ORIGINAL PAPER

Invader in disguise for decades: the plumose sea anemone *Metridium senile* in the Southwestern Atlantic Ocean

Lucas H. Gimenez · Nicolás Battini ·
Ricardo González-Muñoz · Heather Glon

Abstract The attention towards non-native sea anemone introductions has been steadily increasing as multiple species are reported from new locations each year. However, a lack of monitoring efforts and difficulties associated with the detection and identification of these species may result in overlooking introductions in certain areas. In the southern hemisphere, one of these non-native species is *Metridium senile*, whose current taxonomic and invasion status in Argentina is unclear. Here, we pooled scientific and community records to shed light on the past, current and future invasion scenario of this species. First, we clarified the taxonomic and invasion status of suspected *M. senile* populations from Argentina by revising available morphological descriptions and attributes associated with non-native species. Then, we inferred and described the potential dispersal pattern in Argentina from the late 1890s to present day. Finally, we provided a forecast of the species potential distribution range in the Southwestern Atlantic Ocean, along the coast and in off-shore areas. Enough evidence suggests that *M. senile* is a non-native species that has successfully established in Argentina. This species has been mistakenly considered as native for decades due to taxonomic errors and historical and geographical gaps (i.e., *pseudoindigenous* species). Its current distribution range in Argentina covers over 2000 km of coastline with a southward expansion in recent years. Moreover, according to our forecasted potential distribution, this species can spread further and reach novel areas in coastal and off-shore locations. As *M. senile* combines multiple traits of a successful invader, monitoring efforts should be implemented to early detect or prevent its establishment in areas recently colonized or at risk.

L. H. Gimenez (✉)
Programa de Magíster en Ecología Marina, Facultad de Ciencias, Universidad Católica de la Santísima Concepción, Concepción, Chile
e-mail: lucas.hernan.gimenez@gmail.com

N. Battini
Grupo de Ecología en Ambientes Costeros, Instituto de Biología de Organismos Marinos (CONICET), Puerto Madryn, Argentina

R. González-Muñoz
Laboratorio de Biología de Cnidarios, Instituto de Investigaciones Marinas y Costeras (IIMyC-CONICET), Universidad Nacional de Mar del Plata, Mar del Plata, Argentina

H. Glon
Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, OH, USA

Introduction

Over the past several centuries, scientists have documented an increasing flow of species across oceans that is in association with human activities (Carlton et al. 2003; Carlton 2009). Unfortunately, our lack of information about the basic biology and ecology of certain non-native species limits our understanding of their invasion process and status. Such is the case of invertebrate organisms with no historical reports as threats and a little to no commercial value (Zabin et al. 2007). Sources of underestimation of non-native species richness within an area are diverse and include taxonomic, biogeographic, and sampling errors (Carlton 2009). Taxonomic biases are unfortunately common in invasion ecology as researchers seem to target certain taxa, thereby focusing only on certain species within those taxa. This leads to an over-representation of some non-native species in the literature, to the detriment of others (Bailey et al. 2020; Watkins et al. 2021). Likewise, taxonomic errors abound as non-native species can be mistakenly considered as native due to re-descriptions or misidentifications after introduction (defined as *pseudoindigenous* species; sensu Carlton 2009).

Sea anemones (Cnidaria, Anthozoa, Order Actiniaria) are ubiquitous components of benthic marine communities, exhibiting a higher species diversity in temperate latitudes (30°–40° N; Fautin et al. 2013). At least 11 species of non-native sea anemones have been reported world-wide (Gimenez and Brante 2021). Fortunately, sea anemone introductions have been gaining more attention with new reports every year (e.g., Acuña et al. 2020; Glon et al. 2020a; Holmes and Callaway 2021; Pederson et al. 2021; Pereira et al. 2022). However, a lack of monitoring efforts and difficulties associated with the detection and identification of sea anemones likely leads to an underestimation of reports (Häussermann 2004; Glon et al. 2020b; Gimenez and Brante 2021). Non-native sea anemone populations are easier to detect once they reach high abundances and spread beyond the location of first introduction (e.g., Häussermann and Försterra 2001). Unfortunately, at that stage, ecological consequences may be inevitable and hard to mitigate (e.g., Robinson and Swart 2015; Patris et al. 2019).

Metridium senile is a cold-water species native to the northern hemisphere (Glon et al. 2021). Individuals can be found from the intertidal zone to at least 100 m, and prefer hard substrate both at natural and artificial habitats (e.g., rocks, bivalves, docks, shipwrecks, pilings; Carlgren 1933; Hoffmann 1976). This sea anemone is one of the easiest species to identify as adult individuals exhibit an easy to recognize external morphology, including a lobed oral disc, short plumose-like tentacles, presence of collar, unique coloration, and distinct column shape. Non-native populations have been confirmed in different parts of the southern hemisphere: South Africa (Griffiths et al. 1996), Chile (Häussermann and Försterra 2005; Häussermann 2006; Häussermann et al. 2022), and Islas Malvinas/Falkland Islands (Glon et al. 2020a). However, the invasion status of this species in Argentina is unclear.

Currently, *M. senile* has not been considered as a non-native species by Argentine regional non-native species databases (http://www.inbiar.uns.edu.ar/especies, accessed in January 2023), nor by the most updated and comprehensive checklist of marine non-native species of the Southwestern Atlantic Ocean (Schwindt et al. 2020). Two main reasons could explain the unclear status of this species: taxonomic uncertainty and gaps in its historical records. On one hand, suspected records of this species in Argentina date back to at least the late 60 s and were reported as the subspecies *M. senile lobatum* (Riemann-Zürneck 1975) and the species *Paraisometridium pehuensis* (Zamponi 1978). Although doubtful, the subspecies *M. senile lobatum* has been synonymized with the native species *Actinothoe lobata*, whereas the species *P. pehuensis* has been synonymized with the non-native *M. senile* (compiled in Rodríguez et al. 2022 in https://www.marinespecies.org, accessed in June 2022). There is such a taxonomic uncertainty that in recent years the plumose sea anemone from Argentina has been referred to as *M. senile* (Martin et al. 2015; Bravo et al. 2021) and *Actinothoe lobata* (Giachetti et al. 2019; Battini et al. 2021). Clearly, a taxonomic comparison among historical reports is warranted to better understand the status of *M. senile* in the Southwestern Atlantic Ocean. Confirmed introductions in Chile and Islas Malvinas/Falkland Islands support the idea that *M. senile* has been re-described in Argentina which has led to overlooked non-native populations at present. In fact, Häussermann et al.

(2022) proposed to eliminate the subspecies *M. senile lobatum* (and therefore the synonym with *A. lobata*), considering it a misidentification of *M. senile*.

The distribution and potential spread of *M. senile* in Argentina is also unclear as there are just a handful of suspected records, leaving a significant number of historical and geographical gaps. In fact, multiple populations along the Argentine coast remain unreported today (iNaturalist https://www.inaturalist.org/ accessed in January 2022). A comprehensive summary of all populations in Argentina, coupled with the forecast of its potential distribution, would shed some light on the historical invasion pattern of *M. senile*, its current distribution range, and the areas where it might be introduced in the near future. Here, we aimed to (1) clarify the taxonomic and invasion status of suspected *M. senile* populations from Argentina based on comparisons of available morphological descriptions, (2) summarize a combination of scientific and community records to infer the possible dispersal pattern of *M. senile* in Argentina from the late 1890s to present day, and (3) provide a forecast of the species potential distribution range along the Southwestern Atlantic Ocean to identify areas that could be potentially invaded in the future.

