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KEY ASPECTS FOR THE INVASION SUCCESS OF SEA ANEMONES (CNIDARIA, ACTINIARIA)

Por

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FACULTAD DE CIENCIAS

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Por

LUCAS HERNÁN GIMENEZ

Tesis para optar al grado de Magíster en Ecología Marina

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“La página escrita nunca recuerda todo lo que se ha intentado,

sino lo poco que se ha conseguido.”

— Antonio Machado, Prólogo a *Páginas escogidas* (1917)

“And do you know the answers?”

“Oh, no, no, no. Far from it. What I love about science is that,

as you learn, you don’t really get answers. You just get *better* questions.”

— John Green, *Turtles all the way down* (2017)

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ABSTRACT

A number of cnidarian species are known to have become marine invaders across a variety of regions and habitats, including sea anemones of the order Actiniaria. Unfortunately, integrative approaches to identify and describe general patterns and likely drivers of the invasion process of sea anemones have only been of recent interest and using some selected species. The purpose of this research is to better understand the invasion process of sea anemones and which drivers determine their invasion success. Specifically, the aims were: (1) to integrate records of all the non-native sea anemone species reported around the world to describe a general pattern of invasion and unmask potential biases or gaps in our current knowledge, and (2) to perform an invasion risk assessment based on ecological niche modeling and describe the environmental niche dynamics of three globally introduced sea anemones species (*Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis*). I performed a systematic review to summarize and categorize the records of non-native populations of sea anemone species around the world 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. The 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 in marine systems, although some species thrive in human-made habitats and estuarine systems. 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 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. However, some evidence has suggested negative ecological effects associated with non-native sea anemone populations, mediated by predation and competition mechanisms. The conservation of invaded communities is therefore of great concern. In this context, spatially explicit information (e.g., predictions of potential distributions) is essential for the prevention or early detection of sea anemone invasions. I applied ecological niche models to predict areas with invasion risk of *Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis*. Additionally, I assessed the invasion stage of current non-native occurrences and the environmental niche breadth of each species. Then, I evaluated their environmental niche dynamics to determine whether they are colonizing areas with similar environmental conditions as those from their respective native distribution ranges (i.e., climatic match hypothesis). The geographical projections detected areas with potential for new introductions and already colonized areas that could undergo further spread. The three species showed a high proportion of stabilizing populations and broad environmental niche breadths. These results suggest a strong pattern of successful establishment in a wide range of environmental conditions. Two different niche dynamics were found: (1) *D. lineata* showed a strongly conserved niche, suggesting that its invasion success has mainly occurred in areas with similar environmental conditions as those in its native range; and (2) both *E. diaphana* and *N. vectensis* showed levels of niche shift attributed to niche expansions, suggesting they might be adapting to new environmental conditions in their respective non-native ranges. This contribution demonstrates that ecological niche modeling can help to detect areas with sea anemone invasion risk and to shed light on some of the mechanisms operating in their invasion process. On the other hand, the results provide support for the climatic match hypothesis of invasions, especially in the case of *D. lineata*. Finally, I discussed a general pattern for the invasion process of sea anemones and potential ways to reduce some of the biases and gaps found in the current knowledge. I also reflected on future perspectives in the study of sea anemone invasions to develop a better understanding of their invasion ecology.

Keywords: *Anemonia*, *Diadumene*, ecological effects, Ecological niche model, *Exaiptasia*, invasion ecology, *Metridium*, *Nematostella*, *Sagartia.*

RESUMEN

Ciertas especies de cnidarios han sido reconocidas como invasores marinos en distintas regiones y hábitats, incluyendo al grupo de las anémonas de mar del Orden Actiniaria. Desafortunadamente, los enfoques integradores que buscan identificar y describir patrones generales y posibles modulares del proceso de invasión de las anémonas de mar solo han sido de interés recientemente y utilizando algunas especies seleccionadas. El propósito de esta investigación fue entender mejor el proceso de invasión de las anémonas de mar y los factores que determinan su éxito de invasión. Específicamente, los objetivos fueron: (1) integrar registros de todas las especies de anémonas de mar con poblaciones no nativas alrededor del mundo para describir un patrón general de invasión y detectar posibles sesgos o vacíos en el conocimiento actual, y (2) realizar una evaluación de riesgo de invasión basada en modelos de nicho ecológico y describir la dinámica de nicho ambiental de tres especies introducidas globalmente (*Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis*). Llevé a cabo una revisión sistemática enfocada a resumir y categorizar los registros de poblaciones no nativas de todas las especies de anémonas de mar alrededor del mundo para evaluar si existe un patrón común de invasión para este grupo. Un total de 126 artículos fueron analizados con 11 especies con registros de poblaciones no nativas. Los resultados mostraron que las invasiones de anémonas de mar se remontan al menos hasta los finales de la década de 1890 e introducciones nuevas han sido reportadas para distintas especies en los últimos cinco años. Se encontraron posibles sesgos en la literatura respecto al esfuerzo dirigido a las distintas especies, zonas geográficas y enfoques de estudio. La mayoría de los estudios han sido enfocados a una sola especie (*Diadumene lineata*), especialmente en el Atlántico Norte Templado. Se encontró y describió un patrón aparentemente común a lo largo de todas las etapas del proceso de invasión, pero se debe concentrar más esfuerzo en las especies menos reportadas/estudiadas. El transporte ha sido mediado principalmente por vectores asociados a actividades humanas como el tráfico marítimo y la acuicultura. Los individuos recién llegados colonizan mayoritariamente hábitats naturales en ambientes marinos, aunque algunas especies prosperan en hábitats artificiales y ambientes estuarinos. Un conjunto diverso de rasgos ha sido asociado con el éxito de invasión de anémonas de mar, aunque los reportados más frecuentemente en la literatura son la tolerancia abiótica y las estrategias reproductivas. A diferencia de otros invasores bentónicos, los mecanismos de dispersión (tanto primaria como secundaria) y las consecuencias ecológicas y económicas producidas por poblaciones de anémonas de mar no nativas han sido poco exploradas y por lo tanto necesitan más atención. No obstante, existe evidencia que sugiere efectos negativos asociados a las poblaciones no nativas de anémonas de mar mediados por mecanismos de depredación y competencia. Estas consecuencias potenciales despiertan preocupación respecto a la conservación de las comunidades invadidas. Por lo tanto, información espacial explícita (e.g., predicciones de distribuciones potenciales) son necesarias para prevenir o detectar de forma temprana las invasiones de anémonas de mar. En este contexto, apliqué modelos de nicho ecológico para predecir áreas potenciales con riesgo de invasión para *Diadumene lineata*, *Exaiptasia diaphana*, y *Nematostella vectensis*. Además, realicé evaluaciones de la etapa de invasión de las ocurrencias no nativas y cálculos de la amplitud del nicho ambiental de cada especie. Luego, exploré la dinámica del nicho ambiental de estas tres especies para determinar si están colonizando áreas con condiciones ambientales similares a las de sus respectivos rangos de distribución nativa (i.e., hipótesis de similitud climática). La proyección geográfica del modelo seleccionado para cada especie permitió la detección de áreas con potencial para nuevas introducciones y áreas ya colonizadas con potencial para escenarios de dispersión secundaria. Las tres especies mostraron una alta proporción de poblaciones en etapa estable y nichos ambientales amplios. Estos resultados sugieren un patrón fuerte de establecimiento exitoso en un amplio rango de condiciones ambientales. Dos dinámicas de nicho ambiental diferentes fueron encontradas: (1) *D. lineata* mostró un nicho fuertemente conservado, lo que sugiere un éxito de invasión para esta especie principalmente en áreas con condiciones ambientales similares a las de su rango nativo; y (2) *E. diaphana* y *N. vectensis* mostraron cambios de nicho atribuidos a expansiones de nicho, lo que sugiere que estas dos especies podrían estar adaptándose a nuevas condiciones ambientales dentro de sus respectivos rangos de distribución no nativo. Esta contribución demuestra que los modelos de nicho ecológico representan una herramienta útil para detectar áreas con riesgo de invasión de anémonas de mar y para entender algunos de los mecanismos que operan en su proceso de invasión. Por otro lado, los resultados brindan sustento para la hipótesis de similitud climática de las invasiones, especialmente en el caso de *D. lineata*. Finalmente, discutí un patrón general para el proceso de invasión de las anémonas de mar y posibles formas de reducir algunos de los sesgos y vacíos encontrados en el conocimiento actual. También reflexioné sobre las perspectivas a futuro en el estudio de las invasiones de anémonas de mar para desarrollar una mejor comprensión de su ecología de invasión.

Palabras claves: *Anemonia*, *Diadumene*, ecología de invasiones, efectos ecológicos, *Exaiptasia*, *Metridium*, modelo de nicho ecológico, *Nematostella*, *Sagartia.*

CHAPTER 1: INTRODUCTION

Biological invasions include the arrival, establishment, and subsequent spread of species in a community in which they were previously absent (sensu Carlton 1989). The arrival of such newcomers can occur through two main processes: *range expansions* and *introductions.* Range expansions are mediated by natural dispersal mechanisms of species, whereas introductions are facilitated by pathways and vectors associated with human activities (Carlton 1987). Particularly in marine ecosystems, maritime traffic and the aquaculture activity represent the main vectors for non-native species (NNS), translocating representatives of different taxa such as algae, fish, and invertebrates (Molnar et al. 2008). While a considerable number of species arrive at new locations, not all of them survive and persist (Blackburn et al. 2011). However, those that succeed can generate negative ecological, economic, or sanitary effects (e.g., Pimentel et al. 2001; Molnar et al. 2008; Diagne et al. 2020), which are recognized as relevant factors of global change (Ruiz et al. 1997).

Ecological effects of NNS occur at different levels. When a given NNS persists and spreads, it can displace native species, produce changes to the structure or dynamic of communities, or even disrupt ecosystem processes and services (Simberloff et al. 2013). A global analysis of the ecological impact of 329 marine NNS estimated that 57% were harmful at different ecological levels: from disrupting a single species with little to no wider ecosystem impact, to disrupting multiple species or some wider ecosystem function (Molnar et al. 2008). In this context, research on biological invasions has focused on understanding the biology, ecology, and evolution of NNS; identifying and describing pathways and vectors; determining which factors drive invasion success; describing distributional and dispersal patterns; and predicting the effects of NNS on the communities they invade (for an overview see Chan & Briski 2017).

Although the research on marine invasions has increased in the last decade, certain taxa have been less studied, which is not necessarily related to the inexistence of invaders species in those groups or the absence of impacts. For instance, non-native cnidarian species have been recognized as little studied, in contrast to other groups such as crustaceans and mollusks (Molnar et al. 2008). Interestingly, up to 47% of non-native cnidarians have been classified as harmful (sensu Molnar et al. 2008), and some species even represent an invasion threat (sensu Miralles et al. 2021). Unfortunately, non-native cnidarians remain as an unexplored group in marine invasion research: they still are less represented than other non-native invertebrate groups such as tunicates and mollusks (Watkins et al. 2021).

Drivers and mechanisms of the invasion process: What makes a successful invader?

The invasion process can be characterized by progressive stages, and each stage presents a barrier (or filter) that NNS must surpass to reach the next stage (e.g., Richardson et al. 2000). These barriers include geographical, survival, reproductive, and dispersal limitations (Blackburn et al. 2011). A given NNS is considered an invasive species once it has proliferated and spread beyond the area of first introduction (sensu Catford et al. 2009). However, only a small proportion of NNS becomes invasive (Blackburn et al. 2011). This fact has led to numerous hypotheses that address the factors determining invasion success (e.g., Richardson & Pyšek 2006; Catford et al. 2009; Jeschke 2014). The approach of these hypotheses can focus on the invader itself, the invaded ecosystem, or in the invader-invaded community interaction (Perkins & Nowak 2013). Unfortunately, many of these hypotheses have little to no empirical support (see Jeschke et al. 2012). Moreover, the reach of most invasion hypotheses is limited and many of them overlap, complement, or share similarities with others (see Table 2 in Catford et al. 2009). An integrative approach proposed by Catford et al. (2009) defines the invasion process, and its success, as a function of four factors: (1) propagule pressure, (2) abiotic conditions of the invaded ecosystem, (3) biological traits of the receipt community and the invader species, and (4) the influence by human activities. Other authors have proposed similar approaches (see "The invasion triangle" by Perkins et al. 2011 for an example).

Propagule pressure (i.e., the number of dispersal units that arrive to a given location and the frequency of arrivals; sensu Lockwood et al. 2005) directly influences invasion success. However, regardless of propagule pressure, any species that has arrived in a new location must face the features of the abiotic environment (i.e., conditions and resources; abiotic resistance hypothesis) and the biotic environment (i.e., native community; biotic resistance hypothesis). Environmental conditions (e.g., temperature, salinity) and resource availability (i.e., space, food) represent abiotic filters that any NNS must overcome to survive and establish (Mack et al. 2000; Blackburn et al. 2011). When the environmental conditions of a given habitat surpass the physiological tolerance of a NNS, or when its required resources scarce, it will not establish regardless of its invasive potential (Perkins et al. 2011). Likewise, native diversity is associated with community stability and invasion resistance (i.e., biotic filters; Levine & D'Antonio 1999). When native diversity increases, resources scarce and there is a greater chance that a native species with higher competitive ability displaces the newcomer (Perkins & Nowak 2013). Communities with more native diversity also present a greater number of potential enemies (e.g., pathogens, parasites, predators) that can affect the reproduction, growth or even survival of a given NNS through different mechanisms than competition (Perkins et al. 2011).

From a perspective focused on the NNS, certain traits are associated with invasion potential and success, including broad physiological tolerance, generalist diets, competitive ability, phenotypic plasticity, fast individual growth, high fecundity, and short generational time (Perkins & Nowak 2013; Chan & Briski 2017). NNS can arrive at a new location presenting these traits or they can develop a new set of traits after introduction through micro-evolutive changes (Whitney & Gabler 2008). However, it is worth noting that assessing any trait depends directly on the ecological context, which means that a given trait can benefit invasion success to a specific NNS in a specific location, but it can be neutral or even associated with invasion failure in other contexts (Perkins & Nowak 2013).

Influence of environmental conditions on the ecology of sea anemones

Sea anemones (Cnidaria, Anthozoa, Order Actiniaria) are relevant members of benthic communities that play multiple ecological roles, from opportunistic predators to providers of shelter and defense (see Shick 1991). These organisms can form large aggregations and become a relevant component of coastal systems (e.g., temperate and cold waters such as the Chilean coast; Häussermann & Försterra 2005). Distributional patterns of sea anemones, both along latitudinal and intertidal gradients, depend on multiple factors including environmental conditions (Stotz 1979; Richardson et al. 1997; Cha et al. 2004; Amado et al. 2011), aggressive competitive interactions (Brace 1981; Rudin & Briffa 2011), and predation pressure (Shick 1991 p. 279; Augustine & Muller-Parker 1998). Likewise, these factors likely influence the invasion success of non-native sea anemones (Podbielski et al. 2016; Escribano-Álvarez & López-González 2018).

Environmental conditions (e.g., temperature, salinity, air exposure) affect multiple sea anemone biological processes, including their metabolic rate (Walsh & Somero 1981), their osmolality (Amado et al. 2011), their individual growth (Chomsky et al. 2004), their reproduction (Johnson & Shick 1977), and ultimately their survival (Suárez et al. 2020). These organisms rely on multiple physiological, morphological, and behavioral mechanisms to minimize the adverse effects of unsuitable environmental conditions. They can maintain the humidity of their columns by secreting mucus and thus generating a protective cloth that attracts sediment particles, or they can withdraw their tentacles to reduce surface area and limit water lost (Hart & Crowe 1977; Shumway 1978; Stotz 1979). However, these mechanisms are energy expensive because they reduce oxygen diffusion to the body (Shumway 1978). Therefore, other mechanisms are also widely used including water retention and osmolality changes of the gastrovascular cavity (Pierce & Minasian 1974; Stotz 1979), antioxidant compounds synthesis to minimize UV radiation damage (Arbeloa et al. 2010; Cubillos et al. 2018), crowding (Carling et al. 2019), and detachment from the substratum and floating to find better environmental conditions (López et al. 2013; Suárez et al. 2020). The differential use of these strategies among members of the actiniarian sea anemone taxa likely determines whether a given species shows narrow or broad tolerance ranges, which also influences the invasion potential of NNS.

Climatic match hypothesis of invasion success and ecological niche modeling

Temperature is one of the main factors that determine the distributional ranges of marine species (e.g., Sanford et al. 2006; Tittensor et al. 2010). In the case of NNS, broad physiological tolerance ranges to abiotic stress translate into a greater potential to survive and establish in a varied array of habitats (Lenz et al. 2011; Bates et al. 2013). For instance, the invasive kelp *Undaria pinnatifida* presents a broader tolerance range to temperature than the native algae species *Lessonia variegata* and *Ecklonia radiata* (Bollen et al. 2016). Moreover, *U. pinnatifida* seems to tolerate even warmer temperatures than those from its native distribution range (James & Shears 2016). In addition, salinity represents another relevant factor delimiting distribution ranges of marine species (e.g., Smyth & Elliott 2020). Most marine invertebrates are osmo-conformers and sessile: their extracellular fluids are isosmotic to the environment, and they are unable to avoid unfavorable environmental conditions actively and efficiently. Facing these unfavorable conditions demands energy and ultimately affects development, growth, and reproduction (e.g., Hauton 2016). Particularly, it has been demonstrated in sea anemone invasions that environmental conditions outside the optimum range limit their spread and potential geographic extension (in *Diadumene lineata*, Podbielski et al. 2016).

One key hypothesis explaining the fate of species introductions states that the establishment of a self-sustaining population in the non-native range can only succeed within conditions matching the native environmental niche (i.e., climatic match hypothesis, Curnutt 2000; Pauchard et al. 2004; Nuñez & Medley 2011; Cope et al. 2019; Broennimann et al. 2021). Invasiveness can be estimated based on the magnitude of spatial spread, predicted from species environmental requirements (i.e., environmental niche) and represented with ecological niche models (ENMs, see Peterson & Soberón 2012).

ENM is a widely used tool to describe invasion patterns of NNS (Goncalves et al. 2014; Oliveira et al. 2018; Battini et al. 2019). Based on the niche-biotype duality concept, the environmental requirements of a given species can be projected from the environmental niche space to the geographic space to estimate habitat suitability (Phillips et al. 2006; Colwell & Rangel 2009). This approach can provide: (1) predictions of potential distributions (Pearson & Dawson 2003; Phillips et al. 2006); (2) a classification of non-native occurrences into invasion stages (sensu Gallien et al. 2012); and (3) calculations of environmental niche breadth (Warren et al. 2008). On the other hand, this approach also allows an assessment to detect which are the mechanisms mediating the invasion process. Comparisons between the native and non-native niches can evaluate whether a given NNS is occupying similar environmental conditions in the non-native range as those from its native range, testing the climatic match hypothesis (Broennimann et al. 2007, 2012). Environmental niche dynamics can be further decomposed into three basic components (stability, unfilling and expansion) to better understand the invasion process (Petitpierre et al. 2012). For instance, the stability niche area represents the environmental conditions shared between the native and non-native range (i.e., climatic match). On the contrary, the expansion niche area corresponds to the degree of niche shift, showing new environmental conditions occupied in the non-native range (i.e., climatic mismatch).

