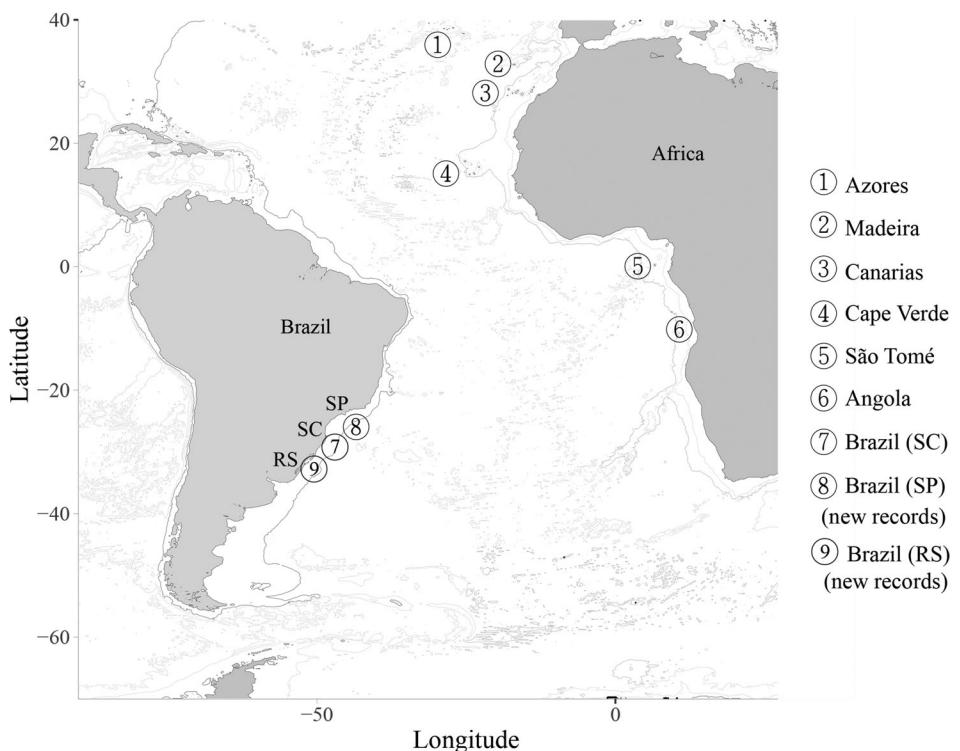


FIGURE 1 Map of *Chromis limbata*'s distribution in 2018. The monitoring of Brazilian established populations in time was conducted in Santa Catarina State (7); monitoring of range extensions (new records) was conducted in São Paulo State (8)

- ① Azores
- ② Madeira
- ③ Canarias
- ④ Cape Verde
- ⑤ São Tomé
- ⑥ Angola
- ⑦ Brazil (SC)
- ⑧ Brazil (SP)
(new records)
- ⑨ Brazil (RS)
(new records)

entropy (MaxEnt) was developed to evaluate habitat suitability for *C. limbata* along the southwest Atlantic coast (Verbruggen et al., 2009), and recent new records of the species from São Paulo State were discussed. For a better understanding of such invasion effects on local reef fish communities, a long-term monitoring programme is urgent.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out on the coasts of three Brazilian states: Santa Catarina (long-term monitoring), São Paulo and Rio Grande do Sul (new records). The monitoring of the expansion of the established population of *C. limbata*, from 2010 to 2019, was conducted in subtropical reefs at Florianópolis, Santa Catarina ($27^{\circ} 35' 41.08''$ S, $48^{\circ} 32' 38.96''$ W). The geomorphology of these rocky reefs is characterized, in its major portion, by steep granitic rocky reefs ending in 12–15 m deep sandy bottoms. The water visibility annual average is 4 m. The temperature range is between 10°C during the harsh austral winters and 28°C in summer. These rocky reefs are regarded as the southernmost limit of distribution of tropical reef fish species that inhabit the tropical northern portion of the Brazilian coast (Anderson et al., 2014, 2015, 2017, 2019). Five islets were selected for sampling because of their logistic accessibility (e.g., distance from the shore and confirmed *C. limbata*'s established populations) (Anderson et al., 2017): Arvoredo, Deserta, Galé, Aranhas and Xavier.

New records and range extension of *C. limbata* to the state of São Paulo are now confirmed from Cabras Island, located in the vicinities of São Sebastião Channel ($23^{\circ} 49' 50''$ S, $45^{\circ} 23' 36''$ W). New records and range expansion towards the southern Brazilian coast are

now confirmed for the state of Rio Grande do Sul (Parcel de Torres – $29^{\circ} 42' 4.60''$ S, $48^{\circ} 28' 40.32''$ W) (Figure 1).

2.2 | Field data collection techniques (Santa Catarina State)

Underwater visual censuses (UVCs) [20×2 m (40 m^2)] were used to quantify fish density along Santa Catarina State. For this methodology, a scuba diver swam 1 m above the substratum along 20 m, recording fish 1 m to each side of the transect (Anderson et al., 2017). During the transects, the diver also sexed the fish according to their colour patterns; females were yellow [ca. 13 cm TL (total length)] (Figure 5a–c), and males were grey blue (young males) to a strong cobalt blue while defending the nest (ca. 15 cm TL) (Figure 5d). The present work is based on 9 years of UVCs conducted by the authors and the database of the Marine Macroecology and Biogeography Laboratory. In total, over 1000 UVCs from 2010 to 2019 were conducted, and then a cut-off of 30 UVCs per site per year was selected for analyses. Samples were collected in the shallow part of the reef ranging from 5 to 14 m depth. All samples were obtained in the same sites, in the mornings during the austral summers (e.g., from early December to March) (Anderson et al., 2015, 2017, 2019).

