



A morphogenetic characterisation of a potentially dominant African marine species in Europe

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Abstract Studying the early stages of the introduction of non-indigenous species (NIS) is crucial as it allows immediate management actions aimed at preventing NIS spread at a time when these actions are more likely to be effective. Recent species introductions present unique opportunities to study key aspects of the invasion process. However, comprehensive information on how and when NIS are first introduced remains rare. We assessed the characteristics

of the introduction of a member of the widespread *Pyura stolonifera* species group (Chordata, Tunicata) in Europe. These ascidians are important bioengineer species that can attain amongst the highest benthic biomass per surface area ever reported. We collected introduced individuals on the coast of the northwestern Iberian Peninsula, an area with high shipping traffic and one of the world's most important mussel farming regions. The specimens were analysed using taxonomic and genetic tools. Both field surveys and taxonomic analysis showed that one of the African members of the species group, *Pyura herdmanni*, has recently been introduced to Europe and, although it

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does not yet form the large aggregates found in the native range, it is already well-established. Genetic data revealed that only the northwest African lineage of *P. herdmani* has been introduced to Europe. Considering the low dispersal capabilities of the early life-history stages of *P. herdmani*, the introduction of this species into Europe can only be explained via human mediated transport of NIS. In order to prevent any detrimental effects on both native biota and/or economically-important anthropogenic activities, regular monitoring of recent NIS introductions is urgently required.

Keywords Biological invasion · Colonisation history · DNA barcoding · Exotic species · Non-native species · Taxonomy

Introduction

Understanding the characteristics of the artificial introduction of non-indigenous species (NIS) is key to determining whether such species will become invasive, potentially causing serious economic and ecological impacts. Such information provides vital knowledge and guidance for immediate management actions aimed at eradicating or at least containing the NIS. Despite a growing body of research on key aspects of species invasions (Ricciardi et al. 2017), information on how and when NIS are first introduced is absent in many cases.

A notorious group of invasive species in marine ecosystems are the members of the class Ascidiacea (Chordata, Tunicata) due to their negative impacts on human activities (Zhan et al. 2015) and their capacity to overgrow and smother native species (Carver et al. 2003). Like many other marine NIS (Bañón et al. 2019; Madon et al. 2023), ascidians are often detected in harbours and marinas (Zhan et al. 2015), and reporting non-native ascidians is key for forecasting future biological invasions (Hudson et al. 2021a). Ascidians are sessile as adults and have an extremely short dispersal phase that often has a duration of less than 24 h (Rius et al. 2017). Thus, the presence of introduced ascidians far away from their native range can often be explained by human mediated transport of NIS.

The solitary ascidians that belong to the *Pyura stolonifera* group (Monniot et al. 2001) currently

comprise the following species: *P. stolonifera* (Heller 1878), *Pyura praeputialis* (Heller 1878), *Pyura doppelgangera* (Rius and Teske 2013), *Pyura herdmani* (Drasche 1884) and *Pyura dalbyi* (Rius and Teske 2011). Out of these five species, at least three have shown potential to become problematic NIS. The first one is the Australian species *P. praeputialis*, which has invaded a bay on the west coast of South America, where it forms dense aggregates that monopolise all available substrata and exclude native species (Castilla et al. 2004). This species exhibits amongst the largest biomass ever reported for an intertidal organism (Castilla et al. 2000). The second species of the group that has the potential of becoming invasive is *P. doppelgangera*. This species is considered native to Tasmania and from there it has established itself on the coastlines of both the Australian mainland and New Zealand, where *P. doppelgangera* can form large aggregates (Rius and Teske 2013; Atalah et al. 2021). The third species that could potentially become introduced is the most widespread African member of the group (*P. herdmani*), which is highly abundant in harbours and lagoons across its native range (Rius and Teske 2011).

In 2015 an unidentified species of the *P. stolonifera* group was for the first time collected in Europe (Rius et al. 2017; Hudson et al. 2021b). More specifically, it was reported in the Rías Baixas, a region in southwestern Europe that hosts a major bivalve aquaculture industry (Supplementary information I, Fig. S1). To date, no detailed species identification of the collected samples has been conducted. Studies have so far reported 23 marine NIS across the Rías Baixas region (Bañón et al. 2019), two of which are ascidians (*Corella eumyota* Traustedt, 1882 and *Styela clava* Herdman, 1881).