Research purpose and thesis structure

The purpose of this research is to better understand the invasion process of sea anemones and which drivers determine their invasion success. Hitherto, at least 12 species of non-native sea anemone species have been reported worldwide (according to González-Duarte et al. 2016). Unfortunately, integrative invasion patterns have only recently begun to be studied using *a priori* selected species (see Glon et al. 2020). In **Chapter 2**, I provide a systematic literature review aimed at integrating global non-native records of all non-native sea anemone species reported to describe a general pattern of invasion and unmask potential biases or gaps in our current knowledge.

Like other benthic invaders (e.g., ascidians, Pereyra & Ocampo Reinaldo 2018), non-native sea anemone species likely generate ecological and economic effects on the communities they colonize. These potential negative effects arouse concern about the conservation of the communities invaded. Preventing the introduction and establishment of non-native marine species has been suggested as the most efficient management alternative to avoid the potential ecological damage and economic costs associated with biological invasions (Floerl et al. 2005; Simberloff et al. 2013; Diagne et al. 2020). This strategy can only be effective when monitoring effort is allocated to specific vectors, pathways, species, and locations (Hayes et al. 2005). Spatially explicit information (i.e., predictions of potential distributions) is thus essential to support decisions aimed at preventing, early detecting, and managing biological invasions (Inglis et al. 2006; Leidenberger et al. 2015). In **Chapter 3**, I addressed the potential of ecological niche modeling to predict introduction and spread scenarios of non-native sea anemone species. I selected three widespread invasive sea anemone species as biological models: *Diadumene lineata*, *Exaiptasia diaphana* and *Nematostella vectensis.* I based my selection on their available information, occurrence reports and well-documented invasion ecology. I modeled their distributions to detect new areas suitable for introduction and spread. I assessed the invasion stage of non-native occurrences for each species. I also calculated their niche breadths to test whether their known broad physiological ranges are represented at macrospatial scale. Finally, I explored the environmental niche dynamics of these three species to test the climatic match hypothesis of invasion success. Even though chapters 2 and 3 are independent, in **Chapter 4** I provide an integration of the main findings of this research and reflect on the future perspectives on the study of non-native sea anemone species.

Hypotheses and Aims

Chapter 2

General aim: Integrate records of all the non-native sea anemone species reported around the world to describe a general pattern of invasion and unmask potential biases or gaps in the current knowledge.

Specific aims:

- Summarize and categorize the published literature on non-native sea anemones (e.g., species, invasion stage, research effort, types of study).
- Identify the main vectors and dispersal mechanisms, describe the environments and habitats colonized, and characterize ecological or economic effects.
- Identify the main biological traits associated with invasion success.

Chapter 3

Hypotheses

1. The invasion process of *Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis* is at advanced stages in concordance with their widespread geographic range and long historical introduction records, but they also have potential for future introduction and spread scenarios.
2. The niche breadths of *Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis* are broad, in concordance with their reported broad physiological tolerance ranges.
3. The environmental niche dynamics of *Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis* are conserved, which means these species colonize similar environmental conditions as those from their respectively native ranges (i.e., climatic match hypothesis).

General aim: Perform an invasion risk assessment based on ecological niche modeling and describe the environmental niche dynamics of three globally introduced sea anemones species (*Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis*).

Specific aims:

- Predict potential distributions based on habitat suitability and detect likely areas for future introduction and spread.
- Assess the invasion stage of current non-native occurrences and estimate the environmental niche breadth of each species.
- Test the climatic match hypothesis of invasion success by exploring the niche dynamic of each species (i.e., to determine whether they have colonized areas with the same environmental conditions as those from their respectively native ranges).

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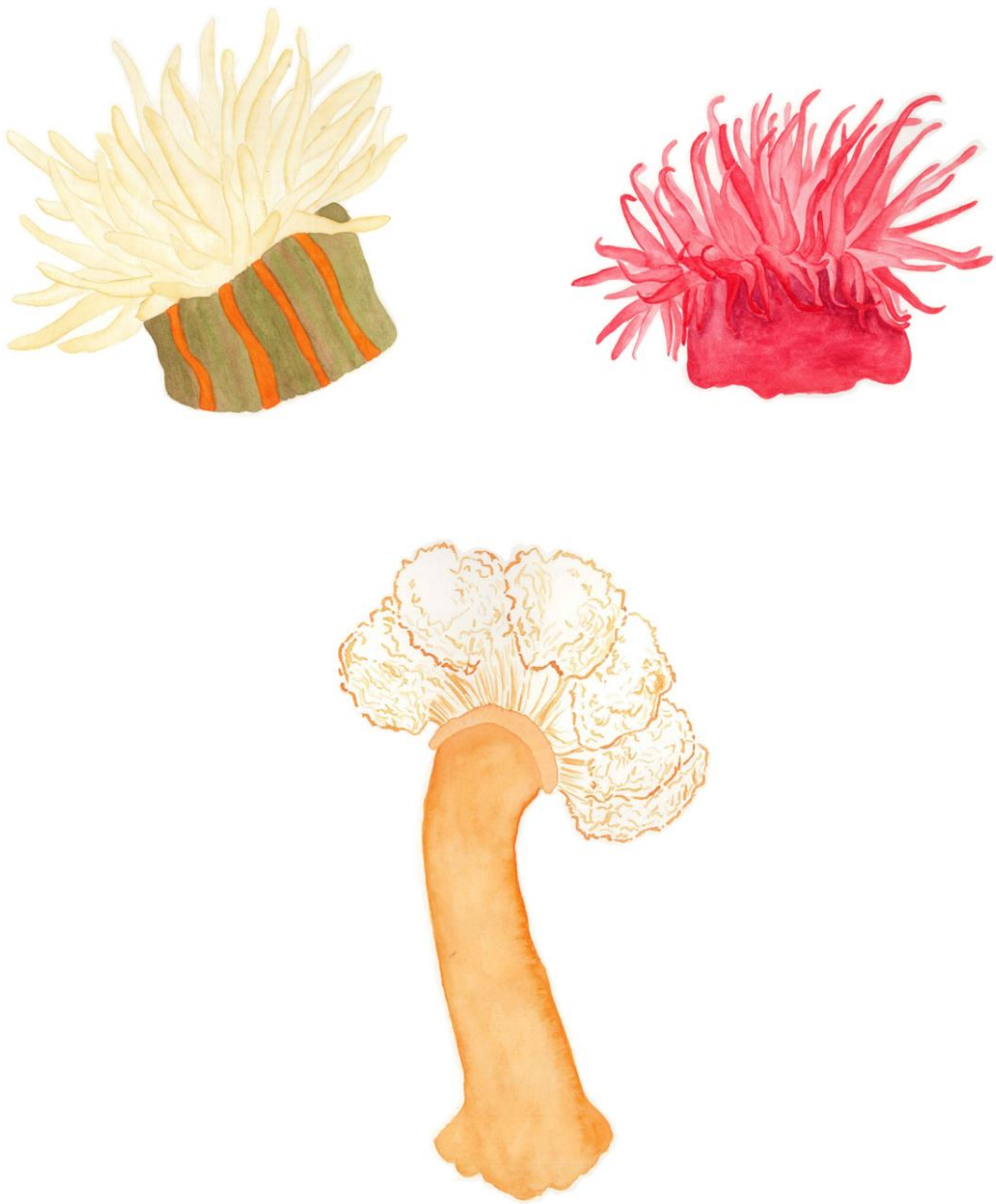
CHAPTER 2: DO NON-NATIVE SEA ANEMONES SHARE A COMMON INVASION PATTERN?



Diadumene lineata, Anemonia alicemartinae and *Metridium senile* in watercolor by Julieta Coronel.

Introduction

Non-native 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* (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.

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 indigenous" 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.

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 is 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 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 Southern Ocean	Categorical classification of the distribution of each record based on the exact location of the populations.
	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.
	Other	Other approaches not considered.

TABLE 1. Continued.

Data	Category	Definition
Environment	Marine	Coastal (intertidal and subtidal) or oceanic systems.
	Estuarine	Within an estuary or its mouth.
	Both	Marine and estuarine systems.
	NA	The study does not provide information regarding the environment.
Habitat	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.
	NA	The study does not provide information regarding the type of habitat.
Dispersal mechanisms	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.
	NA	The study does not focus on and thus lacks information regarding the spread mechanisms.
Effects	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.
	NA	The study does not focus on and thus lacks information regarding the species effects.
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 benefic 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 benefic 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.

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).

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). Table S1 in *Supplementary material* summarizes all the data collected.

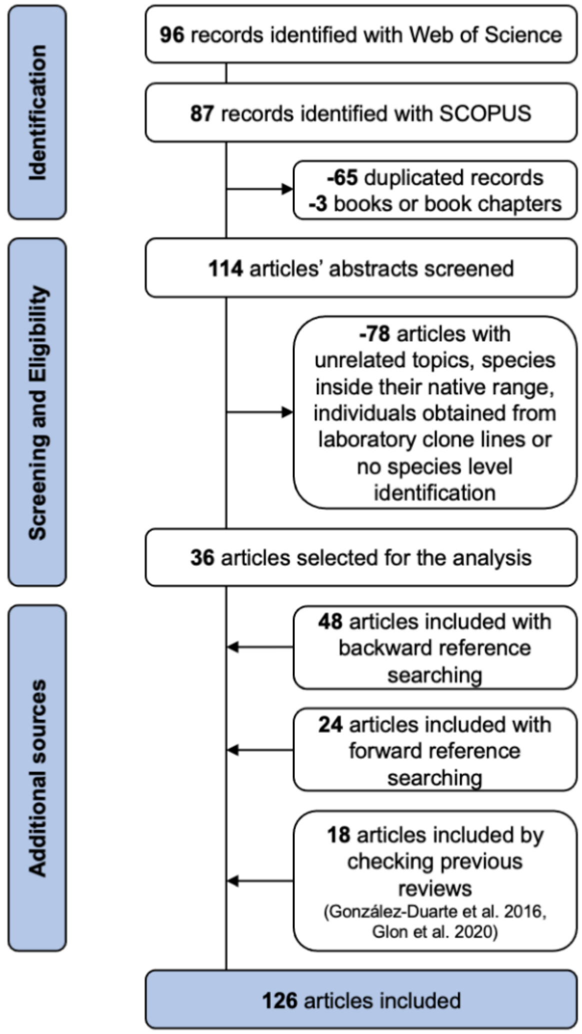


Figure 1. Flow chart detailing the search procedure performed: identification, screening, and selection of the analyzed articles.

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 and Försterra, 2001; *Diadumene cincta* Stephenson, 1925; *D. franciscana* Hand, 1956; *D. leucolena* Verrill, 1866; *D. lineata* Verrill, 1869; *D. paranaensis* Beneti, Stampar, Maronna, Morandini and 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.

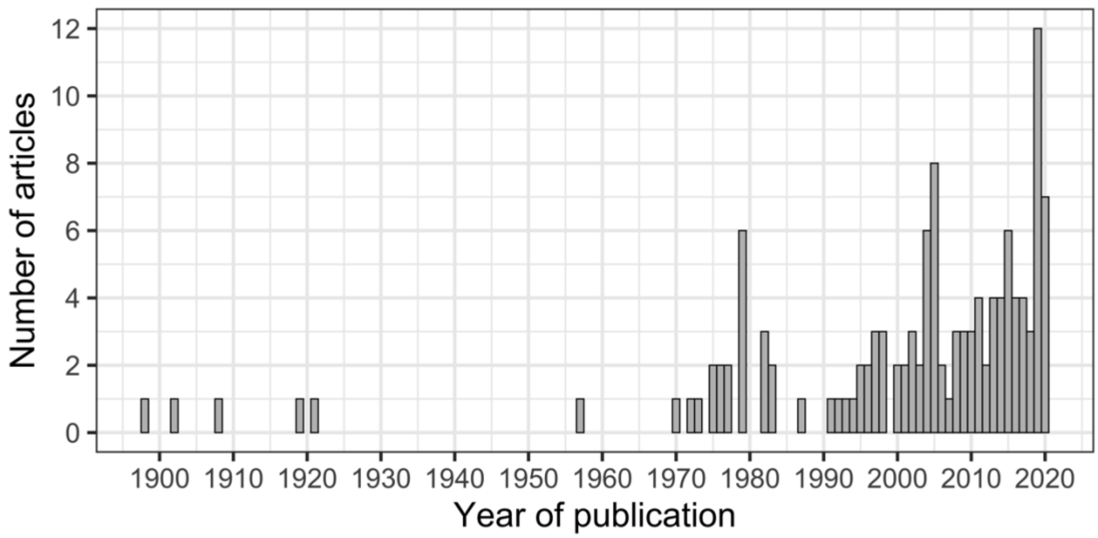


Figure 2. Number of articles published per year. Only studies considered for the analysis are shown. The most recent year (2020) only includes articles published as of August 2020.

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 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 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.

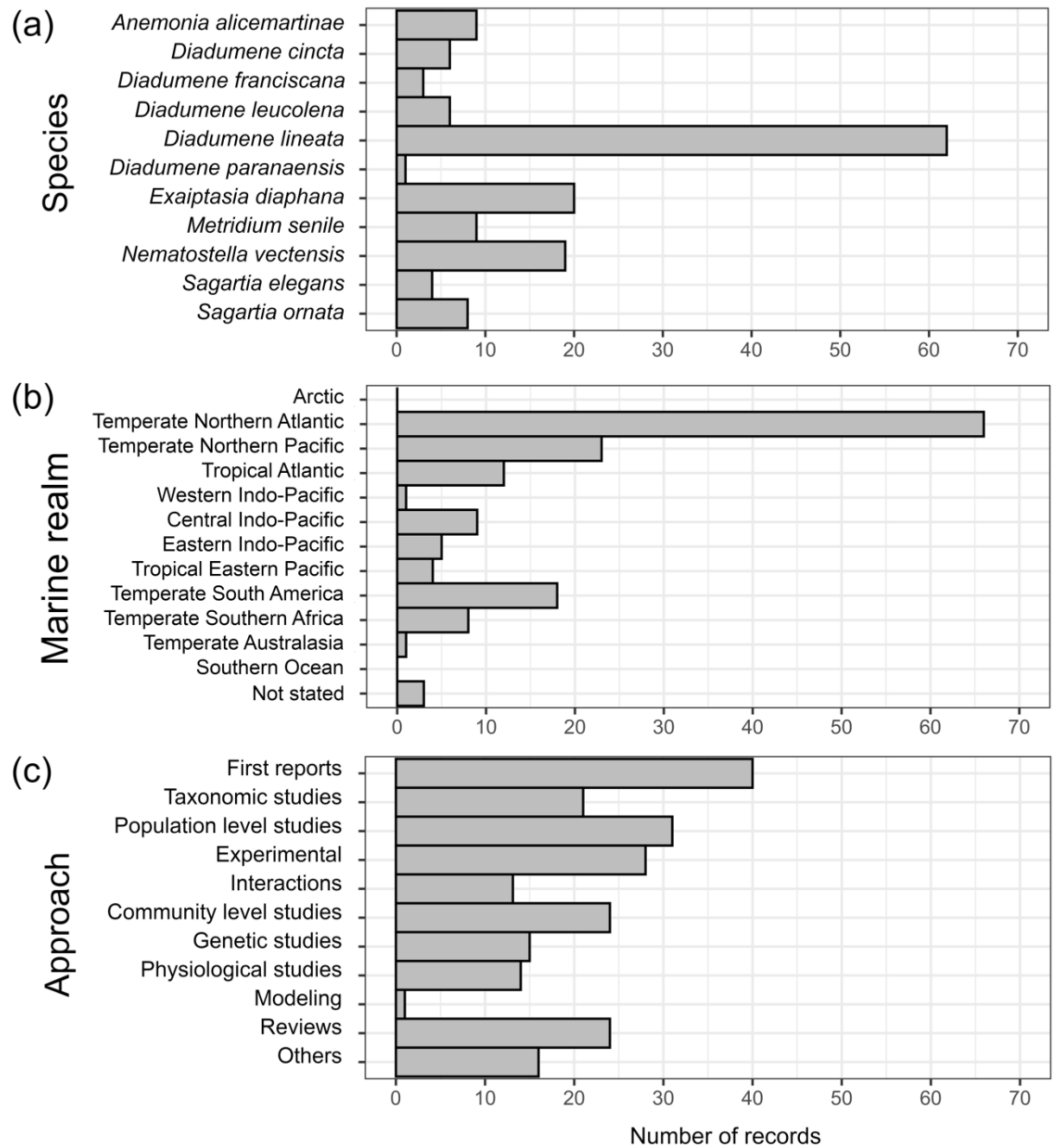


Figure 3. Distribution of the analyzed articles across **(a)** species, **(b)** marine realms (sensu Spalding et al. 2007) and **(c)** study approaches. A given article can represent more than one record.

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 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.

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.

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.