2.3 | New records

Observations in São Paulo State occurred inside the Marine Protected Area of Cabras Island Monitoring Programme, project ECOPERE-SE (Reef Fish Ecology from Southwestern Brazilian Coast), implemented

FIGURE 2 (a) Santa Catarina's population variations from 2010 to 2019. Circles represent the number of individuals detected. Different colours represent different sizes (ontogenetic stages) of individuals. Asterisks indicate significance [generalized linear model (GLM)]. *Chromis limbata* illustration by JPB *imagDOP*. (b) Light green circles represent the total density of *C. limbata* per year. The dashed red line represents the total 9 years' mean density. Asterisks represent the GLM significance $\text{Pr}(>|t|) < 0.05$, and letters represent the Tukey post hoc contrasts test. (c) Purple circles represent the total density per year of recruits (individual ≤ 5 cm TL). The dashed red line represents the total 9 years' mean density. Black dots represent the GLM significance $\text{Pr}(>|t|) = 0.07$ (not significant)

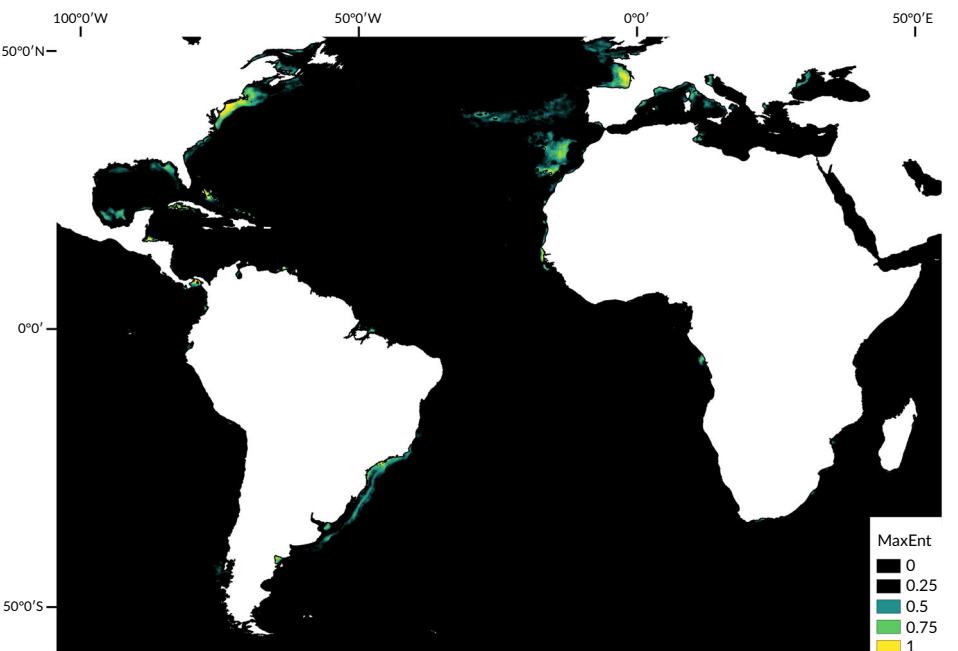
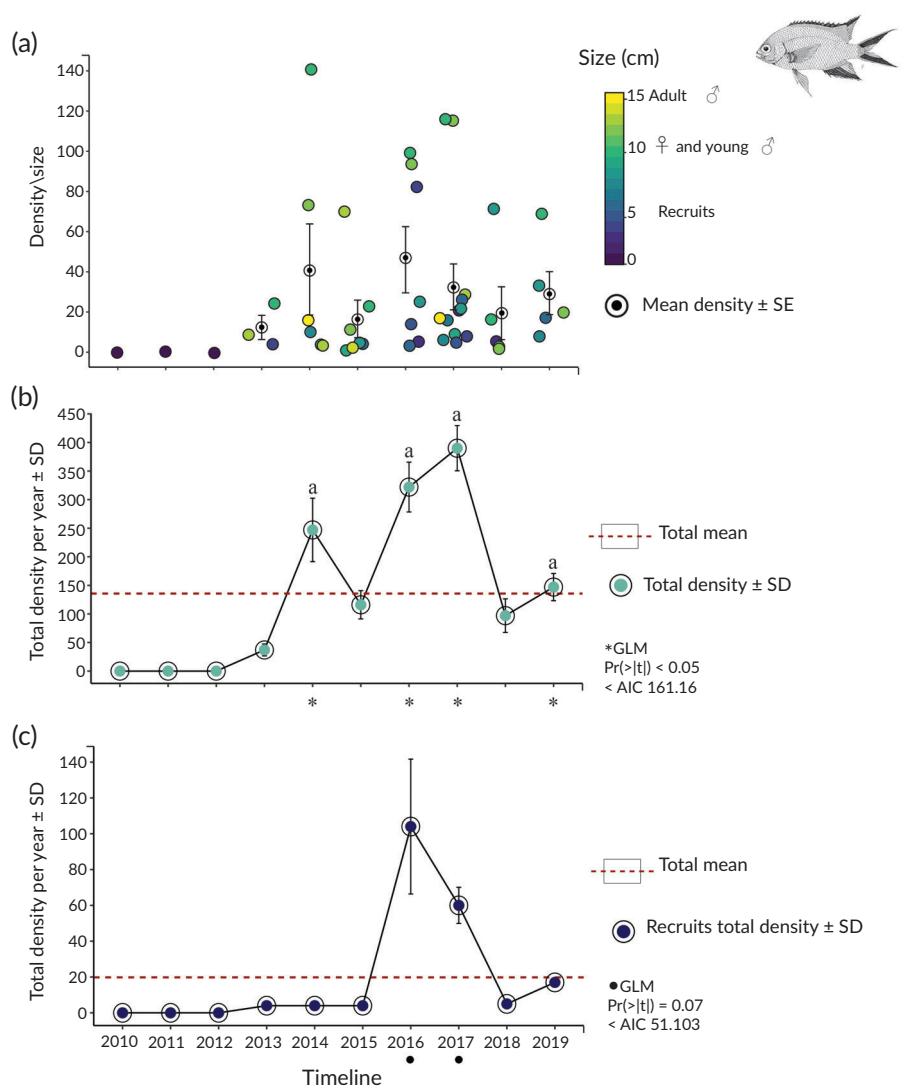