Here, we comprehensively assessed the first ever documented introduction of a species of the *P. stolonifera* group in Europe by: (i) conducting taxonomic and genetic analyses to formally identify the species that has been introduced; and (ii) comparing genetic signatures from native and introduced ranges to unravel its introduction pathway and origin.

Methods

Field sampling

During the period between 2015 and 2019, divers of the Hydronauta Diving Club (www.hydronauta.com/) collected a few unusually large solitary ascidians in the marina of the Port of Ribeira (Table S1) at ~5 m depth. The size of most solitary ascidians found in Europe is < 10 cm, and some of the collected individuals were considerably larger. The largest individuals were attached to harbour chains or ropes, and the rest were smaller ones that were attached directly to the sandy sea floor or harbour seawalls. Specimens were preserved in 4% formalin solution and sent to experts for species identification. Preliminary identification assigned these specimens to the *P. stolonifera* group (X. Turon and E. Vázquez pers. comm., see Rius et al. 2017; Hudson et al. 2021b).

To confirm these initial records and assess the current distribution of the introduced ascidians, rapid assessment surveys (RAS) (Arenas et al. 2006) were conducted along the coast of the Ría de Arousa in March 2022. As ascidians readily attach themselves to hard surfaces in marinas, the underside of floating pontoons, hanging ropes, and buoys were searched from the side of floating pontoons. These surveys included the site of Ribeira where the species was first detected (Table S1), and primarily targeted shallow-water benthic communities living in recreational marinas and harbours. In addition, RAS were carried out along the nearby Ría de Vigo (Table S1) to determine whether these ascidians had spread from their initial point of introduction. The RAS were complemented with SCUBA diving at several locations (Table S1), including harbour seawalls, which allowed conducting observations of deeper substrates (up to 10 m depth).

Taxonomic identification

All ascidians collected in 2022 were transported in insulated containers to the Estación de Ciencias Mariñas de Toralla of the University of Vigo (www.cim.uvigo.gal), where they were dissected and photographed. Several specimens showed the

external characteristics of the *P. stolonifera* group. Some internal structures of the specimens were stained with Masson's haemalum to allow species identification following Monniot et al (2001) and Rius and Teske (2011, 2013).

DNA sequencing and data analyses

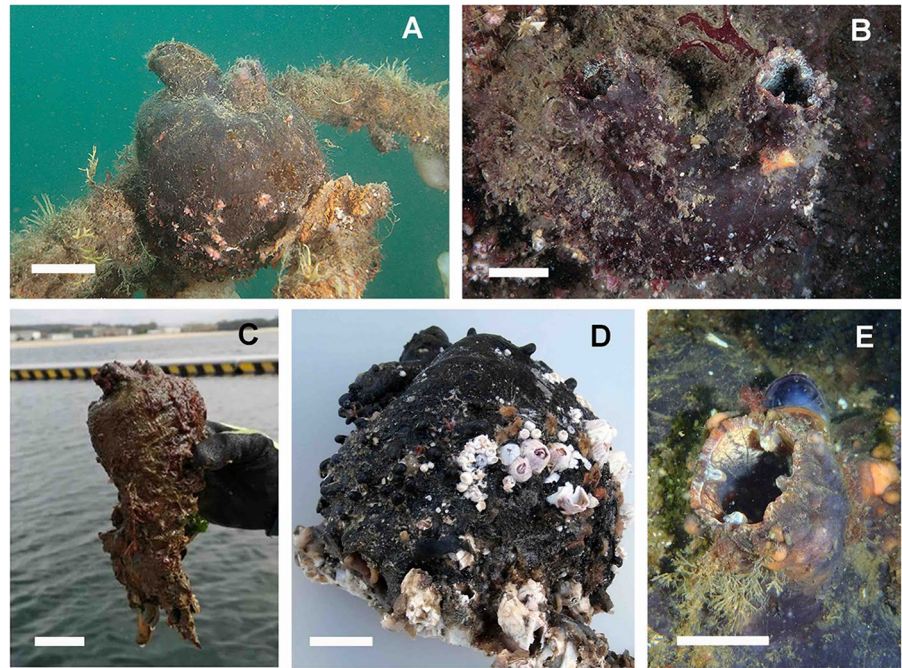
Prior to the morphological examination of the collected individuals, a piece of mantle (mainly muscular tissue) was dissected, placed in absolute ethanol, and stored at −20 °C for subsequent genetic analyses. A portion of the mitochondrial cytochrome oxidase c subunit I (COI) gene was amplified from all the collected individuals using universal primers (Folmer et al. 1994). DNA extraction and amplification conditions followed Rius and Teske (2013). The amplicons were sequenced using both forward and reverse primers at the Genomic Services of the Scientific-Technological Support Centre for Research (Vigo, Spain). We also downloaded all the COI sequences of this species available in GenBank (NCBI) to align them using MEGA7 (Kumar et al. 2016) and assess the phylogenetic placement of the collected samples. We used a single representative of each unique COI haplotype in the phylogenetic analyses to reduce the size of the resulting phylogenetic tree. We used the Bayesian Information Criterion in MEGA7 to identify the most suitable model for the resulting dataset. Phylogenetic analyses were conducted using the neighbour-joining method in MEGA7, with the Tamura and Nei model including a gamma distribution parameter of 0.25. Nodal support was assessed using 1000 non-parametric bootstrap replications. We also constructed a minimum-spanning haplotype network (Bandelt et al. 1999) in POPART (Leigh and Bryant 2015) using all newly generated and published DNA sequences from the evolutionary lineage within which the new sequences were placed in the neighbour-joining tree.