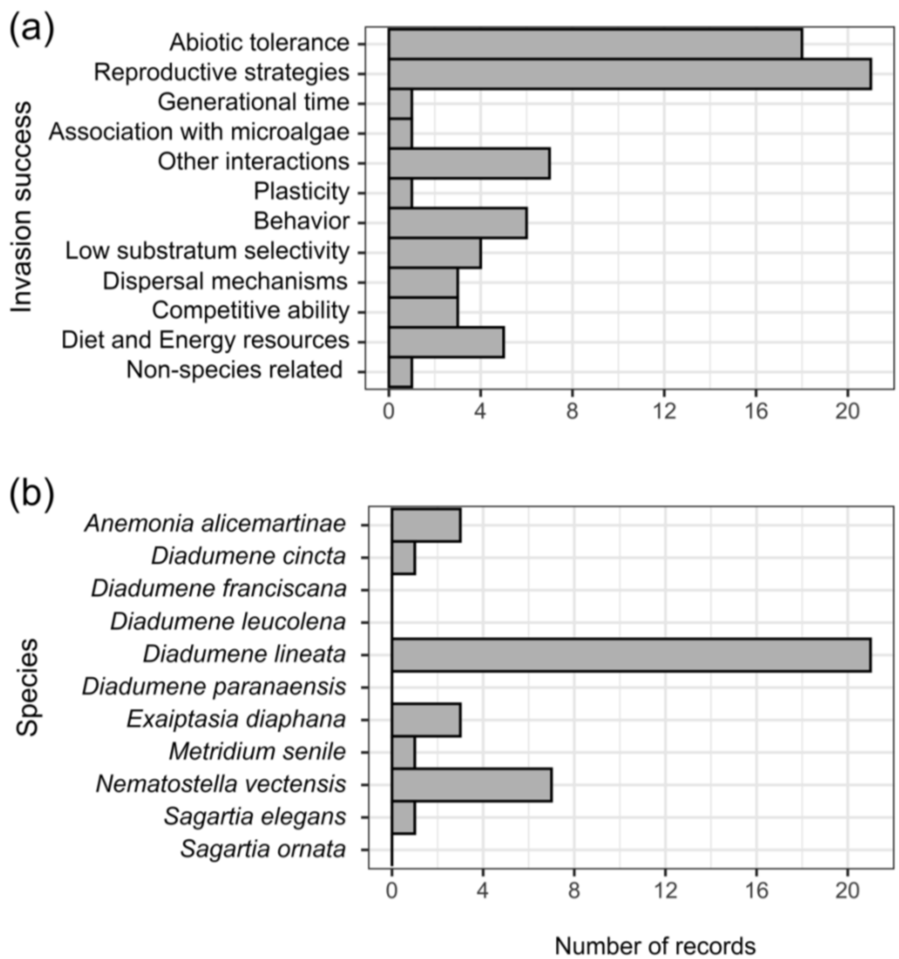


Figure 5. (a) Traits associated with the invasion success of sea anemone species. **(b)** Number of records per species associating abiotic tolerance or reproductive strategies with invasion success. Only records with relevant information regarding this topic are shown (~50%). A given article can represent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

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 *D. 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.

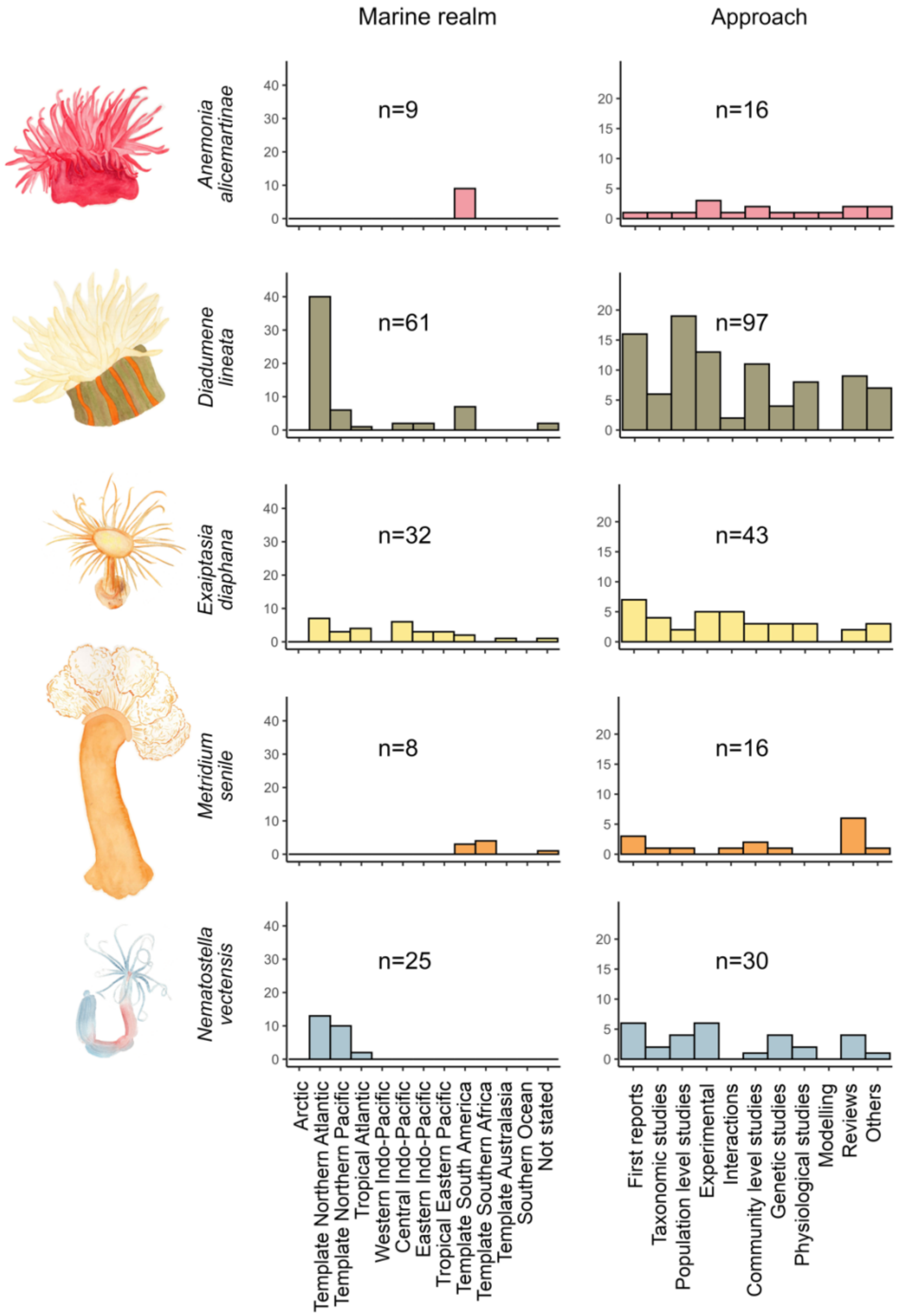


Figure 6. Distribution of records across marine realms (sensu Spalding et al. 2007) and study approaches focused on the five most frequently reported sea anemone species with non-native populations. A given article can represent more than one record. n= Number of total records for each species in the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

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 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 underlaying 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 Gónzalez-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 congenerics (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; Gusmaõ 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 the 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, the former has been 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 limitation 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 (Grebelnyi and Kovtun 2013; Gusmaõ 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). Future research should quantify any economic costs associated with non-native sea anemone populations to determine whether they represent a threat as other marine invertebrate invaders (e.g., mollusks, ascidians).

Limitations

The goal of this review 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 thesis 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. The 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 the procedure *a priori,* it 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 the procedure excluded information in languages other than English. However, the procedure applied here can be used to update this review in the future, and it can also be adapted to other taxa with invasive representatives.

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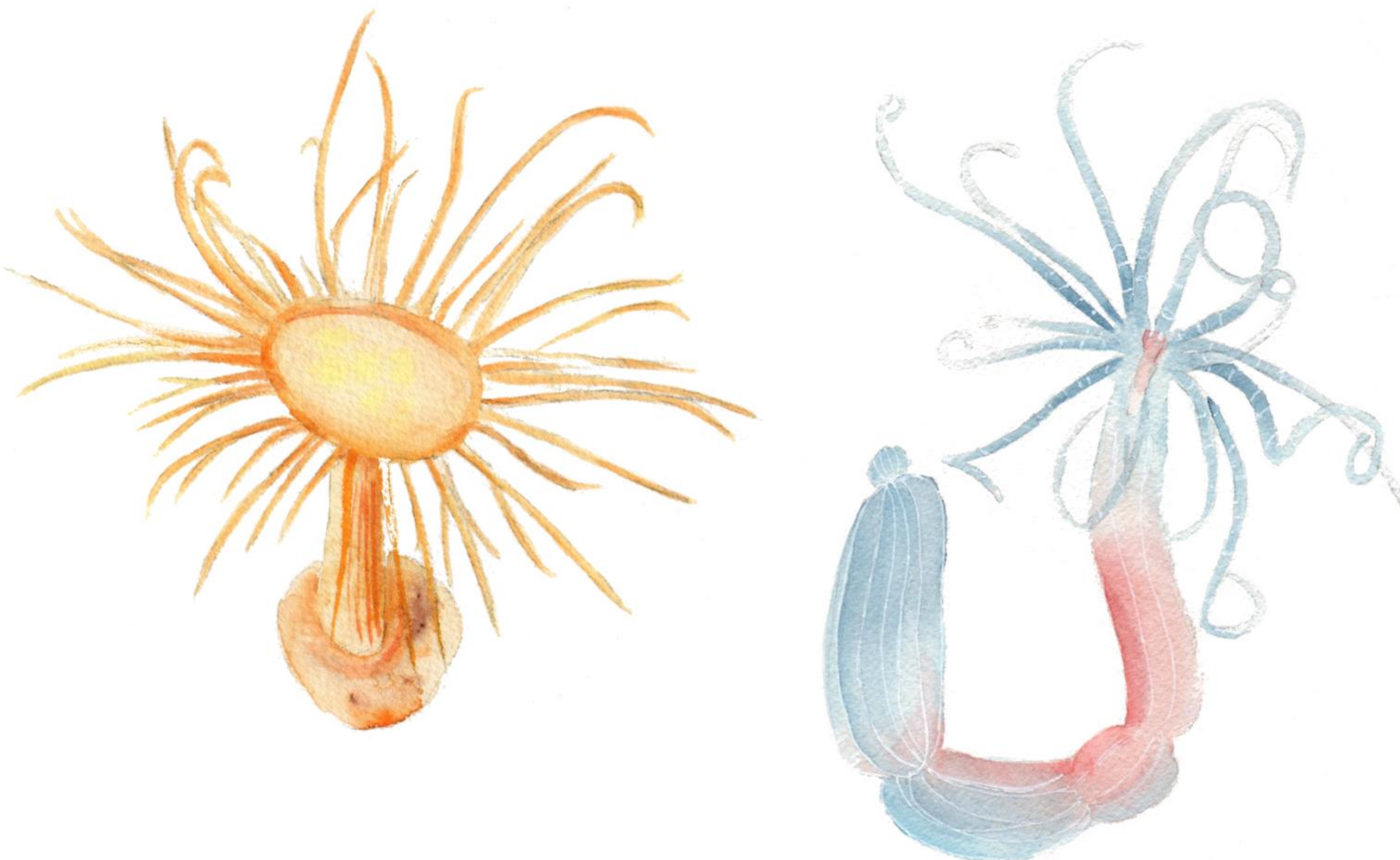
Chapter 3: One step ahead of sea anemone invasions – Potential new introductions, spread, and environmental niche dynamics of three successful invasive species



Exaiptasia diaphana and *Nematostella vectensis* in watercolor by Lucía Ortiz Miralles.

Introduction

Human activities (e.g., maritime traffic, aquaculture) have transported and introduced actiniarian sea anemone species around the world (see Chapter 2). Non-native populations have become established in natural and human-made habitats as a result of adaptive traits that promote their invasion success, including a high dispersal potential, a high asexual reproduction rate, and a broad physiological tolerance to temperature and salinity (for a review see Glon et al. 2020). Once established, non-native sea anemone species can affect the native community mainly through predation pressure and competition (Robinson & Swart 2015; Patris et al. 2019). Therefore, detecting areas at risk is crucial for the prevention or mitigation of potential negative effects on native communities.

Even though it is difficult to predict the future invasion scenario of non-native sea anemone species, multiple tools are currently available to detect potential areas of introduction and spread for a given species based on its current native and non-native distributions. Invasiveness can be estimated from the magnitude of spatial spread, predicted from species environmental requirements (i.e., environmental niche) and represented with ecological niche models (ENMs). ENMs are widely used to predict potential distributions (Pearson & Dawson 2003; Phillips et al. 2006). In addition, these models allow for the interpretation of their ecological significance, e.g., niche dimensions (see Peterson & Soberón 2012). All of the conditions that a species requires to maintain populations in a given area are included in its ecological niche, along with the changes that the species itself generates on its resources, other interacting species, habitats and environments (sensu Peterson et al. 2011). The set of all combinations of environmental variables necessary for the population growth rate to be positive represents the fundamental niche, whereas the realized niche is a subset of environmental conditions that exists in a given region and time and is used by the species after biotic interactions are taken into account (Soberón & Nakamura 2009). At macrospatial scales, the distribution of a species is mainly determined by environmental conditions, whereas biotic interactions mostly operate at microspatial scales (Pearson & Dawson 2003; Soberón 2010).

The ENM approach is based on the niche-biotype duality concept, this states that environmental requirements of a given species can be projected from the environmental niche space to the geographic space to estimate habitat suitability (Phillips et al. 2006; Colwell & Rangel 2009). Particularly, the environmental similarity of native and non-native locations is a key factor in predicting the likelihood of invasion risk in invasion ecology (e.g., climatic match hypothesis, Qiao et al. 2017; but see Gallagher et al. 2010). ENMs can explore the invasion process of non-native species by comparing the environmental requirements in native and non-native ranges, testing the climatic match hypothesis (Broennimann et al. 2007, 2012). In addition, the environmental niche dynamic of a given species can be assessed by dividing its niche into different components: stability, expansion and unfilling (Petitpierre et al. 2012). On the other hand, ENMs can also provide information regarding the invasion stage of populations and the environmental niche breadth of a given species (Warren et al. 2008; Gallien et al. 2012).

Two assumptions underline ENMs: (1) *biogeographic equilibrium*, which means that introduced species can colonize every suitable existing habitat in the new range, and (2) *niche conservatism*, which means that introduced species colonize similar environmental areas as those from their native ranges (Araújo & Pearson 2005; Wiens et al. 2010). However, the biogeographic equilibrium assumption is most likely unfulfilled in early stages of the invasion process (e.g., Battini et al. 2019). In concordance, it has been recently demonstrated that the niche conservatism assumption can also be unfulfilled and, on the contrary, niche shift scenarios can occur (e.g., Langdon et al. 2019). In most cases, niche shifts take place in the realized niche rather than the fundamental niche because the latter is expected to be highly invariant within short to moderate time spans (ten to hundreds of years, Peterson 2011).

Despite their broad use in research on the invasion process of non-native species, ENMs have been little explored in sea anemone invasions (for one example see Pinochet et al. 2019). Here, we selected three cases of widespread sea anemone species with delimited native distribution ranges and non-native populations throughout the world: *Diadumene lineata* Verrill 1869, *Exaiptasia diaphana* Rapp 1829, and *Nematostella vectensis* Stephenson 1935. Using ENMs we aimed: (1) to predict the potential distribution of each species based on their respective current native and non-native distributions; (2) to assess the invasion stage of non-native occurrences and estimate the environmental niche breadth of each species; and (3) to evaluate the environmental niche dynamic in the invasion process of each species to determine whether they have colonized areas with the same environmental conditions as those from their respective native ranges (i.e., climatic match hypothesis).

The selected sea anemone species have shown broad ranges of physiological tolerance to temperature and salinity and have been reported as successful invaders in multiple locations (see *Species* section). Thus, we expected to find: (1) suitable areas that have yet to be colonized (i.e., outside their current distributions) as well as areas suitable for spread scenarios; (2) a high proportion of established populations (i.e., an estimate of invasion success); (3) broad niche breadths in concordance with broad ranges of physiological tolerance; and (4) conserved niche dynamics. These conserved niche dynamics were expected to display high values of overlap between native and non-native ranges (see Broennimann et al. 2012), high values of the stability component (an estimate of niche conservatism, see Petitpierre et al. 2012), and low values of the expansion component (an estimate of niche shift, see Petitpierre et al. 2012).

Methods

Species

Diadumene lineata is the most widely distributed sea anemone (Figure 7a). Even though its native range is restricted to East Asia from Japan to Hong Kong (Uchida 1932), its non-native range includes populations throughout the world (Glon et al. 2020). It is an euryhaline and eurythermal species that tolerates salinities as low as 8‰ and persists in temperatures from below freezing to 30 ºC (Minasian 1979; Minasian & Mariscal 1979; Podbielski et al. 2016; Ryan 2018). However, populations are most successful near oceanic salinity (Podbielski et al. 2016; Konecny & Harley 2019; Ryan & Miller 2019). Survival during wide temperature swings, air exposure and extremely low salinity has enabled this species to endure intertidal conditions, seasonal changes, and transport across wide latitudes (Glon et al. 2020).

Exaiptasia diaphana (often referred to as *E. pallida* or *Aiptasia pallida*) is a tropical sea anemone species used as a model biological system in studies of cnidarian-zooxanthellae symbiosis (e.g., Brown et al. 2017; Dungan et al. 2020). Its native range presumably comprises the Tropical Western Atlantic, while reported non-native populations include tropical and near-tropical areas throughout the world (Figure 7b; Grajales & Rodriguez 2014; Grajales & Rodríguez 2016; Glon et al. 2020). Despite being a tropical species, *E. diaphana* displays broad physiological tolerance: under thermal and salinity stress, *E. diaphana* retains its symbionts unlike other photosymbiotic cnidarians (Gegner et al. 2017). In addition, *E. diaphana* thrives in acidic waters (Hoadley et al. 2015).

Nematostella vectensis is a sea anemone species found in brackish habitats within coastal saltmarshes (Figure 7c; Hand & Uhlinger 1994). It has been used as a model biological system for evolution and development studies (Reitzel et al. 2012). Its native range encompasses the Atlantic Coast of the US (Reitzel et al. 2008) and non-native populations occur along the Pacific Coast of the US, the UK and Brazil (Glon et al. 2020). This species tolerates extreme ranges of temperature and salinity conditions (-1 to 8 ºC and 9-51,5‰ respectively; Hand & Uhlinger 1994), which likely contributes to its invasion success (see Glon et al. 2020).