Methods

Taxonomic revision on suspected *Metridium senile* synonyms

We reviewed the literature on historical reports related to the putative synonyms of *M. senile* (Linnaeus, 1761) in Argentina, including the species names of *Sagartia patagonicha* Carlgren 1899 (synonymized with *Actinothoe patagonica*?), *Metridium senile lobatum* (Carlgren 1899) (synonymized with *A. lobata*?), and *Paraisometridium pehuensis* Zamponi 1978 (synonymized with *M. senile*?). Based on the external and internal anatomy data in these studies, we constructed a comparative table that includes the variable characters among those reported for each of these specific names. With this revision, we searched for potential misidentifications or re-descriptions to gather enough evidence and clarify which historical records correspond with *M. senile*. In addition, we examined the cnidom of the holotype specimen of *P. pehuensis* on loan from the Museo de La Plata (code

number: MLP-Oi 8503), as well as cross and longitudinal histological sections from paratypes held in the collection of the Laboratorio de Biología de Cnidarios, at the Universidad Nacional de Mar del Plata, to corroborate the taxonomic status of this species. Unfortunately, we did not have access to type material of other suspected cases.

Distribution range, historical records and current invasion status

We delimited the distribution range of *M. senile* along the Argentine coast based on records obtained from multiple sources: iNaturalist (accessed in January 2022), research literature, historic visual material (i.e., photos, videos), and reports from local fishermen/divers. We corroborated each *M. senile* report based on its distinctive visible characteristics in adult individuals (e.g., lobed oral discs and short plumose-like tentacles) with the available visual material, discarding any doubtful record. We registered the date, the georeferenced location and, when possible, biological information visible from each report (n = 95). In addition, we reconstructed the historical invasion pattern of *M. senile* from the late 1890s to present day, in order to better understand how the distribution of *M. senile* has changed in the Southwestern Atlantic Ocean over time.

We qualitatively assessed the abundance of *M. senile* on each report when possible. For that, we applied a scale from 1 to 4 with the following abundance categories: (1) presence (i.e., solitary individual), (2) sparse (i.e., few scattered individuals), (3) common (i.e., a patch of *M. senile* among other benthic components), and (4) dense (i.e., *M. senile* dominates > 50% of the visible area). For examples of abundance categories see Figure S3 in Supplementary Information. In addition, we categorized the type of habitat where individuals were recorded into natural or artificial structures and registered any signal associated with asexual reproduction (e.g., pedal laceration, small individuals growing right next to the pedal disc of a larger individual, etc.). Altogether, this information was used to roughly estimate the invasion status of *M. senile*. We also discussed all the evidence to consider *M. senile* as a non-native species introduced to Argentina, following the criteria proposed by Chapman and Carlton (1991).

Species distribution modeling

We modeled the potential distribution of *M. senile* along the Southwestern Atlantic Ocean using correlative species distribution modeling techniques. We only included records with geographic and taxonomic accuracy from the early 2000s to present and we complemented our dataset with additional records from the native range and other non-native regions (Glon et al. 2023). We also estimated the minimum distance to avoid spatial autocorrelation (120 km). The resulting 61 non-autocorrelated records were used for the modeling procedure (Figure S4).

We obtained topographical variables from MARSPEC (Sbrocco and Barber 2013) and environmental variables from Bio-Oracle v2.0 (Tyberghein et al. 2012; Assis et al. 2018). The grid resolution of all layers is 5 arcmin (~10 km), which has been applied for estimating habitat suitability of coastal species including sea anemones (e.g., Derviche et al. 2021; López-Farran et al. 2021; Castro et al. 2021; Gimenez et al. 2022). We selected variables with biological relevance for *M. senile* such as temperature and salinity (Glon et al. 2019), and we also assessed the collinearity among predictors (Figure S5) as highly correlated variables can affect the interpretation of the modeling outputs (Dormann et al. 2012). After eliminating collinearity, 8 predictors were selected for modeling: bathymetry/depth (m), mean temperature (°C), maximum temperature (°C), minimum temperature (°C), temperature range (°C), minimum salinity (PSS), minimum primary production (g m^{-3} day^{-1}), and primary production range (g m^{-3} day^{-1}).

We selected the pseudo-absences for the models combining two different widely used approaches as proposed by Chapman et al. (2019): the accessible area and habitat unsuitability selection criteria. Then, we used an ensemble model approach combining the outputs of seven different algorithms: 'MARS' (multivariate adaptive regression splines), 'GLM' (generalized linear models), 'GBM' (general boosted regression models), 'CTA' (recursive partitioning and regression trees), 'SRE' (surface range envelope), 'RF' (random forests) and 'MAXENT' (maximum entropy). We ran 700 individual models per algorithm by combining different sets of pseudo-absences. Individual models were combined into an ensemble by scaling their predictions through a binomial GLM, using the area under the receiver operating characteristic curve values (AUC) as an averaging weighting parameter and excluding the poorest performing models ($z < -1$) as proposed by Chapman et al. (2019). This method allows for better performing models to have a greater contribution to the final ensemble. The final ensemble was projected onto the Southwestern Atlantic Ocean using the same predictors and resolution as for model calibration. Modeling was performed using the 'biomod2' package (Thuiller et al. 2009) in R (R Core Team 2022). The importance of each variable was calculated using 'biomod2' default procedures. For a more detailed description of the modeling procedure see the Supplementary Information.

Results

Taxonomic revision: Different names, same species?

For the purpose of this comparison, each description is referred to as originally named (Table 1). Most of the morphological characteristics described for the different suspected synonyms of *M. senile* from Argentina are within the known level of variation for this species, including column structure, presence of collar, and number of tentacles. However, some forms lack information due to incomplete descriptions as it is the case of *S. patagonicha*.

The column of *M. senile* is divided into capitulum and scapus, in the same way as indicated for *M. senile lobatum* and *P. pehuensis*. This feature is not mentioned for *S. patagonicha*, probably because it was overlooked by the small size of the individuals or due to the poor state of conservation of the specimens. The presence of the collar that characterizes *M. senile* is only indicated for *M. senile lobatum*. In the type specimen of *P. pehuensis* (Figure S1), we did find a slight bend in the upper part of the column. It is a very small specimen that is poorly preserved so we could not rule out that it may possess a collar similar to *M. senile*. To further suggest that the species may have a collar, we observed a mesogleal thickening in the upper column in the longitudinal section examined, which may indeed be indicative of a collar due to the difference in tissue texture. This area examined was alongside the mesogleal marginal sphincter (Figure S2a). Likewise, the

Table 1 Comparison of distinctive morphological characteristics of *Metridium senile* with its suspected synonyms in Argentina

Species name	Column structure	Collar	Number of tentacles	Marginal sphincter	Retractor muscles	Cnidom	Site according to reference	Type specimens availability (according to Fautin 2016)	References
Metridium senile	Smooth, divided in capitulum and scapus	Present	From dozens to several hundreds	Mesogleal, well-developed, maybe absent or weak in small specimens	Well-developed, diffuse	Spirocysts, basitrichs, atrichs, holotrichs, *p*-amastigophores, *p*-mastigophores, *b*-mastigophores	Widespread through the northern Atlantic and Pacific Oceans; South America; South Africa	Holotype unavailable	Hand (1955), Riemann-Zürneck (1975), Manuel (1981), Griffiths et al. (1996) and Häussermann et al. (2022)
Sagartia patagonicha	Smooth	–	96	Mesogleal, well-developed	Well-developed	–	Puerto Madryn, Chubut Province (intertidal)	Syntypes in the Naturhistoriska Riksmuseet, Sweden, Zoologisches Museum Hamburg, and Museum of Zoology, Sweden	Carlgren (1899)
Metridium senile lobatum	Smooth, divided in capitulum and scapus	Present	At least 400	Mesogleal, finely alveolar	Well-developed, circumscript-diffuse	Spirocysts, basitrichs, *p*-mastigophores	Argentine Continental Shelf (95–120 m depth)	Unknown	Riemann-Zürneck (1975)
Paraisometridium pehuensis	Smooth, divided in capitulum and scapus	Absent (*Present?)	Numerous (*more than 160)	Mesogleal, palmate circumscript, in all the capitulum and upper scapus	Well-developed, circumscript-diffuse (*restricted-diffuse)	Spirocysts, *b*-mastigophores, *p*-mastigophores (*basitrichs, holotrichs, *p*-amastigophores)	Pehuen-Có, Bahía Blanca, Buenos Aires Province (intertidal)	Holotype in the Museo de La Plata (code number: MLP-Oi 8503)	Zamponi (1978)

