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Plicopurpura patula and *Monoplex parthenopeus* (Gastropoda: Caenogastropoda): New evidence of the tropicalization of the Bay of Biscay (NE Atlantic)

Ricardo López-Alonso^{a, c}, Omar Sánchez^a, Esteban Pascual-Parra^a, Yaisel J. Borrell^b, Javier Martínez-Pérez^d, Andrés Arias^{a,*}

^a Department of Organisms and Systems Biology (Zoology), University of Oviedo, Oviedo 33071, Spain

^b Department of Functional Biology, University of Oviedo, Oviedo 33007, Spain

^c Regional Service for Agri-Food Research and Development (SERIDA), Animal Health Area, Spain

^d Grupo de Investigación Marina del Principado de Asturias (GIMPA), Spain

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ABSTRACT

Recent changes in climate and oceanographic conditions have been affecting the dynamics and composition of species communities worldwide, increasing the occurrence of tropical-subtropical species within a specific biogeographic area. This phenomenon defined as tropicalization is occurring in the Cantabrian Sea (Bay of Biscay), a transitional zone between two different regions of the North Atlantic. In this study we present new records of the tropical-subtropical gastropod species *Plicopurpura patula* and *Monoplex parthenopeus* in the European Atlantic, which constitute their northernmost distribution in the Atlantic Ocean to date. We provide a detailed characterization of both species, combining morphological and molecular features. Finally, supported by provided evidence and justification, we propose both species as two new potential bioindicators of the tropicalization phenomenon in the North Atlantic waters.

1. Introduction

In recent years, global change has been modifying climate and oceanographic conditions, affecting the species dynamics and composition of ecological communities worldwide (Occhipinti-Ambrogi, 2007). These triggered anomalies are evidenced by disturbances in the sea temperature, the upwelling dynamics, the sea-level and weather conditions (Gissi et al., 2021). The global sea temperature has been increasing 0.159 °C per decade thoughout the last century (Brown et al., 2019) and the frequency, intensity and duration of the heat waves have risen as well (Arafeh-Dalmau et al., 2019; Smale et al., 2019). One of the most outstanding ecological effects of the temperature increase is the species distribution shift known as tropicalization (Vergés et al., 2014; Peleg et al., 2019). This phenomenon can be defined as the spreading of tropical and subtropical species to the surrounding temperate areas by their own means. This is facilitated by global warming in a direct way (i. e., by their own temperature rise) and also indirectly, both by the increase in the mortality rates of boreal-like species, or by forcing them to migrate to colder areas, generating empty niches that can be used by the

tropical species (McLean et al., 2021).

Although the worldwide occurrence of tropical and subtropical species outside their original distributions has increased in the last decades, the Cantabrian Sea (in the Bay of Biscay) is a particularly interesting area to study this phenomenon. This regional sea constitutes a transitional zone between two different regions, one with predominantly boreal biota and other one with subtropical Atlantic one (Fischer-Piette, 1957; Arias et al., 2023). Therefore, evidence of tropicalization has become usual on the shore of the Cantabrian Sea, mainly represented by the new occurrence of fish species such as Caranx crysos (Mitchill, 1815), Pseudocaranx dentex (Bloch et al., 1801), Seriola rivoliana Valenciennes, 1833, Seriola fasciata (Bloch, 1793), Kyphosus sectatrix (Linnaeus, 1758), Fistularia petimba Lacepède 1803 or Lagocephalus laevigatus (Linnaeus, 1767) (Bañón-Díaz and Casas-Sánchez, 1997; Fernández-Cordeiro and Bañón-Díaz, 1997; Bañón-Díaz and Garazo, 2006; Bañón-Díaz and Sande, 2008; Bañón and Mucientes, 2009; Bañón-Díaz and Santás, 2011; Arias et al., 2014; Bañón-Díaz et al., 2017). However, tropicalization indicators of invertebrate phyla have been neglected or underestimated in most studies (Arias and Crocetta,

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^{*} Corresponding author. E-mail address: ariasandres@uniovi.es (A. Arias).

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2016).