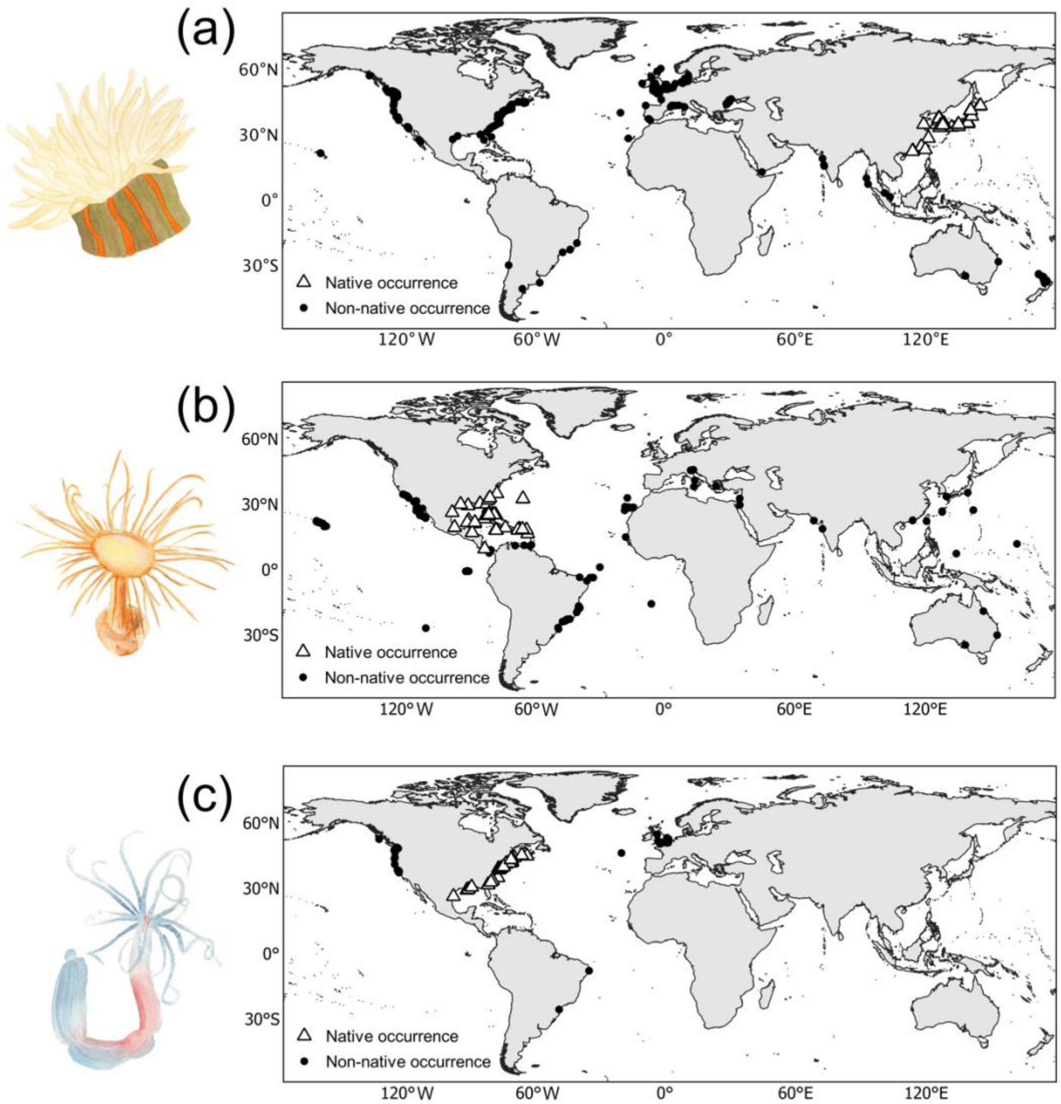


Figure 7. Current distributions of **(a)** *Diadumene lineata*, **(b)** *Exaiptasia diaphana*, and **(c)** *Nematostella vectensis* based on available occurrence data.

Occurrence records

Georeferenced occurrences were mainly compiled from two specialized repositories: the Global Biodiversity Information Facility (GBIF, https://www.gbif.org/ accessed in September 2020) and the Ocean Biodiversity Information System (OBIS, https://www.obis.org/ accessed in September 2020). After removing duplicates, these records were classified into the native or non-native range of each species following currently available maps of distribution (Glon et al. 2020). Additional records from the non-native range of each species were obtained from recent literature (past 10 years, reviewed in Chapter 2).

Typical records from databases and literature revisions may be influenced by spatial biases due to differences in sampling efforts (García-Roselló et al. 2015), which interfere in ecological niche modeling (Elith et al. 2011). To avoid such biases, we applied a spatial thinning to our occurrence records, eliminating records within ~10 km of another record. This procedure was performed using the *spThin* package v0.2.0 (Aiello-Lammens et al. 2015). After thinning, occurrence records were 317 for *D. lineata*, 146 for *E. diaphana* and 73 for *N. vectensis*. These three final occurrence datasets were used in the following analyses and are shown in Figure 7 and Table S1 (*Supplementary material*).

Environmental predictors

To supply the ENMs with environmental data, we used the open database Bio-ORACLE v2.1 (https://www.bio-oracle.org/; Tyberghein et al. 2012; Assis et al. 2018). We first selected nine surface variables with biological relevance for sea anemones: temperature (mean and range), salinity (mean and range), dissolved oxygen (mean and range), primary productivity (mean and range) and pH. Changes in temperature or salinity affect sea anemone biology at different levels, including their metabolic rate, osmolarity, growth, reproduction and ultimately survivorship (Johnson & Shick 1977; Chomsky et al. 2004; Amado et al. 2011; Suárez et al. 2020). In particular, non-native sea anemones show broad tolerance ranges to temperature, salinity and, in some cases, to oxygen depletion events, all of which have been associated with their invasion success (Hand & Uhlinger 1994; Jewett et al. 2005; Podbielski et al. 2016; Ryan et al. 2019; Suárez et al. 2020). Primary productivity was selected as a proxy of food availability or photosynthetic activity in the case of symbiotic species (*E. diaphana*, Gegner et al. 2017). On the other hand, pH was selected because at least one species has proven to be tolerant to acidic waters (*E. diaphana*, Hoadley et al. 2015).

Finally, to establish our species-specific predictors, we performed a subsequent selection of variables using the variance inflation factor (VIF) to evaluate and eliminate collinearity among predictors at the points of occurrence for each species. Following a stepwise approach, we only included variables with VIF < 3 (Zuur et al. 2010). This procedure was performed using the *pedometrics* package v0.7.0 (Samuel-Rosa 2020). Based on this analysis, we chose four predictors for *D. lineata* (temperature range, mean salinity, mean primary productivity and pH), five for *E. diaphana* (mean temperature, temperature range, mean salinity, primary productivity range and pH), and five for *N. vectensis* (temperature range, salinity range, dissolved oxygen range, mean primary productivity and pH).

Predictions of potential distributions

Using the whole pool of occurrences (native and non-native), we generated a model for each species to geographically project their potential distributions beyond their respective current distributional ranges. We built the models using the Wallace platform v1.0.6.2 (Kass et al. 2018). We utilized the Maxent algorithm (Phillips et al. 2006), which uses presence-only records to predict habitat suitability and has been demonstrated to perform well in a diverse set of modeling scenarios (Elith et al. 2006, 2011). Maxent has been widely used in a great number of studies in ecology, biogeography, and conservation (Costa et al. 2007; Silva et al. 2014) and has been particularly useful in invasion ecology studies (Oliveira et al. 2018; Battini et al. 2019; Langdon et al. 2019).

We generated models for each species using the partition "random k-fold" method (folds = 5) and considering 10,000 background points. We generated different models for each species, selecting five different feature class combinations: L, LQ, H, LQH and LQHP; where L = Linear, Q = Quadratic, H = Hinge and P = product (for more details about feature classes see Elith et al. 2011). We also selected the regularization multipliers (RM), ranging in a sequence from 1 to 10 with increments of 1. These feature class combinations and RM impose constrains and determine the potential shape of response curves to create models with differing complexities and permit statistical evaluations with the most optimal settings. For instance, linear features are less complex than quadratic features; whereas high RM values decrease the chance that the model could result overly complex or overfit (Shcheglovitova & Anderson 2013). The parameter selection was performed using the *ENMeval* package v2.0 (Muscarella et al. 2014).

We evaluated the performance and selected the best model for each species by applying three criteria: Akaike information criterion (AICc), the area under the receiver operating characteristic curve (AUC), and the Boyce's index. First, we selected the model with the lowest AICc, which is a measure of relative adjustment, proportional to the likelihood of the model and the number of parameters (Burnham & Anderson 2004). Then, we used the area under the receiver operating characteristic curve (AUC) to assess the performance of the selected models (Phillips et al. 2006). The AUC ranges from 0 to 1, where scores lower than 0.5 indicate a performance worse than random, a 0.5 score implies a discrimination that is no better than a random guess, and a 1 score indicates perfect discrimination (Pearce & Ferrier 2000).

It is worth noting that the AUC has received criticism for not considering true absences, weighing omission and commission errors equally, and omitting information regarding the spatial distribution of model errors, among other issues (Lobo et al. 2008; Peterson et al. 2008). In this context, we also calculated the Boyce's index as an estimate of model performance, which is calculated using presence-only records (Boyce et al. 2002). The Boyce index was calculated as the relationship between the density of occurrence within predicted habitats for the given species and the total occurrences (i.e., Spearman correlation, Boyce et al. 2002; Hirzel et al. 2006). We used those occurrences eliminated by spatial thinning to calculate the Boyce's index, procuring a robust number of occurrences for evaluation (~30% from total occurrences used for modeling). Values for the Boyce's index range from -1 to 1: positive values indicate a model with presence predictions consistent with the distribution of presences in the evaluation dataset, values close to zero indicate that the model is no different from a random model, and negative values indicate counter predictions, i.e., predicting poor quality areas where presences are more frequent (Hirzel et al. 2006). AICc and AUC values were returned by Maxent in the Wallace platform, whereas the Boyce's index calculations were performed with the *ecospat* package v3.2 (Di Cola et al. 2017).

Invasion stage and niche breadth

We classified non-native occurrences into invasion stages following the framework developed by Gallien et al. (2012). This approach compares a global niche model built considering all of the available occurrences (native and non-native) with a regional niche model built to only consider occurrences in the non-native range. Global niche models are a proxy of the fundamental niche, whereas the regional niche models are a proxy of the realized niche (Vetaas 2002). By displaying the global and regional suitability values in the niche space (i.e., a scatter plot, where the X-axis corresponds to the global model and the Y-axis to the regional model), each occurrence point can be classified into four invasion stages: (1) *stabilizing population*, in which both models return high suitability values, meaning those individuals have established or will most likely become established; (2) *sink population*, in which both models predict a low suitability, meaning that those individuals will most likely not persist; (3) *regional colonization*, in which the global model predicts a high suitability, while the regional model predicts a low suitability, meaning that individuals are arriving, but are far from becoming established; and (4) *regional adaptation*, in which the regional model predicts a high suitability even though the global model predicts a low suitability, meaning that the populations may have adapted to new environmental conditions. The description of the invasion stages can then be inferred by comparing the proportions of each stage (e.g., Langdon et al. 2019).

We calculated the environmental niche breadth of each species using the selected global habitat suitability models. These models were imported to the *ENMtools* package v1.0.2 (Warren et al. 2010, 2021) to estimate niche breadth by calculating B1 (inverse concentration) and B2 (uncertainty) as suggested by Levins (1968). As implemented in *ENMtools*, these two metrics are based on the uniformity of the distribution of each species in association with environmental variation. According to Levins (1968), there is not enough evidence to prefer one metric over the other and in both cases higher values represent a broader environmental niche. However, we focused on the inverse concentration metric (B1) because it does not require the application of a threshold to produce predictions of presence and absence, but rather directly uses the continuous estimates of habitat suitability produced by Maxent (Mandle et al. 2010). Moreover, *ENMtools* returns a standardized version of this metric with values ranging from 0 to 1, indicating minimum and maximum niche breadth, respectively (Warren et al. 2008).

Niche dynamics: testing the climatic match hypothesis of invasion success

The climatic match hypothesis can be tested by estimating the overlap between the environmental conditions occupied in native and non-native ranges (Broennimann et al. 2007, 2012). We restricted the native and non-native backgrounds to ecologically plausible areas surrounding the points of occurrence to avoid potential effects of background selection (see Elith et al. 2011). We cropped each species-specific predictor rafter to encompass areas surrounding the native and non-native occurrences. This was performed with the software QGIS (QGIS Development Team 2020, v3.14, https://www.qgis.org/). We created buffers of 5' (~ 9 km) around each occurrence point, which we then used as masks to extract the area of interest from each environmental raster.

Before comparisons were carried out, we evaluated whether native and non-native environmental conditions for each species were analogs (i.e., comparable). For that, we used the multivariate environmental similarity surface (MESS). MESS evaluates how similar a point is in relation to a set of reference points with respect to a set of predictive variables (Elith et al. 2010). The MESS analysis was run using the *NicheToolBox* (NTBOX) v0.4.6.0 (Osorio-Olvera et al. 2020). This analysis ranges from negative to positive values; negative values represent areas where at least one variable has a value outside the range of conditions in the reference points (Elith et al. 2010), which is the native range in this study.

We made comparisons between the native and non-native ranges of each species by assessing niche overlap. We followed the framework proposed by Broennimann et al. (2012), which consists of three steps: (1) calculating the density of occurrences and environmental predictors along the environmental axis of a multivariate analysis, (2) measuring niche overlap along the gradients of the multivariate analysis, and (3) carrying out statistical tests of niche equivalency and niche similarity. We used a principal component analysis calibrated on the combination of predictors across the environmental background for the native and non-native ranges and their occurrences (i.e., PCA-env). Using the densities of occurrence, we assessed niche overlap with the Schoener's D metric, which ranges from 0 to 1, indicating no niche overlap or identical niche models, respectively (Warren et al. 2008).

To evaluate whether non-native niches of each sea anemone species changed relative to their native niches, we performed two hypothesis tests: niche equivalency and niche similarity (Warren et al. 2008). Niche equivalency assesses whether two niches are identical by pooling all occurrences and then randomly partitioning the identification of original occurrence records, extracting two new random samples and calculating D. The null distribution of the simulated values is compared against the observed value of D in a one-tail test to evaluate the null hypothesis that niches are more identical than expected by chance (Warren et al. 2008, 2010, 2021). Niche similarity assesses whether one niche can predict another based on their environmental conditions. In other words, this test examines whether the overlap between the observed niches in two ranges is different from the overlap between the observed niche in one range and random niches generated for the other range (Broennimann et al. 2012). Null distributions of D values were generated by comparing the niche in one range (i.e., real occurrences and their oceanographic conditions) with niches created with random occurrences drawn from the background of the other range. This was performed twice, first comparing native vs. non-native and then non-native vs. native similarity; rejection of the null hypothesis indicates that the niche models are more similar (or different) than would be expected by chance (Warren et al. 2008, 2010, 2021). If the observed D value is higher than those in the null hypothesis, the compared models are more similar than expected by chance. Niche equivalency and niche similarity tests were performed with 999 permutations using the *ENMtools* package v1.0.2 (Warren et al. 2010, 2021).

To further explore the environmental niche dynamics, we followed the framework developed by Petitpierre et al. (2012), which decomposes the comparison between native and non-native environmental conditions into three basic components: stability (S), unfilling (U) and expansion (E). The stability niche is an estimation of niche conservatism because it represents the environmental conditions shared by native and non-native ranges. On the contrary, the expansion niche corresponds to the degree of niche shift, showing new environmental conditions occupied in the non-native range. The unfilling niche denotes environmental conditions from the native range unoccupied by populations in the non-native range (i.e., an estimate of biogeographic equilibrium). All of these analyses and interpretations were conducted in the environmental niche space. These analyses were performed using the *ecospat* package v3.2 (Di Cola et al. 2017).

All of the analyses described in this study were performed in R (R Core Team 2020).

Results

Potential introduction and spread scenarios

The AUC values for the selected model of each species were higher than 0.75, with the greatest value for *N. vectensis* (Table 2). The Boyce's Index for the three species was higher than 0.70, with the greatest value for *D. lineata* (Table 2). Both metrics suggest that each selected model performed well, and they therefore hold an accurate predictive capacity. Predictor contribution varied among species, while primary productivity and temperature variables contributed to the models selected for *D. lineata* and *E. diaphana*, dissolved oxygen and primary productivity contributed to the model selected for *N. vectensis* (Table S2 in *Supplementary material*). A summary of model selection and evaluation is shown in Table 2, with additional information provided as *Supplementary material* (Figures S1-S3).

Table 2. Summary of model selection and evaluation. Best models are represented by the feature class combinations (FC) and regularization multiplier (RM). Three criteria were used to select and evaluate the performance of the best models: Akaike information criterion (AICc), area under the receiver operating characteristic curve (AUC) and the Boyce's index. AUC and Boyce's index values closer to 1 denote a well performance. H=hinge, L=linear, Q=quadratic.

Species	Best model (FC and RM)	AICc	AUC	Boyce's index
Diadumene lineata	H9	8005.13	0.95	0.93
Exaiptasia diaphana	LQ1	4166.83	0.77	0.88
Nematostella vectensis	LQH3	1575.48	0.98	0.77

The geographic projection of the selected model for each species followed a mostly coastal pattern. Particularly, the potential distribution of *E. diaphana* showed high suitability values in oceanic areas. However, the three species addressed in this study mainly inhabit coastal ecosystems and therefore we only focused on those areas. In all three cases, the predictions encompassed the current native and non-native distributions of each species, but also included areas beyond those hitherto reported. Figure 8 shows the geographical projection for the native and non-native ranges of each species, in contrast with their current distributions. Figure S4 in *Supplementary material* shows each projection omitting the current occurrences to highlight how the models encompass the distribution of each species.

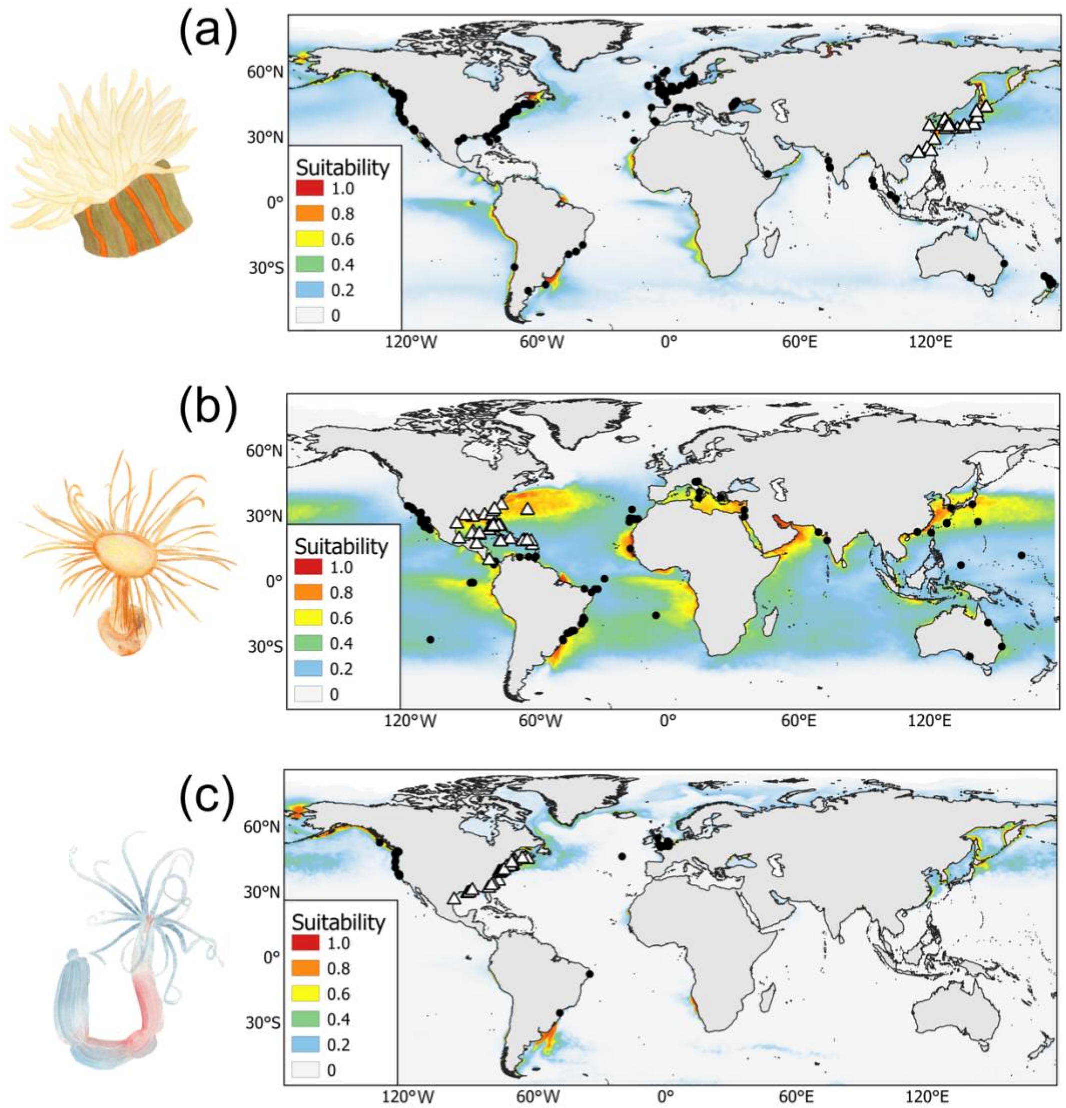


Figure 8. Potential distribution of **(a)** *Diadumene lineata*, **(b)** *Exaiptasia diaphana* and **(c)** *Nematostella vectensis* based on habitat suitability. Each model was built including all of the occurrences of each species (i.e., native and non-native). The current native (white triangle) and non-native (black dot) occurrences are shown to highlight areas with no reports.

