

Review

Do non-native sea anemones (Cnidaria: Actiniaria) share a common invasion pattern? – A systematic review

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Abstract

A number of cnidarian species are known to have become marine invaders across a diversity of regions and habitats, including sea anemones of the order Actiniaria. Unfortunately, integrative approaches to identify and describe general patterns and likely drivers of their invasion process have only been of recent interest. The goal of this systematic review is to summarize and categorize the literature published on non-native populations of sea anemone species and to assess whether these records exhibit a shared common invasion pattern. A total of 126 articles were analyzed, in which 11 species presented records of suspected non-native populations. Our results showed that sea anemone invasions date back to at least the late 1890s and new introductions have recently been reported for different species in the last five years. Some potential biases in the literature were found in relation to species, marine realms and study approaches. Most study efforts have been focused on a single species (*Diadumene lineata*), especially in the Temperate Northern Atlantic. A seemingly common shared pattern was found and described throughout all stages of the invasion continuum, but more effort should be focused on the less reported/studied species. Transport has mainly been mediated by human-associated vectors, such as maritime traffic and aquaculture. Newly arrived individuals colonize mostly natural habitats, although some species thrive in human-made habitats. A diverse array of traits has been associated with the invasion success of sea anemones, although the two most frequently reported traits in the literature were abiotic tolerance and the reproductive strategies. Unlike other benthic invaders, the dispersal mechanisms (both primary and secondary spread) and the ecological or economic consequences produced by non-native sea anemone populations have been little explored and thus need more attention. We discuss potential ways to reduce some of the gaps and research biases found and thus develop a better understanding of the invasion ecology of sea anemones.

Key words: *Anemonia*, *Diadumene*, ecological effects, *Exaiptasia*, invasion ecology, marine realm, *Metridium*, *Nematostella*, *Sagartia*

Introduction

Non-native marine species are associated with negative ecological and economic effects (Ruiz et al. 2000; Pimentel et al. 2001; Carlton et al. 2019). These species may reach new communities through natural dispersal

mechanisms (i.e. range expansions) or associated with human activities (i.e. introductions), such as maritime traffic and aquaculture (Carlton 1987; Molnar et al. 2008). Preventing the introduction and establishment of non-native marine species seems to be the most efficient way to avoid the potential damages and costs associated with biological invasions (Floerl et al. 2005 and references therein). Unfortunately, poor baseline reports on the native diversity in addition to an absence of historical records on non-native species has led to underestimations of the number of non-native marine species present in a given area (see Carlton 2009). In addition, non-native populations of some taxonomic groups, such as fishes and cnidarians, have been less studied in comparison to those of other taxa, such as mollusks, ascidians or algae (Molnar et al. 2008).

Cnidarian species are frequently introduced in areas far from their native ranges, expanding rapidly due to their sexual and asexual reproductive strategies (see González-Duarte et al. 2016 and references therein for different examples). Some species have been successfully transported on ship hulls, on natural or human-made flotsam helped by currents, or in association with fauna in aquaculture (Grizel and Heral 1991; Carlton and Hodder 1995; Gollasch and Riemann-Zürneck 1996; Hoeksema et al. 2012). Non-native populations have become established in human-made and natural habitats, frequently as a result of secondary spread (Sammarco et al. 2004, 2010; Canales-Aguirre et al. 2015; Pinochet et al. 2019).

Within the phylum Cnidaria, sea anemones of the order Actiniaria are important members of benthic communities (see Shick 1991), playing a variety of ecological roles and becoming dominant in some habitats (Häussermann and Försterra 2005). At least 12 non-native sea anemone species have been reported worldwide (González-Duarte et al. 2016). As a group, sea anemones show adaptive traits that promote their invasion success, including a high dispersal potential, high asexual reproduction rate, and broad tolerance to environmental conditions (Glon et al. 2020b). When established, sea anemones can affect the native communities they invade. For instance, *Exaiptasia diaphana* Rapp, 1829 (often referred to as *E. pallida* or *Aiptasia pallida*) dominated a marine lake within the first six years of its arrival, and the increase in its abundance was negatively correlated with native benthic components, such as sponges and algae (Patris et al. 2019).

In spite of the importance of sea anemones as invader species in the marine realm, their general invasion patterns have only recently begun to be studied. In their recent review, Glon et al. (2020b) explored life history traits that could promote the introduction and establishment of non-native populations of ten selected sea anemone species. In addition, they provided updated information regarding the native and non-native distributions of the studied species. This contribution represents the first step towards a better understanding of sea anemone invasions. However, a more systematic revision is needed to unmask the main gaps in our current knowledge

regarding the invasion process of sea anemones, which must be addressed in the future. This systematic revision must collect, review, categorize and summarize all of the available information on non-native sea anemone species in order to visualize the aspects of their invasion ecology that have been of greatest interest, and reveal the main biases of the research effort.

Here, a systematic review on non-native sea anemone species is conducted in order to achieve the following goals: (1) to summarize and categorize the published literature, (2) to identify the main vectors and dispersal mechanisms related to their invasion (natural or human associated), (3) to characterize ecological or economic effects of invader anemones, and (4) to identify main biological traits associated with their invasion success.

Materials and methods

A literature search on invasion topics focused on sea anemones was conducted in June 2020 using the Web of Science Core Collection and SCOPUS. The search expression was stated as follows: (anemone OR actiniari*) AND (invasi* OR invader OR “introduced species” OR “non-native” OR “non native” OR “non-indigenous” OR “non indigenus” OR alien OR exotic OR “naturalized species” OR “naturalised species” OR “established species” OR cryptogenic OR cosmopolitan) AND (sea OR seawater OR ocean OR marine OR estuar* OR brackish). Only articles in English were considered; books or book chapters were excluded.

The metadata of all of the articles found was exported to the Zotero software (free access at <https://www.zotero.org>). Duplicated articles were eliminated and then each abstract was screened to determine its suitability. Studies carried out in marine or estuarine systems were included but those in which species level identification was not specified were excluded (e.g. *Bonodeopsis* sp., *Aiptasia* sp.) to isolate records with taxonomic certainty. When the taxonomic classification of a given non-native sea anemone has changed over time (e.g. *Diadumene lineata*; Hancock et al. 2017), its scientific name was updated to the one currently accepted according to the World Register of Marine Species (WoRMS, <http://www.marinespecies.org>). If two or more non-native sea anemones were considered in the same article, they were classified as “Multispecies”. If the focal species was used as a biological model system (e.g. evolutionary and developmental studies in *Nematostella vectensis*; Reitzel et al. 2012), the article was excluded, unless it included some aspects relevant to the invasion process. Studies carried out on laboratory culture lines of a given species were also excluded, unless the exact location of the population of origin was stated.

The search was amplified with a backward and forward reference searching. Going backward allowed for the incorporation and analysis of relevant articles cited by those found and selected with the search expression. Whereas going forward allowed for the inclusion of relevant articles citing those found and selected with the search expression. These incorporated

articles were searched using the Web of Science and SCOPUS platforms to quickly screen, select and find relevant information. Those articles not included in the Web of Science or SCOPUS were searched in Google Scholar. This procedure was performed once, meaning there was no going backward nor forward in those articles that were included with the amplified search. In addition, articles cited by two previous reviews, one on invasive cnidarians in general (González-Duarte et al. 2016) and another on invasive sea anemones of the order Actiniaria in particular (Glon et al. 2020b), were also screened and selected if they were suitable for the analysis.