*The characteristics observed in this study in the holotype and the paratypes specimens of *P. pehuensis*

retractor muscles were restricted to diffused (Figure S2b), instead of circumscribed to diffused as originally described. Although the histological section was in poor condition, no more than 12 pairs of sterile mesenteries were observed between the first longest cycles (Figure S2c), instead of the 16 pairs originally reported. As for the cnidom, the types of cnidocysts found in the *P. pehuensis* holotype agree well with those described for *M. senile* by Hand (1955) and Östman et al. (2010a, b, c) (Figure S2d–r) with the exception of small basitrichs in the acontia, and the large holotrichs in catch-tentacles described by Hand (1955) which were not observed. It is worth noting, though, that catch-tentacles were not observed in this specimen.

On the other hand, the number of tentacles of *M. senile* ranges from dozens to hundreds depending on the size and degree of development of the individuals. Therefore, the number of tentacles of all suspected synonyms is within this range of variation. While originally there was no clear mention of the number of tentacles in the type specimen of *P. pehuensis*, we observed the presence of more than 160 tentacles.

All descriptions mention forms with a well-developed mesogleal sphincter, although in *M. senile* it can be absent in small individuals. Most notable is the mention of an alveolar mesogleal sphincter in the description of *M. senile lobatum*, although no image is provided of this structure. Likewise, the retractor muscles are described as well-developed in all forms, although a tendency from diffuse to circumscribed is also indicated in *M. senile lobatum*. Cnidae types described for *M. senile lobatum* are generally consistent with the known cnidom of *M. senile*; any differences between them are likely related to the different nomenclatures implemented to classify the cnidae types.

Invasion status and distribution: from first record to recent spread

Metridium senile is currently found along a broad latitudinal range off the Argentine coastline, from Las Grutas (40° S) to Ushuaia (55° S) (Fig. 1). The presence of *M. senile* in the coast of Argentina could date back to the late 1890s if the record of *S. patagonicha* is a re-description of young *M. senile* individuals, and it could represent the earliest record for the Southwestern Atlantic Ocean (1896, ~42° S). However,

the earliest confirmed report (as *M. senile lobatum*) only dates back to 1966 from the continental shelf off Chubut province (~43°–48° S; Fig. 1; Riemann-Zürneck 1975). Zamponi (1978) also reported the presence of *M. senile* (as *P. pehuensis*) at Bahía Blanca (~40° S), although now it is seemingly absent as local researchers did not find it in field surveys (S. Fiori, pers. comm.).

During the early 90 s, *M. senile* was registered in coastal habitats of Puerto Madryn and Península Valdés (~42° S) according to photographs and videos provided by local divers (Fig. 2). They also mention the species being present earlier, during the 70 s and 80 s, although they were unable to provide us with images to support these observations (H. Monsalve, pers. comm.). However, its presence in the area has been registered in different years and persists until today. In Puerto Deseado (~48° S), it was confirmed as present in the early 2000s. Between 2010 and 2015, it appeared in San Jorge gulf (44° S–47° S) and Puerto San Julián (~49° S). More recently, between 2016 and 2020, it was detected in new areas to the north (Las Grutas; ~40° S) and south (Ushuaia; ~54° S). Unfortunately, it could not be confirmed whether *M. senile* inhabits areas in the coast between Puerto San Julián (~49° S) and Ushuaia (~54° S).

Interestingly, the records suggest a persistence of some populations over the years and a spread especially to the south (Fig. 1). Populations associated with artificial habitats especially thrive, such as those within the North Patagonian gulfs (Figure S3d). Based on the information we could gather from visual records, there was a higher number of observations in natural than in artificial habitats. However, in human-made structures the species showed denser abundances than in natural substrata (Table S2). Asexual reproduction was evident in 75% of records in which the species showed levels of pedal laceration with the presence of large individuals surrounded by smaller ones (Table S2).

Modeling output: potential for further spread

Based on habitat suitability, *M. senile* has a wide potential distribution in Argentina and Islas Malvinas/Falkland Islands (Fig. 3). This potential distribution suggests that the invasion of *M. senile* in the Southwestern Atlantic Ocean can further spread from colonized locations to their surroundings, mostly
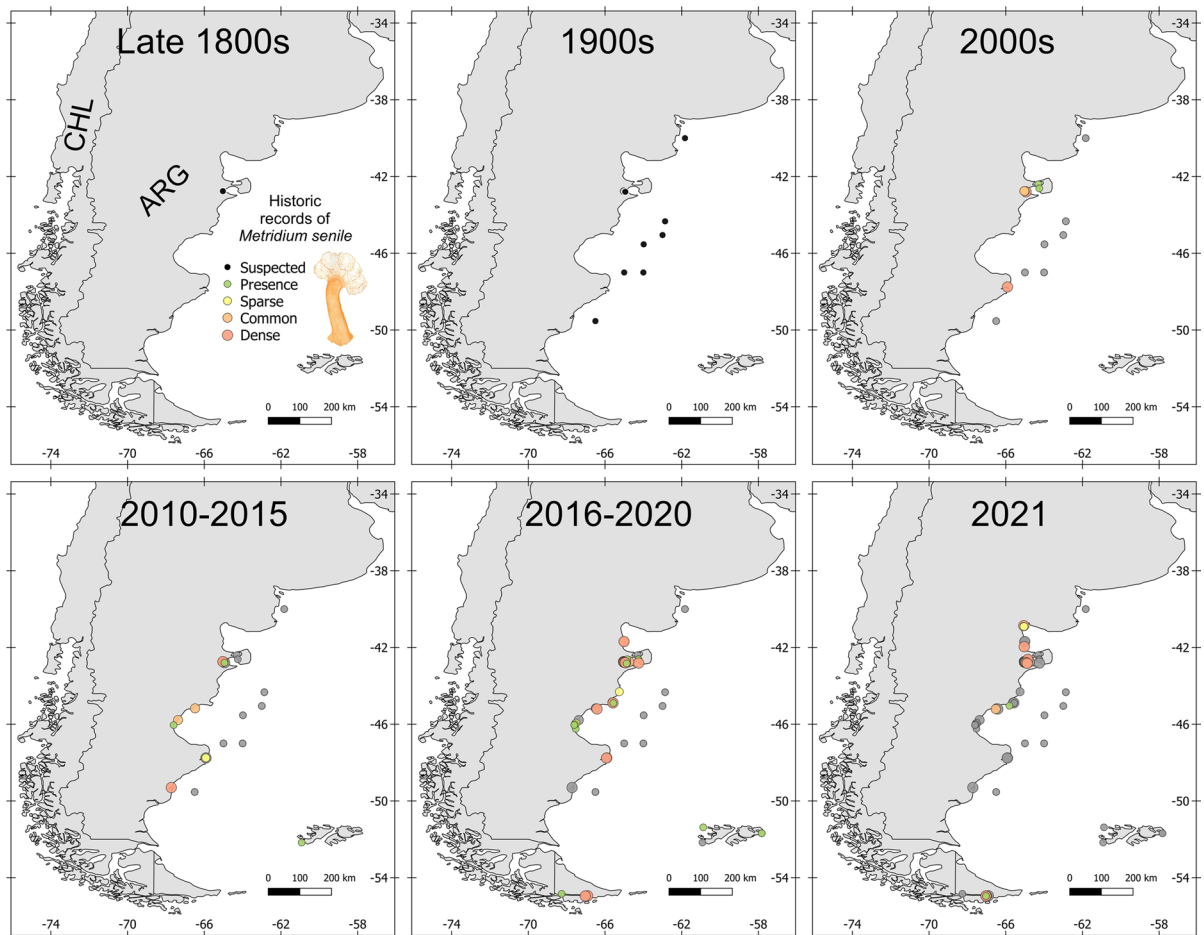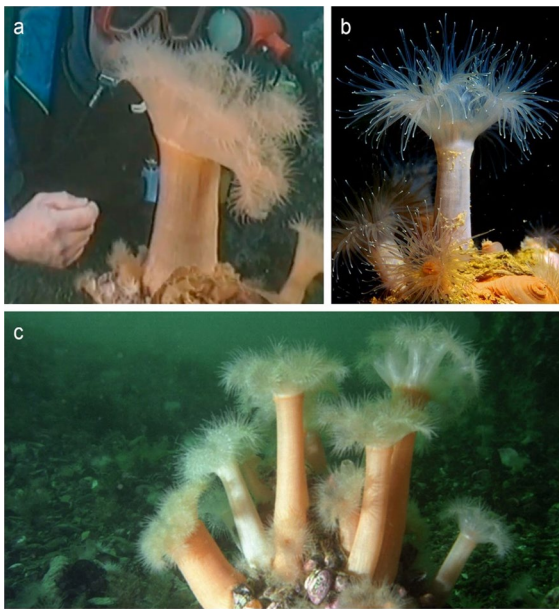
Fig. 1 Historic records of *Metridium senile* in the Southwestern Atlantic Ocean and its potential dispersal pattern along the coast of Argentina since its suspected first report (1890s) to present. *ARG* Argentina, *CHL* Chile

