



Mediators of invasions in the sea: life history strategies and dispersal vectors facilitating global sea anemone introductions

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Abstract Widespread non-native species tend to demonstrate an apparent lack of selectivity in habitat requirements, feeding regimes, and reproductive needs, while displaying a tendency to thrive in human-modified habitats. The high phenotypic plasticity typical of sessile, substrate-attached marine species may enhance their chances of survival and spread in a new region. Anthropogenic activities have changed marine habitats over a wide range of phenomena, including water temperature, community species composition, and the types of available substrates, creating new physical and biotic regimes that may contribute to the potential for successful species introduction. Here we examine ten species of sea anemones that have been introduced outside of their native range, and elucidate specific characteristics that are common among globally introduced sea anemones. Various life history strategies enable these

species to survive and flourish through transport, introduction, establishment and spread, leading to the successful colonization of a new geographic area. Considering life history strategies and weighing of vector potential, we suggest conditions that facilitate introduction of these species, and identify species of sea anemones that may be introduced in the future in the face of changing climate and increased anthropogenic activities.

Keywords Sea anemone · Cnidaria · Actiniaria · Introduced species · Vector

Introduction

Marine biological invasions are being amplified by increasing anthropogenic dispersal and environmental alterations, including stressed habitats and climate change. Anthropogenic activities have enabled linkages of donor regions with new recipient regions that may not otherwise be connected, overcoming natural barriers which may have long kept many regions isolated (Carlton 1996; Ruiz et al. 1997). High-latitude regions are experiencing the poleward expansion of many species in the face of warming ocean temperatures (Jurgens 2018).

Biological invasions may proceed through four basic stages (Blackburn et al. 2011): Transport, Introduction, Establishment, and Spread (Fig. 1). At

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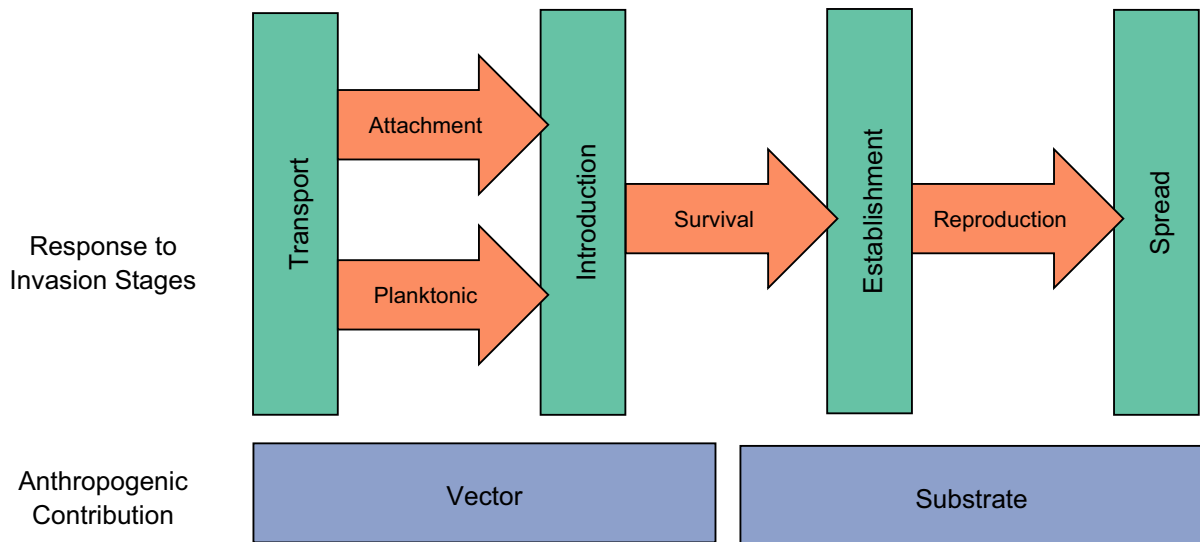


Fig. 1 Stages of invasion adapted from Blackburn et al. (2011), including the associated biological responses as well as where anthropogenic contributions may facilitate invasions

each of these invasion stages a species may exhibit different characteristics or strategies due to changing transport or environmental conditions or interactions with members of the invaded communities (Lodge 1993; Blackburn et al. 2011). Additionally, human activities may influence the potential for a species to pass to the next stage, either by providing a transport vector or by creating new suitable habitat.