Here we present new records of two tropical/subtropical gastropod species (*Plicopurpura patula* (Linnaeus, 1758) and *Monoplex parthenopeus* (Salis Marschlins, 1793) in the Cantabrian Sea, which constitute their northernmost distribution in the Atlantic Ocean so far and the first formally published record of *P. patula* in the Eastern Atlantic. We provide a morphological and molecular characterization of both species and, based on a comprehensive analysis of their biological history, we propose them as two new potential bioindicators of the tropicalization phenomenon in the Atlantic waters. Furthermore, a complementary statistical analysis of the Cantabrian Sea temperature change along the last decades is also provided, as well as a brief discussion about the possible effects of the occurrence of both species in the Cantabrian Sea and the Bay of Biscay.

2. Material and methods

2.1. Specimen collection, morphological analysis, and taxonomic procedures

Four specimens of *P. patula* were collected between 2012 and 2016 in Punta del Carmen, Aramar rocky shore (Gozón), Bañugues rocky shore (Gozón) and Rodiles rocky shore (Villaviciosa) in Asturias, northern Spain, Bay of Biscay (Fig. 1). Five specimens of *M. parthenopeus* were collected in 2011, 2013 and 2018 in Aramar, Rodiles and El Rinconín in Asturias, northern Spain (Fig. 1). All specimens were prepared for preservation in situ, relaxed in MgCl₂, fixed and stored in 70% ethanol. The specimens were deposited in the Collection of the Department of organisms and system (BOS) of the University of Oviedo (https://bos.uniovi.es/). Specimens were examined under a dissecting stereomicroscope Optika SZM-2; $0,7-4,5\times$. Selected specimens were dissected to observe their internal anatomy. Photographs were taken with a Canon EOS 1200D Digital SLR Camera with EF-S 18–55 mm f/3.5–5.6 III Lens. Systematics and nomenclature follow World Register of Marine Species (n.d).

2.2. DNA extraction, PCR amplification and sequencing

The foot tissues of each studied specimen, preserved in ethanol, were used to extract DNA using the E.Z.N.A Mollusc DNA Kit (Omega Bio-tek, Norcross, GA, USA) following the manufacturer's protocol. The extraction success was verified through horizontal electrophoresis (1% agarose gel), and the DNA samples were then stored at -20 °C. To amplify the mitochondrial cytochrome *c* oxidase subunit I (COI) gene, polymerase chain reaction (PCR) was performed in a total volume of 25 µL, using the universal primers LCO1490 and HCO2198 (Folmer et al., 1994). For the PCR reaction, 2.5 µL of template DNA was mixed with 2.5 µM MgCl₂, 1.25 µM deoxyribonucleotides triphosphate, 0.5 µM of each primer, 0.2 U Taq polymerase and the appropriate buffer at a final concentration of 1×. The PCR conditions consisted of an initial denaturation step of 94 °C for 4 min, followed by 45 cycles of 94 °C for 30 s, 48 °C for 1 min, 72 °C for 2 min, and finally an extension step of 72 °C for 7 min and 20 $^\circ$ C for 1 min. The PCR products (25 μ L) were purified using the Agarose-Out DNA Purification Kit (EURx Ltd. 80-297 Gdańsk



Fig. 1. Geographical situation of (A) the Asturian coast (blue) in Bay of Biscay and (B, C) the location of the sampled localities for *Plicopurpura patula* (green circles) and *Monoplex parthenopeus* (blue circles). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Poland), following the manufacturer's instructions. The purified products were then subjected to horizontal electrophoresis (2% agarose gel) with 0.05 L/mL of SimplySafe™ (EURx Ltd. 80–297 Gdańsk Poland) and subsequently sent for forward and reverse sequencing to MACROGEN (Madrid, Spain) using the standard Sanger sequencing method (Sanger and Coulson, 1975).