Results

Field sampling and taxonomic identification

We did not find any individuals belonging to the *P. stolonifera* group during the RAS surveys (Table S1). However, 15 individuals ranging from 10 to 25 cm in

Fig. 1 Morphological identification of *Pyura herdmani* in the field: **A**, **B** underwater view of two individuals, **C** collected individual out of the water, **D** same individual as in **B** after formalin preservation (note the darkening of the tunic), **E** enlarged underwater view of the oral siphon of a different specimen, showing short orange papillae on the tunic. Scale bars: **A**, 3 cm; **B**: 2 cm; **C**: 4 cm; **D**: 2 cm; **E**: 1.5 cm



length (Fig. 1) were collected during the SCUBA surveys in Ribeira (see Table S1), close to where the first individuals were initially found in 2015 and 2019. These individuals were collected at depths of between 2 and 6 m on vertical harbour walls and did not form the characteristic aggregates found in the native range (Rius and Teske 2011).

Morphological characters conformed well with the descriptions of *P. herdmani* by Rius and Teske (2011, 2013). The presence of pointed papillae on the tunic, gonadal lobes in a single row, and a sponge-like dorsal tubercle, are the main characters distinguishing this species from related congeners (i.e. *P. stolonifera*, *P. praeputialis*, *P. doppelgangera* and *P. dalbyi*) (Rius and Teske 2011; 2013). A detailed taxonomic description of the specimens examined can be found in Supporting information II and Fig. S2.

Genetic data

We generated 14 high-quality COI sequences from the collected individuals (GenBank accession numbers: OR364501-OR364514). The results showed three unique haplotypes, two of which were identical to previously published sequences (accession numbers JF961925 and JF961919). Previous genetic analyses identified four different mitochondrial

lineages of *P. herdmani* (Teske et al. 2011). One of these lineages is found on the northwest coast of Africa, two are found in temperate regions of South Africa, and a fourth lineage inhabits tropical and subtropical regions of southern Africa (including eastern South Africa and southern Mozambique). When we combined the newly generated COI sequences with a single representative of all the previously published *P. herdmani* COI haplotypes, the final trimmed alignment had a length of 534 base pairs. The neighbour-joining tree (Fig. 2A) showed the four mitochondrial lineages of *P. herdmani* previously identified in Teske et al. (2011), with the European samples clustering among haplotypes from the north-western African lineage. The haplotype network (Fig. 2B) indicated that this lineage has a pivotal, numerically dominant haplotype that occurs in both Spain and Morocco, while the other four haplotypes (including the one that has so far only been found in Ribeira) are comparatively rare, and differ from it by a single nucleotide change each. Our genetic data showed that the source region of the introduction of *P. herdmani* to Europe was the Atlantic coast of north-western Africa. In this region, *P. herdmani* has been reported along the coastline of Morocco (Monniot and Bitar 1983; Rius and Teske 2011) and in Dakar, Senegal