Once an article was included in the analysis, relevant information was obtained and categorized as described below. The native/non-native status of the sea anemones was categorized according to the geographic location of the populations and complementary literature (distribution maps from Glon et al. 2020b). Invasion status was characterized according to the stages proposed by Blackburn et al. (2011) as introduced, naturalized or invasive (see Table 1 for definitions). This approach has been applied in other studies on invasion ecology (Villaseñor-Parada et al. 2017; Pereyra and Ocampo Reinaldo 2018; Figueroa López and Brante 2020; Glon et al. 2020b). When the invasion category was unclear, it was recorded as undetermined (i.e. NA). Each article was also classified according to its study approach: first report, taxonomic studies, population level studies, experimental, interactions, community level studies, genetic studies, physiological studies, modelling, review and others (see Table 1 for more details). A given article could be considered for two or more study approach categories.

For each study, the environmental system was noted and categorized as marine and/or estuarine; whether samples were recorded from natural (e.g. rocky shores, tidal pools) and/or human-made substrata (e.g. ship hulls, marinas, ports, docks, etc.) was also documented to categorize the habitat. The location of the invaded sites was registered and then assigned to the respective “marine realm” sensu Spalding et al. (2007). Dispersal mechanisms were classified as natural and/or human-associated, and for anthropic mechanisms the specific vector was noted if it was reported (e.g. maritime traffic, aquaculture). Information on ecological and economic effects of each species was obtained when possible. Here, we used the term “effect” rather than “impact” since the definition of the latter is generally biased and ambiguous (see Chew and Carroll 2011; Davis et al. 2011). If any species trait was demonstrated to be associated with invasion success (sensu Catford et al. 2009), it was classified into one of the following categories: abiotic tolerance, generational time, reproductive strategies, association with microalgae, other interactions, behavior, low substratum selectivity, competitive ability, diet and energy resources, dispersal mechanisms and non-species related (see Table 1 for definitions). When no information was found regarding the systems, habitats, dispersal mechanisms, effects or traits associated with invasion success, those categories were registered as not stated/not evaluated (i.e. NA).

Table 1. Data retrieved from the articles included in the analysis and criteria used for classification.

Data	Category	Definition
Species	One species	Only one sea anemone species is reported/studied.
	Multispecies	Two or more sea anemone species are reported/studied. Species level identifications are registered.
Status (according to Blackburn et al. 2011)	Introduced	The species occurs in an area outside its native range due to human-mediated transportation.
	Naturalized	The species has been introduced and its populations can reproduce and grow.
	Invasive	The species has colonized an area beyond the point of first introduction and it might have ecological or economic effects.
	NA	The information given in the article is not enough to determine the status of the non-native populations.
Marine realm (according to Spalding et al. 2007)	Arctic	Categorical classification of the distribution of each record based on the exact location of the populations.
	Temperate Northern Atlantic	
	Temperate Northern Pacific	
	Western Indo-Pacific	
	Central Indo-Pacific	
	Eastern Indo-Pacific	
	Tropical Eastern Pacific	
	Temperate South America	
	Temperate Southern Africa	
	Temperate Australasia	
NA	The study does not provide information regarding the exact location of samples.	
Approach	First reports	A new record of introduction for a given species or an update of its status.
	Taxonomic studies	Taxonomic descriptions or re-descriptions or broad taxa revisions.
	Population level studies	Aspects of life history (at any life stage) or population structure/dynamics are evaluated. This includes larval drift, recruitment, reproductive biology, growth, and other aspects within the population level.
	Experimental	One or more field or laboratory experiments are carried out.
	Interactions	Aspects of interaction between two or more species, including at least one non-native sea anemone, are explored (e.g. competition, predation, commensalism).
	Community level studies	Community aspects are evaluated (e.g. assemblages, succession, biodiversity estimations).
	Genetic studies	Genetic tools or techniques are applied with a methodologic, taxonomic, biogeographic or evolutive approach.
	Physiological studies	Aspects at individual, inter or intracellular levels are evaluated (e.g. tolerance assessments).
	Modelling	Mathematical, spatial or simulation modelling tools are applied with an ecological approach (e.g. niche assessments).
	Reviews	Conceptual, bibliographical or taxonomic reviews. It also includes literature searches for checklists.
Environment	Other	Other approaches not considered.
	Marine	Coastal (intertidal and subtidal) or oceanic systems.
	Estuarine	Within an estuary or its mouth.
	Both	Marine and estuarine systems.
Habitat	NA	The study does not provide information regarding the environment.
	Natural	Natural substrata (e.g. rocky slopes, tidal pools, marshes).
	Human-made	Human-made substrata or structures (e.g. docks, ports, marinas).
	Both	Natural and human-made substrata.
Dispersal mechanisms	NA	The study does not provide information regarding the type of habitat.
	Natural	The species spread through natural mechanisms such as larvae drift, rafting, oceanic currents, etc.
	Human-associated	The species is transported by human associated activities such as shipping or aquaculture.
	Both	The species spread through natural and human-associated mechanisms.
Effects	NA	The study does not focus on and thus lacks information regarding the spread mechanisms.
	Ecological	The species causes native species displacements, community shifts or ecosystem services disruptions.
	Economic	The presence of the species generates economic losses.
	Both	There are both ecological and economic effects involved with the presence of a given species.
Effects	NA	The study does not focus on and thus lacks information regarding the species effects.

Table 1. (continued).

Data	Category	Definition
Invasion success	Abiotic tolerance	Broad tolerance ranges to at least one environmental variable such as temperature, salinity, oxygen depletion, pH level, etc.
	Reproductive strategies	Sexual or asexual reproductive strategies observed in a given species allow it to grow fast after introduction.
	Generational time	Short generational times (and thus rapid population growth) is present.
	Association with microalgae	Symbiosis with microalgae benefits the non-native sea anemone establishment/spread.
	Other interactions	Interactions other than symbiosis benefit the non-native sea anemone establishment/spread.
	Plasticity	Short-time morphological or physiological changes due to environmental clues.
	Behavior	Aggressive or evasive behavior, low intraspecific competition and other types of behavior that benefit the non-native sea anemone establishment/spread.
	Low substratum selectivity	The non-native anemone thrives attached to a diverse array of substrata.
	Dispersal mechanisms	The species can spread through natural mechanisms.
	Competitive ability	The species outcompetes native species or it avoids being displaced.
	Diet and Energy resources	The species withstands starvation or uses a diverse array of energy sources.
	Non-species related	The invasion success is not associated with the traits of the species. It might be associated with aspects of the community invaded or other factors.
	NA	The study does not focus on and thus lacks information regarding the invasion success.

Results

The search expression detected 114 articles, but only 36 were suitable for the analysis. Articles were mostly excluded because they covered unrelated topics or were carried out within the native range of a known invader. Articles were also excluded if they lacked species level identification or the geographic location of the non-native populations from which culture lines were established. However, the reach of the search was amplified to a total of 126 articles with the application of a reference searching procedure and the incorporation of articles cited by two previous reviews (see Figure 1 for details). Supplementary material Table S1 summarizes all of the data collected.

The first record of a non-native sea anemone species dates back to 1898. The number of articles regarding non-native sea anemones has increased during recent decades (Figure 2). Eleven species with records of suspected non-native populations were found, alphabetically: *Anemonia alicemartinae* Häussermann & Försterra, 2001; *Diadumene cincta* Stephenson, 1925; *D. franciscana* Hand, 1956; *D. leucolena* Verrill, 1866; *D. lineata* Verrill, 1869; *D. paranaensis* Beneti, Stampar, Maronna, Morandini & Da Silveira, 2015; *Exaiptasia diaphana* Rapp, 1829; *Metridium senile* Linnaeus, 1761; *Nematostella vectensis* Stephenson, 1935; *Sagartia elegans* Dalyell, 1848; and *S. ornata* Holdsworth, 1855. Most articles focused on a single species and less than 15% applied a multispecies approach. The most frequently studied anemone was *D. lineata*, followed by *E. diaphana* and *N. vectensis* (Figure 3a). The rest of the species were less represented. In fact, one of them, *D. franciscana*, was only found in multispecies studies.