2.3. Genetic analysis

The consensus sequences were edited and aligned using ClustalW in the freeware BIOEDIT (Hall, 1999). To attempt preliminary genetic species identification, nBlast was used to search the BOLD (https ://www.boldsystems.org/index.php/IDS OpenIdEngine) and GenBank (https://blast.ncbi.nlm.nih.gov/Blast.cgi) databases. For phylogenetic analysis, 17 COI sequences from Plicopurpura and other closely related genera were downloaded from Genbank, with the type species of Drupa Röding, 1798, and Mancinella Link, 1807 chosen as outgroups based on their phylogenetic proximity in Claremont et al. (2013). The nucleotide substitution model that best fits the data was predicted using the Model Test software included in IQ-TREE (Nguyen et al., 2015; Trifinopoulos et al., 2016) based on Bayesian information criteria (BIC) scores (Nei and Kumar, 2000), with the Hasegawa-Kishino-Yano model with gamma distribution (HKY + G) (Hasegawa et al., 1985) selected as the best fitting model. A Maximum Likelihood (ML) tree was inferred using a Neighbor Joining starting tree and the Nearest-Neighbor Interchange (NNI) as the rearrangement method. Statistical support for the topology branches was estimated by performing 10,000 ultrafast bootstrap replicates (Minh et al., 2013; Chernomor et al., 2016; Hoang et al., 2018).

2.4. Temperature search and data collection

Sea surface temperature was analysed and collected by NOAAs' radiometer infrared sensor of high resolution (AVHRR), which is corrected in situ by boats and sea buoys in order to make an optimal interpolation and minimize any kind of error in the satellite measurements (Reynolds et al., 2007). It is a monthly type of temporal resolution, which started on January 15th 1982 and finished on February 15th 2020. An average of the averages was also performed, which has a resolution of ¹/₄ degree, having one degree per 110 Km. The total extension of the study area is limited by the coordinates 43.50, -9.20 east, 45.50, -1.60 west.

Once the data were extracted, they were treated and analysed with the RStudio software (RStudio Team, 2020). Firstly, the data were deseasonalised, thus removing the average so we can only analyze the tendency of the set of data for the selected area. This way we eliminate the seasonal effect of the sharp variations between warm and cold periods of the year observed in this region. For this purpose, a linear regression model was chosen, strengthened by a non-parametric test of Mann-Kendall, using the statistical program Kendall (McLeod and McLeod, 2015) for the last one. The graphics of the temperature tendency over time were performed with the package 'ggplot2' (Wickham, 2011).

3. Results

3.1. Morphological characterization

3.1.1. Plicopurpura patula (Linnaeus, 1758) 'Purple snail'

3.1.1.1. Examined material. One specimen from Aramar rocky shore (Gozón, Asturias, northern Spain), coll. A. Arias, 12 March 2016; two specimens from Bañugues rocky shore (Gozón, Asturias, northern Spain), coll. A. Arias, 16 october 2012; One specimen from Rodiles rocky shore (Villaviciosa, Asturias, northern Spain), coll. A. Arias, 16 October 2012.

3.1.1.2. Diagnosis. Shell oval in outline with 7-8 spiral rows of blunt knots and moderately marked axial growth threads (Fig. 2A). Colour, from cream to grey, with dark spiral bands and sometimes yellowish splotches. Aperture lip more than three-fourths of shell height, elliptical and crenulated on outer edge, blotched with black on and between crenulations on inner side (Fig. 2B). Orangey flattened, wide columella frequently with sizable dark brown patch on parietal region. Siphonal canal short, shallow (Fig. 2D). Reddish-brown pear-shaped opercle, horny and smaller than the opening, concentric growth lines, occupying the dorsal surface of the foot (Fig. 2C). Wide body, cylindrical snout with an aperture in the anterior margin (Fig. 2D). Two large tentacles with a short ommatophore in the outer surface (Fig. 2D). Hypobranchial gland located in the first spiral of the mantle producing a purple spot (Fig. 2E). Female gonads adopt yellowish hues, located on the last spirals of the shell, penis is located in the anterior part, near the tentacles (Fig. 2E). Several cases of imposex have been reported in females of the genus Plicopurpura (Domínguez Ojeda et al., 2009).

3.1.1.3. *Remarks.* Collected specimens ranged in shell length between 23 mm and 31 mm. At the new localities in the Cantabrian Sea, *P. patula* may be only misidentified with *Stramonita haemastoma* (Linnaeus, 1758) (Fig. 4A-C). However, *S. haemastoma* can be distinguished from the former by having a smooth to finely nodulose shell with four spiral rows of knobs (Fig. 4A, B), whereas *P. patula* has a coarsely sculptured shell with six spiral rows of blunt knobs (Fig. 2A, B, D). Furthermore, in *S. haemastoma* the aperture and columella are bright orange, red or yellow (Fig. 4C), whilst in *P. patula* the columella is dirty orange-pink-grey and the aperture wall straw, purple-black or green-brown (Fig. 2A, B).