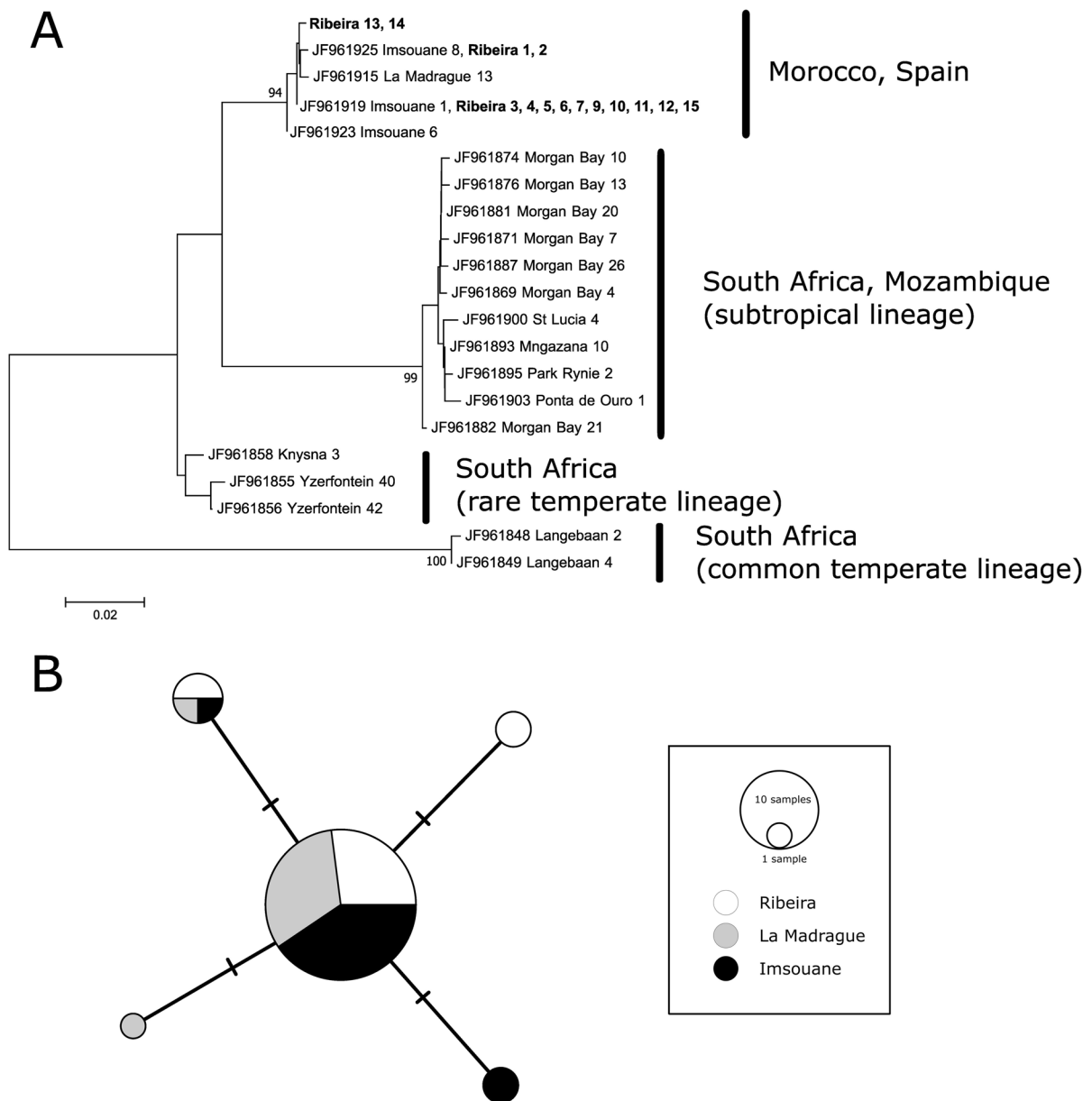


Fig. 2 Phylogenetic placement of the *Pyura herdmani* samples from Ribeira, Spain. **A** Neighbour-joining phylogenetic tree reconstructed from cytochrome oxidase c subunit I (COI) sequences, including a single representative of all haplotypes generated to date. The samples from Ribeira are shown in bold. Bootstrap values >75% are shown below some nodes. Geographic regions where the four distinct genetic lineages occur are shown on the right. **B** Minimum-spanning haplotype network of the samples from Ribeira and all published COI