Diadumene lineata showed high suitability values on the NW and SW coasts of Africa, two areas with no prior reports of introduction for this species (Figure 8a). Other suitable areas with no previous records for *D. lineata* include the coast of Peru, Ecuador (continental territory and the Galapagos Islands), northern Brazil and Alaska (US). According to our model, in its native range *D. lineata* could spread northwards. Some areas in its non-native range presented a suitable pattern for spread: the western and eastern coasts of the United States, in addition to Canada, Argentina, and Chile.

The predicted distribution of *E. diaphana* is clearly limited to tropical and near tropical areas (Figure 8b). Areas with no reports of *E. diaphana* introductions showed high suitability values for its presence, including, for example: The Red Sea, the Persian Gulf, the NW coast of Africa, and areas in northern and southern Brazil. High suitability values for the presence of *E. diaphana* were found for the Gulf of Mexico, part of its native range, and farther north, suggesting a likely area for spread. The eastern side of the Mediterranean Sea was found to be a potential area for spread in its non-native range.

Interestingly, the case of *N. vectensis* showed a restricted pattern, mostly represented by near estuarine systems (Figure 8c). High suitability values were found in Alaska, NW Canada, East Asia, the SW coast of Africa, and the estuary of De la Plata River (Argentina-Uruguay). According to our model, a potential spread scenario appeared along the western coast of the US, expanding its non-native range northwards to Alaska.

Invasion stage and niche breadth: evidence for invasion success

The three species showed a high proportion of stabilizing populations (equal to or greater than 30%), but overall different patterns arouse (Figure 9). *Diadumene lineata* presented a high proportion of stabilizing populations (64.3%), followed by sink populations (25.6%), populations with regional adaptations (5.9%), and populations at the regional colonization stage (2.3%). Occurrences of *E. diaphana* were mostly sink populations (41.7%), followed by stabilizing populations (30.1%), populations at the regional colonization stage (20.3%), and populations with regional adaptations (7.8%). Regarding *N. vectensis*, this species presented a high proportion of stabilizing populations (58.1%), followed by populations at the regional colonization stage (20.9%), populations with regional adaptations (11.6%), and sink populations (9.30%). The geographic representation of global and regional modeling for each species are presented in Figures S5-S7 in the *Supplementary material*.

Measurements of niche breadth (B1, inverse concentration metric) based on habitat suitability (i.e., at the geographic space) were higher than or equal to 0.90 for the three species. *Exaiptasia diaphana* showed the greatest value (B1 = 0.95), followed by *D. lineata* (B1 = 0.93) and *N. vectensis* (B1 = 0.90). According to these results, the three species seem to have broad environmental niches.

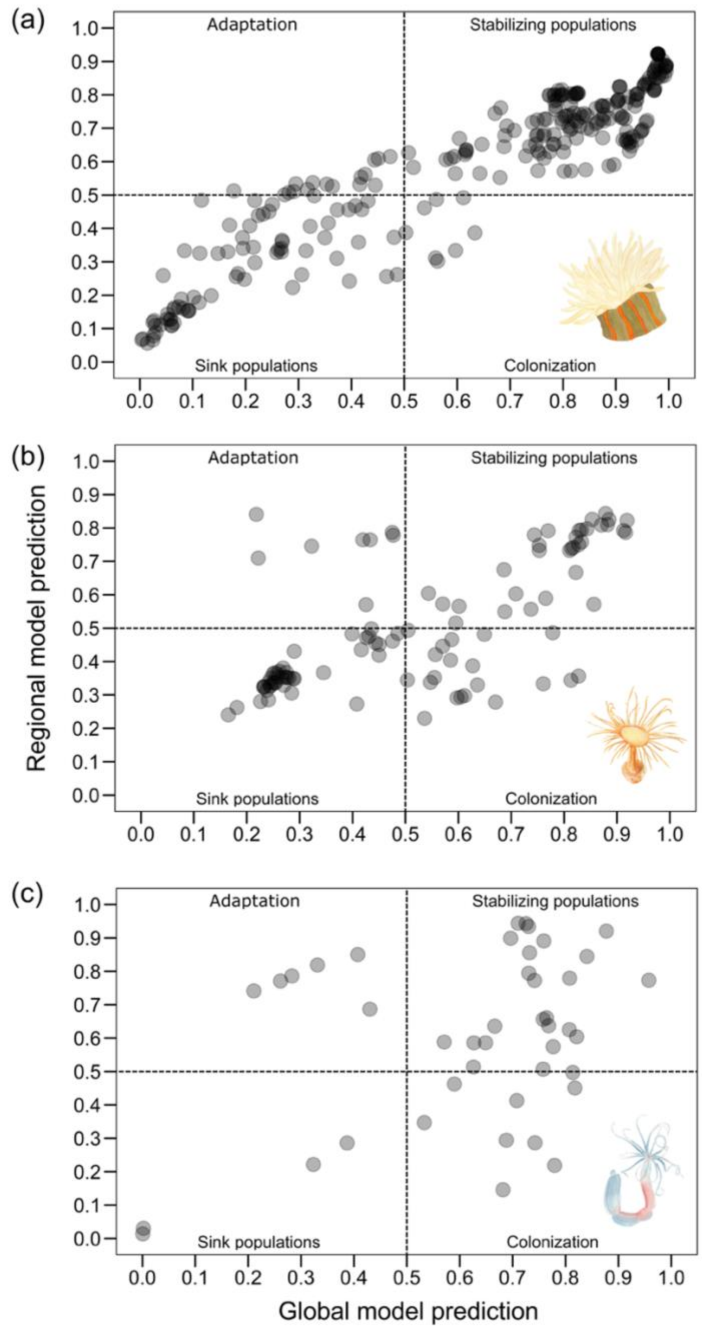


Figure 9. Invasion stages for **(a)** *Diadumene lineata*, **(b)** *Exaiptasia diaphana*, and **(c)** *Nematostella vectensis*. This analysis is based on comparisons between global and regional model predictions (estimated habitat suitability values). Each scatterplot is divided to classify each population in one of four stages by establishing an arbitrary threshold of 0.5 (sensu Gallien et al. 2012).

Niche dynamics: support for the climatic match hypothesis and niche shifts

According to the MESS analyses, the non-native ranges of each species presented analog conditions to those presented in their respective native ranges (Figure S8 in *Supplementary material*). The PCA-env analyses showed that the PC1 and PC2 axis explained approximately 70% of the total variance or more depending on the case (*D. lineata* = 72.5%; *E. diaphana* = 69.3%; *N. vectensis* = 73.7%; see Figures S9-S11 in *Supplementary material*).

Niche overlap between native and non-native ranges showed intermediate values for the three species. *Diadumene lineata* presented the highest overlap, whereas *E. diaphana* and *N. vectensis* showed equal overlap values (Table 3). We found no evidence for rejecting the niche equivalency hypothesis between the native and non-native ranges for any of the studied species (Table 3). These results suggest that the native and non-native ranges of each species are identical. However, niche similarity tests provided mixed results (Table 3). Significant values for niche similarity were found for *D. lineata* and *N. vectensis* when comparing the native vs. non-native range directions, but the comparisons in the other direction turned out to be non-significant. These results demonstrate that the native niches of these two species can predict the non-native niches, but the non-native niches cannot predict the native niches. The similarity test for *E. diaphana* showed no significant values for any direction, meaning that neither niche can predict the other for this species. Additional information regarding all of the niche equivalency and similarity tests are provided in *Supplementary material* (Figures S12-S14).

Table 3. Summary of results (p-values) obtained in comparison tests of equivalency and similarity between the native and non-native niches. Significant values for niche equivalency occur when observed values are more different than expected by chance. On the contrary, similarity occurs only when the test is significant in both possible directions (native versus non-native and vice versa).

* indicates significant values.

Species	Overlap (D)	Equivalency	Similarity	
			Native vs. Non-native	Non-native vs. Native
Diadumene lineata	0.44	0.93	0.00*	0.17
Exaiptasia diaphana	0.29	0.99	0.31	0.15
Nematostella vectensis	0.29	0.99	0.03*	0.09

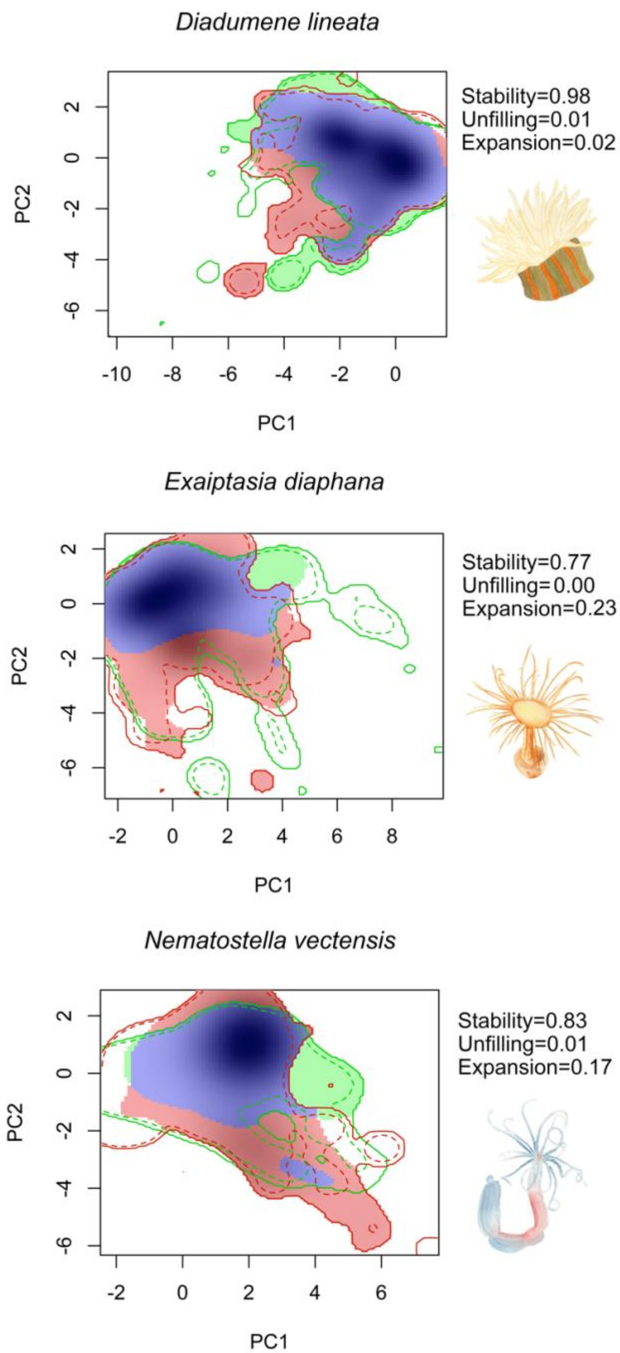


Figure 10. Environmental niche dynamics of *Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis*. Niche comparisons were made between the native and non-native ranges of each species. Colored areas represent niche components: stability (blue), unfilling (green) and expansion (red). Values for each component are found to the right of each panel. Solid and dashed line delimit the 100% and 75% of the available background environments considered in the analyses.

A conserved environmental niche dynamic was found for *D. lineata*, whereas both *E. diaphana* and *N. vectensis* showed some level of niche shift (Figure 10). The three species showed high stability (i.e., overlap between native and non-native ranges), with the highest value for *D. lineata*, followed by *N. vectensis* and *E. diaphana*. These results suggest that these species successfully invade similar environmental conditions as those from their respective native ranges. However, environmental mismatches were found, mostly attributed to niche expansions (i.e., areas occupied in the non-native range not overlapping with the native range) in the case of *E. diaphana* and *N. vectensis*. These results suggest that these two species might be adapting to new environmental conditions. In contrast, low niche expansion was found for *D. lineata*, suggesting no niche shift for this species. On the other hand, the three species showed low unfilling values, meaning that almost all native niche conditions have been occupied in the non-native range (i.e., they have virtually reached the biogeographic equilibrium).

Discussion

Preventing the introduction and establishment of non-native marine species has been suggested as the most efficient management alternative to avoid the potential ecological damage and economic costs associated with biological invasions (Floerl et al. 2005; Simberloff et al. 2013; Diagne et al. 2020). This can only be effective when monitoring efforts are focused on specific vectors, pathways, species, and locations (Hayes et al. 2005). Spatially explicit information (e.g., predictions of potential distributions) is thus necessary to support decisions aimed at the prevention, early detection, and management of biological invasions (Inglis et al. 2006; Leidenberger et al. 2015). In this study, we detected potential areas for the introduction and spread of three important widespread sea anemone species: *Diadumene lineata*, *Exaiptasia diaphana*, and *Nematostella vectensis*. Additionally, we determined the invasion stage of non-native occurrences and calculated the environmental niche breadth of each species bringing new insights to their invasion process. Our results showed high proportions of stabilizing populations and broad niche breadths, which suggest that these three species succeed in a wide range of environmental conditions. Finally, we tested the climatic match hypothesis of invasion success by assessing the environmental niche dynamic of each species, comparing the environmental conditions occupied inside the native range with those occupied in the non-native range. Two types of environmental niche dynamics were found: (1) a strongly conserved niche for *D. lineata*, and (2) some level of niche shift for both *E. diaphana* and *N. vectensis*.

We corroborated that ecological niche modeling provides a helpful tool to detect areas at risk of introduction and spread of non-native sea anemones at macrospatial scales. These areas of risk should be the focus of future attempts to detect introductions early on and prevent spread scenarios. Interestingly, there was a recent report of introduction of *E. diaphana* (Isla del Coco National Park, Costa Rica; Acuña et al. 2020) within an area with high suitability values according to our models. This “fulfilled prediction” seems to support the potential of this approach for the early detection of sea anemone introductions. This potential is relevant considering that visual detection and identification are often problematic in this group and most monitoring programs do not seem to be aimed at or designed to find sea anemone introductions, which results in an underestimation of reports (Chapter 2). The chance to detect a new introduction is enhanced once a population has grown to a point where it can easily be seen in the field (e.g., Häussermann & Försterra 2001). Unfortunately, the invasion process is almost impossible to stop at this point of population abundance and secondary spread (see Patris et al. 2019).

Different negative ecological effects on the native communities have been associated with sea anemone invasions. In fact, *D. lineata* has proven to have a great chance (>90%) of becoming an invasion threat, with demonstrated impacts (according to the “Invasion Threat Score” created by Miralles et al. 2021). In accordance with laboratory experiments, the presence of *D. lineata* (an established non-native species) and *E. diaphana* (a potential invader) could lead to changes in the assemblage composition of native sea anemone species through aggressive behavior (Escribano-Álvarez & López-González 2018). The outcome of the interactions between non-native sea anemones and the native community could ultimately result in a domination pattern by the invader. Such a domination pattern has been described for *E. diaphana* in the Jellyfish Lake (Palau, Oceania); this new sea anemone dominated the lake perimeter within six years after introduction, and its increasing abundance was associated with decreases of native benthic components (Patris et al. 2019). On the other hand, *N. vectensis* represents an opportunist predator of estuarine marshes (reviewed by Hand & Uhlinger 1994). This likely predation pressure by *N. vectensis* on native prey could ultimately have unexplored ecological consequences (similar to *Sagartia ornata* in South Africa, Robinson & Swart 2015). The ENM approach applied here thus holds a great potential to detect areas at risk and prevent potential negative effects generated by these non-native sea anemone species.

Advanced stages of invasion have been reported for all three species, and it is plausible that the spread scenarios predicted by our models may occur in the near future. According to our results, a high proportion of stabilizing populations suggest that these three species successfully establish non-native populations. For instance, *D. lineata* has become established in Argentina and seasonal abundance monitoring surveys in Bahía Blanca demonstrate the persistence of this population throughout the year (Molina et al. 2009). In concordance, our results suggest that the *D. lineata* population from Bahía Blanca is indeed in the stabilizing stage. Allegedly, *E. diaphana* has established non-native populations on the eastern side of the Mediterranean Sea and Taiwan (Chen et al. 2008; Schlesinger et al. 2010). However, our models suggest that *E. diaphana* populations inside the Mediterranean Sea are in the regional colonization stage rather than established. Interestingly, the *E. diaphana* population from Taiwan seems to be a sink population. This result is plausible given that new individuals might arrive at Taiwan from suitable adjacent areas; populations from Hong Kong and southern Japan are in the stabilizing stage and represent likely sources. On the other hand, *N. vectensis* mostly occurs in the Northern Hemisphere, with successful non-native populations on the Pacific Coast of the US and England (Reitzel et al. 2008). A southward expansion has been suggested for this species along the Brazilian coast (Brandao et al. 2019). Conversely, our results showed that *N. vectensis* populations from Brazil seem to be sink populations and new introductions further south might have been mediated by vector availability. A rapid and successful secondary spread has been confirmed for *D. lineata* in the Baltic Sea and *E. diaphana* in the Jellyfish Lake, Palau (Podbielski et al. 2016; Patris et al. 2019).