Certain species within given taxonomic groups are more likely to be candidates for successful introduction based on their ecological and biological traits. Within the actinarian sea anemones, there is an amazing array of life history strategies regulating reproduction, dispersal, and tolerance to abiotic factors such as temperature and salinity (Shick 1991). A general predisposition among many anemone species towards hardiness and potentially rapid proliferation creates a group well-adapted for introduction.

Here we address how life history strategies and dispersal vectors impact the success and history of marine invasions, using sea anemone species as models of introduction across the world. Sea anemone invasions leverage multiple anthropogenic activities and are inferred to span timescales from historical (pre-1900) to recent (and ongoing). Our goal is to consolidate our current understanding of examples of anemone invasions while highlighting and comparing the intersection of life history and ecological strategies and modes of introductions. This synthesis thus

provides a baseline to predict future effects and risks of human-mediated dispersal of sea anemones.

Species

We consider here ten species of sea anemones that are globally known as introduced throughout the world. Eight species belong to the Acuticulata clade of the superfamily Metridioidea, one species is in the superfamily Actinoidea, and one is in the superfamily Edwardsioidea. The ten species are presented in an

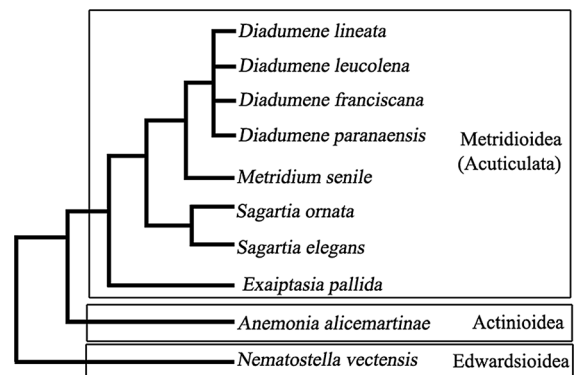


Fig. 2 Current understanding of the phylogenetic relationships of the ten species or purported species included in this review, based primarily on Rodríguez et al. (2014), with the major clades to which each belongs highlighted

order that reflects our current understanding of their phylogenetic relationships (Figs. 2, 3; see Rodríguez et al. 2014). Several of these species (*Diadumene lineata*, *Exaiptasia pallida*, *Metridium senile*, and *Nematostella vectensis*) have been well studied, while others are less well known or only recently described. Sea anemones have a reputation for being difficult to identify, and thus are historically overlooked in surveys and are prone to misidentification, thus these species serve as a starting point in our understanding of sea anemone introductions. Our focus is on the life history traits and biology (Table 1) that may regulate

introduction, with notes on their native and introduced ranges, rather than a complete review of the introduction history of each species, particularly as there may be cryptic diversity present within some introduced ranges. In addition, we consider several additional species whose potential introduction histories remain to be determined.

Diadumene lineata (Verrill, 1869)

Diadumene lineata (previously known as *Haliplanella luciae* (Verrill, 1898)) is the most widely distributed