FIGURE 3 Maximum entropy niche model (MaxEnt). Representative model map of maximum entropy for *Chromis limbata*. Warmer colours indicate better predicted conditions

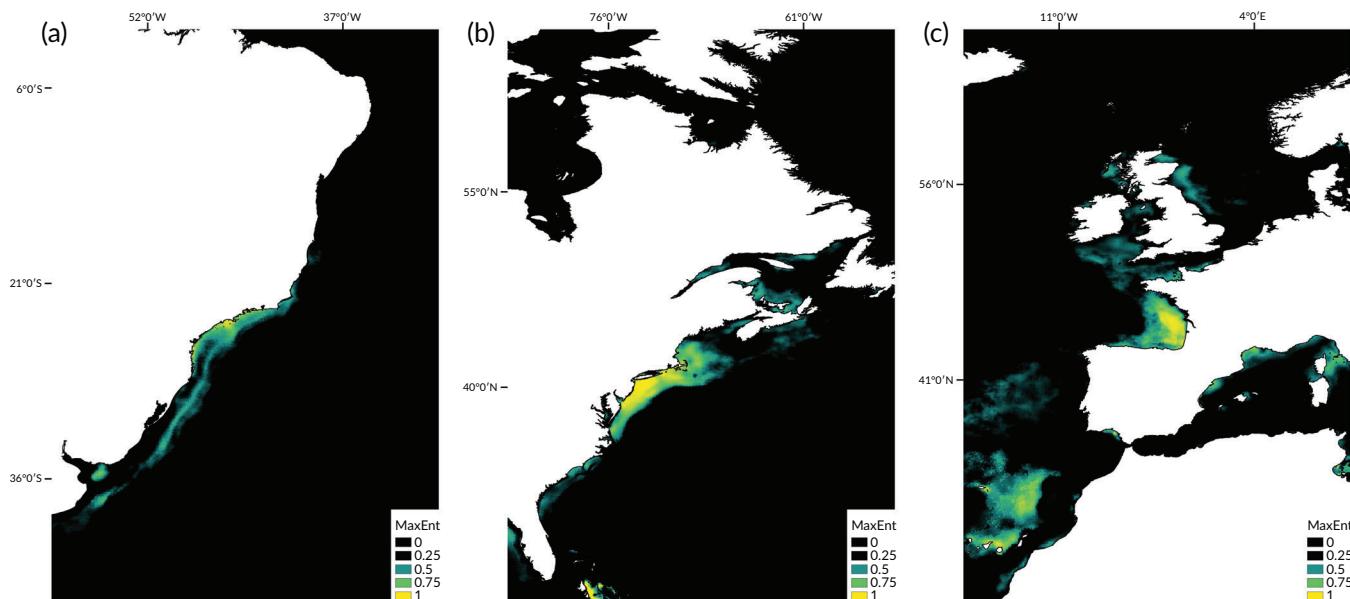


FIGURE 4 Maximum Entropy Niche model (MaxEnt): a) *C. limbata* suitable habitats for the Brazilian coast; b) suitable habitats for the Northwestern Atlantic coast; c) suitable habitats for the Northeastern Atlantic coast

in January 2005. The Monitoring Programme comprised monthly sampling periods, including diurnal and nocturnal scuba dives (depth range: 4–13 m) and freediving (depth range: surface to 3 m), surrounding Cabras Island, to record all rocky reef fish species. The dives' average time was 60 min for scuba and 40 min for freediving. Photographs of *C. limbata* were taken using a point-and-shoot camera (Canon G9) in Ikelite housing and two Sea & Sea Strobes YS-110.

Photos were taken in macro mode as close to the fish as possible and recorded in RAW and JPEG file modes. In every photographic record, the diver took notes of the fish size. As a measure of reference and to avoid distortions in the assessment, the diver positioned a 5 cm ruler on the substrate close to the site occupied by the fish. Images were analysed after edition using free software Image J 1.49 (<http://imagej.nih.gov/ij/>) to obtain meristic data and measurements to confirm the fish identification followed (Canestrini, 1872; Froese & Pauly, 2019).