Non-native sea anemone populations are reported from all marine realms, except in the Arctic and the Southern Ocean (Figure 3b). The Temperate Northern Atlantic was the marine realm with the greatest number of records, followed by the Temperate Northern Pacific and Temperate South

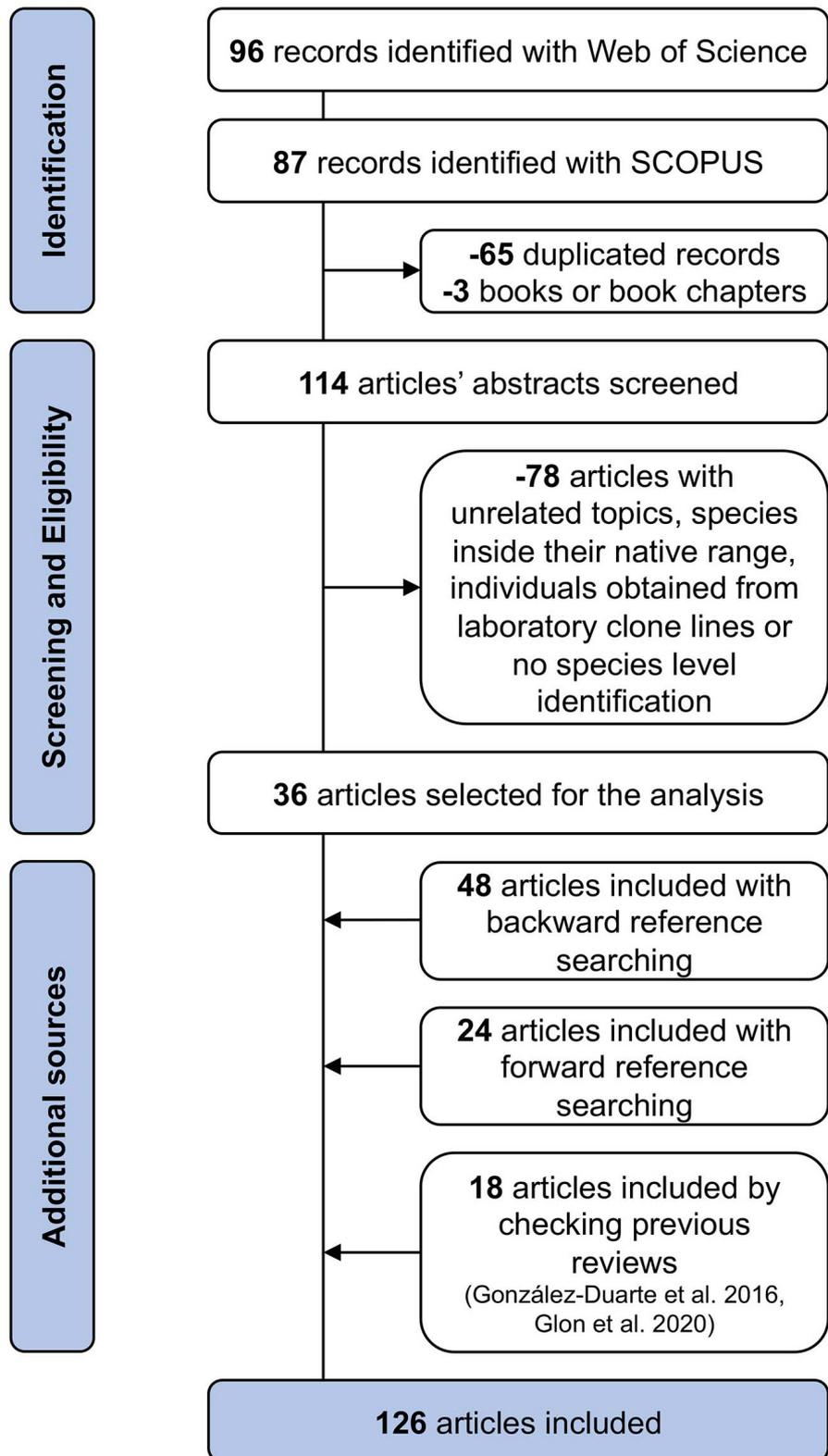


Figure 1. Flow chart detailing the search procedure performed: identification, screening and selection of the analyzed articles.

America. On the contrary, the Western Indo-Pacific and Temperate Australasia were less represented. Diverse study approaches investigating non-native sea anemones were found (Figure 3c). First reports and population level studies were the most represented, followed by experimental and

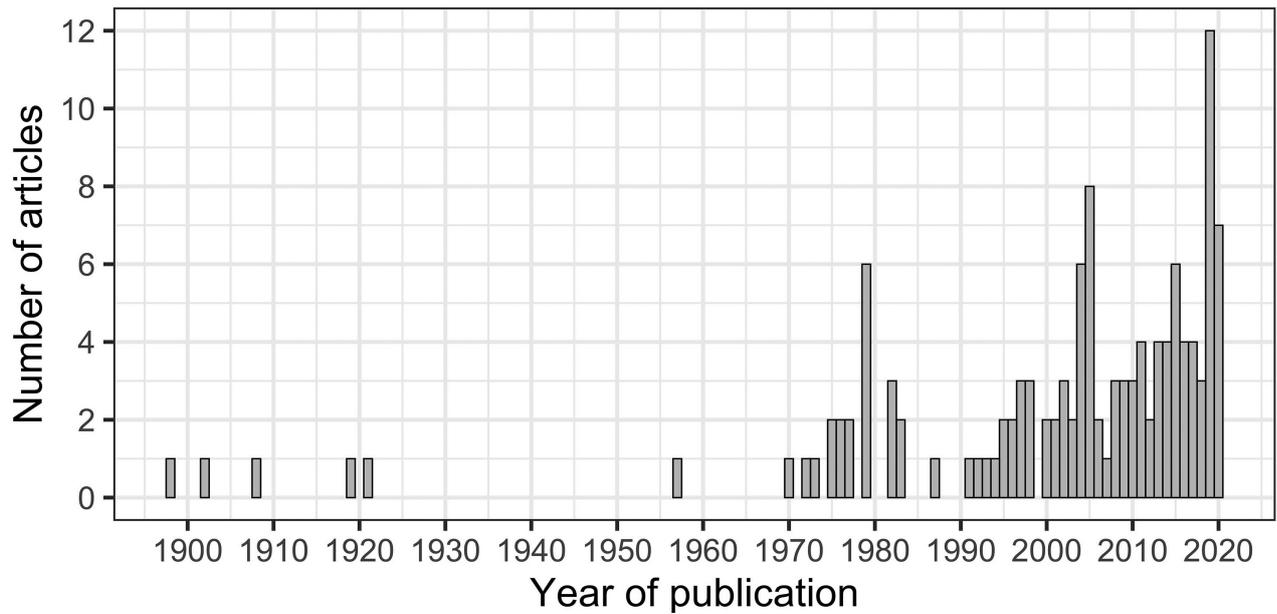


Figure 2. Number of articles published per year. Only studies considered for the analysis are shown. The most recent year (2020) only includes articles published as of August 2020.