in coastal areas. Particularly in the Argentine coast, this sea anemone could reach areas northwards to the coast of Buenos Aires and southwards to locations with no historical nor current reports. Some off-shore areas in the continental shelf of Argentina might also be vulnerable to the introduction of *M. senile* including the Namuncurá Marine Protected Area.

Overall, the resulting ensemble model had a good performance both in discrimination (mean AUC = 0.96) and calibration (Boyce index = 0.75). The AUC for individual models varied depending on the algorithm and ranged from 0.36 to 0.93, with models with an AUC < 0.6 excluded from the final ensemble (Figure S6). The environmental predictors that most contributed to the model were depth, productivity range and temperature variables such

as mean and maximum (Figure S7). As expected based on previous information, predicted suitability values sharply decreased for depths greater than 250 m and when maximum annual temperature at the maximum depth exceeded 23 °C. Based on our ensemble model, predicted suitability was highest for annual mean temperatures between 2 and 10 °C and when productivity ranged between 0.012 and 0.050 g m^{-3} day^{-1}. In the case of salinity, our model did not account for values of minimum annual salinity lower than 15 PSU, but suitability decreased when it exceeded 32 PSU (hypersaline environments) (Figure S8).

Fig. 2 Photographic records of *Metridium senile* in the area of Puerto Madryn during the period 1993–1997. Photo credits: Héctor Elías Monsalve (**a**, **b**) and Marcelo Mazza (**c**)
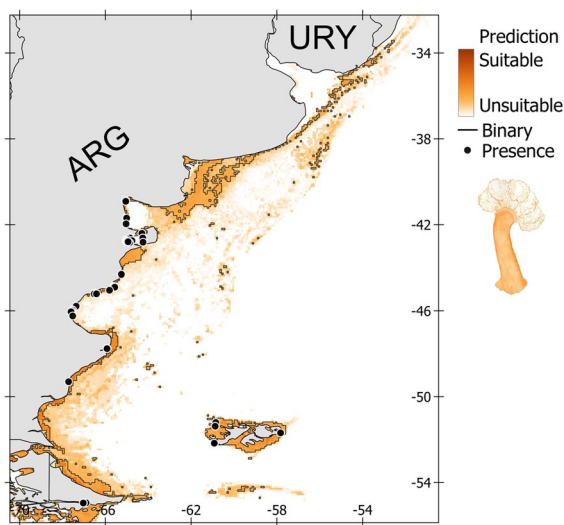
Fig. 3 Forecasted potential distribution of *Metridium senile* in the Southwestern Atlantic Ocean. Current occurrence records are shown to highlight suitable areas for new introductions or spread. Habitat suitability values range from 0 (unsuitable) to 1 (suitability), and they are the mean of an ensemble prediction of multiple models with different algorithms weighted on their area under the receiver operating characteristic curve values (AUC; i.e., model discrimination). A thresholded prediction, using the maximum sum of sensitivity and specificity criterion, is shown as a solid line to produce a binary prediction of the habitat suitability for *M. senile*. *ARG* Argentina, *URY* Uruguay

Discussion

Our study highlights four main findings: (1) there has been a great taxonomic confusion in the records of *M. senile* in the Southwestern Atlantic Ocean, which has led to many overlooked non-native populations in Argentina; (2) some reported populations combine multiple criteria to be considered as successful introductions while others need to be monitored; (3) historically, *M. senile* may have been in Argentina since the late 1890s, but confirmed records abound since the 1960s with an apparent dispersion pattern over the years and a current distribution range of over 2000 km; and (4) the potential distribution suggests this species can keep spreading northwards and southwards along the Argentine coast.

Taxonomic entanglement

Metridium senile is known to exhibit a high level of morphological plasticity, as individuals can vary widely in size, shape, and color (Glon et al. 2020a). This high level of variation has led to suggestions of taxonomic subspecies or varieties within the northern hemisphere, including *M. senile senile* (Hand 1955), *M. senile dianthus* (Dons 1945), *M. senile fimbriatum* (Carlgren 1936), and *M. senile pallidum* (Stephenson 1935). However, all of them are simply accepted as *M. senile*, a single, highly variable species (compiled in Rodríguez et al. 2022).

According to Riemann-Zürneck (1975), *M. senile lobatum* is largely identical to *M. senile* from the North Atlantic Ocean, with only a few differences such as smaller sizes, an unusually strong lobed edge of the pedal disc, the smaller *p*-mastigophores of the tentacles, and the greater tendency of the retractor muscles towards the circumscribed form. However, she noted that these deviations may have been caused by differences in ecological conditions, a plausible scenario after an introduction to a novel area. The morphological plasticity of *M. senile* includes the small differences described by Riemann-Zürneck (1975) for *M. senile lobatum*. For instance, the small *p*-mastigophores in the tentacles of *M. senile lobatum* have been documented in *M. senile* specimens from the northern hemisphere by Östman et al. (2010c; reported as *p*-amastigophores). On the other hand, Zamponi (1978) distinguished *P. pehuensis* from *M.*

senile by the lack of a collar on the upper column, among other minor differences. Our examination of the type material and of histological sections from paratypes of *P. pehuensis* are inconclusive regarding the presence of a collar due to the poor preservation of the specimen, although we found a tissue texture change that might indicate the presence of a collar. This suggests that there may have been a collar overlooked in the original description due to the small size of the specimen or its poor state of preservation. Therefore, based on our observations of the cnidom, as well as of the internal and external characteristics of the type material of *P. pehuensis*, we can't dispute the suggestion of den Hartog and Ates (2011), but feel that to truly consider this species to be a junior synonym of *M. senile* we would need additional evidence.