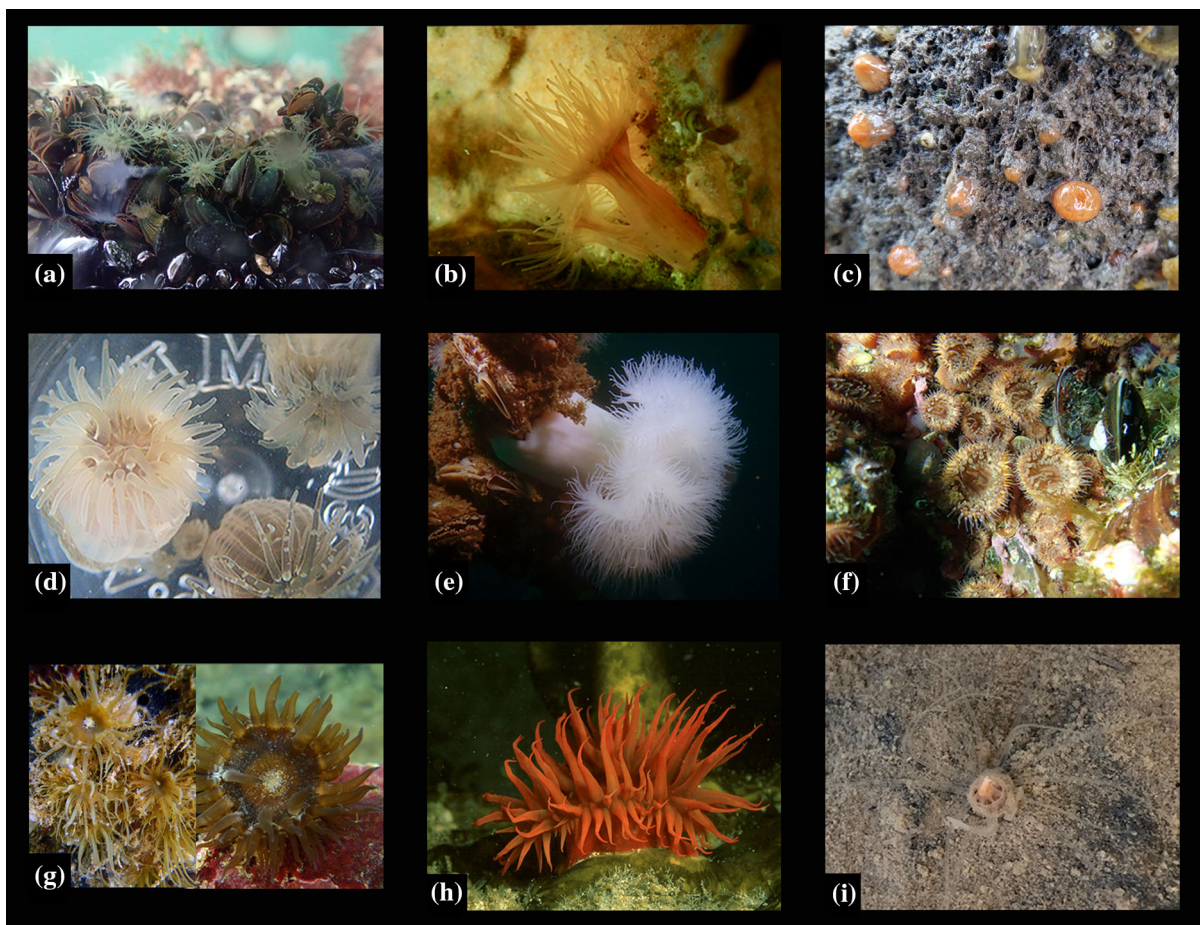


Fig. 3 Photographs of sea anemone species with notable introduction events: **a** *Diadumene lineata* (Photo: Heather Glon, Nova Scotia, Canada, 2018); **b** *Diadumene leucolena* (Photo: Heather Glon, Cape Cod, Massachusetts, 2018); **c** *Diadumene franciscana* (Photo: used with permission from Damon Tighe, California, 2015); **d** *Diadumene paranaensis* (Photo: used with permission from Sérgio Stamper, Brazil, 2010); **e** *Metridium senile* (Photo: Heather Glon, Iceland, 2019); **f** *Sagartia elegans*

(Photo: Heather Glon, Norway, 2018); **g** *Exaiptasia pallida* (Photo: used with permission from Alejandro Grajales, Sea of Cortez & Hawaii, 2012) **h** *Anemonia alicemartinae* (Photo: used with permission from Vreni Häussermann, Chile, 2001); **i** *Nematostella vectensis* (Photo: used with permission by Whitney Leach, Massachusetts, 2016) (Not pictured: *Sagartia elegans*; see cover of Biological Bulletin December 2019 (volume 237, number 3) for color photo)

Table 1 Summary of the habitat and life history traits for each of the species included in this review