In December 2016 one vagrant individual of *C. limbata* was detected and photographed in Queimada Grande Island, also in São Paulo State ($24^{\circ} 29' 14.55''$ S, $46^{\circ} 40' 36.76''$ W), by L. Francine. New records from Rio Grande do Sul State were collected from recreational divers' videos posted online. Those were recorded on 4 March 2017 at the Parcel de Torres – a rocky outcrop located 20–25 km offshore ($29^{\circ} 42' 4.60''$ S, $48^{\circ} 28' 40.32''$ W), at depths ranging from 22 to 30 m (video https://www.youtube.com/watch?v=uZoNhCf_iNE&t=386s).

2.4 | Data analyses

2.4.1 | Population expansion in Santa Catarina

Generalized linear models (GLM) were used to evaluate the effect of time on *C. limbata*'s densities in Santa Catarina State. Individuals'

densities were used as a dependent variable and time (year) as an independent variable according to Chatfield (1989) and Rencher and Schaalje (2008). For significant differences, Tukey contrasts were used to analyse variations between years. Tukey post hoc test contrasts were performed using the "multicomp" R packages (Hothorn et al., 2016), "lsmeans" (Lenth & Lenth, 2018) and "multicompView" (Graves et al., 2015). Assumptions of normality and homoscedasticity were assessed using Kolmogorov-Smirnov/Lilliefors and Bartlett's tests. Data were log transformed ($\log(X + 1)$) to meet the assumptions of normality (Snedecor & Cochran, 1989; Underwood, 1981; Zar, 1999). The analysis was performed in R environment (R Core Team 2019).

2.4.2 | Niche modelling procedures

Macroecological niches of *C. limbata* were modelled using the MaxEnt – a machine learning algorithm (R package dismo v1.1–4) which consists of a technique based on the principle of maximum entropy – using species' presence data as proposed by Phillips and Dudík (2008). This algorithm has been tested worldwide in several studies and is considered an adequate tool to be used in such contexts (see Elith & Leathwick, 2009; Hernandez et al., 2006; Phillips & Dudík, 2008). Only accurate data (i.e., published papers) collected in literature regarding occurrence of species were applied to elaborate the model (Verbruggen et al., 2009) (Appendices 1 and 2).

2.4.3 | Presence data and environmental variables

A total of 708 georeferenced occurrences were used to model *C. limbata* niche availability. Occurrence records were obtained from scientific journal articles (Appendix 2). For later use in the modelling procedures, the

background (i.e., "pseudo-occurrences") was generated with respect to a circumference of 500 km around the occurrence records as proposed by Elith et al. (2011). To avoid spatial autocorrelation, occurrences located <1 km apart were randomly selected and removed, as well as duplicate entries.

The data set of environmental variables (global scale) (see Appendix 3) was used to generate the model and was downloaded from Bio-Oracle data set (Assis et al., 2018; Tyberghein et al., 2012). Predictive variables were selected considering relationships among *C. limbata*'s biology, ecology and collinearity between environmental variables (Assis et al., 2018; Tyberghein et al., 2012).

The best-fit model was selected according to the following steps. (a) The multicollinearity test was conducted using Pearson's correlation coefficient (*R*) to examine the cross-correlation between environmental variables (Farashi & Naderi, 2017). (b) Variables with a cross-correlation coefficient value >0.9 were excluded from further analysis (see Appendix 3) (Farashi & Naderi, 2017). (c) GLMs were used to test the significance of environmental variables (Appendix 4) and then to select the best-fitted model according to the AIC (i.e., the preferred model is the one with a minimum AIC value) (Appendix 4) (Akaike, 1998). (d) Such procedures resulted in a subset of 15 variables used as the best-fitted input for the model (Figure 4, Appendices 4 and 6). Both presence data and environmental variables were processed and analysed in R (R Development Core Team, 2019). (e) The performance of the models was measured using the area under the curve (AUC) (Philips & Dudík, 2008; Phillips et al., 2011; Verbrugge et al., 2009).

3 | RESULTS

3.1 | The invasive populations in Santa Catarina

A total of 780 strip transects were conducted during the austral summers (i.e., December to April) from 2010 to 2019, covering a

total area of 31,200 m² and corresponding to ca. 117 h of underwater observation. This work resulted in 10 years' monitoring of *C. limbata*'s populations in the coast of Santa Catarina, southern Brazil (Figure 2).

The invasive Pomacentrid populations in Santa Catarina vary significantly in time [GLM Pr(>|t|) < 0.05] (Figure 2b; Appendix 5). Considering species' population structure in time, large schools of small individuals (e.g., ≤5 cm) were detected in 2016, 2017, 2018 and 2019. Despite the large numbers of recruits detected, no significant differences were found over time [GLM Pr(>|t|) = 0.07] (Figure 2c; Appendix 5). The number of adult female and young male feeding aggregations has increased since 2010 (Figure 2a). Large adult males' densities also increased along Santa Catarina coast in the same period (Figure 2a). Despite their populational significant variations in time (Figure 2b), no significant differences were detected among years (Figure 2b; Appendix 5).