Another species that has been synonymized with *M. senile lobatum* is *Actinothoe lobata* since Riemann-Zürneck (1975) considered that *Sagartia lobata* (Carlgren 1899) and *Metridium parvulum* McMurrich, 1907 from Chile were synonyms of *M. senile lobatum*. Riemann-Zürneck (1975) placed *S. lobata* as the senior synonym of this subspecies, but Carlgren (1949) had previously placed *S. lobata* in the genus *Actinothoe*. These acts caused that *M. senile lobatum* was later synonymized with *A. lobata* (compiled in Rodríguez et al. 2022), but this seems to be a mistake and it is still considered a doubtful case (e.g., Häussermann and Försterra 2005; Fautin 2016). In fact, Häussermann et al. (2022) already suggested that the subspecies *M. senile lobatum* should be eliminated. Interestingly, Rodríguez et al. (2012) included nuclear and mitochondrial marker sequences from a specimen identified as *M. senile lobatum* from Puerto Madryn in their phylogenetic analysis of acontiate sea anemones (D. Lauretta pers. comm.) and found that it formed a monophyletic clade with other *M. senile*, including a specimen labeled as *M. senile fibratum* from Japan.

The case of *S. patagonicha* (synonymized with *A. patagonica*?) is intriguing as it is a species reported in the late 1890s but seemingly with no contemporary populations. Although its description is incomplete, Carlgren (1899) described it as very similar to *S. lobata*, but apparently with 96 tentacles. The fact that in Puerto Madryn there are no other sea anemones that can be easily mistaken with *M. senile*, suggests that either *S. patagonicha* was an endemic

species that has become locally extinct during the last 100 years, or it was a re-description of *M. senile*. Although the latter seems more plausible, either hypothesis is possible and we cannot shed more light on this matter unless an examination of the type material of *S. patagonicha* is performed. In Chile, a similar scenario could have happened if the records of *S. lobata* (synonymized with *A. lobata*?) and *M. parvulum* (synonymized with *A. lobata*?) are also re-descriptions of *M. senile* introductions that have failed to establish (see Table S1 in Supplementary Information for a summary of the features reported for these two species, not included in our analysis). However, solving the taxonomic status of *S. lobata* and *M. parvulum* is beyond the aims of this study as it requires an examination of type material (if available and well preserved) or new collected specimens from the type localities in Chile (if found).

Evidence suggests that *M. senile lobatum* and *P. pehuensis* may be re-descriptions of *M. senile* introductions, although we are more confident in the case of *M. senile lobatum* than *P. pehuensis*. The case of *S. patagonicha* remains dubious but it could likely be a re-description as well. Therefore, *M. senile* in Argentina clearly represents a pseudoindigene, a non-native species mistakenly considered as native for decades due to taxonomic errors, specifically a re-description as a new species after introduction in spite of being already described in its native range. Carlton (2009) has mentioned that pseudoindigenous species represent an important, yet overlooked, source of invasion diversity underestimation. Some examples he mentions include the European green crab *Carcinus maenas* described as *C. granulatus* in 1817 in North America, and the American slipper limpet *Crepidula plana* described as *C. sinuosa* in 1852 in Europe. The issues associated with the detection and identification of non-native sea anemone species have already led to many gaps and mistakes throughout the invasion history of certain species (e.g., *Anemonia alicemartinae, Diadumene lineata, Nematostella vectensis,* and *Sagartia elegans*; for reviews see Glon et al. 2020b; Gimenez and Brante 2021). It is not surprising that other sea anemone species represent cases of pseudoindigenes, including *D. lineata* and *N. vectensis* (Carlton 2009).

Past, current, and future invasion status of *Metridium senile* in Argentina

Our results clearly suggest that taxonomic uncertainty and a long-lasting presence of *M. senile* in Argentina have led to many overlooked non-native populations. Currently, some of these populations seem to be thriving and dominating large patches. By pooling scientific and community records, we captured a glimpse of the past, current, and potential future spread of *M. senile* in the Southwestern Atlantic Ocean.

One of the most obvious criteria to define a species as non-native is its sudden appearance in a location where it was not previously found despite being a sufficiently sampled area (*Criterion 1* by Chapman and Carlton 1991). The overlooked invasion of *M. senile* in the Southwestern Atlantic Ocean could have started long before the first confirmed records in Argentina, and certainly much earlier than the development of regional taxonomic expertise. If *S. patagonicha* is a re-description of *M. senile*, the earliest record in Argentina could date back to the late nineteenth century in Puerto Madryn. This port could therefore represent the most likely point of introduction for this species. In fact, it is an area that has experienced intense maritime traffic during the eighteenth century prior to the opening of the Panama Canal and during the time when scientific expeditions, whalers and sealers had a very frequent destination in Patagonia (Haller and Vezub 2018). Hence, it is not unreasonable to suggest that the introduction of *M. senile* could date back to the nineteenth century or even before, with maritime traffic as its plausible vector (*Criterion 3* by Chapman and Carlton 1991). In addition, Puerto Madryn (~42° S) is an enclosed area well-known as a non-native diversity hotspot (*Criterion 4* by Chapman and Carlton 1991), with 46 introduced species, including crustaceans, tunicates, and macroalgae (Schwindt et al. 2020).

First confirmed records of *M. senile* have been located in the continental shelf off Chubut (1966; ~43°–48° S) and maybe in southern Buenos Aires (1978; ~40° S) as *M. senile lobatum* and *P. pehuensis,* respectively (Riemann-Zürneck 1975; Zamponi 1978). Unfortunately, the presence of *M. senile* could not be confirmed by the first ecological assessment of subtidal communities in that area in the early 60 s due to poor taxonomic resolution, even though "numerous species of Actiniaria" were reported (Olivier et al.

1966). In the early 2000s, Häussermann and Försterra (2005) mentioned that it was found inhabiting shallow waters around Península Valdés and Buenos Aires. Since the late 2000s, records of *M. senile* are more frequent in the literature as it has been spotted both in southern Argentina and central Chilean Patagonia (Häussermann 2006; Häussermann and Försterra 2009; Lauretta et al. 2011; Martin et al. 2015). More recently, *M. senile* has been reported inhabiting the northern and southern Argentinian Patagonia on the intertidal shore, subtidal rocky reefs, and fouling communities associated to steer piles (Martin et al. 2015; Giachetti et al 2019 as *Actinothoe lobata*; Bravo et al. 2021). However, in southern Buenos Aires the species seems to be currently absent as local researchers did not find it in field surveys (S. Fiori, pers. comm.).

During the twentieth century, *M. senile* seemingly spread southwards through Argentina, and its appearance in southern Patagonia may be relatively recent (*Criterion 2* by Chapman and Carlton 1991). It is not surprising that populations have rapidly spread in South America either through range expansion or new introductions as its temperate marine habitats are likely similar in abiotic features to the native range of *M. senile*. In Puerto Deseado (47° S), the absence of records of *M. senile* in 1982 and earlier (Martin et al. 2015), suggests an arrival date between late 1980s and 2006, when we could confirm the presence of the species based on video recordings from the HMS Swift sloop archaeological survey (https://www.youtube.com/watch?v=DYL9bVd3TH0). In Bahía San Julián (49° S), it was reported as abundant in the lower intertidal by 2009 (Martin et al. 2015) but was not reported in previous descriptions of the lower intertidal macrobenthos in 2007 (Zaixso et al. 2017), suggesting an arrival date around that period. In Islas Malvinas/Falkland Islands, it seems to have arrived during the late 2010s (Glon et al. 2020a), and in the Beagle Channel (55° S) it was not found until very recently in 2020 (Häussermann et al. 2022; this study). We found a geographic gap in our reports for *M. senile* in Argentina in the area between ~49° S and ~55° S. Therefore, the arrival of this species in the Beagle Channel and Ushuaia may have originated in Chile, as this species has been spreading and increasing its abundance in northern, central and southern Patagonia (Häussermann et al. 2022). Although the absences in certain areas from Argentina can be also

explained due to biases in ecological or taxonomic sampling design, there is a consistent dispersal pattern over time.