Species	Reproduction type	Depth	Substrate type	Temperature tolerance	Salinity tolerance
	Introduced range	Native and introduced ranges			
<i>Diadumene lineata</i>	Asexual (both?)	Intertidal, shallow	Hard and Soft	Broad	Broad
<i>Diadumene leucolena</i>	Sexual	Shallow	Hard	Medium	Broad
<i>Diadumene franciscana</i>	Both	Shallow	Hard	Broad	Broad
<i>Diadumene paranaensis</i>	Asexual	Shallow	Hard	Medium	Broad
<i>Metridium senile</i>	Both	Intertidal to > 100 m	Hard	Medium	Broad
<i>Sagartia</i> sp. “South Africa”	Parthenogenic	Shallow	Hard	Medium	Broad
<i>Sagartia elegans</i>	Both	Shallow (native to 90 m)	Hard	Medium	Medium
<i>Exaiptasia pallida</i>	Asexual (both?)	Shallow	Hard	Medium	Broad
<i>Anemonia alicemartinae</i>	Asexual	< 25 m	Hard	Narrow	Narrow
<i>Nematostella vectensis</i>	Both	Intertidal	Soft	Broad	Broad

Reproduction type refers to the strategy recorded in the introduced range (“both” refers to asexual and sexual strategies). Depth encompasses their most commonly reported depth. Substrate type is the preferred substrate that a species can be found attaching or burrowing into. Tolerance to temperature and salinity extremes is based on our current understanding of adult tolerance throughout native and introduced ranges. Temperature categories: Narrow = restricted to stable temperatures within a single temperature zone; Medium = adapted to a more than one temperature zone; Broad = able to persist extreme temperature swings outside of native range. Salinity categories: Narrow = restricted to full ocean salinity; Medium = adapted to ephemeral salinity fluctuations; Broad = adapted to estuarine and marine conditions

sea anemone in the world and among the most well-studied of the non-native sea anemones, occurring broadly throughout the northern and southern hemispheres (Fig. 4; Shick 1976; Shick and Lamb 1977; Ting and Geller 2000; Fautin and Hand 2007). A shallow-water species, reaching 3 cm in height, it is commonly found in the intertidal zone (Fukui 1991) and in shallow subtidal fouling communities (Ting and Geller 2000; Jewett et al. 2005). It is a habitat generalist (Hausman 1919) with individuals found on hard natural substrates such as pebbles, rocks, and oyster shells, on artificial substrates such as docks and piers, and as a common epibiont on other organisms including ascidians, barnacles, sponges, and seaweeds (Uchida 1932; Miyawaki 1951; Sassaman and Mangum 1970; Z. Currimjee and M. Flenniken, personal observations). In certain locations, *D. lineata* is also a common species on mudflats and in salt marsh sediments, with each individual either loose in a small depression or attached to debris or hard substrate under the mud surface, manifested as a cluster of tentacles at the sediment surface at low tide, but a sea

of expanded crowns at high tide (J. T. Carlton, personal observations, 2019, Coos Bay, Oregon).

Diadumene lineata is euryhaline and eurythermal (Miyawaki 1951; Sassaman and Mangum 1970; Shick 1976, 1991; Dunn 1982). It is a well-known estuarine species, characteristic of harbors, bays, and lagoons, where it tolerates salinities as low as 8‰ (Podbielski et al. 2016) and survives freshwater conditions for short periods of time (Miyawaki 1951). Notably, the presence of *D. lineata* in the Baltic Sea spans a range of salinities (Podbielski et al. 2016). It is generally not found in hypersaline habitats, suggesting that it is more tolerant of reduced versus elevated salinities. However, populations are most successful near oceanic salinities, and decline in lower salinities as seen by the reduction in feeding, growth and fission between 14 and 24‰ (Podbielski et al. 2016; Konecny and Harley 2019; Ryan and Miller 2019). It persists in temperatures from below freezing to 30 °C, and can exist short-term at higher temperatures (Minasian and Mariscal 1979; Ryan 2018). Survival during wide temperature swings, air exposure, and extremely low salinities has equipped the species to endure intertidal

