

An updated phylogeny of the redlip blenny genus *Ophioblennius*

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An updated molecular phylogeny of the blenny genus *Ophioblennius*, with a focus on two geographically disjunct morphotypes observed in Brazil, is presented. The analyses showed that specimens from the north-eastern Brazilian coast are the endemic redlip blenny *Ophioblennius trinitatis*, but specimens from the southern Brazilian coast are conspecific to an undescribed east Atlantic Ocean (Gulf of Guinea) species, previously unknown in Brazil. Possible explanations for this geographical pattern include: natural larval dispersal and rafting across the Atlantic; an unknown ecological attribute that enabled this species to colonize southern Brazil; oil platforms as introduction vectors.

KEYWORDS

Atlantic Ocean, Blenniidae, dispersal, marine biogeography, mtDNA, reef fish

The Atlantic redlip blennies, genus *Ophioblennius* Gill 1860, were originally considered a single reef-fish species with two subspecies, *Ophioblennius atlanticus atlanticus* (Valenciennes in Cuvier & Valenciennes 1836) and *Ophioblennius atlanticus macclurei* (Silvester 1915) (Springer, 1962). They have since been divided into five species (Muss *et al.*, 2001; Patzner *et al.*, 2009; Rangel & Mendes, 2009): *Ophioblennius atlanticus* (Valenciennes 1836) in Lusitania (Azores, Madeira and Canaries) and Cape Verde, *Ophioblennius macclurei* (Silvester 1915) in the Caribbean, *Ophioblennius trinitatis* Miranda Ribeiro 1919 in the Brazilian Province and two species yet to be described, one in the Gulf of Guinea (São Tomé and Príncipe) in the Tropical east Atlantic Ocean (TEA) and one in the Mid-Atlantic islands of Ascension and St. Helena. In Brazil, *Ophioblennius* populations occur from the north-east (including oceanic islands) to the south of Santa Catarina state (Anderson *et al.*, 2015), with a gap between Bahia and the north of Santa Catarina, where only a few stray individuals have been reported (Moura *et al.*, 1999).

The life history of *Ophioblennius* includes benthic eggs that hatch after 5 days (Marraro & Nursall, 1983; Muss *et al.*, 2001; Robertson *et al.*, 1990) and a planktonic larval phase of c. 50 days (Labelle & Nursall, 1992). Individuals of *Ophioblennius* in Brazil appear to be polymorphic, with two distinct morphotypes observed (Mendes, 2007). Adults in the north-east and oceanic islands normally reach a maximum

total length (L_T) of 4 to 10 cm (up to 15 cm in Bahia) and are lightly coloured, while adults in the south (Santa Catarina) reach L_T of 10 to 20 cm and are black in colour, with white stripes on the head and red mouths. Despite these marked differences, it is still unclear whether these populations are genetically distinct. To evaluate the genetic distinctiveness of *Ophioblennius* populations along the Brazilian coast, phylogenetic analyses of *Ophioblennius* were conducted throughout the Atlantic Ocean, with an emphasis on the two disjunct populations in Brazil.

Muscle tissue samples were collected by removing the right pectoral fin of *Ophioblennius* individuals collected from five locations: the Archipelago of Fernando de Noronha and the states of Bahia and Santa Catarina in Brazil, as well as Ascension Island in the Mid-Atlantic and São Tomé Island. Tissue samples were stored in 96% ethanol. For each tissue (individual), DNA was extracted using a Qiagen DNeasy Blood & Tissue kit (www.qiagen.com) and amplified using PCR procedures. An 820 bp segment of mtDNA cytochrome *b* (*cytb*) was amplified with two primers: a heavy-strand primer (5'-GTGATCTGAA AAACCACCGTTG-3'; Song, 1994) and a light-strand primer (5'-AATA GGAAGTATCATTGCGGTTTGATG-3'; Taberlet *et al.*, 1992). PCR amplifications were modified from Muss *et al.* (2001) and included an initial denaturing step at 94°C for 120 s, followed by 35 to

40 amplification cycles (94°C for 42 s, 54°C for 30 s, 72°C for 55 s) and a final extension at 72°C for 30 s.