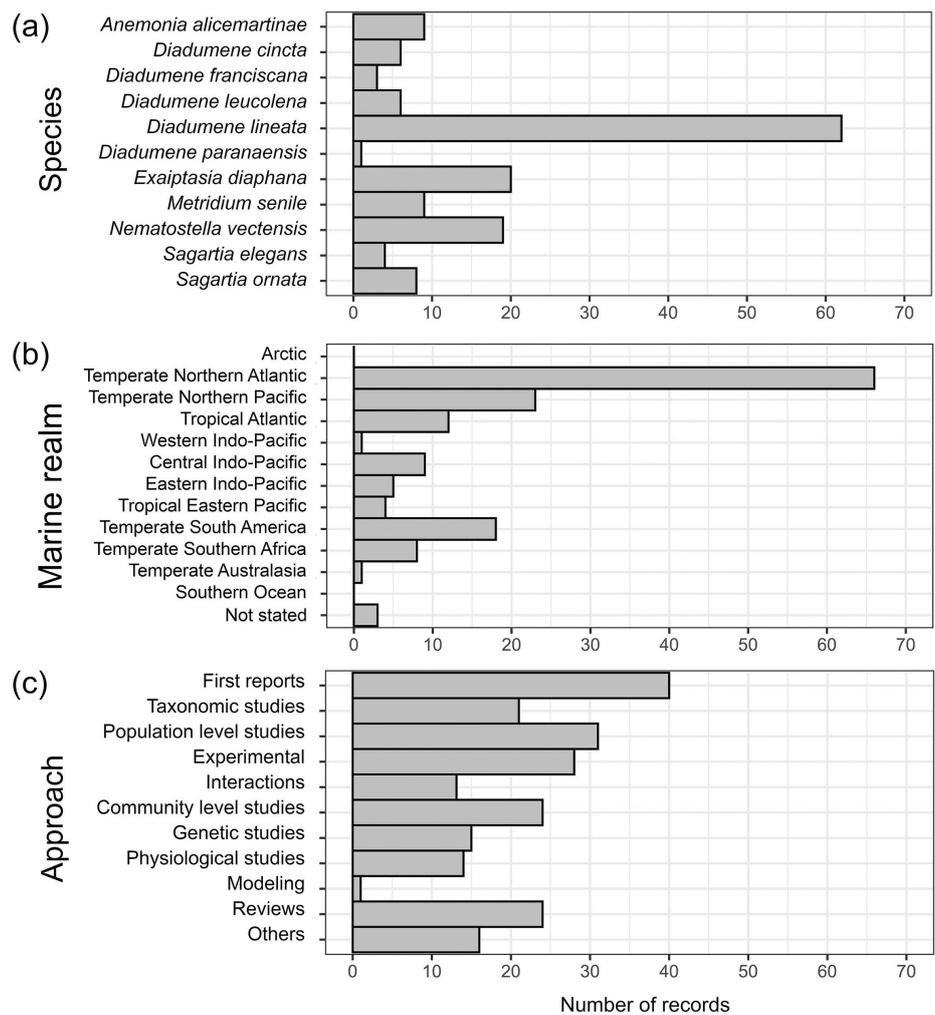


Figure 3. Distribution of the analyzed articles across (a) species, (b) marine realms (sensu Spalding et al. 2007) and (c) study approaches. A given article can represent more than one record.

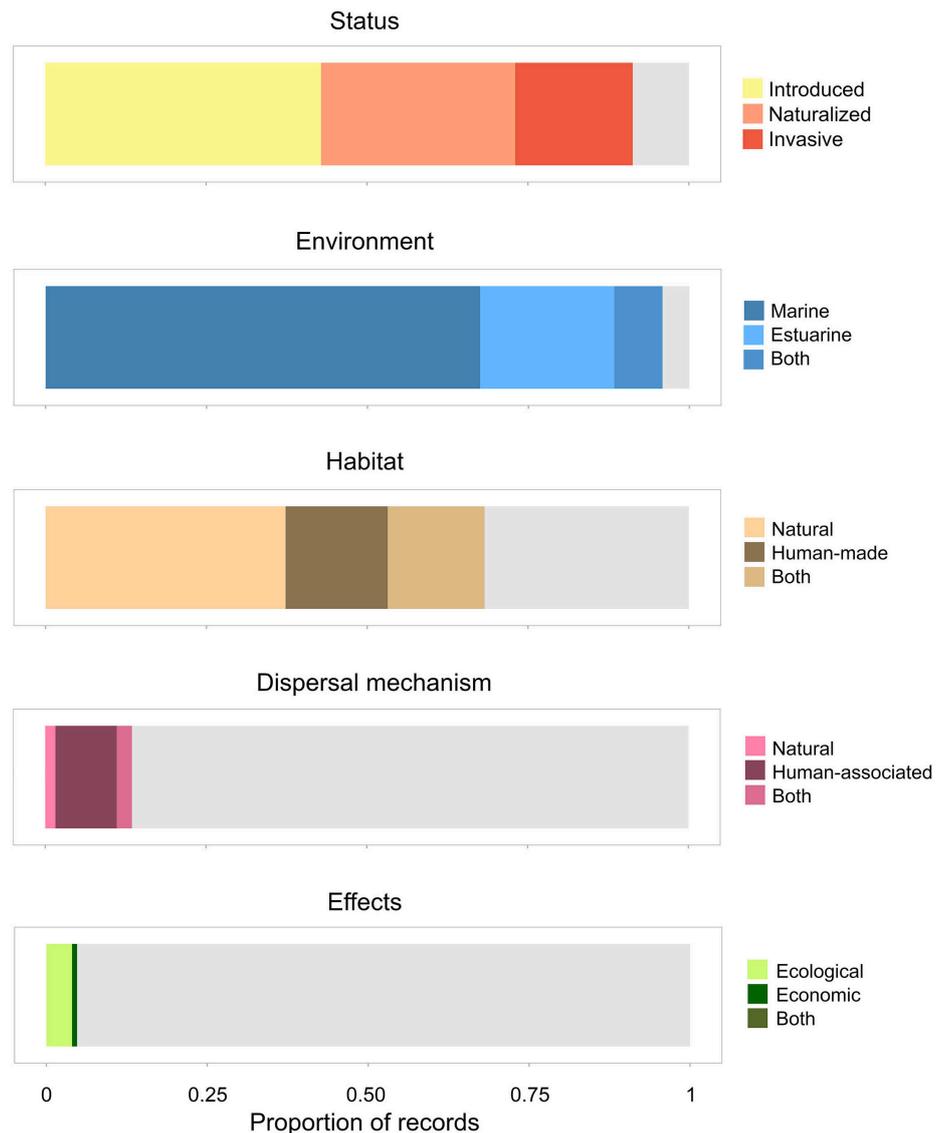


Figure 4. Summary of the common invasion pattern based on the records of all of the suspected non-native sea anemones species included in the analysis. *Status* within the invasion continuum proposed by Blackburn et al. (2011). *Environment* and *Habitat* from which individuals have been collected or reported. *Dispersal mechanisms* involved. *Effects* demonstrated to be associated with their presence. Grey bars represent records with no data for a given category.

community level studies. Reviews were also represented, mostly by non-native species checklists in different geographical areas which were supported by literature searches. Modeling (e.g. ecological niche modeling) was the least represented study approach, with only a single record found. Other approaches that were identified, but not considered in the *a priori* classification included, for instance, biogeographical and behavioral studies.

Most of the records included in our analysis showed that non-native populations were in the introduced or naturalized stages of the invasion continuum, and less than a quarter of the records were in the invasive stage (Figure 4). However, such a pattern may be biased as one species accounted for most of the records (*D. lineata*, Figure 3a). Records were mainly from marine systems, although some species were found in brackish waters. Only