3.1.1.4. Distribution and biology. The purple snail is a common carnivorous snail native from the coasts of Florida to Venezuela, including the Gulf of Mexico and the Caribbean Sea (Wellington and Kuris, 1983) (Fig. 3). We can differentiate P. patula from its sister species P. columellaris (Lamarck, 1816) (=P. pansa (Gould, 1853)), by its smaller size and by the colour of the shell opening, which is less white than in *P*. columellaris (Muñoz-Mancilla et al., 2007). Plicopurpura spp. have an intra-capsular development that takes between 5 and 8 weeks, going through different larval stages, trochophore, preveliger and veliger (some authors consider also an additional post-veliger stage) (Naegel and Gómez del Prado-Rosas, 2004). This is a dioecious species, and each female can produce up to 50,000 eggs per reproductive period, showing high mortality rates during its first stages of larval development (Spight, 1975). The eggs are contained inside capsules, that reach approximately about 1.7 mm in height, 4.3 mm in length, and 3.3 mm in width. Inside each capsule more than 400 eggs can be found, depending on the capsule size (Naegel, 2004).

3.1.2. Monoplex parthenopeus (Salis Marschlins, 1793), 'giant hairy triton'

3.1.2.1. Material examined. Two living specimens from El Rinconín rocky shore (Gijón, Asturias, northern Spain), coll. A. Arias, 8 February 2018); One shell from Rodiles rocky shore (Villaviciosa, Asturias, northern Spain), coll. A. Arias. 12 March 2013; Two shells from Aramar rocky shore, (Gozón, Asturias, northern Spain), coll. A. Arias, 5 July 2011. Three shells occupied by hermit crabs of the species *Clibanarius erythropus* (Latreille, 1818).

3.1.2.2. Diagnosis. Big shell, up to 120 mm larger than its width. Spiral and moderately marked axial growth lines, outer lip with 5 to 7 brown spots with 2 to 4 white denticles (Fig. 5A, D). Slight opening reinforced on the exterior size (Fig. 5B- 5E). Brownish periostracum (Fig. 5C), with dark brown dots on the exterior of the opening, columella dark reddish brown with white and raised plicate.



Fig. 2. Photographs of *Plicopurpura patula* specimens collected in Asturias (northern Spain). (A, B, D) dorsal and ventral views of the shell of three specimens; (C) detail of the opercle (inner and outer views); (E) frontal view of male specimen showing soft body morphology: M-mantel; HG-hypobranchial gland; *E*-eye; F-foot; T-tentacles; S-snout; P-Penis.



Fig. 3. Global distribution of *Plicopurpura patula*, red circle: locality from the present study, lilac shading: localities from bibliography data. Main Atlantic oceanic currents after Sissini et al. (2017). CC, Caribbean Current; EUC, Equatorial Undercurrent; GS, Gulf Stream; NAD, North Atlantic Drift; NBC, North Brazil Current; NEC, North Equatorial Current; SEC, South Equatorial Current. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

3.1.2.3. Remarks. Monoplex parthenopeus may be misidentified with Monoplex corrugatus (Lamarck, 1816) and Cabestana cutacea (Linnaeus, 1767), two cymatid snail species that occur sympatrically with *M. parthenopeus* in the Cantabrian Sea. Both Monoplex corrugatus (up to 9 cm) and *C. cutacea* (up to 10 cm) are smaller than *M. parthenopeus* (up to 15 cm) and their periostraca are strictly different: thicker and darker in colour in *M. corrugatus* and (Fig. 4D, E) and shorter, delicate and more translucent in *C. cutacea* (Fig. 4F, G). Other conchological differences can be appreciated in Fig. 4.

3.1.2.4. Distribution and biology. The giant hairy triton is a relatively common species in the Atlantic Ocean. In the East Atlantic it is distributed from the South of the Iberian Peninsula to Angola, including the Canary Islands, Madeira, Cape Verde and the Azores archipelagos. In the East Atlantic *M. parthenopeus* occurs from North Carolina to Brazil.