In contrast to successful establishments, a considerable number of occurrences of these three sea anemone invaders are in unsuitable areas and most likely represent populations that have failed or will fail to establish. In concordance, it has been demonstrated that *D. lineata* has failed to persist in Nova Scotia, Canada where some local non-native populations have gone extinct (Ma et al. 2020). According to our results, *D. lineata* populations from Nova Scotia represented both sink populations and populations at the regional colonization stage. However, farther north of Nova Scotia there seems to be a suitable area for *D. lineata* establishment. On the other hand, an “introduction-failure-reintroduction” pattern has been observed in a *D. lineata* population from Texas, US (Hancock et al. 2017). Hancock et al. (2017) mentioned that *D. lineata* has succeeded to establish at the Galveston area, whereas the Port Aransas population has failed. Our results demonstrated that the Galveston population is in the stabilizing stage, whereas individuals at Port Aransas represent a sink population. These similarities between our ENMs and empirical observations highlight again the potential of this approach in sea anemone invasions. Interestingly, although *E. diaphana* showed a high proportion of sink populations, there were also high suitability values for this species in oceanic areas. This result suggests a plausible potential for *E. diaphana* to withstand transportation that could partly explain how sink populations might persist long periods of time, an aspect that deserves further exploration in the future.

Unfortunately, most non-native sea anemone populations seem to remain unmonitored after their first report (see Chapter 2). In Chile, *D. lineata* was reported in 2015, but no further information has been provided about this population since (Häussermann et al. 2015). This has also occurred for both *E.*

diaphana and *N. vectensis* in the Galapagos Islands and Brazil, respectively (Silva et al. 2010; Carlton et al. 2019). According to our results, both *D. lineata* and *E. diaphana* either have established or will likely establish in Chile and the Galapagos Islands, respectively. On the contrary, the non-native *N. vectensis* populations in Brazil represent sink populations. Future research should thus focus on monitoring non-native populations of these three species (and others) to elucidate which have successfully established and which have failed (as demonstrated by Ma et al. 2020).

The invasion success of a species may be attributed to different causes, at biological and ecological levels. At a biological level, successful non-native sea anemone species have been highly associated with broad physiological tolerance ranges to temperature and salinity, in addition to asexual reproductive strategies (Glon et al. 2020; Chapter 2). The association between broad tolerance range and invasion success has only been assessed by observational and experimental approaches. In this study, our results demonstrated that such relationship also occurs when applying a macroecological approach (see Vasconcelos et al. 2012). The distribution of the occurrences of each species and their environmental conditions resulted in high values of niche breadth in concordance with the aforementioned broad physiological tolerance ranges (see *Species* section). Other non-native sea anemone species have also shown broad physiological tolerance ranges, such as *Anemonia alicemartinae* and *Metridium senile* (Glon et al. 2019; Suárez et al. 2020). Alternatively, at an ecological level, other likely mechanisms accounting for invasion success include interspecific interactions (e.g., *D. lineata* has found hard substratum and protection provided by Spartina sp., Molina et al. 2009) and lack of natural enemies (e.g., *E. diaphana* seems to have found no predator or competitor at the Jellyfish Lake, Patris et al. 2019).

One key hypothesis explaining the fate of species introductions states that the establishment of a self-sustaining population in the non-native range can only succeed within conditions matching the native environmental niche (i.e., climatic match hypothesis; see Broennimann et al. 2021). ENMs allow for the exploration of the invasion process of non-native species on a macrospatial (i.e., biogeographic) scale by comparing the native and non-native ranges (Broennimann et al. 2012; Petitpierre et al. 2012). Here, we tested the climatic match hypothesis in the invasion of three globally introduced sea anemone species by assessing their environmental niche dynamics (i.e., overlap between environmental conditions in the native and non-native ranges). The results from the niche equivalency test suggest that each species showed an identical niche when comparing the overlap between their respective native and non-native niches. Furthermore, we found two contrasting scenarios when exploring the niche dynamics of each species. On one hand, *D. lineata* revealed a strongly conserved niche dynamic, which means that the invasion success of this species has occurred mainly in areas with similar environmental conditions as those from its native range (i.e., niche conservatism assumption and climatic match hypothesis were fulfilled). On the other hand, although *E. diaphana* and *N. vectensis* revealed almost conserved dynamics, both species showed levels of niche expansion, particularly greater for *E. diaphana*. In addition, both species showed a considerable proportion of populations at the regional adaptation stage, particularly greater for *N. vectensis*. These results provide support for the climatic match hypothesis, but also suggest that these two species might be adapting to new environmental conditions in their non-native ranges (i.e., niche shifts).

Niche shifts can be the result of two main possible mechanisms: unfilling and expansion. In a niche unfilling, the conditions occupied in the non-native range are a subset contained in the native niche (i.e., there is an unfilled area), and the invasion is an ongoing process at early stages where there are still suitable areas to be colonized. For example, Battini et al. (2019) found that the non-native neurotoxic sea-slug *Pleurobranchaea maculata* has yet to reach biogeographic equilibrium in the SW Atlantic Ocean, which means this invasion phenomenon is at early stages. In this study, the three sea anemone invasion phenomena showed unfilling niche values of practically 0. These results demonstrate that the three species have occupied all of the suitable environmental conditions from their native ranges in the non-native ranges (i.e., biogeographic equilibrium) and their invasion processes seem to be overall at advanced stages.

Alternatively, in a niche expansion the non-native niche can be partially or completely different from the native niche (i.e., the species thrives under new environmental conditions). This pattern can result from changes in dispersal and biotic restrictions or a sampling bias (Soberón & Nakamura 2009). However, a sample bias is unlikely in this study because we attempted to minimize possible sources of bias in the occurrence records and the environmental predictors (see *Methods*). Assuming there were no sampling biases, the arrival of *E. diaphana* and *N. vectensis* at new locations with different dispersal or biotic restrictions from those that limit their native distributions could explain why they are colonizing new environmental conditions. Another plausible mechanism resulting in niche expansion could be a founder effect, a common phenomenon among non-native populations during the invasion process (e.g., Oliveira et al. 2018). Particularly, in sea anemone invasions certain individuals successfully overcome transport and introduction, often involving wide environmental fluctuations (Gollasch & Riemann-Zürneck 1996). Local populations then establish due to asexual reproduction with high proportions of certain successful genotypes that could likely result in acclimatation and ultimately in adaptation to new environmental conditions (see Ryan 2018; Ryan & Miller 2019; Ryan et al. 2019). Regardless of the mechanism, the invasion potential of *E. diaphana* and *N. vectensis* has likely begun to increase due to adaptations to environmental conditions absent in their native ranges. Future research should assess to which extent these species have adapted to new conditions, if any, and explore which mechanisms are operating.

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CHAPTER 4: CONCLUSION AND FUTURE PERSPECTIVES

An increasing flow of species across oceans in association with human activities has been evident over the past centuries, but many questions remain unanswered about the drivers and processes mediating marine invasions (Carlton 2003, 2009; Darling & Carlton 2018). Effort has been aimed at distinguishing the traits that determine which non-native species survive and persist in novel environments and what other factors influence invasion success (Catford et al. 2009; Blackburn et al. 2011; Perkins et al. 2011; Chan & Briski 2017). Unfortunately, a lack of information about the basic biology and ecology of certain non-native species limits our understanding of their invasion process (e.g., invertebrate organisms with no historical reports as pests and little to no commercial value; Zabin et al. 2007). Invasion ecology researchers seem to target certain taxa and certain species within those taxa leading to an over-representation of some non-native species in detriment of others (Bailey et al. 2020; Watkins et al. 2021). Unsurprisingly, such a trend partly explains why many introductions and invasions happen silently without being noticed (Miglietta & Lessios 2009).

The phylum Cnidaria includes representatives well-known as invaders. The azooxanthellate coral *Tubastraea coccinea* is the most studied non-native cnidarian species (Watkins et al. 2021). This coral species has dominated certain environments, with rapid spread and ecological consequences (Fenner & Banks 2004; Creed 2006; Mantelatto et al. 2011; Riul et al. 2013; Da Silva et al. 2014). Other cnidarian species recognized as invaders include the octocoral *Unomia stolonifera*, the spotted jellyfish *Phyllorhiza punctata*, and the venomous rhizostamatid jellyfish *Rhopilema nomadica* (Bolton & Graham 2004; Giallongo et al. 2021; Ruiz-Allais et al. 2021). At least 11 species of non-native actiniarian sea anemones have been reported world-wide. Fortunately, these cases have been gaining more attention with new reports every year (e.g., Acuña et al. 2020; Glon et al. 2020a; Holmes & Callaway 2021; Pederson et al. 2021).

In the systematic review provided here (Chapter 2), the general pattern of sea anemone invasions was described throughout all stages: transport, introduction, establishment, and invasion (Figure 11). Non-native sea anemones have reached areas far from their native distribution ranges mainly in the adult stage and aided by human activities such as maritime traffic and aquaculture. The aquarium trade industry represents a new vector for the introduction of sea anemones and should be more explored in the future. Individuals colonize mostly marine systems and natural habitats, although they also thrive in estuarine systems and human-made habitats. Broad tolerance ranges to abiotic stressors (e.g., temperature, salinity) and non-selective resource requirements (e.g., food, space) partly explain the successful introduction of non-native populations. Then, asexual reproduction strategies enable population growth and persistence to assure establishment. Both natural and human-associated dispersal mechanisms likely facilitate secondary spread. However, while some populations establish and undergo secondary spread reaching the invasion stage, others may remain stable for years and even disappear due to multiple factors, such as abiotic stress (e.g., severe winters). Negative ecological effects have been demonstrated for some species, especially linked to changes in the abundance of native species. However, both the ecological and economic consequences of sea anemone invasions have seldom been studied. Interestingly, *D. lineata* presents a chance >90% of becoming a biological invasion threat with demonstrated impacts (according to the "Invasion Threat Score" created by Miralles et al. 2021). This fact highlights how much attention should be focused on ecological and economic consequences associated with sea anemone invasions.

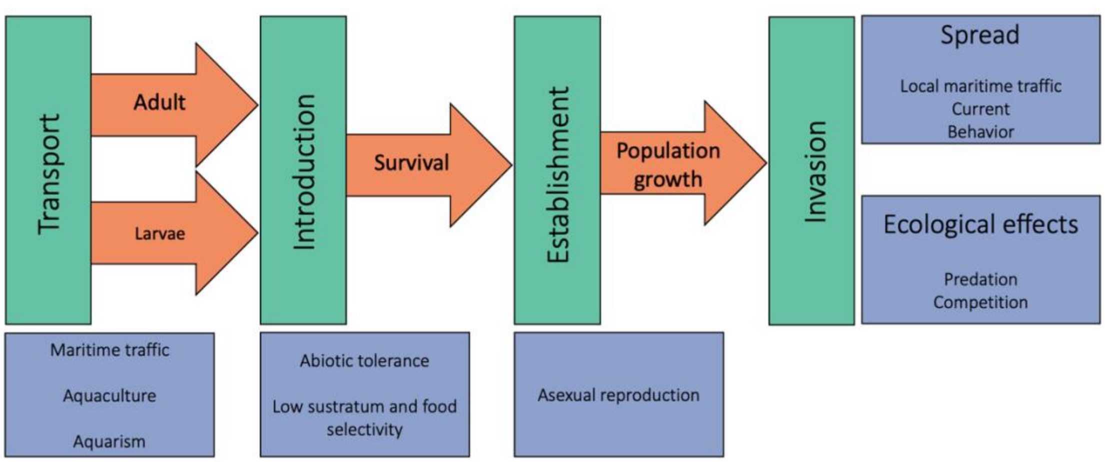

Figure 11. Stages of sea anemone invasions (modified from Glon et al. 2020b).

Different issues were detected in the study of non-native sea anemone species. Both geographic and taxonomic biases were observed: most reports come from the Northern Hemisphere, and they are focused mainly in three species (*Diadumene lineata*, *Exaiptasia diaphana* and *Nematostella vectensis*). I demonstrated that most research effort has been aimed at *D. lineata*, the "poster children" of sea anemone invasions (sensu Watkins et al. 2021). Therefore, the general pattern described above is most likely biased, and more attention should be focused on less studied/reported species. Similar biases were found for marine invasions in general (Watkins et al. 2021). Fortunately, in the case of sea anemone invasions, new species are gaining attention, especially in the Southern Hemisphere (*Metridium senile*, *Anemonia alicemartinae* and *Sagartia ornata*). However, most reports for all species world-wide seem to remain unmonitored after first detection. Therefore, future monitoring surveys must be aimed at determining which populations have successfully established and which have failed (see Ma et al. 2020 for an example). On the other hand, some species suspected as non-native need more information to better determine whether they represent new cases of introductions.

Sea anemone species of the order Actiniaria represent a broad taxon suitable for invasion ecology research (Glon et al. 2020b; Chapter 2). As discussed in Chapter 2, some species, marine realms, and approaches require more research effort to eliminate biases and gaps in the current knowledge. Multiple approaches in the future can help to minimize the research biases and fill in the gaps in our current knowledge about sea anemone invasions. Ecological impact assessments need to be carried out to determine which populations represent a threat to native communities. Predation pressure and competition represent the main mechanisms leading to ecological effects associated with non-native sea anemones. Prey composition in the gastrovascular content of non-native sea anemones and changes in native community composition are an easy way to evaluate effects mediated by predation pressure (e.g., Robinson & Swart 2015). Competition is hard to assess, but changes in native distribution and abundance and aggressive interaction experiments represent two possible ways to explore competitive interactions (Escribano-Álvarez & López-González 2018; Brante et al. 2019). Comparisons between native and non-native populations will also provide relevant information to better understand which traits lead to invasion success (as demonstrated in plant invasions, Hierro et al. 2005). For instance, *M. senile* has proven to be tolerant to abiotic stress in its native range (Glon et al. 2019), but what about its non-native populations in the Southern Hemisphere? Interesting patterns could emerge when comparing different aspects of native vs. non-native populations, as has been demonstrated in *D. lineata* studies (Uchida 1932; Ryan and Miller 2019; Newcomer et al. 2019). Furthermore, the application of genetic and phylogenetic tools could shed light on uncertain cases, helping to establish species delimitation and their native ranges. On the other hand, ecological interactions between non-native sea anemones and members of the invaded community have only recently gained attention (e.g., Molina et al. 2009, Martin et al. 2015), but the processes involved have not yet been fully described. These are only a few examples for potential future research on non-native sea anemones and I encourage fellow researchers to explore all of these possibilities and more.

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 reported. 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 positivity 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.

Spatially explicit information (e.g., predictions of potential distributions) is necessary to support decisions aimed at the prevention, early detection, and management of biological invasions (Inglis et al. 2006; Leidenberger et al. 2015). In this research (Chapter 3), I addressed the potential of ecological niche modeling in sea anemone invasions to achieve three goals: (1) to provide a useful tool to predict potential introductions and spread scenarios of non-native sea anemone species; (2) to determine the invasion stage of non-native occurrences and calculate the environmental niche breadth of each species; and (3) to assess the environmental niche dynamics during the invasion process and determine whether these three species have colonized areas with similar environmental conditions as those from their respectively native ranges (i.e., climatic match hypothesis). This approach has been widely used in other taxa with non-native representatives such as plants, other terrestrial organisms, and marine invasive algae (Gallien et al. 2010; Marcelino & Verbruggen 2015).

The model projections reveled likely scenarios for introductions of *Diadumene lineata*, *Exaiptasia diaphana* and *Nematostella vectensis* in areas beyond their hitherto reported non-native ranges. Even though a biogeographic equilibrium seems almost reached in the invasion process of these three sea anemone species, likely scenarios for spread may occur in the future, both in their native and non-native ranges. A high level of non-native populations in the stabilizing invasion stage suggests a strong pattern of successful establishment for these three species, arousing concern about the lack of monitoring surveys aimed at the early detection of introductions. In concordance, all three species showed broad environmental niche breadths, suggesting they colonize a wide range of environmental conditions. Finally, two different scenarios of niche dynamics were found: (1) *D. lineata* showed a strongly conserved dynamic, which suggests that invasion success has mainly occurred in areas with similar environmental conditions as those from its native range; and (2) *E. diaphana* and *N. vectensis* showed niche shifts attributed to niche expansions, suggesting they might be adapting to new local environmental conditions in their non-native ranges. Overall, the results suggest that the three species succeed when colonizing non-native location with similar environmental conditions as those from their respective native distributions. Therefore, strong evidence has been provided to support the climatic match hypothesis of invasions. However, *E. diaphana* and *N. vectensis* have likely begun to increase their invasive potential by adapting to environmental conditions absent in their respective native distributions. This contribution demonstrates that ecological niche modeling can help to detect areas with sea anemone invasion risk and to shed light on mechanisms that could help to better understand the invasion process of sea anemones.

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SUPPLEMENTARY MATERIAL

Chapter 2

Table S1. Summary of the data obtained from the analyzed articles in the systematic review.

This table can be provided as a .xlsx file by request at lucas.hernan.gimenez@gmail.com

Chapter 3

Table S2. Native and non-native occurrence records used in this study for *Diadumene lineata*, *Exaiptasia diaphana* and *Nematostella vectensis*.

This table can be provided as a .xlsx file by request at lucas.hernan.gimenez@gmail.com

Table S3. Summary of contribution and importance of each species-specific predictor to the models used to build the potential distribution maps.

Species	Predictors	Contribution (%)	Importance
Diadumene lineata	Mean primary productivity	68.78	69.29
	Temperature range	30.72	30.22
	Mean salinity	0.50	0.50
	pH	0.00	0.00
Exaiptasia diaphana	Primary productivity range	36.28	14.44
	Temperature range	27.11	53.67
	Mean temperature	14.16	19.89
	Mean salinity	11.48	6.23
	pH	10.96	5.77
Nematostella vectensis	Dissolved oxygen range	60.53	75.23
	Mean primary productivity	30.43	14.85
	pH	4.22	5.81
	Salinity range	4.08	4.10
	Temperature range	0.74	0.00

Figure S1. Model selection (delta AICc) and performance assessment (average AUC) for *Diadumene lineata*. The model selected was the H9 (features = Hinge; regularization multiplier = 9).