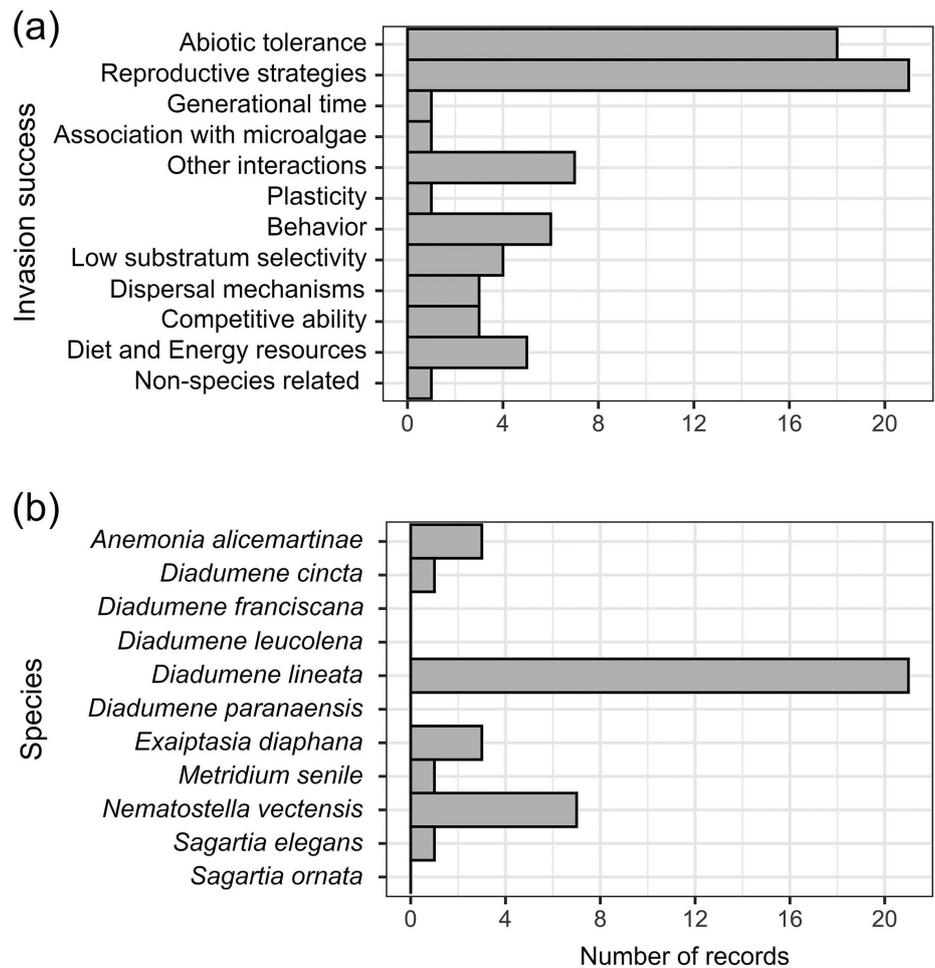


Figure 5. (a) Traits associated with the invasion success of sea anemone species. Only records with relevant information regarding this topic are shown (~ 50%). (b) Number of records per species associating abiotic tolerance or reproductive strategies with invasion success. A given article can represent more than one record.

one species, *N. vectensis*, exclusively inhabited estuaries. The main habitats occupied by non-native sea anemones were natural substrata, including rocky shores and tidal pools with some species inhabiting sandy beaches and marshes. However, some populations were recorded in human-made habitats, such as docks, marinas, offshore oil-platforms, and ship hulls, among others.

Information regarding dispersal mechanisms and effects was less available, with ~ 13% and less than 5% of the articles providing data on these aspects, respectively (Figure 4). Human-associated transport was the most frequently reported dispersal mechanism, with maritime traffic and aquaculture representing the main vectors. The presence of some non-native sea anemones has been linked to negative ecological effects on native communities, but these effects were not well-documented. The main effect seemed to be a decline in native species abundances due to competition or predation pressure. Only one record for a potential economic effect was found, which involved maintenance costs to control fouling on offshore structures.

Abiotic tolerance and reproductive strategies were the two main traits associated with the invasion success of sea anemones (Figure 5a). Non-native

sea anemones have proven to be tolerant to different abiotic stressors, especially temperature, salinity and oxygen depletion. These species reproduce mainly asexually, most of them by longitudinal, transversal fission, or pedal laceration. A diverse array of other traits was also found, including aggressive or evasive behaviors, low substratum selectivity and energy resources to withstand starvation. An interesting aspect was the participation of non-native sea anemones in interactions with oysters, mussels and even halophilic plants (*Spartina* sp.), which was associated with invasion success. Invasion success proved to be unrelated to species traits in only one community, where presumably it was instead driven by the absence of biotic filters (i.e. competitors and predators). However, there seems to be a biased research effort in the assessment of traits associated with invasion success because *Diadumene lineata* accounted for most of the studies that reported either abiotic tolerance or reproductive strategies favoring invasion; the rest of the species were less represented (Figure 5b).

By analyzing the specific cases of the five most studied species, some different geographic patterns arose (Figure 6). Even though *D. lineata* was the most frequently reported and studied non-native anemone, its distribution was clearly biased, with a greater number of records for the Temperate Northern Atlantic compared to other areas. In fact, no records of this species were found for the Western Indo-Pacific, Tropical Eastern Pacific, Temperate Australasia and Temperate Southern Africa. In contrast, the records for *E. diaphana* were fewer, but distributed throughout more marine realms, lacking records only in the Western Indo-Pacific and Temperate Southern Africa. The non-native populations of *N. vectensis* have been mostly reported in the Northern Hemisphere, with only two records for the Southern Hemisphere in the Tropical Atlantic. Interestingly, some species were exclusively non-native to the Southern Hemisphere: *A. alicemartinae*, *M. senile* and *S. ornata* (Figure 6, Table S1).

A diversity of study approaches has been focused on the five most frequently reported species, but the number of records per category is clearly different when comparing cases (Figure 6). For instance, *D. lineata* presented numerous records of studies addressing different aspects of its invasion ecology. In contrast, while different aspects of the invasion ecology of *A. alicemartinae* and *M. senile* have been of interest, the number of records was clearly fewer than those found for *D. lineata*. However, this diversity of approaches could suggest that these species are gaining more attention.

Discussion

This systematic review highlights three main findings: (1) even though the number of articles on non-native sea anemones has increased in recent years, biases and gaps were identified in the published literature; (2) the invasion