sequences belonging to the genetic lineage among which the Ribeira samples clustered in the neighbour-joining tree. Each circle represents a unique haplotype, with haplotype frequencies indicated by the size of the circles. Each cross-bar represents a single nucleotide difference between haplotypes. Colours represent the proportion of a particular haplotype from up to three sites where this species has been detected (i.e. Imsouane, La Madrague and Ribeira)

(Lafargue and Wahl 1986–1987). Genetic results to date have shown a unique lineage of *P. herdmani*

present in North Africa, although no samples from Senegal have been sequenced yet.

Discussion

Reporting NIS as soon as they arrive in a new habitat is crucial for implementing any management plan to control their spread. In addition, a clear understanding of the species' current range, taxonomy and genetics is key for understanding the factors that shape the early introduction stages and subsequent invasiveness. In this study, we reported the introduction of an African NIS (*P. herdmani*) into Europe, showing that only one lineage of this NIS has been introduced. Following Ricciardi et al. (2017), the introduced *P. herdmani* appears to be at the "establishment" stage, i.e. reproductively active since mature gonads with gametes were found in several specimens (Fig. S2) and individuals are temporally sustained (2015–2022). However, the species has neither spread nor formed the characteristic large aggregates found in the native range. Unravelling such NIS' attributes is key not only for understanding how a species introduction can unfold, but also for establishing plans for managing subsequent stages of the invasion process, especially if the particular NIS has the potential to become an aggressive invasive species.

The first sign of the presence of a member of the *P. stolonifera* species group was the size of this solitary ascidian, which can be up to around 30 cm (Rius and Teske 2011). Despite numerous field surveys targeting NIS along the coastlines of the Galician Rías prior to our sampling in 2022 (see details Supplementary information I), no solitary ascidian reaching such sizes has ever been recorded. The absence of previous reports of such particularly large and conspicuous ascidians indicates that the introduction of *P. herdmani* into European shores has been recent. Here we report the northernmost point of the distribution of *P. herdmani* to date and, although this could suggest a climate-induced poleward range expansion, we ruled out this possibility mainly due to the absence of this species along other parts of the south European coastline, and the nature of its early life history stages (i.e. very short-lived dispersal phases that do not allow natural dispersal over long distances). Thus, the introduction of *P. herdmani* at a distant site (in this case, around 1000 km between Morocco and northwest Spain) can only be explained by human mediated transport of this species. The fact that it was first sighted in 2015 suggests a prolonged initial introduction stage, which is not uncommon in

ascidians. For instance, *Microcosmus squamiger* was first detected in Europe in 1963, long before its recognised expansion (Monniot 1981; Turon et al. 2007). Another example is the introduced ascidian *Clavelina oblonga*, which has apparently been confined to its initial zone of introduction on the Mediterranean coast for decades (Ordóñez et al. 2016).

The specimens examined conformed well with previous descriptions of *P. herdmani* (Monniot et al. 2001; Rius and Teske 2011, 2013). Our morphological identification was confirmed by the COI sequences, which placed the European samples within the lineage of north-western African haplotypes (Fig. 2). The fact that Ribeira did not contain a large number of haplotypes together with the absence of large aggregates of this species individuals in the introduced range confirm that the arrival of this species in Europe represents a recent introduction. Future studies using more informative molecular markers such as genome-wide single nucleotide polymorphisms (e.g. Hudson et al. 2021a) and/or genetic markers specifically designed for the target species will help to refine our understanding of *P. herdmani*'s colonisation history.

Bivalve aquaculture activities are common entryways of NIS (Carver et al. 2003), but the species exchanges in Galicia are mostly with nursery areas at southern European sites, where *P. herdmani* has not yet been reported. Fishing vessels operating across the Canary-Saharan bank often dock in Moroccan harbours and then return to their bases in Galicia a few times a year for maintenance and crew rest. These boats could have easily translocated individuals of *P. herdmani* from Morocco to Galicia and thus, this represents the most likely introduction pathway. To date, our evidence for the identification of the introduced range of *P. herdmani* comes solely from Ribeira and future surveys along the Iberian coast are needed to assess whether the size of the introduced range of *P. herdmani* is expanding or not.