The affinity of *M. senile* for artificial substrate is well-known, including pontoons, shipwrecks, pilings, etc. (Hiscock et al. 2010; Nelson and Craig 2011). In North Patagonian gulfs, this species thrives in artificial habitats but it is not as abundant in natural reefs (N. Battini pers. obs.). This concurs with our findings that dense populations of *M. senile* are mostly found on artificial rather than natural substrates. Either due to substrate availability, surface slope, biotic interactions or modified hydrodynamics, *M. senile* is the dominant sea anemone on artificial substrates, reaching extremely high abundances (Martin et al. 2015) that are not easily observed in natural rocky reefs. This prevalence in artificial environments in Argentina is characteristic of many marine non-native species (*Criterion 5* by Chapman and Carlton 1991), such as ascidians, bryozoans, hydrozoans, etc. However, in Chile there is evidence that this species is forming large patches with high abundance on natural substrate (Molinet et al. 2022). As long as suitable hard substrate is available and conditions are within its broad tolerance range, it is relatively straightforward for this species to establish and spread into novel areas (Glon et al. 2020b).

Furthermore, *M. senile* has other traits to be a rampant, successful invader in Argentina from a biological standpoint. It has the ability to either reproduce asexually under favorable conditions or undergo seasonal sexual reproduction, which contributes to the potential rapid growth of a population (Lombardi and Lesser 2010; Glon et al. 2019). Interestingly, invasive sea anemones mostly reproduce asexually in their non-native range (e.g., *D. lineata*, *Exaiptasia diaphana*, as discussed in Glon et al. 2020b; Gimenez and Brante 2021). This "reduction" in reproductive strategies to exclusively asexual reproduction might also be true for *M. senile* in Argentina. While sexual reproduction has not yet been reported in the non-native range, the high abundance and morphological variability in Argentina suggests two potential hypotheses for future studies: *M. senile* is indeed reproducing sexually, or there have been multiple introductions from different source areas. The latter was reported for a number of marine species such as *Cyclope neritea* (Bachelet et al. 2004), *Mnemiopsis leidyi* (Ghabooli et al. 2011) and *Diadumene lineata*

(Newcomer et al. 2019), although it may be a much more common process than currently acknowledged (Roman 2006).

Another aspect currently unknown is whether *M. senile* might represent a potential threat to native communities or economic activities in Argentina as it can dominate patches in high abundance, especially in artificial habitats such as steel piles and artificial reefs (Martin et al. 2015; this study). In Chile, its presence and high abundance in certain regions have been associated with a lower abundance of commercially relevant species such as sea urchins and a lower species diversity of the benthic community in general (Häussermann et al. 2022; Molinet et al. 2022). This situation has caused concerns among local fishermen who now encounter large patches of this non-native sea anemone instead of their target species, urging for management actions (Häussermann and Försterra 2009; Molinet et al. 2022). In contrast, in Argentina there is no evidence suggesting that *M. senile* is currently or potentially interfering with local fisheries. This could be due to the differences in the types and targets of fisheries, or either a perception driven by the long-lasting presence of *M. senile* in some areas, coupled with its unrecognized status as an invasive species. In any case, our work highlights the importance of regional non-native species assessments as a means to prevent their spread and introduction to nearby regions. Once introduced, control and eradication actions are highly costly and challenging. Any future management initiatives aimed to prevent or control this species will definitely need further biological and ecological information from the many populations in the region.

Overall, the plausible high abundance and asexual reproduction of certain non-native populations, along with their long persistence in the area, suggest that *M. senile* has successfully established in Argentina. However, a suspected historical record places *M. senile* in areas where it is now seemingly absent (southern Buenos Aires, as *P. pehuensis*). Similarly, another suspected record from Chile (as *S. lobata*, synonymized with *A. lobata?*) was reported in the 1890s, but during the late 1990s and early 2000s it was reported as absent (Häussermann and Försterra 2005). These suspected records might represent mistaken identifications, signs of population expansion and retractions, or an invasion failure (i.e., the

failure of the species to successfully establish self-sufficient populations in the area). Future genetic analyses may bring new insights to better understand the invasion of *M. senile* in South America, for example, answering whether the current distribution results from a single or multiple introduction events. Glon et al. (2020a) have already found two introduction events in the Islas Malvinas/Falkland Islands. Likewise, the different dispersal patterns in Chile (Häussermann et al. 2022) and Argentina (this study) suggest that there might have been at least two different successful introduction events, an older one in Argentina and a more recent one in Chile which might be now merging in the southern tip of Tierra del Fuego.

Concluding remarks

Metridium senile is a non-native species in Argentina and has successfully established populations in multiple locations. This sea anemone combines different traits as an invader: broad tolerance to abiotic factors, dense abundance associated with artificial habitats in enclosed areas connected by human activities (local and international maritime traffic), high asexual reproduction rates, and wide dispersal potential. Suspected records suggest that its introduction to Argentina could have happened in the late 1890s, but confirmed records only date back to the late 1960s. Recent reports showed a northward and southward spread pattern along the Argentine coast, with a current distribution of over 2000 km and potential to expand. Different biological and ecological aspects of *M. senile* populations in Argentina should be assessed to better understand the factors accounting for its invasion success as many populations seem to be persisting and thriving. Monitoring efforts should determine whether recent populations will establish or fail, and hopefully early detect and prevent novel introductions in those areas at risk according to our species distribution model. Lastly, many questions remain, mainly whether this species is reproducing sexually, whether it represents a threat to the native communities, and how populations are connected within Argentina and with other non-native and native regions.

References

Acuña FH, Cortés J, Garese A, González-Muñoz R (2020) The sea anemone *Exaiptasia diaphana* (Actiniaria: Aiptasiidae) associated to rhodoliths at Isla del Coco National Park, Costa Rica. Rev Biol Trop 68:S283–S288. https://doi.org/10.15517/rbt.v68iS1.41191

Assis J, Tyberghein L, Bosch S et al (2018) Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Glob Ecol Biogeogr 27:277–284. https://doi.org/10.1111/geb.12693

Bachelet G, Simon-Bouhet B, Desclaux C, Garcia-Meunier P, Mairesse G, de Montaudouin X, Raigné H, Randriambao

K, Sauriau PG, Viard F (2004) Invasion of the eastern Bay of Biscay by the nassariid gastropod *Cyclope neritea*: origin and effects on resident fauna. Mar Ecol Prog Ser 276:147–159. https://doi.org/10.3354/meps276147

Bailey SA, Brown L, Campbell ML et al (2020) Trends in the detection of aquatic non-indigenous species across global marine, estuarine and freshwater ecosystems: a 50-year perspective. Divers Distrib 26:1780–1797. https://doi.org/10.1111/ddi.13167

Battini N, Giachetti CB, Castro KL et al (2021) New invasive predator reduces the abundance of native prey in a cold-temperate marine fouling community. Aquat Conserv Mar Freshw Ecosyst 31:2842–2854. https://doi.org/10.1002/aqc.3681