Outside the Atlantic Ocean, the species inhabits the Mediterranean Sea, South Africa and the Pacific and Indic Ocean (Scheltema, 1965; Gofas et al., 2011) (Fig. 6). *Monoplex parthenopeus* is a dioecious species whose egg clutch has a diameter of 6.5 cm and contains approximately 200 individual egg capsules per clutch. This species has a protective behaviour that increases the egg's possibilities of survival (i.e., protecting them from nematode predation) (Turner et al., 2020), and an indirect development with a teloplanic larvae (long-distance dispersing) that can survive up to three months in the water column, but it normally lasts one month. Its veliger larvae can be easily recognized by its dark foot (Scheltema, 1965). Its larvae have been reported from different parts of the Gulf Stream and the North Atlantic drift and the number of eggs they lay are around 50,000, and the mortality rates are also high, almost 99% of the larvae do not survive to the veliger stage (Scheltema, 1965).



Fig. 4. Photographs of the shells of comparison used species (dorsal and ventral views): A-C Stramonita haemastoma; D-F Cymatium corrugatum; G-H Cabestana cutacea.



Fig. 5. Photographs of *Monoplex parthenopeus* specimens collected in Asturias (northern Spain). (A, B, D, E) dorsal and ventral views of the shell of two specimens; (C) detail of the periostracum. All scale bars 20 mm.



Fig. 6. Global distribution of *Monoplex parthenopeus*, red circle: locality from the present study, lilac shading: adult localities from bibliography data, or-ange shading: distribution of *M. parthenopeus* larvae from Scheltema (1965). Map of the main Atlantic oceanic currents after Sissini et al. (2017). CC, Caribbean Current; EUC, Equatorial Undercurrent; GS, Gulf Stream; NAD, North Atlantic Drift; NBC, North Brazil Current; NEC, North Equatorial Current; NECC, North Equatorial Current; SEC, South Equatorial Current. (For interpretation of the reader is referred to the web version of this article.)

3.2. Genetic results

Fragments of 648-bp COI were successfully obtained from two studied specimens of P. patula (genetic analyses did not amplify any regions in M. parthenopeus) and two different haplotypes were obtained and deposited in GenBank under accession numbers MZ004434 and MZ004435 respectively. The Bold identification engine identified unambiguously MZ004434 as P. patula with 100% of similarity with the Genbank specimens under the registries HE584360 (collected in Costa Rica (Manzanillo)) and HE584362 (Florida, USA), both reported by Claremont et al. (2012) and also with the Genbank registry MK308436 (Martinique: Baie de Fort-de-France) (unpublished). The Bold identification procedure for MZ004435 revealed 99.85% of similarity with the registries already mentioned above (HE584360 and HE584362). The phylogenetic analysis of the family Muricidae (see Barco et al. (2010), Marko et al. (2014) and López-Chávez et al. (2016)) is not the focus of this work (more data are needed) but here are clustered all the P. patula sequences with a 87% of bootstrap support and they are located phylogenetically close to the other species within the genus Plicopurpura (P. pansa and P. collumellaris) (Fig. 7).

3.3. Temperature analysis

For the data taken from the satellite, the linear regression model (*P*-value = 2×10^{-16} ; $R^2 = 0.2412$) and the Mann-Kendall non-parametric test (tau = 0.315; P-value = 2×10^{-16}) have a statistical significance, showing a rising tendency of 7.404 $\times 10^{-5}$ per month, which ends in a rise in the temperature of the sea surface of 0.034 °C for the next 38

years, 0.01 °C per decade approximately (Fig. 8).

4. Discussion

Plicopurpura patula and M. parthenopeus are other examples from a long list of species that are reaching new areas, due to the action of global change and global warming, as it is the case of Umbraculum umbraculum (Lightfoot, 1786) (Arias and Crocetta, 2016). The arrival of both species of gastropods to the Cantabrian Sea appears to be consistent with trans-Atlantic passive larval dispersal by ocean currents, favored by the global warming. The provided revision of their biological and biogeographical traits confirms their amphi-Atlantic distribution, which appears consistent with the distribution of the main Atlantic currents (Figs. 3 and 6). The water currents play an important role in the distribution of different species of marine invertebrates with indirect development (Briggs, 2003; Carmona et al., 2011; Arias and Paxton, 2020). Plicopurpura patula and M. parthenopeus long-term planktonic larvae are capable of dispersal or rafting, serving as a vector of gene flow between distant populations and explaining the current amphi-Atlantic distribution of both species. Thus, it is very likely that larvae of both species of gastropods have been able to disperse through the Gulf Stream and North Atlantic Drift, from the American Atlantic, and reach the Cantabrian Sea in the Bay of Biscay. This process was most likely allowed and/or facilitated by the temperature increase experienced in the last decades. Furthermore, the provided biological evidence argues in favor of this hypothesis, i.e., both species produce a large number of eggs per reproductive period that develop into long-term planktotrophic larvae (Scheltema, 1965; Naegel, 2004; Naegel and Gómez del