3.2 | Fundamental niche availability model

The model predicts highly probable suitable habitats for *C. limbata* in the northwestern Atlantic to the coasts of New Jersey, Connecticut and Massachusetts (Figures 3 and 4), the southern Brazilian coast, from Espírito Santo State to Rio Grande dos Sul State and in the northeastern Atlantic to the coast of France (Figures 3 and 4). Among the 15 environmental predictors analysed, the most significant variables are related to primary productivity and oceanographic conditions (Table 1; Appendix 6). The models presented a good performance with an AUC value of 0.99. Results were closer to a perfect prediction, indicating that most essential environmental variables which determine species distributions were considered in the data set (Table 1; Appendix 6) (Verbrugge et al., 2009).

TABLE 1 Environmental variables used in the MaxEnt model and their contribution to the model predictions.

Environmental variables	Unit	Contribution (%)	Permutation importance
Diffuse attenuation mean	m ⁻¹	23.3	47.9
Dissolved oxygen mean	mol m ⁻³	22.2	0
Current velocity maximum	m ⁻¹	13	12.4
Primary productivity maximum	g m ⁻³ day ⁻¹	10.3	10.4
Current velocity minimum	m ⁻¹	8.2	9.4
Par maximum	E m ⁻² day ⁻¹	8.2	5.7
Cloud cover maximum	%	4.3	5.8
Par mean	E m ⁻² day ⁻¹	1.9	1.2
Temperature maximum	°C	1.8	0.9
Calcite mean	mol m ⁻³	1.7	0.8
Phosphate maximum	mol m ⁻³	1.5	0
Chlorophyll mean	mol m ⁻³	1.2	1
Phosphate minimum	mol m ⁻³	0.8	2.2
Silicate minimum	mol m ⁻³	0.8	0.2
Surface pH	-	0.8	2.1

Bold values are shown Variables with higher permutation importance.

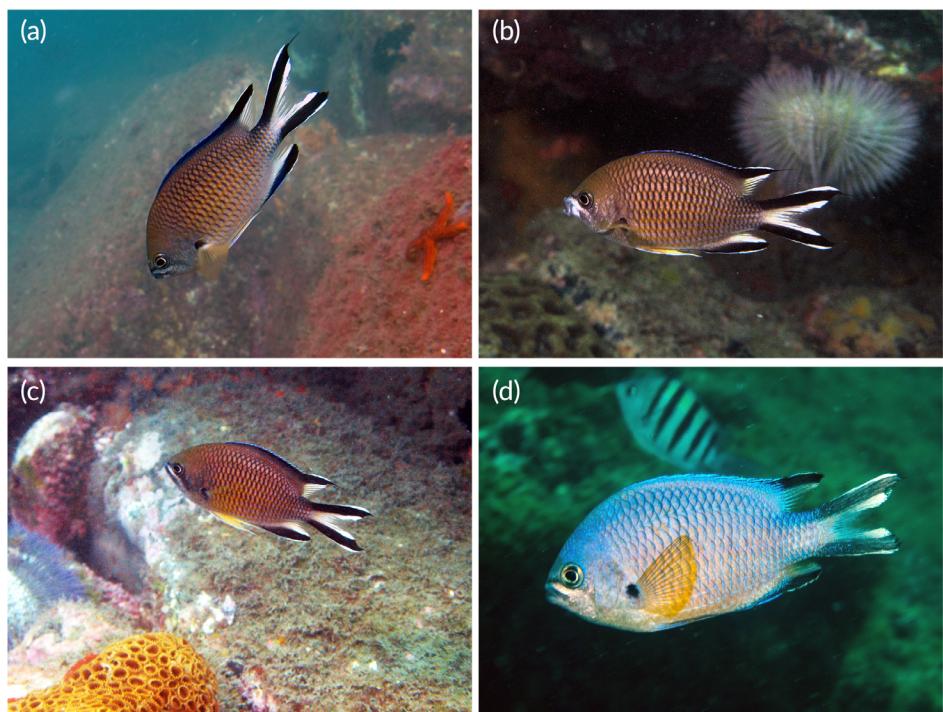


FIGURE 5 Pictures of *Chromis limbata* (♀) from (a) Santa Catarina State (image A. B. Anderson), (b and c) São Sebastião (Cabras Island) (♀), São Paulo State (images J. P. Silva) and (d) Queimada Grande Island (♂), São Paulo State (image L. Francini)

3.3 | Brazilian populations' range expansion (new records)

Vagrant individuals of *C. limbata* were recorded in the southeastern Brazilian coast from 2008 to 2019. During the Monitoring Programme of the Marine Protected Area of Cabras Island, four individuals of *C. limbata* were recorded. The site for all records was São Sebastião Channel, east coast of São Sebastião Island ($23^{\circ} 49' 50''$ S, $45^{\circ} 23' 36''$ W). Among these records, a vagrant individual of *C. limbata* [8–10 cm standard length (SL)] was repeatedly detected at the vicinity of Cabras Island every month from June 2008 to June 2009. In the same area, another fish, 12 cm, was recorded in January and April 2011. From March to May 2012, another individual, 10 cm, was recorded, and finally in May 2014 an 8 cm fish was monitored until July 2015, when it reached 10 cm (Figure 5). Since then, no further records have been reported from Cabras Island.