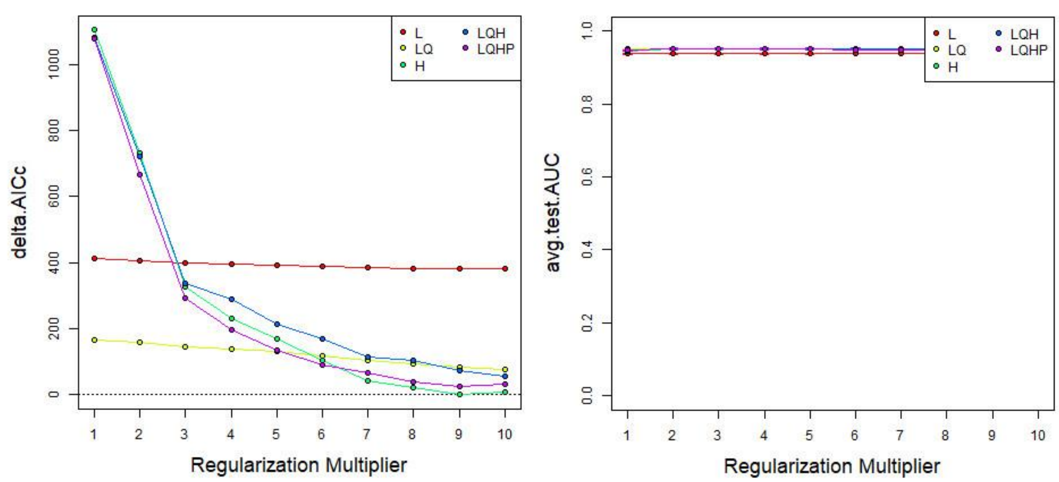


Figure S2. Model selection (delta AICc) and performance assessment (average AUC) for *Exaiptasia diaphana*. The model selected was the LQ1 (features = Linear + Quadratic; regularization multiplier = 1).

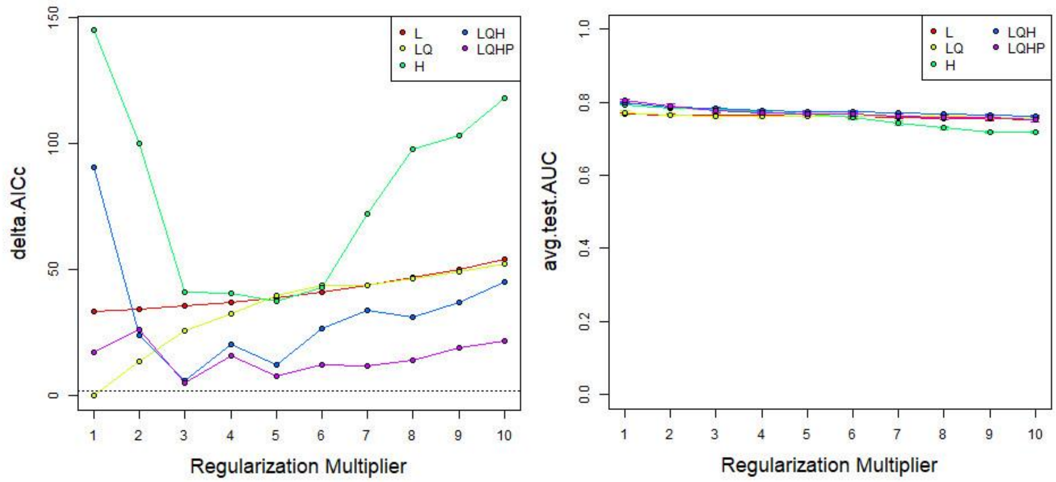


Figure S3. Model selection (delta AICc) and performance assessment (average AUC) for *Nematostella vectensis*. The model selected was the LQH3 (features = Linear + Quadratic + Hinge; regularization multiplier = 3).

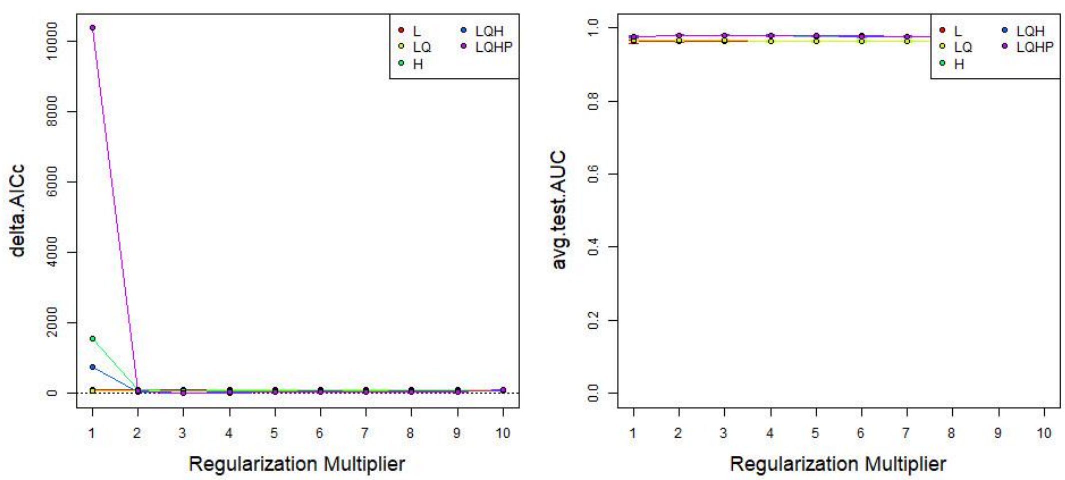


Figure S4. Potential distribution of **(a)** *Diadumene lineata*, **(b)** *Exaiptasia diaphana* and **(c)** *Nematostella vectensis*. Each model was built including all of the occurrences of each species (i.e., native and non-native). The current native and non-native occurrences are omitted to show how the models encompass the distribution of each species.

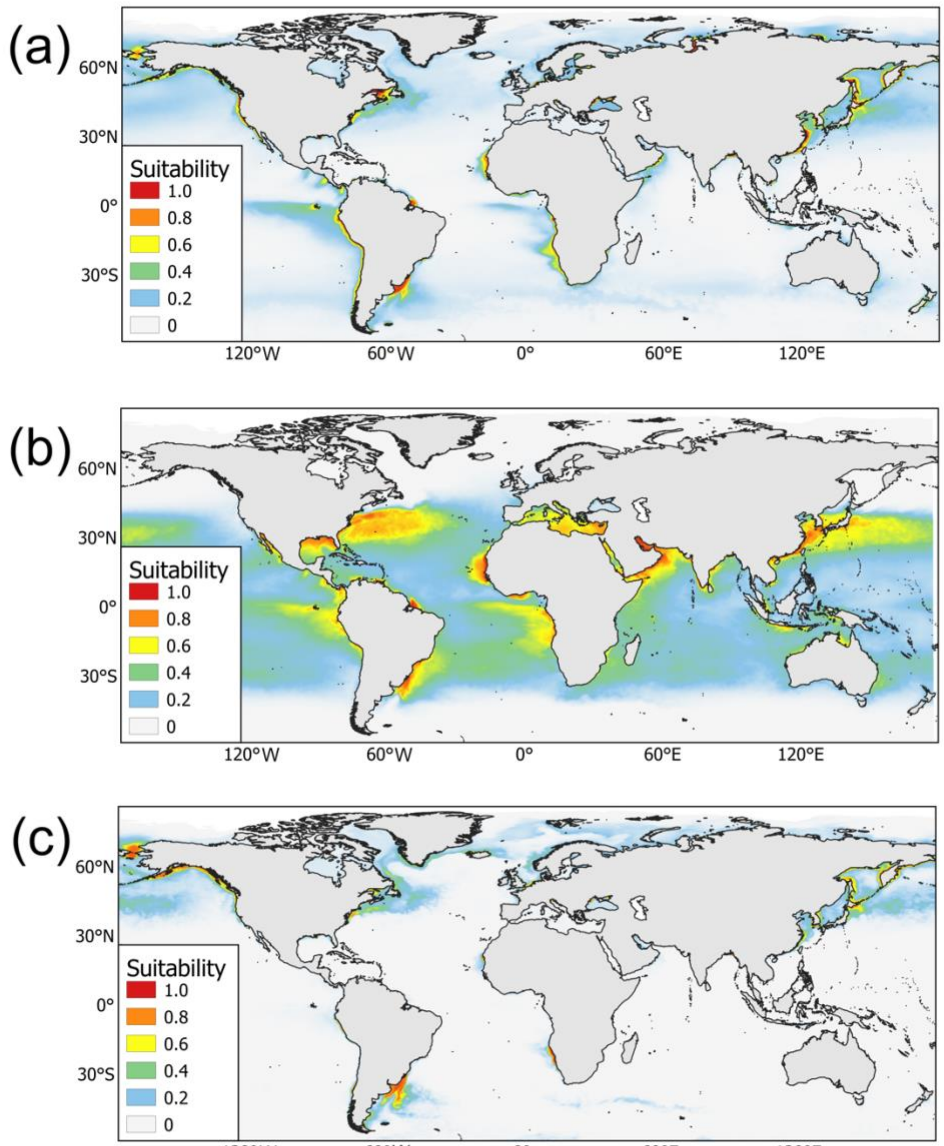


Figure S5. Global model (yellow) and regional model (blue) used to classify *Diadumene lineata* non-native occurrences (black dots) into invasion stages. Green areas denote the overlap between both models. Both models were transformed to a binary prediction establishing an arbitrary threshold of 0.5. Occurrences can be categorized into four different stages: stabilizing populations (green area), sink populations (white area), colonization (yellow area) and adaptation (blue area).

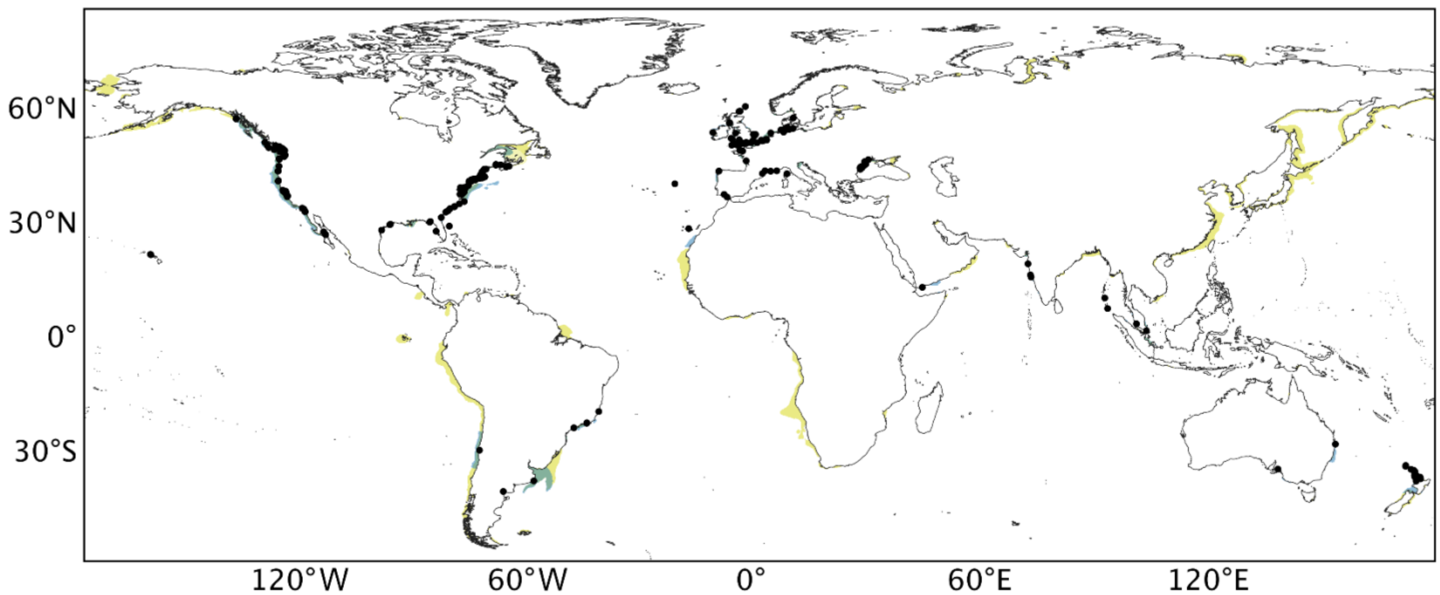


Figure S6. Global model (yellow) and regional model (blue) used to classify *Exaiptasia diaphana* non-native occurrences (black dots) into invasion stages. Green areas denote the overlap between both models. Both models were transformed to a binary prediction establishing an arbitrary threshold of 0.5. Occurrences can be categorized into four different stages: stabilizing populations (green area), sink populations (white area), colonization (yellow area) and adaptation (blue area).

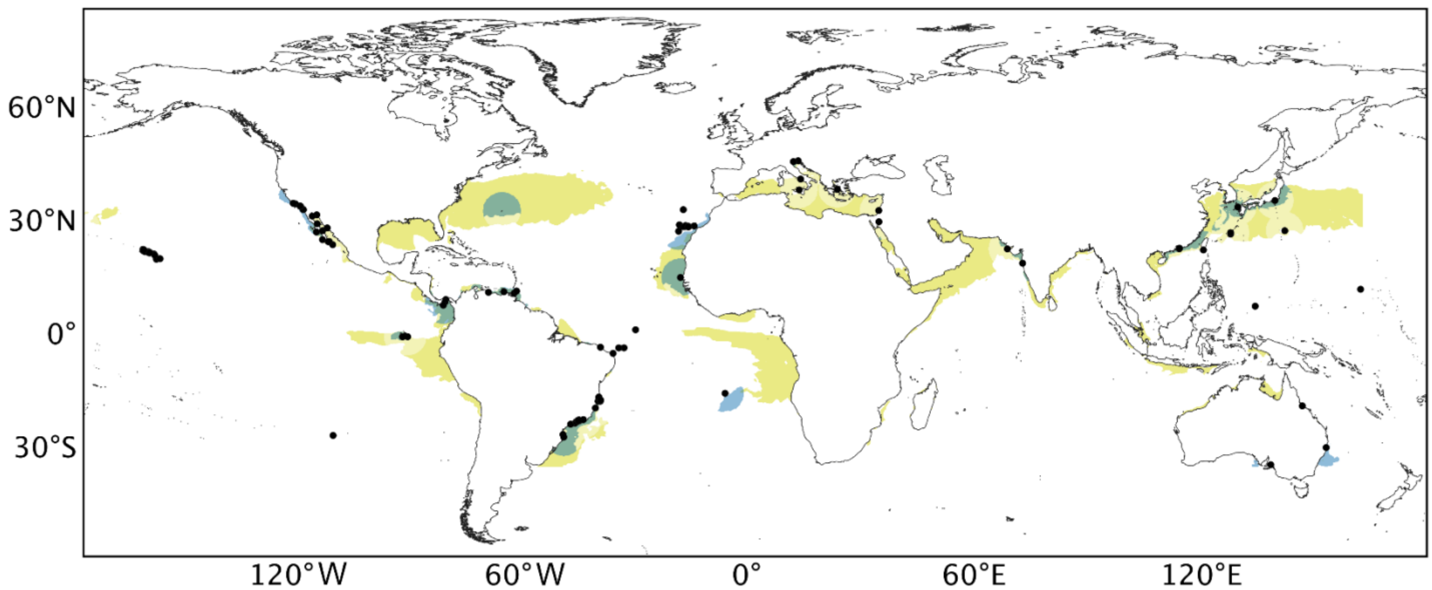


Figure S7. Global model (yellow) and regional model (blue) used to classify *Nematostella vectensis* non-native occurrences (black dots) into invasion stages. Green areas denote the overlap between both models. Both models were transformed to a binary prediction establishing an arbitrary threshold of 0.5. Occurrences can be categorized into four different stages: stabilizing populations (green area), sink populations (white area), colonization (yellow area) and adaptation (blue area).

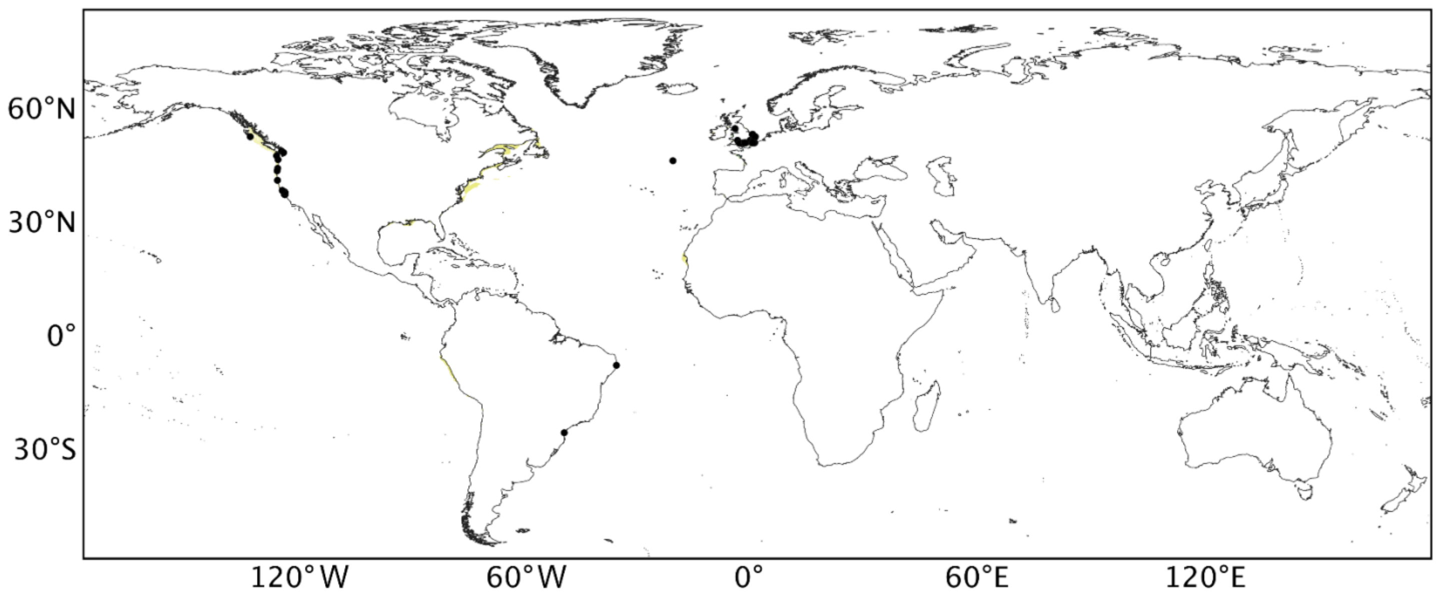


Figure S8. Environmental analogy between the native and non-native ranges of (**a**) *Diadumene lineata*, (**b**) *Exaiptasia diaphana* and (**c**) *Nematostella vectensis* based on the multivariate environmental similarity surface analysis (MESS). Lower (especially negative) values denote non-analog areas.