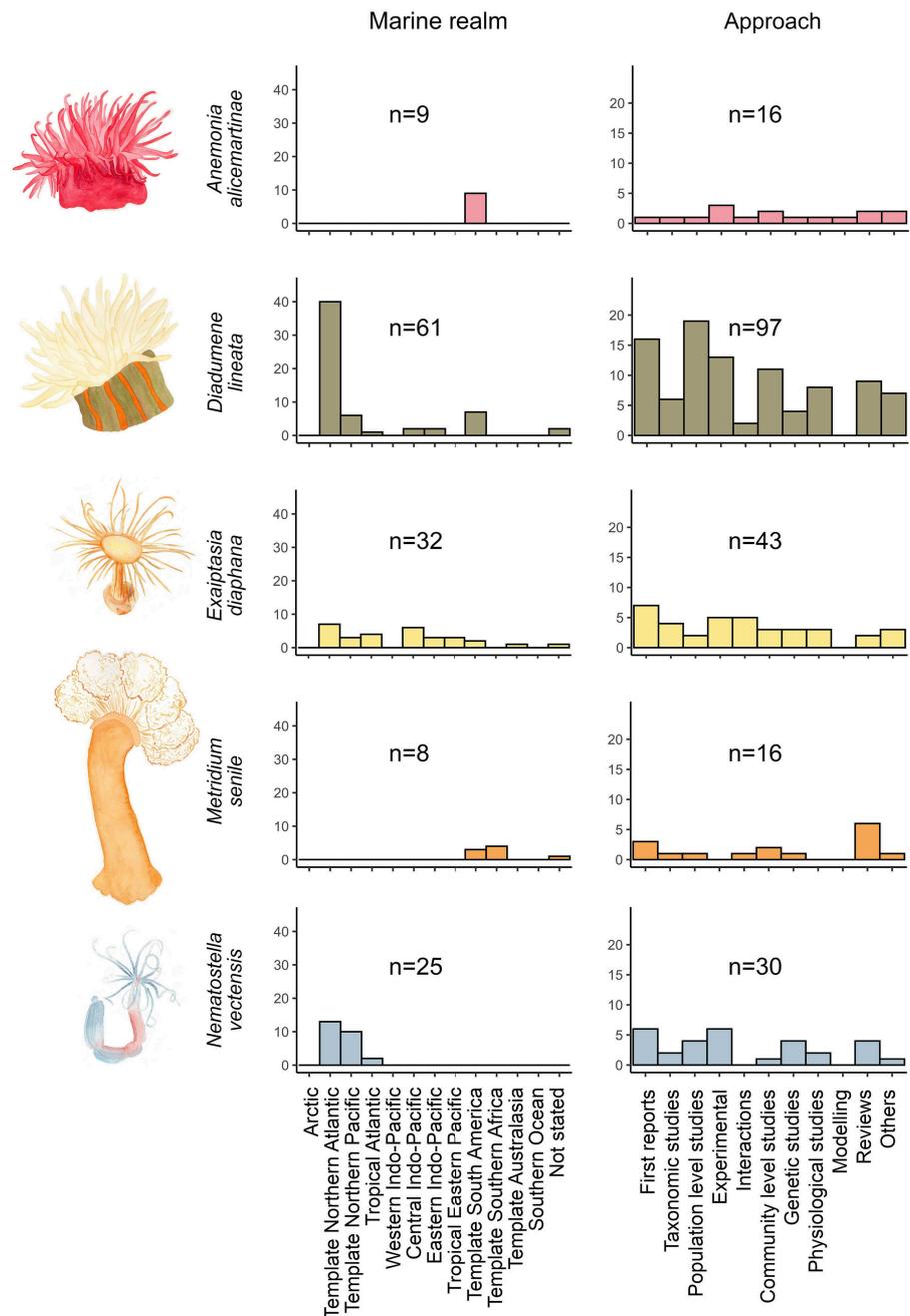


Figure 6. Distribution of records across marine realms (sensu Spalding et al. 2007) and study approaches focused on the five most frequently reported sea anemone species with non-native populations. A given article can represent more than one record. n= Number of total records for each species in the given category.

success of the reported non-native sea anemone populations appears to be mainly associated with a broad abiotic tolerance and asexual reproductive strategies, although this is not certain as few species accounted for the majority of records (especially *D. lineata*); and (3) despite being widely introduced around the world, the dispersal mechanisms (both primary and secondary spread) and the potential ecological or economic consequences of non-native sea anemones have been little explored. In addition, our

review clearly highlights the need to increase the study effort of less represented species and regions in order to unmask the underlying mechanisms of the invasion process of sea anemones, and to implement policies and actions to prevent, mitigate or reduce their likely (but mostly unexplored) negative effects on marine ecosystems.

A total of 11 non-native sea anemone species were found. This result is similar to the number of examples provided by González-Duarte et al. (2016) in their review on invasive cnidarians. However, four species reported by these authors were not considered in this review: *Bunodeopsis* sp., due to taxonomic uncertainty; *Aiptasiomorpha minima*, a synonym for *Exaiptasia diaphana* (WoRMS, <http://www.marinespecies.org>); *Synandwakia hozawai*, whose distributional range has been delimited to Japanese coasts with no information regarding its invasion status (Kostina 2000); and *Cereus pedunculatus*, a species native to the Northeast Atlantic that was not found with our searching procedure. All ten species reviewed by Glon et al. (2020b) were found and considered here. The inclusion of a given non-native species in our analysis was based on the available information retrieved from the selected articles, although the lack of knowledge about most species could have skewed the results and interpretation. For example, whether *A. alicemartinae* and *D. cincta* have been respectively introduced to South America and Europe from another continent or represent range expansions is unknown (see Glon et al. 2020b). The case of *D. franciscana* is another example of little information available because this species has only appeared as part of multispecies studies, along with congeners (especially *D. lineata*). Whether these cases continue to be categorized as non-native sea anemone species in the future will depend on how much more information is developed about the different aspects of their invasion processes. In addition, new species will most likely be reported as non-native in the future.

The study of non-native sea anemones

It has been inferred that sea anemone invasions span great time scales, from historical to recent and ongoing (Glon et al. 2020b). Our results showed that sea anemone invasions date back to at least the late 1890s. New introductions have recently been reported for different species (e.g. *N. vectensis* in Brazil, Brandao et al. 2019; *E. diaphana* in the Galapagos Islands, Carlton et al. 2019; *M. senile* in the Frankland Islands, Glon et al. 2020a). The number of new reports increased when considering the past five years (e.g. Häussermann et al. 2015; Martin et al. 2015; Podbielski et al. 2016; Gusmao et al. 2018). Even though these were new reports, it is unclear whether these introductions occurred recently. In fact, the number of non-native species and populations is likely to be underestimated, both in the literature and in surveys, as has been noted for marine taxa in

general (Carlton 2009). In particular, sea anemones have historically been overlooked in surveys because they are difficult to detect and identify (Glon et al. 2020b). The problematic detection and identification of certain sea anemones could partially explain why some species have been more frequently reported than others. Visual detection and identification are easier in some cases (e.g. *D. lineata*, *M. senile*, *A. alicemartinae*), whereas others must be identified by experts or with genetic tools. In fact, Häussermann and Försterra (2001) argued that the bright red color of *A. alicemartinae* makes it difficult to be ignored by observers; therefore, its recent report along Chilean coasts supports the idea of an invasion phenomenon.

Another issue that could be involved in detecting new records of non-native sea anemones is that most invasive species monitoring programs do not seem to be aimed at or designed to find sea anemones. For instance, Moore et al. (2014) reported a new record for *D. lineata* in Nova Scotia, Canada and mentioned that no further attempt at determining the extension of the species was underway, in spite of the Aquatic Invasive Species (AIS) monitoring program. The chance to detect a new introduction is most likely enhanced once a population has grown to a point where it can easily be seen in the field. Unfortunately, the invasion process is almost impossible to stop at this point of population abundance and secondary spread (as was the case of *E. diaphana* in Jellyfish Lake, Patris et al. 2019). Hopefully, monitoring programs will pay more attention to non-native sea anemones in the future to quickly detect new introductions before populations become dominant.

We evidenced that some marine realms have been more reported/studied than others. According to our results, reports in the Northern Hemisphere are more frequent than in the Southern Hemisphere. This pattern may represent a biased research effort, rather than the “whole picture” of sea anemone invasions. Such a bias could be explained by one or more factors, including: (1) the lack of sea anemone taxonomists and ecologists in some areas; (2) the costs associated with sending samples to experts or using genetic tools for identification, especially in developing countries; and (3) the inaccessibility of some coastal areas. However, the distribution of records shown here could also result from other factors related to the invasion process, such as differences in vector availability, species requirements for establishment and the resistance imposed by the native community.

Three species have been the main focus of interest: *D. lineata*, *E. diaphana* and *N. vectensis*. Two of these species have been used as models for evolution and development (*N. vectensis*, Reitzel et al. 2012) and cnidarian-zooxanthellae symbiosis (*E. diaphana*, Brown et al. 2017; Dungan et al. 2020). This has led to the development of culture lines to explore different aspects of their biology (Stefanik et al. 2013; Tortorelli et al. 2020). Given

the increasing interest in these two species and their close relatives, additional approaches have been applied to define their taxonomic status, population genetic structure and phylogenetic relationships (Darling et al. 2004; Grajales and Rodríguez 2016; Brown et al. 2017). Other species, such as *A. alicemartinae*, *M. senile* and *S. ornata* have only recently gained attention and different aspects of their invasion process are being studied. However, most of the records analyzed here represent first reports, suggesting that most non-populations are being detected and identified, but no further monitoring is being carried out.