All encounters occurred in the same rocky-bottom area of ca. 20 m^2 . Individuals were usually observed feeding together with large aggregations of *Abudefduf saxatilis* (Linnaeus, 1758), and only in the last records *C. limbata* was detected feeding together with a single individual of its congener *Chromis multilineata* (Guichenot, 1853). The differences between the sizes and time of occurrence indicated the presence of more than one individual during the time of observations.

In December 2016 one adult male was photographed in Queimada Grande Island, São Paulo State coast, representing a new record and range extension of *C. limbata*'s populations for the Brazilian coast (Figure 5d). In February, 2017 a video was uploaded showing several individuals of *C. limbata* in the Parcel de Torres, Rio Grande do Sul State ($29^{\circ} 34.501'$ S, $048^{\circ} 07.567'$ W), extending the southernmost distribution limit of the invasive Pomacentridae and

corroborating the model predictions regarding the fundamental niche availability for southern Brazil (https://www.youtube.com/watch?v=uZoNhCf_INE). The video shows mature females, large males (blue individuals) and a small school of recruits, which suggests a growing population.

4 | DISCUSSION

4.1 | Santa Catarina's established populations and the "Arc of Capricorn" region influence

New populations of invasive marine fish species along the western Atlantic coast have been monitored with greater concern since the establishment of the Indo-Pacific lionfish species, *Pterois volitans* (Linnaeus, 1758) and *Pterois miles* (Bennett, 1828), along the Atlantic coast of the United States (Schofield, 2009). From 1999 to 2015 the species also colonized the Caribbean, extending their range to the southern Brazilian coast (Ferreira et al., 2015; Schofield, 2009). Experiments with intentional introductions of 11 marine predatory fish (e.g., grouper, snapper and emperor fish) were conducted in the Hawaiian Islands from 1955 to 1961 to produce new fishery resources (Johnston & Purkis, 2016). Within 15 years eight species' populations crashed, and three established self-sustained populations. Two species, *L. kasmira* (Forsskål, 1775) the common bluestripe snapper and *C. argus* (Schneider, 1801) the Peacock hind, are classified as invasive (Johnston & Purkis, 2016). In 2013 the Indo-West Pacific damselfish, known as Regal demoiselle *Neopomacentrus cyanomos* (Bleeker, 1856), was first recorded in the west Atlantic, when it was reported to be common on reefs near Coatzacoalcos, in the extreme southwest Gulf of Mexico corner (Robertson et al., 2016). From 2013 to 2015 the

species was observed on six nearshore reefs adjacent to Veracruz City, Veracruz, Mexico (Robertson et al., 2016). Robertson et al. (2016) also suggested that *N. cyanomos* may compete with native planktivorous damselfishes [e.g., the Brown chromis *C. multilineata* (Guichenot, 1853)] and have adverse effects on populations. This 10-year monitoring study of *C. limbata*'s populations in the southern Brazilian coast, compared to the works mentioned earlier, seems to follow the same invasive pattern of establishment and expansion. In a near future, *C. limbata* may represent a threat to local native damselfishes competing for resources such as food, shelter and nesting areas (Anderson et al., 2017).

The establishment of a new population will depend on abiotic (e.g., topography, temperature, nutrient availability) and biotic [e.g., initial colonizers (healthy propagules, larvae, adults), mating success, new mutations, elimination of deleterious alleles, repeated inflow of new genotypes, competition, predation] factors (Anderson et al., 2017; Kaňuch et al., 2014). The low genetic diversity detected in Santa Catarina's established populations compared to native populations from Macaronesia (Anderson et al., 2017) suggests a small larval pulse or the arrival of a small group of individuals.

Populations in Santa Catarina seem to be varying significantly (Figure 2). Blue males with large harems of females and large schools of small individuals (<5 cm) were detected in all studied sites from 2013 to 2019 (Figure 2a). This may well point to a healthy increasing population, with potential for spatial domination (e.g., higher density and biomass than local congener *C. multilineata* and other Pomacentrids such as *A. saxatilis*) in the near future (Anderson et al., 2017).

The southwestern Atlantic biogeographic ecotone is also known as the Arc of Capricorn (i.e., encompassing the states of Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul) and represents the southernmost limit of distribution for most tropical organisms (Anderson et al., 2015, 2017). Moreover, the region is considered a warm temperate biogeographic province (Bernardes et al., 2018; Horta et al., 2001). This part of the Brazilian coast, especially Santa Catarina State, presents seasonal patterns of temperate variations with a monthly average of $25.6 \pm 0.5^\circ\text{C}$ in winter and $27.0 \pm 0.9^\circ\text{C}$ in summer (Anderson et al., 2015, 2017; Bernardes et al., 2018). This seasonal pattern is determined by both warm tropical waters from the Brazilian Current (originating from the north and flowing southwards) and cool waters from the South Atlantic Central Water, flowing north. This mass of water intrudes on the shallow coastal shelf of this region, especially during the spring and summer northeastern winds, and features temperatures of $\leq 16^\circ\text{C}$ (Anderson et al., 2015; Bernardes et al., 2018). Such characteristics seem to work as an optimum habitat for *C. limbata* and may have influenced the establishment of a healthy population. Otherwise, further north along the coast of São Paulo State, with slightly warmer water masses, *C. limbata* was also detected, albeit in modest numbers (Anderson et al., 2017).