Bravo G, Livore JP, Battini N et al (2021) Rocky reef biodiversity survey: Punta Pardelas, Argentina. Biodivers Data J 9:e72081. https://doi.org/10.3897/BDJ.9.e72081

Carlgren O (1899) Zoantharien. Hambg Magalhaensische Sammelreise 4:1–48

Carlgren O (1933) Zoantharia and actiniaria: the godthaab expedition 1928. Medd Gronland 79:1–55

Carlgren O (1936) Some west American sea anemones. J Wash Acad Sci 26:16–23

Carlgren O (1949) A survey of the Ptychodactiaria, Corallimorpharia and Actiniaria. Kungl Svenska Vetenskapsakademiens Handlingar, pp 1–121

Carlton JT (2003) Community assembly and historical biogeography in the North Atlantic Ocean: the potential role of human-mediated dispersal vectors. In: Jones MB, Ingólfsson A, Ólafsson E et al (eds) Migrations and dispersal of marine organisms. Springer, Dordrecht, pp 1–8

Carlton JT (2009) Deep invasion ecology and the assembly of communities in historical time. In: Rilov G, Crooks JA (eds) Biological invasions in marine ecosystems. Springer, Berlin Heidelberg, pp 13–56

Castro KL, Battini N, Giachetti CB et al (2021) Early detection of marine invasive species following the deployment of an artificial reef: Integrating tools to assist the decision-making process. J Environ Manag 297:113333. https://doi.org/10.1016/j.jenvman.2021.113333

Chapman JW, Carlton JT (1991) A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). J Crustac Biol 11:386–400. https://doi.org/10.2307/1548465

Chapman D, Pescott OL, Roy HE, Tanner R (2019) Improving species distribution models for invasive non-native species with biologically informed pseudo-absence selection. J Biogeogr 46:1029–1040. https://doi.org/10.1111/jbi.13555

den Hartog JC, Ates RML (2011) Actiniaria from Ria de Arosa, Galicia, northwestern Spain, in the Netherlands Centre for Biodiversity Naturalis, Leiden. Zool Meded 85:11–53

Derviche P, Saucsen A, Spier D, Lana P (2021) Distribution patterns and habitat suitability of the non-native brittle star *Ophiothela mirabilis* Verrill, 1867 along the Western Atlantic. J Sea Res 168:101994. https://doi.org/10.1016/j.seares.2020.101994

Dons C (1945) Norges strand fauna XXXII Hexakoraller. Kongelige nor Vidensk Selsk Forh 18:17–20

Dormann CF, Schymanski SJ, Cabral J et al (2012) Correlation and process in species distribution models: bridging a dichotomy. J Biogeogr 39:2119–2131. https://doi.org/10.1111/j.1365-2699.2011.02659.x

Fautin DG (2016) Catalog to families, genera, and species of orders Actiniaria and Corallimorpharia (Cnidaria: Anthozoa). Zootaxa 4145:1–449. https://doi.org/10.11646/zootaxa.4145.1.1

Fautin DG, Malarky L, Soberón J (2013) Latitudinal diversity of sea anemones (Cnidaria: Actiniaria). Biol Bull 224:89–98. https://doi.org/10.1086/BBLv224n2p89

Ghabooli S, Shiganova TA, Zhan A et al (2011) Multiple introductions and invasion pathways for the invasive ctenophore *Mnemiopsis leidyi* in Eurasia. Biol Invasions 13:679–690. https://doi.org/10.1007/s10530-010-9859-8

Giachetti CB, Battini N, Bortolus A et al (2019) Macropredators as shapers of invaded fouling communities in a cold temperate port. J Exp Mar Biol Ecol 518:151177. https://doi.org/10.1016/j.jembe.2019.151177

Gimenez LH, Brante A (2021) Do non-native sea anemones (Cnidaria: Actiniaria) share a common invasion pattern?—A systematic review. Aquat Invasions 16:365–390. https://doi.org/10.3391/ai.2021.16.3.01

Gimenez LH, Rivera RJ, Brante A (2022) One step ahead of sea anemone invasions with ecological niche modeling: potential distributions and niche dynamics of three successful invasive species. Mar Ecol Prog Ser 690:83–95. https://doi.org/10.3354/meps14044

Glon H, Haruka Y, Daly M, Nakaoka M (2019) Temperature and salinity survival limits of the fluffy sea anemone, *Metridium senile* (L.), in Japan. Hydrobiologia 830:303–315. https://doi.org/10.1007/s10750-018-3879-2

Glon H, Costa M, de Lecea A et al (2020a) First record of the plumose sea anemone, *Metridium senile* (Linnaeus, 1761), from the Falkland Islands. BioInvasions Rec 9:461–470. https://doi.org/10.3391/bir.2020.9.3.02

Glon H, Daly M, Carlton JT et al (2020b) Mediators of invasions in the sea: life history strategies and dispersal vectors facilitating global sea anemone introductions. Biol Invasions 22:3195–3222. https://doi.org/10.1007/s10530-020-02321-6

Glon H, Quattrini A, Rodríguez E et al (2021) Comparison of sequence-capture and ddRAD approaches in resolving species and populations in hexacorallian anthozoans. Mol Phylogenet Evol 163:107233. https://doi.org/10.1016/j.ympev.2021.107233

Glon H, Häussermann V, Brewin PE, Brickle P, Kong S, Smith ML, Daly M (2023) There and back again: the unexpected journeys of *Metridium* de Blainville, 1824 between the old oceans and throughout the modern world. Biol Bull. In press

Griffiths CL, Kruger LM, Smith CE (1996) First record of the sea anemone *Metridium senile* from South Africa. Afr Zool 31:157–158. https://doi.org/10.1080/02541858.1996.11448407

Haller S, Vezub JE (2018) Interoceanic connections of the 19th century Patagonian coast: maritime history background. Anuario IEHS 33:15–38

Hand C (1955) The sea anemones of Central California, Part III. The acontiarian anemones. Wasmann J Biol 13:186–251

Häussermann V (2004) Identification and taxonomy of soft-bodied hexacorals exemplified by Chilean sea anemones; including guidelines for sampling, preservation and examination. J Mar Biol Assoc UK 84:931–936. https://doi.org/10.1017/S0025315404010215h

Häussermann V (2006) Biodiversity of Chilean sea anemones (Cnidaria: Anthozoa): distribution patterns and zoogeographic implications, including new records for the fjord region. Investig Mar 34:23–35. https://doi.org/10.4067/s0717-71782006000200003

Häussermann V, Försterra G (2001) A new species of sea anemone from Chile, *Anemonia alicemartinae* n sp (Cnidaria: Anthozoa). An invader or an indicator for environmental change in shallow water? Org Divers Evol 1:211–224. https://doi.org/10.1078/1439-6092-00018

Häussermann V, Försterra G (2005) Distribution patterns of Chilean shallow-water sea anemones (Cnidaria: Anthozoa: Actiniaria, Corallimorpharia); with a discussion of the taxonomic and zoogeographic relationships between the actinofauna of the South East Pacific, the South West Atlantic and the Antarctic. Sci Mar 69:91–102. https://doi.org/10.3989/scimar.2005.69s291

Häussermann V, Försterra G (2009) Marine benthic fauna of Chilean patagonia. Nature in Focus, Santiago

Häussermann V, Molinet C, Díaz Gómez M et al (2022) Recent massive invasions of the circumboreal sea anemone *Metridium senile* in North and South Patagonia. Biol Invasions. https://doi.org/10.1007/s10530-022-02878-4