Given the ecological dominance and biomass of the members of the *P. stolonifera* species group in many localities in their area of distribution (Castilla et al. 2000; Rius et al. 2017), this introduction has the potential to colonise important areas of the Ría de Arousa where there is a well-developed aquaculture industry. It is thus imperative to carry out SCUBA-based sampling to determine the full extent of the introduction of *P. herdmani*, and to urgently

implement NIS mitigation measures. The role of recreational divers, who routinely visit subtidal sites along this coastline, is crucial in documenting and reporting the presence of this NIS. In addition, online platforms that allow citizens to alert the scientific community as to the discovery of NIS are key to report the onset of species introductions as soon as these happen. We emphasise here the need for underwater observation, as RAS examining shallow areas did not prove useful to detect introduced individuals of *P. herdmani*. Future studies are needed to unveil the role of time since first introduction and the lag period for this and other NIS. The study of *P. herdmani* in Europe provides a unique opportunity to advance our understanding of the mechanisms involved in the early introduction stages of coastal NIS.

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Author contribution MR and EV designed the study and conducted and/or supervised fieldwork; MR, XT and EV dissected specimens for taxonomic examination; XT prepared figures; PM obtained genetic data from tissue samples; JP and BA detected the introduced individuals for the first time and assisted with fieldwork; PT did phylogenetic analyses. MR led the writing, and the co-authors revised the different drafts.

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Declarations

Competing interests The authors declare no competing interests. The lead author is a member of the editorial board of the journal Biological Invasions.

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References

- Arenas F, Bishop JDD, Carlton JT, Dyrinda PJ, Farnham WF, Gonzalez DJ, Jacobs MW, Lambert C, Lambert G, Nielsen SE, Pederson JA, Porter JS, Ward S, Wood CA (2006) Alien species and other notable records from a rapid assessment survey of marinas on the south coast of England. *J Mar Biol Assoc* 86:1329–1337
- Atalah J, Fletcher LM, Forrest BM (2021) Impacts of a putative invasive ascidian on rocky shore communities. *Mar Environ Res* 168:105308
- Bandelt H, Forster H, Rohl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Mol Biol Evol* 16:37–48
- Bañón R, Almón B, Trigo J, Pérez-Dieste J (2019) Especies marinas exóticas e inmigrantes en las costas de Galicia. In: *Especies exóticas invasoras*. Editorial Universidad de Alcalá, pp 81–94
- Carver CE, Chisholm A, Mallet AL (2003) Strategies to mitigate the impact of *Ciona intestinalis* (L.) biofouling on shellfish production. *J Shellfish Res* 22:621–631
- Castilla JC, Guíñez R, Alvarado JL, Pacheco C, Varas M (2000) Distribution, population structure, population biomass and morphological characteristics of the tunicate *Pyura stolonifera* in the Bay of Antofagasta, Chile. *Mar Ecol* 21:161–174
- Drasche R (1884) Ueber einige neue und weniger bekannte aussereuropasche einfache Ascidien. *Denkschr Acad Wiss Wien* 48:369–386
- Castilla JC, Guíñez R, Caro AU, Ortiz V (2004) Invasion of a rocky intertidal shore by the tunicate *Pyura praeputialis* in the Bay of Antofagasta, Chile. *Proc Natl Acad Sci* 101:8517–8524
- Folmer O, Black M, Hoeh W, Lutz R, Vrijenhoek R (1994) DNA primers for amplification of mitochondrial cytochrome c oxidase subunit I from diverse metazoan invertebrates. *Mol Mar Biol Biotech* 3:294–299
- Heller C (1878) Beitrage zur nahern Kenntniss der Tunicaten. *Sitzber Acad Wiss Wien* 77:2–28
- Herdman WA (1881) Preliminary report on the Tunicata of the Challenger expedition. Cynthiidae. *Proc Roy Soc Edinburgh* 11:52–88
- Hudson J, Castilla JC, Teske PR, Beheregaray LB, Haigh ID, McQuaid CD, Rius M (2021a) Genomics-informed models reveal extensive stretches of coastline under threat by an ecologically dominant invasive species. *Proc Natl Acad Sci* 118:e2022169118
- Hudson J, McQuaid CD, Rius M (2021b) Contemporary climate change hinders hybrid performance of ecologically dominant marine invertebrates. *J Evol Biol* 34:60–72
- Kumar S, Stecher G, Tamura K (2016) MEGA7: molecular evolutionary genetics analysis version 7.0 for bigger datasets. *Mol Biol Evol* 33:1870