Overall, a well-documented historical record coupled with a well-delimited species identification are pivotal in the study of the invasion patterns of sea anemones. Hitherto, *D. lineata* has been the most studied sea anemone species in invasion ecology, with a well-registered historical record and species delimitation (Hancock et al. 2017). This has allowed scientists to delineate its native and non-native ranges and compare different ecological aspects of its native and non-native populations (Uchida 1932; Ryan and Miller 2019; Newcomer et al. 2019). However, in the beginning *D. lineata* was misidentified and re-described several times, which led to gaps in its historical records (reviewed by Hancock et al. 2017). Unfortunately, this is a common situation among some sea anemones with non-native populations and thus cases such as these require more research to better understand their invasion status. For instance, the introduction of *S. ornata* from Europe to South Africa has been of interest in the literature (Acuña and Griffiths 2004; Acuña et al. 2004; Robinson et al. 2004, 2005; Haupt et al. 2010; Mead et al. 2011), but its identification has been recently doubted and must therefore be revised (Glon et al. 2020b). Another example of misidentification due to taxonomic synonyms is *S. elegans*: this species seems to have been introduced in China, but these populations have been reported as the synonym *S. rosacea* (Yan and Yan 2003; Li et al. 2011).

Some species have been reported as introduced, but their native ranges have not been delimited. This is the case of *A. alicemartinae*, whose native range has been suggested as southern Peru, though this remains undefined (Canales-Aguirre et al. 2015). Other species lacking a delimited native range are *D. cincta*, *D. franciscana* and *D. paranaensis* (Wasson et al. 2001; Beneti et al. 2015; Mavraki et al. 2020). Even with an undelimited native range it is possible to classify a given species as non-native, especially when there is enough baseline information in the newly colonized location (see the case of *D. paranaensis* discussed by Glon et al. 2020b). However, establishing the native range of both suspected and confirmed non-native species is crucial. Interestingly, it has been demonstrated in sea anemone invasions that delimiting the native and non-native ranges is difficult and can lead to mistakes. For example, *N. vectensis* had been classified as in danger of extinction in England for years, but, in fact, those populations have now been classified as non-native (Reitzel et al. 2008).

Other sea anemones not considered here may represent introductions: *Actinia equina* (suggested by Glon et al. 2020b), *Synandwakia hozawai* (suggested by González-Duarte et al. 2016) and *Culicia rachelfitzhardingeae* (suggested by Carlton 2009). *Actinia equina* has a “cosmopolitan” distribution and most likely represents a species complex given its morphological and genetic variability (see Glon et al. 2020b). However, whether the broad distribution of *A. equina* includes introduction and establishment scenarios remains unknown. As mentioned before, *S. hozawai* is distributed along Japanese coasts, but there is no information about its invasion status (Kostina 2000). On the other hand, *C. rachelfitzhardingeae* has been described as introduced in Hawaii with a presumably (but yet unknown) native range in the Indo-Pacific (see Table 2.3 from Carlton 2009). Clearly, more research is needed in order to shed light on these cases and determine whether they represent non-native species.

Invasion of sea anemones: an integrative approach

Similar mechanisms for the successful invasion process of non-native sea anemones have been detected. Sea anemones travel beyond their native ranges mainly because of human-associated transport, especially maritime traffic. For instance, *D. lineata* has been found fouling on ship hulls in Germany and Brazil (Gollasch and Riemann-Zürneck 1996; Farrapeira et al. 2007). Along their journeys, sea anemones most likely experience environmental fluctuations that they must withstand in order to survive the trip to new areas. Gollasch and Riemann-Zürneck (1996) documented the worldwide route travelled by individuals of *D. lineata* and the environmental fluctuations they overcame: salinity reduction and air exposure. Aquaculture activity has also been a relevant vector for sea anemone introductions. For example, *E. diaphana* and *S. ornata* have been introduced in association with oyster farming in France and South Africa, respectively (Grizel and Heral 1991; Haupt et al. 2010). Other likely human-associated vectors may include aquarium trade (e.g. *E. diaphana*, Rhyne et al. 2004).

While natural dispersal mechanisms may occur during both larval and adult stages, these were less reported in the literature. Planula larvae of sea anemones live at least 3–8 weeks (in *Anthopleura elegantissima*, Schwarz et al. 2002) and may drift short or long distances. However, with the search procedure performed here, no information was found regarding the potential dispersal of non-native sea anemone species in the larval stage. On the other hand, adult stages of some species can detach from the substratum and float short distances or even raft long distances. This detach-float-reattach behavior has been observed as a way to find suitable conditions when faced with abiotic stress and to avoid stronger competitors or predators (Edmunds et al. 1976; López et al. 2013; Brante et al. 2019). Even though it is unlikely that this mechanism represents an introduction

pathway, it may favor the secondary spread of established non-native populations.

Once non-native anemones arrive to a new area, a broad physiological tolerance to abiotic stressors (e.g. temperature, salinity), non-selective resource requirements (e.g. food, space) and reproductive strategies (mainly asexual) would favor their persistence and spread. Non-native sea anemones display different mechanisms to withstand abiotic stress, harness available resources and ensure population survival and growth. Changes in temperature, salinity and air exposure can affect different physiological and ecological processes of sea anemones, such as their metabolic rate (Walsh and Somero 1981), osmolality (Amado et al. 2011), growth (Chomsky et al. 2004), reproduction (Johnson and Shick 1977) and survival (Suárez et al. 2020). Broad tolerance ranges to temperature, salinity and oxygen depletion have been observed both in non-native (Hand and Uhlinger 1992; Jewett et al. 2005; Podbielski et al. 2016; Ryan et al. 2019; Suárez et al. 2020) and native populations (e.g. *M. senile* Glon et al. 2019). In addition, sea anemones count on different strategies to withstand conditions outside their tolerance ranges, including mucus secretion and tentacle withdraw (Hart and Crowe 1977; Shumway 1978; Stotz 1979), water retention and osmoregulation of the gastrovascular cavity (Pierce and Minasian 1974; Stotz 1979), and crowding (Carling et al. 2019).

It is unlikely that food availability represents an impediment for introduction and establishment because sea anemones are opportunist polyphagous predators and some species also depend on their photosynthetic symbionts (Schlichter 1978; Sebens 1981). It has been demonstrated that some non-native species, such as *D. lineata*, can withstand starvation even while undergoing asexual reproduction (Minasian 1979); this suggests some energy storage that could facilitate both transport and early introduction. At least one species, *E. diaphana*, presents photosynthetic symbionts and this trait seems to favor its invasion success. Unlike other symbiotic organisms, *E. diaphana* seems to be non-selective when incorporating symbionts (Tortorelli et al. 2020), which is likely to favor its arrival to new areas. In addition, *E. diaphana* seems to retain its symbionts even when exposed to non-favorable salinity or thermal conditions (Gegner et al. 2017).

Space availability is not a limited resource given that sea anemones often display low substratum selectivity. Most non-native sea anemone populations develop on hard substrata and our results suggest a greater use of natural habitats than human-made habitats (Grebelyni and Kovtun 2013; Gusmao et al. 2018; Glon et al. 2020a; Suárez et al. 2020). This contrasts with other groups of benthic invaders that flourish mainly on human-made substrata, such as ascidians (Pereyra and Ocampo Reinaldo 2018).

Interactions between non-native sea anemones and the invaded community are diverse. Some communities may lack competitors and potential enemies, enabling invasion success (e.g. *E. diaphana* in Palau, Oceania,

Patris et al. 2019). Sometimes, non-native sea anemones dominate native sea anemones in aggressive encounters, as is the case of *D. lineata* and *E. diaphana* (Escribano-Álvarez and López-González 2018). In other cases, non-native sea anemones depend on evasive behaviors when faced with more aggressive native competitors; *A. alicemartinae* has been observed evading attacks from the native sea anemone *Phymactis papillosa* by escaping elsewhere (Brante et al. 2019). The results from this review suggest that non-native sea anemones also participate in interactions that, in some cases, facilitate invasion success by providing protection or substrata (Molina et al. 2009; Haupt et al. 2010; Martin et al. 2015). For instance, *D. lineata* finds substrata in the roots of *Spartina* sp. in sandy marshes; also, the shade provided by these plants protects the sea anemone from direct sun exposure and reduces high temperatures in the summer (Molina et al. 2009).