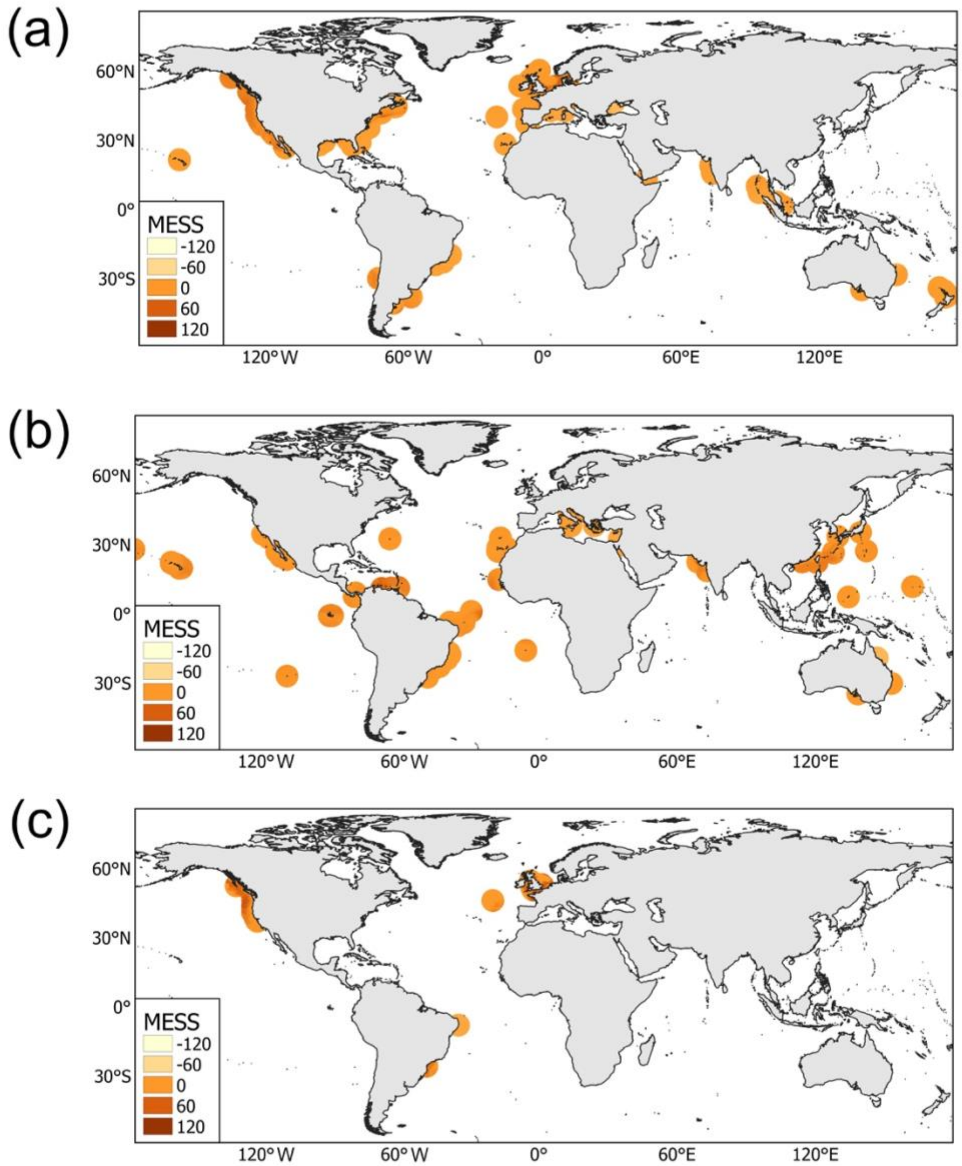


Figure S9. PCA-env for specific predictors selected for *Diadumene lineata*.

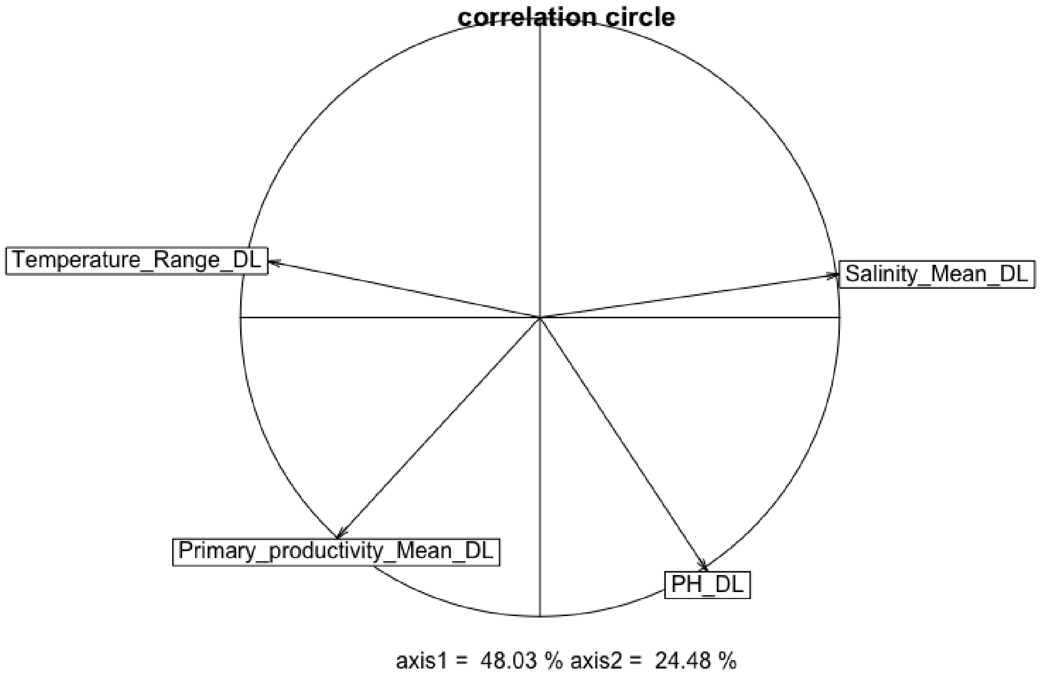


Figure S10. PCA-env for specific predictors selected for *Exaiptasia diaphana*.

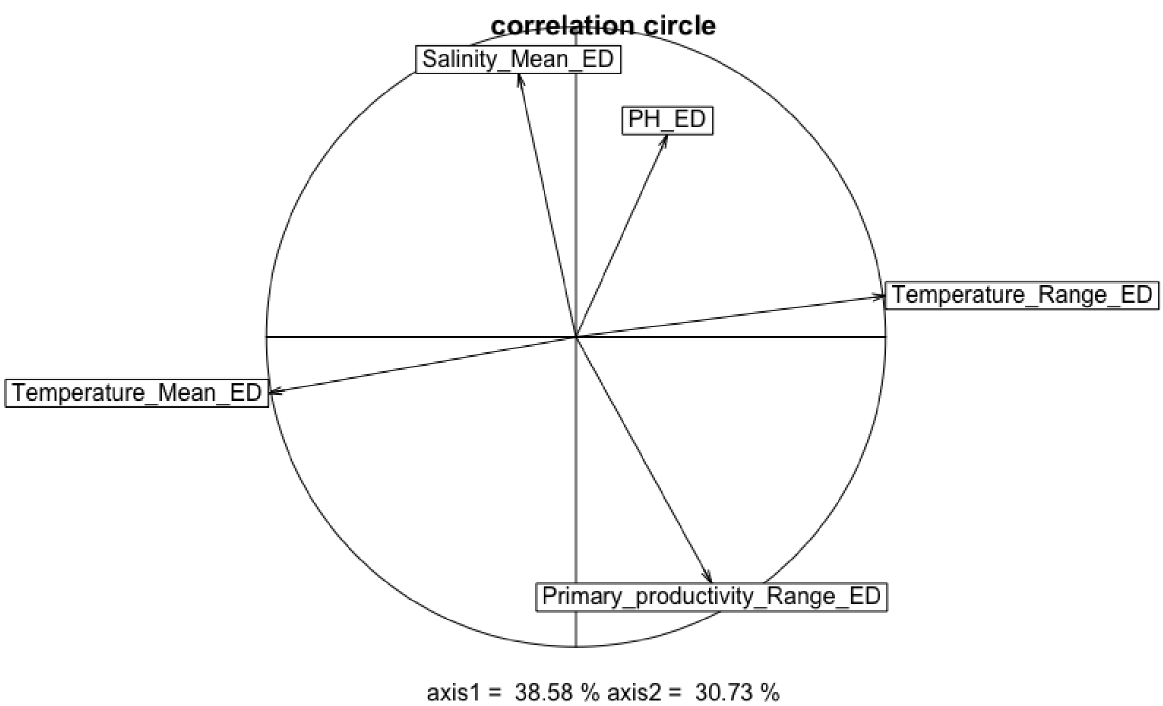


Figure S11. PCA-env for specific predictors selected for *Nematostella vectensis*.

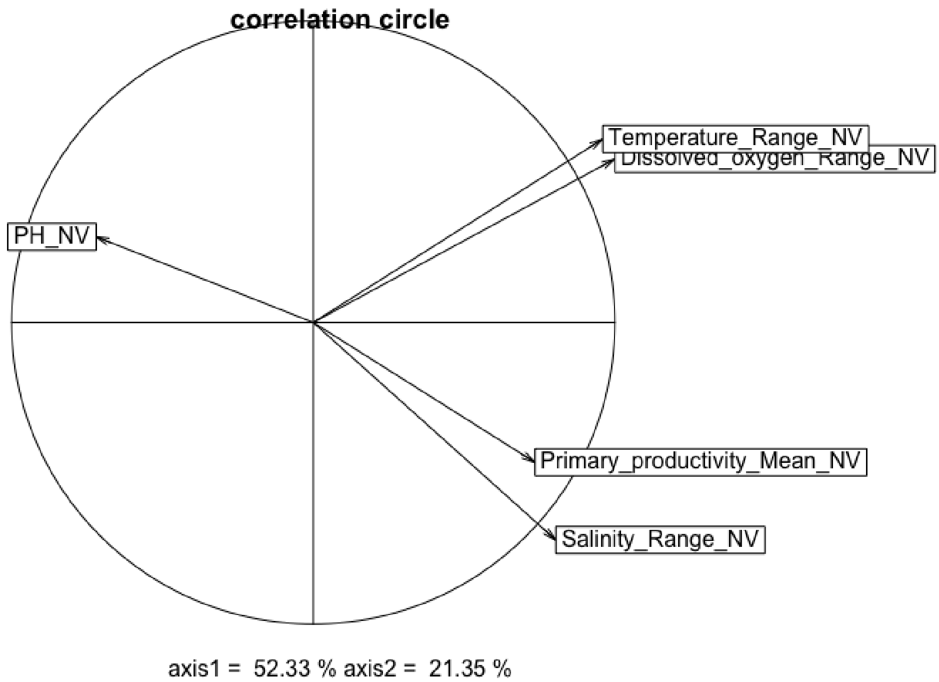


Figure S12. Statistical tests for niche comparison between native and non-native range for *Diadumene lineata*. Observed values for niche overlap index (D) in relation to expected frequencies for p=0.05.

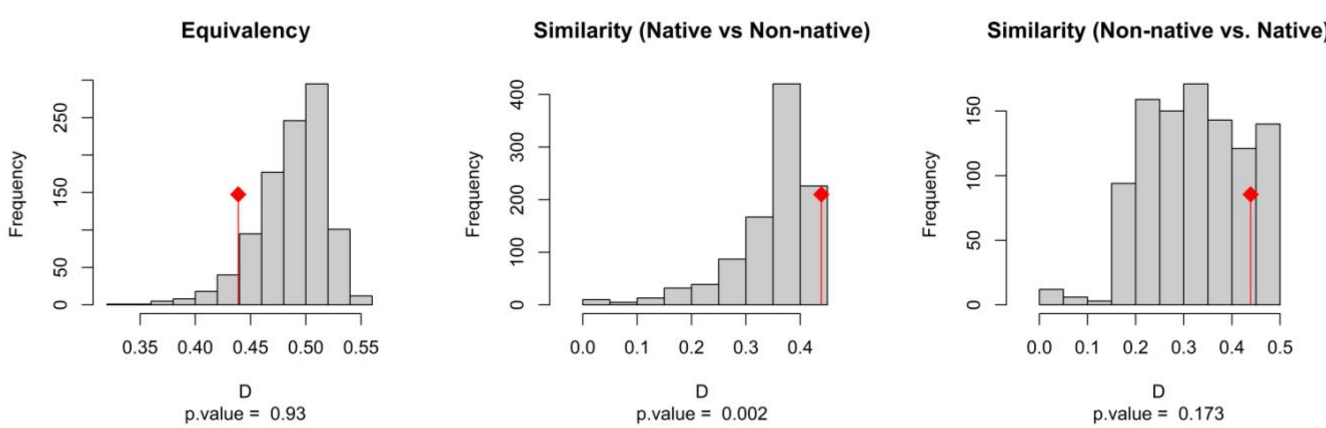


Figure S13. Statistical tests for niche comparison between native and non-native range for *Exaiptasia diaphana*. Observed values for niche overlap index (D) in relation to expected frequencies for p=0.05.

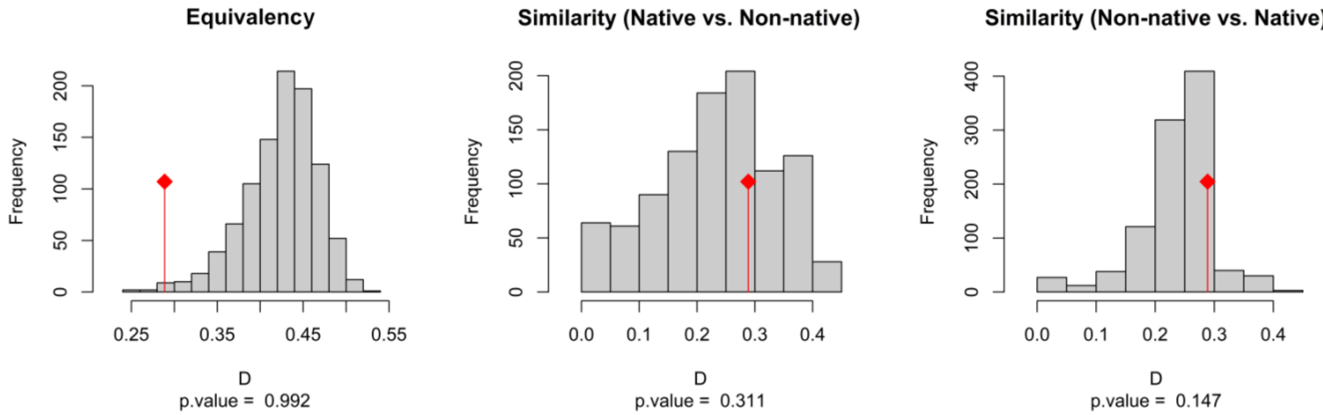
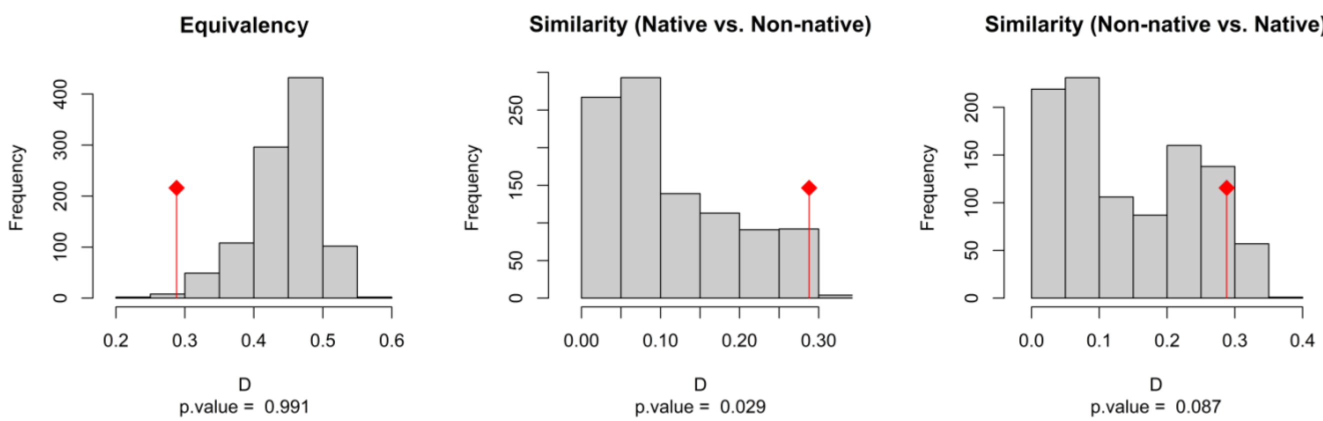


Figure S14. Statistical tests for niche comparison between native and non-native range for *Nematostella vectensis*. Observed values for niche overlap index (D) in relation to expected frequencies for p=0.05.



PUBLICATIONS AND CONTRIBUTIONS

Publications derived from this thesis

- **Gimenez LH**, Brante A. (2021). Do non-native sea anemones (Cnidaria, Actiniaria) share a common invasion pattern? – A systematic review. Aquatic Invasions 16(3): 365-390.

Authors' contributions: LHG and AB conceived the idea and designed the study. LHG designed the methodology, revised the articles, collected the data, prepared the figures, and led the writing of the manuscript. LHG and AB interpreted the data. AB significantly contributed to manuscript writing and critical review.

- **Gimenez LH**, Rivera R, Brante A. One step ahead of sea anemone invasions: Potential new introductions, spread, and environmental niche dynamics of three successful invasive species. In prep.

Authors' contributions: LHG, RR and AB conceived the idea and designed the study. RR designed the methodology. LHG searched and organized the occurrence and environmental data, performed the analyses, and prepared the figures. LHG, RR and AB interpreted the results. LHG led the writing of the manuscript. RR and AB significantly contributed to the manuscript writing and critical review.

Other publications generated during the MEM Program, but not related to this thesis

- **Gimenez LH**, Doldan MS, Zaidman PC, Morsan EM. (2020). The potential of *Glycymeris longior* (Mollusca, Bivalvia) as a multi-decadal sclerochronological archive for the Argentine Sea (Southern Hemisphere). Marine Environmental Research. 155: 104879.

- **Gimenez LH**, Doldan MS, Zaidman PC, Morsan EM. (2020). Age and growth of *Glycymeris longior* (Sowerby, 1832) clam at the southern edge of its distribution (Argentine Sea). Helgoland Marine Research. 74: 2.

Contributions to Scientific meetings

- **Gimenez LH**, Rivera R, Brante A. 2021. Distribución geográfica potencial y dinámica de nicho de la anémona invasora *Diadumene lineata*. XL Congreso de Ciencias del Mar. Punta Arenas, Chile. (TALK)
- **Gimenez LH**, Brante A. 2021. Uso de microhábitat y composición de presas de la anémona invasora *Anemonia alicemartinae* y la anémona nativa *Anthothoe chilensis*. XL Congreso de Ciencias del Mar. Punta Arenas, Chile. (POSTER)