- Lafargue F, Wahl M (1986–1987) Contribution to the knowledge of littoral ascidians (Ascidacea, Tunicata) of the Senegalese coast. *Bulletin de l'IFAN* 3–4: 386–402
- Leigh J, Bryant D (2015) POPART: full-feature software for haplotype network construction. *Methods Ecol Evol* 6:1110–1116
- Madon B, David R, Torralba A, Jung A, Marengo M, Thomas H (2023) A review of biodiversity research in ports: let's not overlook everyday nature! *Ocean Coast Manag* 242:106623
- Monniot C (1981) Apparition de l'ascidie *Microcosmus exasperatus* dans les ports Méditerranéens. *Tethys* 10:59–62
- Monniot C, Bitar G (1983) Sur la présence de *Pyura stolonifera* (Tunicata, Ascidacea) a Ras Achaccar (Cote Nord Atlantique Marocaine). Comparaison anatomique distinctive avec *Pyura praeputialis*. *Bull L'institut Scientifique, Rabat* 7:83–91
- Monniot C, Monniot F, Griffiths CL, Schleyer M (2001) South African ascidians. *Annals of the South African Museum* 108
- Ordóñez V, Pascual M, Fernandez-Tejedor M, Turon X (2016) When invasion biology meets taxonomy: *Clavelina oblonga* (Ascidacea) is an old invader in the Mediterranean Sea. *Biol Invasions* 18:1203–1215
- Ricciardi A, Blackburn TM, Carlton JT, Dick JTA, Hulme PE, Iacarella JC, Jeschke JM, Liebhold AM, Lockwood JL, MacIsaac HJ, Pyšek P, Richardson DM, Ruiz GM, Simberloff D, Sutherland WJ, Wardle DA, Aldridge DC (2017) Invasion science: a horizon scan of emerging challenges and opportunities. *Trends Ecol Evol* 32:464–474
- Rius M, Teske PR (2011) A revision of the *Pyura stolonifera* species complex (Tunicata, Ascidacea), with a description of a new species from Australia. *Zootaxa* 2754:27
- Rius M, Teske PR (2013) Cryptic diversity in coastal Australasia: a morphological and mitonuclear genetic analysis of habitat-forming sibling species: cryptic diversity in coastal Australasia. *Zool J Linn Soc* 168:597–611
- Rius M, Teske PR, Manríquez PH, Suárez-Jiménez R, McQuaid CD, Castilla JC (2017) Ecological dominance along rocky shores, with a focus on intertidal Ascidians. In: Hawkins SJ, Evans AJ, Dale AC, Firth LB, Hughes DJ, Smith IP (eds) *Oceanography and marine biology*. CRC Press, pp 55–85
- Teske PR, Rius M, McQuaid CD, Styan CA, Piggott MP, Benhissoune S, Fuentes-Grünwald C, Walls K, Page M, Attard CR, Cooke GM, McClusky CF, Banks SC, Barker NP, Beheregaray LB (2011) “Nested” cryptic diversity in a widespread marine ecosystem engineer: a challenge for detecting biological invasions. *BMC Evol Biol* 11:176
- Traustedt MPA (1882) Vestindiske Ascidiae Simpliciter, Forsie Afdeling. Phallusiadae. *Vid Meddel Nat For Kjobenhavn* 1881:257–288
- Turon X, Nishikawa T, Rius M (2007) The spread of *Microcosmus squamiger* (Ascidacea: Pyuridae) in the Mediterranean Sea and adjacent waters. *J Exp Mar Biol Ecol* 342:185–188
- Zhan A, Briski E, Bock DG, Ghabooli S, MacIsaac HJ (2015) Ascidians as models for studying invasion success. *Mar Biol* 162:2449–2470

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