DNA sequences were edited using Sequencher 5.4.1 and aligned using ClustalX with *Ophioblennius cytb* sequences previously generated by Muss *et al.* (2001) for the tropical eastern Pacific Ocean, Caribbean, Oceanic Islands in the Atlantic Ocean and north-eastern Brazil. A maximum likelihood phylogenetic tree was inferred using PhyML (Guindon *et al.* 2010). Node support was evaluated using 1000 non-parametric bootstrap pseudoreplicates. The nucleotide substitution model used, estimated using the Akaike information criterion (AIC) in jModelTest 2.1.10 (Darriba *et al.*, 2012; Guindon & Gascuel, 2003), was GTR + γ + I. Following Muss *et al.* (2001). The tree was rooted using the east Pacific species *O. steindachneri* as an outgroup for the Atlantic lineages.

A total of 149 *Ophioblennius* sequences were analyzed after the addition of three sequences from Fernando de Noronha, two from Bahia, four from Santa Catarina, one from Ascension and one from São Tomé generated in this study. The latter sequences were trimmed to the same length (630 bp) used by Muss *et al.* (2001), with the exception of three shorter sequences. GenBank accession numbers: MF990190 to MF990200.

The phylogenetic analysis of *Ophioblennius* in the Brazilian province revealed that the north-eastern Brazilian coast (Hump of Brazil and Bahia) plus the oceanic islands of St. Paul's Rocks, Fernando de Noronha and Trindade constitute a monophyletic group (*O. trinitatis*) while the Santa Catarina (Southern Brazil) population is conspecific to an undescribed *Ophioblennius* species from São Tomé and Príncipe