Even though most records are in the introduced and naturalized stages, the results presented here suggest that some non-native sea anemone populations have indeed spread and become invasive. For instance, historical records and field observations have suggested that *A. alicemartinae* has spread southward along the Chilean coast with a rate of 38 km year⁻¹ (Häussermann and Försterra 2001). Another example, that has already been mentioned, is the case of *E. diaphana*, which rapidly colonized the whole perimeter of the marine Jellyfish Lake within the first six years of its introduction (Patris et al. 2019). Secondary spread is most likely mediated by both natural and human-associated mechanisms. Rafting is likely both an introduction vector and a secondary spread mechanism, which often involves both natural and human-associated factors. Different sea anemones have been recorded on natural and human-made flotsam, such as macroalgae, volcanic pumice and plastics (see Thiel and Gutow 2005 for a review). For instance, sea anemone species found on the anthropogenic debris originated from the 2011 Japanese tsunami travelled through the North Pacific and arrived at North America and Hawaii (Carlton et al. 2017). Interestingly, even though this journey took longer than that of a typical ship route, individuals of *D. lineata* were found to be alive and reproductive once they landed at their new destinations (Carlton et al. 2017). On the other hand, the relevance of local maritime traffic on biological invasions has increased in past decades and recent years, and some authors have suggested its particular role in the introduction and secondary spread of sea anemone invasions (Wasson et al. 2001; Darling et al. 2009; Canales-Aguirre et al. 2015; Pinochet et al. 2019).

While some populations flourish and spread beyond their points of first introduction, others fail to establish and even disappear after establishment. A clear example is the introduction of *S. elegans* into Massachusetts, USA, which was first reported in 2000, but has been absent in different intensive searches since 2010 (Wells and Harris 2019). According to laboratory and field experiments, temperature drops in the winter reach values outside the

tolerance range of *S. elegans* and thus affect its reproduction, growth and survival (Wells and Harris 2019). Even species known and recognized as successful invaders can fail in some areas. It has been demonstrated in field surveys in Nova Scotia, Canada that *D. lineata* has not spread and, on the contrary, has disappeared in locations previously reported as colonized (Ma et al. 2020). Interesting, *D. lineata* has been reported to disappear and then reappear on the coast of Texas, USA (Hancock et al. 2017). These different scenarios highlight the relevance of monitoring each population, both spatially and temporally in order to gather more information regarding their invasion process.

The ecological effects of invasive non-native sea anemone populations have been seldom studied; only a handful of examples could be found. Non-native sea anemones may affect the native community due to predation pressure or competition. For instance, *S. ornata* preys on native polychaeta and amphipod species in South Africa and it has been demonstrated that its presence has changed the community composition (Robinson and Swart 2015). On the other hand, *M. senile* seems to have displaced the native sea anemone *Anthothoe chilensis* in southern Chile, altering its abundance and distribution (Häussermann 2006). Potential displacements were also demonstrated in laboratory experiments: *D. lineata*, an established non-native species, and *E. diaphana*, a potential invader, changed the interaction hierarchy of a native sea anemone assemblage which could lead to alterations in its composition (Escribano-Álvarez and López-González 2018). An extreme example of domination is the case of *E. diaphana* in the marine Jellyfish Lake (Oceania), whose increase in abundance was correlated with declines of native benthic components, such as algae and sponges (Patris et al. 2019). These cases of negative ecological effects, although few, arouse concern about the conservation of those communities invaded by sea anemone species. Future research on non-native sea anemones populations should thus assess their ecological effects more frequently to better understand the magnitude of their associated potential damages.

The lack of information regarding the economic consequences associated with non-native sea anemones is most likely due to a lack of exploration on this topic, rather than an absence of consequences. It is plausible that non-native sea anemones could negatively affect economic activities, such as the aquaria industry and human energy resources. In fact, the presence of *S. elegans* (referred to as *S. rosacea*) fouling on offshore structures has been associated with economic maintenance costs (Yan and Yan 2003). On the other hand, *E. diaphana* is considered an aquarium pest and protocols of biological control have been proposed to mitigate its negative effects (Rhyne et al. 2004).

Limitations and future work

The goal of this study was to systematically analyze the available literature in order to fundamentally describe the invasion patterns shared by sea

anemones of the order Actiniaria. Describing the historical records for each species goes beyond the aims of this paper and future reviews should focus on this topic to continue revealing sea anemone invasion patterns in even more detail. Here, we applied a systematic approach when analyzing the literature found in order to reduce any potential biases. In addition, this procedure can be used to update this review in the future, and it can also be adapted to other taxa with invasive representatives. Our selection and classification criteria were rather strict to ensure that all data were supported in some way by the articles we read, either by observations, experiments or other approaches. We are well aware that by establishing our procedure *a priori*, we may have left aside some literature published in books and other sources, such as reports. In addition, some species discussed here have been widely studied in their native range, which also represents literature that was not included here. It is also important to note that our procedure excluded information in languages other than English.

Sea anemone species of the order Actiniaria represent a broad taxon suitable for invasion ecology research (Glon et al. 2020b; this study). As discussed here, some species, marine realms and approaches require more research effort to eliminate potential biases and gaps in the current knowledge. For instance, *M. senile* has proven to be tolerant to abiotic stress in its native range, but what about its non-native populations in the Southern Hemisphere? Interesting patterns could emerge when comparing different aspects of native versus non-native populations, as has been demonstrated in *D. lineata* studies (Uchida 1932; Ryan and Miller 2019; Newcomer et al. 2019). On the other hand, the application of genetic and phylogenetic tools could shed light on uncertain cases, helping to establish species delimitation and their native ranges. Furthermore, different common aspects can be studied in the future to better understand the invasion of sea anemones. For instance, diet has been widely studied in sea anemones in general (Chintiroglou and Koukouras 1992; Acuña et al. 2001; Quesada et al. 2014; Ivanova and Grebelnyi 2017), but studies on the diet of non-native populations are uncommon and represent an easy way to assess potential negative effects on native prey and competitors (as demonstrated by Robinson and Swart 2015). Ecological interactions between non-native sea anemones and members of the invaded community have only recently gained attention (e.g. Escribano-Álvarez and López-González 2018; Brante et al. 2019; Patris et al. 2019), but the processes involved have not yet been fully described.

Interestingly, ecology niche modeling has been little explored in sea anemone invasions and has potential for detecting suitable areas for introduction that could help direct sampling efforts for each of the species discussed here. It is worth noting that ecological niche modeling is a widely used tool in the invasion ecology of plants, other terrestrial organisms and marine invasive taxa such as algae (Gallien et al. 2010; Marcelino and Verbruggen 2015). The work of Pinochet et al. (2019) on *A. alicemartinae*

represents a first step in the ecological niche modeling of non-native sea anemone species. According to their results, the abundance of *A. alicemartinae* seems to be positively correlated to local maritime traffic, suggesting that the secondary spread of this species is facilitated by human activities. In addition, the projection of the habitat suitability model built by Pinochet et al. (2019) predicted that the distribution of *A. alicemartinae* could expand farther south to areas with no records of introductions (e.g. Chiloé Island). Recently, new reports near Chiloé Island and even farther south have been found (Ocean Biodiversity Information System, OBIS, <https://www.obis.org/>), but they must be corroborated in the field. The application of ecological niche modeling to the invasion scenarios of other non-native sea anemone species could shed light on subjacent mechanisms and potential distributional patterns of different species. These are only a few examples for potential future research on non-native sea anemones and we encourage fellow researchers to explore all of these possibilities and more.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Summary of the data obtained from the analyzed articles.

This material is available as part of online article from:

http://www.reabic.net/aquaticinvasions/2021/Supplements/AI_2021_Gimenez_Brante_SupplementaryMaterial.xlsx