Fig. 7. ML consensus tree based on COI sequences of *Plicopurpura, Drupa* and *Mancinella*. The tree is drawn to scale, with branch lengths measured in the number of substitutions per site. The *P. patula* clade is highlighted in light green, red rectangles represent Cantabrian Sea samples, and light orange the *P. columellaris* (= *P. pansa*) clade. The GenBank accession numbers are indicated after the specific scientific name. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



Fig. 8. Tendency for the seasonally adjusted temperature data along a temporal line in the Cantabrian Sea.

Prado-Rosas, 2004). These veliger-like larvae can survive long periods of time (up to 3 months in *M. parthenopeus*) in the water column allowing its passive dispersal through the water currents (Scheltema, 1965; Pechenik, 1984; Muthiah and Sampath, 2000a, 2000b; Naegel and

Gómez del Prado-Rosas, 2004; Turner et al., 2020) (Fig. 6). In a complementary way, in the case of *M. parthenopeus*, the origin of the Cantabrian Sea specimens may be the result of larval dispersal of north African or Mediterranean populations, potentially explained and favored by global warming as well. However, its introduction linked to maritime shipping, through larval transportation in ballast waters or through floating debris, cannot be ruled out. On the other hand, the successful DNA analysis of *P. patula* revealed the presence of two distinct COI haplotypes within the Cantabrian Sea specimens, suggesting at least two episodes of colonization or the colonization by waves of larvae of different populations/subpopulations. According to our results and the provided ecological and biological information of the treated species, we consider the occurrence of *P. patula* and *M. parthenopeus* in the Cantabrian Sea as a direct result of the tropicalization phenomenon and recommend the use of the new occurrences and the northern expansion of both species as a reliable bioindicator of this phenomenon in the Bay of Biscay.

Up until now, no ecological effects have been reported by the expansion of the treated gastropods. Their recent appearance and their occurrence in low numbers may account for this. Plicopurpura patula is a high intertidal predatory gastropod, but most information of its biology and ecology is somewhat confused and intermixed with that of other similar species (P. columellaris), which were previously considered as forms or subspecies of the former. Furthermore, unlike P. columellaris, which is an edible species (Barraza, 2009; Domínguez Ojeda et al., 2009), *P. patula* is not greatly used for the extraction of the purple dve which diminished the interest in its study (Muñoz-Mancilla et al., 2007). As a member of the subfamily Rapaninae, it plays an important role in the structure of communities due to its predatory nature, that could mean biodiversity loss in the receiving ecosystems (Claremont et al., 2012). Cases of predation on benthic invertebrates such as chitons and other bivalves have been reported in Plicopurpura patula sensu lato (Domínguez Ojeda et al., 2009). Also, P. patula could display a competitive relationship with a resident member of its subfamily, S. haemastoma, which presents the same ecological requirements in terms of food and shelter. Regarding to M. parthenopeus, as mentioned before, it is a carnivorous snail and a typical member of the Ranellidae family. This species mostly feed on bivalve molluscs and tunicates, thanks to the expelling of acid secretions through its salivary glands (Gofas et al., 2011). Cantabrian sea specimens of the hairy triton may impacton resident food webs, competing with other members of the families ranellids or even muricids.

Tropicalized species may involve ecological, and even socioeconomic damage, through direct and indirect impacts on native species and ecosystem services and function, as it can occur with the arrival of new species to a new area (Diagne et al., 2021). Although, so far, no negative effects have been associated with these two species of gastropods, a comprehensive approach should be undertaken to avoid potential future conflicts by, for instance, implementing a monitoring program to evaluate their abundance, distribution and evolution at the new localities. Likewise, it is also peremptory to enforce studies on their reproductive biology and their trophic ecology under the new ecological and environmental conditions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

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