4.2 | Fundamental niche availability

The main predictors which have influenced the model were variables related to primary productivity, temperature, oceanographic and topographic conditions (Table 1). Therefore, the model reinforces the affinity of the species to areas with cooler waters and high primary

production (e.g., regions with upwelling) (Anderson et al., 2017). All main regions highlighted by the model have distinct oceanographic characteristics regarding temperature, currents, upwellings and resurgence phenomena, which directly affect primary productivity [e.g., the Gulf Stream in the northwestern Atlantic, the Iberian Poleward Current system in the northeastern Atlantic and the Brazil current in the southwestern Atlantic (Bernardes et al., 2018; Bukata et al., 2018; Peliz et al., 2005)].

Many northwestern and northeastern Atlantic sites do not present topographic conditions such as complex rocky coastlines with small archipelagos, islands or nearshore islets. Moreover, temperature seems to be a limiting factor for *C. limbata*'s dispersal. These abiotic and biotic factors – such as predations and competition – may explain why *C. limbata* does not occur, so far, in those regions.

Considering that the Brazilian populations of *C. limbata* (São Paulo and Santa Catarina States) have the same age (i.e., in both cases, first records were documented in 2008–2009), the low densities from São Paulo (warmer oceanic water masses) may emphasize that the larger Brazilian populations have affinities to colder, nutrient-rich and more productive waters, such as those in Santa Catarina's coasts, where upwelling is a constant phenomenon and primary productivity is higher when compared to northerner parts of the Brazilian coast (Anderson et al., 2017; Bernardes et al., 2018). Temperature may be a limiting factor to the expansion of *C. limbata* towards the northern Brazilian coast, considering the average sea surface temperature of such regions (Anderson et al., 2017; Matano et al., 2010; Olson et al., 1988). Otherwise, deeper and colder reefs (a depth of 50 m maximum) may represent a refuge and also work as "stepping stones" for *C. limbata*'s northward expansion (e.g., Vitória-Trindade Sea Mount Chain) (Pinheiro et al., 2017). Mediterranean and African populations of Chromis species have been recorded from 10 to 40 m depth (Bertонcini et al., 2010; Domingues et al., 2005; Domingues et al., 2007).

4.3 | São Paulo vagrant specimens and new record origins

Leite et al. (2009) described that all the encounters of *C. limbata* in Santa Catarina State occurred in the same rocky-bottom area of ca. 20 m^2 , suggesting a restricted occupation area based on specific substrate conditions and/or behavioural interactions (e.g., reproductive and feeding behaviours), which indicates site fidelity and small residential range. This study suggests that *C. limbata* may have similar territorial behaviours on Brazilian-colonized areas. The differences between sizes and time of occurrence of *C. limbata* indicate the presence of more than one individual during the observations. In this particular case, different sizes and record timing could be explained through recurrent introductions of *C. limbata* in the São Sebastião canal. It is possible to apply Williamson & Fritter's "rule of ten" (1996) for this. In other words, the probability of success of an introduction is very low, and most introductions fail to establish and spread. It has been suggested that only 1 out of every 10 introductions survives,

only one-tenth of these become established and spread and only a tenth of these become invasive (Williamson & Fitter, 1996).

Since 2008 *C. limbata* has been recorded in the vicinities of São Sebastião, São Paulo State, Brazil; the most recent one was from Queimada Grande Island, in December 2016. According to Leite et al. (2009), the first record of *C. limbata* in Santa Catarina occurred in that same year, which suggests that both records may have the same origin. Otherwise, recent records in São Paulo may well be a natural dispersal from Santa Catarina's established populations. The genetic study published by Anderson et al. (2017) concluded that Santa Catarina's populations do not share haplotypes with Macaronesian populations, which may imply that the source of both populations probably originated from western Africa. When considering species' morphology (Figure 5), specimens from São Paulo and Santa Catarina are remarkably similar. Nevertheless, no *C. limbata* have been found yet along the relatively small Paraná coastline. This is important for discussion because this state borders São Paulo (north) and Santa Catarina (south).

4.4 | The long-distance dispersal

Ocean currents can drift fish larvae to new destinations although distance is a prime factor in determining which species will prevail. Distance apparently acts as a natural filter and probably excludes species with short larval stages, such as damselfishes (Pomacentridae), and selects others with long larval lives such as surgeon fishes (Acanthuridae) (Luiz et al., 2004, 2012, 2015). Cowen et al. (2006) showed that typical larval dispersal distances for the wider Caribbean, providing ecologically significant numbers of settlers, were only on a scale of 50–100 km for most species with a relatively high rate of local retention or recruitment from adjacent locations. Recent invasion events to the Brazilian coast were related to a supposed flow of the superficial currents on the tropical Atlantic flowing westward from Africa to Brazil or via natural larval dispersal from the Caribbean towards the Brazilian coast (Anderson et al., 2015; Anderson et al., 2017; Ferreira et al., 2015; Leite et al., 2009; Luiz et al., 2004).