Hiscock K, Sharrock S, Highfield J, Snelling D (2010) Colonization of an artificial reef in south-west England—ex-HMS 'Scylla.' J Mar Biol Assoc UK 90:69–94. https://doi.org/10.1017/S0025315409991457

Hoffmann RJ (1976) Genetics and asexual reproduction of the sea anemone *Metridium senile*. Biol Bull 151:478–488. https://doi.org/10.2307/1540501

Holmes S, Callaway R (2021) Fouling communities and non-native species within five ports along the Bristol Channel, South Wales, UK. Estuar Coast Shelf Sci 252:107295. https://doi.org/10.1016/j.ecss.2021.107295

iNaturalist (2022) Available from https://www.inaturalist.org. Accessed 13 Jan 2022

Lauretta D, Rodríguez E, Penchaszadeh PE (2011) A new vermiform sea anemone (Anthozoa: Actiniaria) from Argentina: *Harenactis argentina* sp. nov. Zootaxa 3027:9–18. https://doi.org/10.11646/zootaxa.3027.1.2

Lombardi MR, Lesser MP (2010) The annual gametogenic cycle of the sea anemone *Metridium senile* from the gulf of maine. J Exp Mar Biol Ecol 390:58–64. https://doi.org/10.1016/j.jembe.2010.04.004

López-Farrán Z, Guillaumot C, Vargas-Chacoff L et al (2021) Is the southern crab *Halicarcinus planatus* (Fabricius, 1775) the next invader of Antarctica? Glob Change Biol 27:3487–3504. https://doi.org/10.1111/gcb.15674

Manuel RL (1981) British Anthozoa. Linnean Society of London and the Estuarine and Brackish-water Sciences Association. Academic Press, London

Martin JP, Garese A, Sar A, Acuña FH (2015) Fouling community dominated by *Metridium senile* (Cnidaria: Anthozoa: Actiniaria) in Bahía San Julián (southern Patagonia, Argentina). Sci Mar 79:211–221. https://doi.org/10.3989/scimar.04082.21a

Molinet C, Häussermann V, Astorga M, Barahona N, Espinoza K, Diaz M, Díaz P, Henríquez J, Matamala T, Soto D (2022) Population expansion of the invasive sea anemone *Metridium senile* in the spatial mesoscale of a sea urchin bed in north-western Patagonia. Biol Invasions. https://doi.org/10.1007/s10530-022-02965-6

Nelson ML, Craig SF (2011) Role of the sea anemone *Metridium senile* in structuring a developing subtidal fouling community. Mar Ecol Prog Ser 421:139–149. https://doi.org/10.3354/meps08838

Newcomer K, Flenniken MM, Carlton JT (2019) Home and away and home again: discovery of a native reproductive strategy of the globally invading sea anemone *Diadumene lineata* (Verrill, 1869) in a satellite population. Biol Invasions 21:1491–1497. https://doi.org/10.1007/s10530-019-01940-y

Olivier SR, Kreibhom de Paternoster I, Bastida R (1966) Estudios biocenóticos en las costas de Chubut (Argentina) I. Zonación biocenológica de Puerto Pardelas (Golfo Nuevo). Bol Inst Biol Mar 10:1–73

Östman C, Kultima JR, Roat C, Rundblom (2010a) Acontia and mesentery nematocysts of the sea anemone *Metridium senile* (Linnaeus, 1761) (Cnidaria: Anthozoa). Sci Mar 74(3):483–497. https://doi.org/10.3989/scimar.2010.74n3483

Östman C, Kultima JR, Wong SYG (2010b) Dart formation in nematocysts of the sea anemone *Metridium senile* (Linnaeus, 1761) (Cnidaria: Anthozoa). Sci Mar 74(3):499–510. https://doi.org/10.3989/scimar.2010.74n3499

Östman C, Kultima JR, Roat C (2010c) Tentacle cnidae of the sea anemone *Metridium senile* (Linnaeus, 1761) (Cnidaria: Anthozoa). Sci Mar 74(3):511–521. https://doi.org/10.3989/scimar.2010.74n3511

Patris S, Martin LE, Bell LJ, Dawson MN (2019) Expansion of an introduced sea anemone population, and its associations with native species in a tropical marine lake (Jellyfish Lake, Palau). Front Biogeogr 11:e41048. https://doi.org/10.21425/f5fbg41048

Pederson J, Carlton J, Bastidas C et al (2021) 2019 Rapid Assessment Survey of marine bioinvasions of southern New England and New York, USA, with an overview of new records and range expansions. BioInvasions Rec 10:227–237. https://doi.org/10.3391/bir.2021.10.2.01

Pereira AM, Silva MM, Mateus O (2022) First record of *Phymactis papillosa* (Lesson, 1830), a Pacific south sea anemone in European shores. J Mar Biol Assoc UK 102:1–4. https://doi.org/10.1017/S0025315422000571

R Core Team (2022) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/

Riemann-Zürneck K (1975) Actiniaria des südwestatlantik. Helgol Wiss Meeresunters 27:70–95. https://doi.org/10.1007/BF01611687

Robinson TB, Swart C (2015) Distribution and impact of the alien anemone *Sagartia ornata* in the West Coast National Park. Koedoe 57:1246. https://doi.org/10.4102/koedoe.v57i1.1246

Rodríguez E, Barbeitos M, Daly M et al (2012) Toward a natural classification: phylogeny of acontiate sea anemones (Cnidaria, Anthozoa, Actiniaria). Cladistics 28:375–392. https://doi.org/10.1111/j.1096-0031.2012.00391.x

Rodríguez E, Fautin D, Daly M (2022) World list of actiniaria. Available from https://www.marinespecies.org/. Accessed 8 June 2022

Roman J (2006) Diluting the founder effect: cryptic invasions expand a marine invader's range. Proc R Soc B Biol Sci 273(1600):2453–2459. https://doi.org/10.1098/rspb.2006.3597

Sbrocco EJ, Barber PH (2013) MARSPEC: ocean climate layers for marine spatial ecology. Ecology 94:979–979. https://doi.org/10.1890/12-1358.1

Schwindt E, Carlton J, Orensanz J et al (2020) Past and future of the marine bioinvasions along the Southwestern Atlantic. Aquat Invasions 15:11–29. https://doi.org/10.3391/ai.2020.15.1.02

Stephenson TA (1935) The British sea anemones, vol II. The Ray Society, London

Thuiller W, Lafourcade B, Engler R, Araújo MB (2009) BIO-MOD—a platform for ensemble forecasting of species distributions. Ecography 32:369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x

Tyberghein L, Verbruggen H, Pauly K et al (2012) Bio-ORA-CLE: a global environmental dataset for marine species distribution modelling. Glob Ecol Biogeogr 21:272–281. https://doi.org/10.1111/j.1466-8238.2011.00656.x

Watkins HV, Yan HF, Dunic JC, Côté IM (2021) Research biases create overrepresented "poster children" of marine invasion ecology. Conserv Lett 14:e12802. https://doi.org/10.1111/conl.12802

Zabin CJ, Zardus J, Pitombo FB et al (2007) A tale of three seas: consistency of natural history traits in a Caribbean-Atlantic barnacle introduced to Hawaii. Biol Invasions 9:523–544. https://doi.org/10.1007/s10530-006-9056-y

Zaixso HE, Sar AM, Lizarralde ZI, Martin JP (2017) Macrobenthic assemblages with presence of mytilids of San Julián bay (Southern Patagonia, Argentina). Rev Biol Mar Oceanogr 52:311–323. https://doi.org/10.4067/S0718-19572017000200010

Zamponi MO (1978) Sobre la anémona *Paraisometridium pehuensis*, gen. y sp. nov. (Actiniaria: Metridiidae). Neotropica 24:117–122