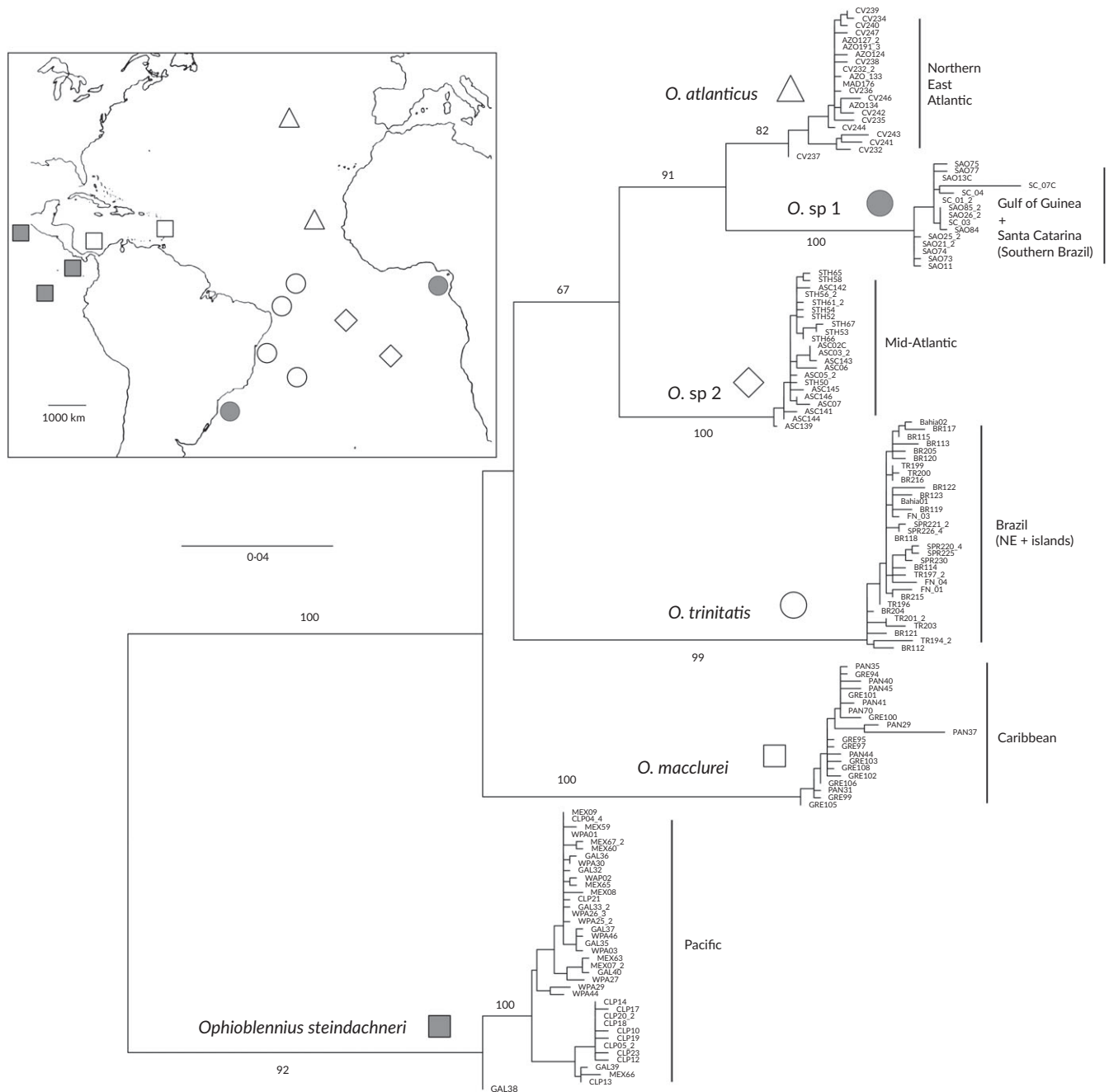


FIGURE 1 Maximum likelihood tree of *Ophioblennius* mtDNA cytochrome *b* lineages (nodes with >70% bootstrap support are indicated) and a map showing the distribution of common genetic linkages

(Figure 1). An 11% sequence divergence was observed between the Santa Catarina population and the northeastern *O. trinitatis* clade.

This study is the first to show that Brazilian populations of *Ophioblennius*, which were previously believed to be a single species (*O. trinitatis*; Rangel & Mendes, 2009) that was widely distributed from north-eastern to southern Brazil and the Brazilian oceanic islands, are in fact two distinct species. The species *O. trinitatis* occurs in north-eastern Brazil (Bahia as the southern limit) and the Brazilian oceanic islands, while the species that occurs in Santa Catarina, southern Brazil, is the same undescribed species that occurs in São Tomé and Príncipe in the Gulf of Guinea, Africa.

There is a range of possible non-mutually exclusive explanations for the occurrence of the same *Ophioblennius* species in southern Brazil and in the Gulf of Guinea, Africa. These include natural larval dispersal and rafting across the Atlantic: *Ophioblennius* larvae have a planktonic phase of approximately 50 days (Labelle & Nursall, 1992; Muss *et al.*, 2001), which would allow them sufficient time to traverse the Atlantic. *Ophioblennius* larvae are probably endowed with enough thermal tolerance to survive the cold current (20°C) between Africa and Brazil, a distance which could be traversed in 35–105 days (Scheltema, 1971) or even 43–70 days (Chesher, 1966), theoretically within the larval duration range of the genus. In this scenario, the dispersal would have originated south of the Gulf of Guinea, e.g. between Gabon and Angola, via the South Equatorial Current or the Benguela Current and could have ended up in southern Brazil with the aid of the southward Brazilian Current. The very small geographic range in southern Brazil compared with the range in the Eastern Atlantic reinforces the Eastern to Western direction of colonization. A second possibility is that some unknown ecological attribute (or a generalist behaviour) could have enabled this species to colonize southern Brazil but not the north-eastern coast of Brazil, where this lineage would have to co-occur with a congener. Thirdly, the movement of oil platforms from place to place could have served as introduction vectors (Falcón *et al.*, 2015; Pajuelo *et al.*, 2016). Although *Ophioblennius* is present among oil platforms off Gabon (Friedlander *et al.*, 2014), the movement of oil platforms in Southern Brazil is very low compared with other parts of Brazil.

The fact that the Mid-Atlantic islands' species is not found in Brazil despite its closer proximity compared with the Gulf of Guinea can be explained by a lower larval output of the small resident populations in the two Mid-Atlantic islands, compared with much larger populations in the TEA. Moreover, the coastal environment of south Brazil is very different from the oligotrophic marine environment around the Mid-Atlantic islands, which could pose another hurdle to establishment.

Putative examples of colonisations of the Brazilian coast from the relatively depauperate eastern Atlantic Ocean are accumulating (Luiz *et al.*, 2004; Anderson *et al.*, 2017). The recent arrival and establishment of the eastern Atlantic damselfish, the Azores chromis *Chromis limbata* (Valenciennes 1833), in southern Brazil supports the hypothesis of natural dispersal and indicates that colonization of southern Brazil from the TEA may be more common than previously thought (Anderson *et al.*, 2017).

This study confirms that the genus *Ophioblennius* is diversified in the Atlantic Ocean (Muss *et al.*, 2001) and provides evidence that

there is no connectivity between the north-eastern and southern populations of this genus in Brazil. Moreover, we confirm that southern Brazilian populations and an undescribed Gulf of Guinea species are conspecific. A thorough description of this undescribed species is required.

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