Semi-submersible oil rigs are notorious to transport entire communities of marine organisms through oceans (Anderson et al., 2017; Wanless et al., 2010). Recently, the presence of the Pomacentrids *Abudefduf hoeftleri* (Steindachner, 1881) and *A. saxatilis* in the Canaries has been attributed to oil rigs (Pajuelo et al., 2016). Damselfishes, especially within the genus *Abudefduf*, *Neopomacentrus* and *Chromis*, have been detected rafting in plastic debris, algae and flotsam (Luiz et al., 2015; Robertson et al., 2016), which led us to consider the "hitchhiker's hypothesis" as the most plausible (Anderson et al., 2017). Other records of invasive species can be interpreted in a different way, suggesting ballast water among the most important vectors of introduced species in the marine realm, with a high risk to coastal habitats (Ferreira et al., 2004a, 2004b, 2009, 2015; Lopes et al., 2009).

Because invasion mediated by ships is the main pathway of exotic species, it is evident that there is a need to monitor areas adjacent to harbours together with the application of rigorous

controls of ballast water. Despite the increasing rate in exotic species reports, Brazil does not have an effective control system for ballast water. NORMAM (Brazilian Navy Authority Rules/Directives) determines that ships exchange ballast water within an isobath of 200 m, to reduce the risk of spreading exotic species. Nonetheless, the control of any species present is not effective (de Paula Costa et al., 2011).

Considering the growth in the number of ship visits to Brazilian harbours (Wilmsmeier & Monios, 2016), the increase in their transit speeds and the possibility of ballast water to function as an incubator during the cruise for some planktonic species and the fact that *C. limbata* larvae and juveniles prey upon zooplankton (Bax et al., 2003; Gollasch et al., 2000), it is plausible to consider the hypothesis of shipping transport for *C. limbata* larvae to Brazil (Anderson et al., 2017). In contrast, there are no evidences of any Pomacentridae listed in samples collected directly from ship ballast waters (Williams et al., 1988; Wonham et al., 2000).

4.5 | The impacts in local communities

Considering the high level of primary productivity which occurred in the recently colonized areas, the invader *C. limbata* may not pose a threat to local planktivorous fish, regarding competitive behaviours towards food resource (Anderson et al., 2017). On the contrary, the aggressive behaviour of adult males during reproduction may pose a severe threat to their congeners, other Pomacentridae and species which have the same demersal reproductive behavioural patterns [e.g., *C. multilineata*, *Stegastes fuscus* (Cuvier, 1830), *A. saxatilis*, *Stegastes pictus* (Castelnau, 1855), *Stegastes variabilis* (Castelnau, 1855)] (Anderson et al., 2017; Laglbauer et al., 2017). Moreover, the aggressive reproductive behaviour of *C. limbata* adult males may cause detrimental effects on shelter availability for local fish. In rocky reef systems, shelter availability (e.g., holes and crevices) is a valuable resource to species which rely on the environment as protection against predation and parental care (Anderson et al., 2017, 2019). The need for behavioural studies in the invaded areas is urgent for a better understanding of patterns, such as reproductive seasonality, spawning characteristics and habitat use.

According to Pinnegar (2018), large populations of *C. chromis* play a fundamental role in the Mediterranean Sea by transferring nutrients from pelagic systems to the littoral in the form of solid and liquid wastes. In addition, *C. chromis* represents a major prey item for predators and mesoconsumers in Mediterranean food webs (Pinnegar, 2018). It is also considered a major consumer of fish eggs and therefore may have a strong influence on the dynamics of other fish species (Pinnegar, 2018). Therefore, the increasing numbers of the invasive *C. limbata* in southern Brazil may have, in a near future, the same effects of the system described by Pinnegar (2018), regarding the populations of its Atlanto-Mediterranean congener *C. chromis*. Long-term monitoring of such impacts is crucial for a better understanding of ecological impacts of invasive species in marine ecosystems.

5 | CONCLUSIONS

This study indicated that *C. limbata* populations in Santa Catarina State vary over time and are expanding in space, obeying the general patterns of invasive species. Specimens detected in São Paulo State in the early stages of the colonization (2008) may have the same origin as Santa Catarina's populations, and may also have originated the most recent records (2017). Despite the wide availability of fundamental niches for *C. limbata* worldwide, temperature seems to be a limiting factor for their dispersal. From all the dispersal hypotheses which could account for this invasion in south Brazil, the oil rig transportation and "hitchhikers" or rafting seem more plausible.

The present population of this invader in Brazilian waters and their eventual effects on native reef fish communities are still not possible to evaluate. The rocky reefs of southern Brazil are positioned in a biogeographic climatic transition zone, affected by several oceanographic and climatic phenomena (e.g., upwellings, current shifts, La Niña and El Niño southern oscillations, cold ocean water intrusions during the austral winters). Such climatic complexity affects local ichthyofauna population's density and biomass, which can underestimate the real effects of *C. limbata*'s invasion on local communities. A long-term monitoring programme (including genetic studies) of this invasion would be crucial to elucidate the drivers of such unique dispersal and evaluate *in situ* the impacts of a species invasion in a new environment.

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AUTHOR CONTRIBUTIONS

A.B.A. contributed the original idea and helped with data generation, data analysis, manuscript preparation and reviews; S.R.F., J.P.S. and J.P.S.B. contributed the original idea and helped with manuscript preparation, reviews and funding; R.S. and C.L.B.F. contributed to manuscript preparation.

CONFLICTS OF INTEREST

All authors declare that they have no conflict of interest.

ETHICAL APPROVAL

All applicable international, national and/or institutional guidelines for the care and use of animals were followed.

SAMPLING AND FIELD STUDIES

All necessary permits for sampling and observational field studies were obtained by the authors from competent authorities.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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