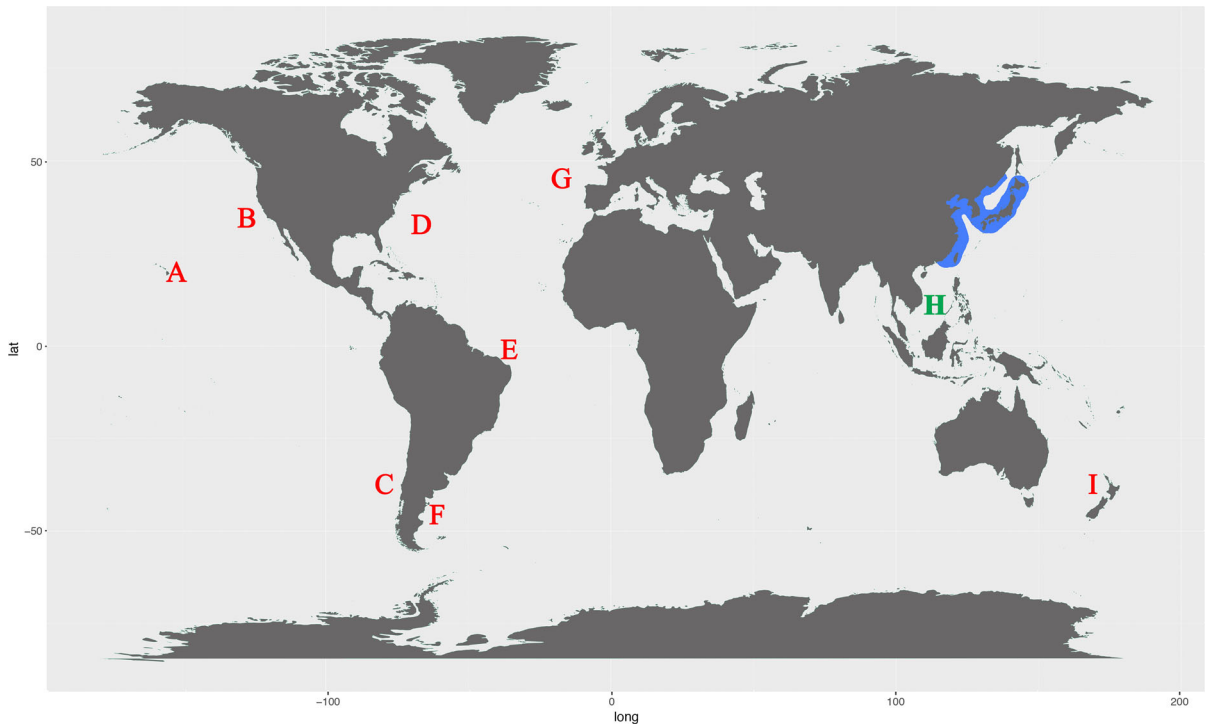


Fig. 4 Map of the native (blue shading), introduced (red letters), and cryptogenic (green letter) distribution of *Diadumene lineata*. References including dates of original regional detection and/or of additional distribution data: a Hawaii (Zabin et al. 2004; Carlton and Eldredge 2015); b Pacific coast of North America from Sitka, Alaska to San Diego Bay, California (Carlton 1979a, b; Fofonoff et al. 2019a, b, c; J. T. Carlton, personal observations, iNaturalist observations); c Chile (Häussermann et al. 2015); d Canadian Maritimes to the Gulf

of Mexico (Verrill 1898; Shick 1976; Hancock et al. 2017; Fofonoff et al. 2019a, b, c; Ryan and Miller 2019; Ryan et al. 2019; Ma et al. 2020; all authors, personal observations); e Brazil (Belém and Monteiro 1977); f Argentina (Molina et al. 2009); g Western Europe south to the Canary Islands, through the Mediterranean to the Black Sea (Stephenson 1935; Podbielski et al. 2016; Fofonoff et al. 2019a, b, c; iNaturalist observations); h Malaysia and Indonesia (Dunn 1982); i Australia and New Zealand (Dunn 1982)

conditions (Verrill 1898; Sassaman and Mangum 1970; Shick 1991), seasonal climates, and no doubt through transport episodes across wide latitudes. In northern latitudes, individuals of *D. lineata* may shrink to a dormant phase during the winter to the point of a population nearly disappearing or becoming regionally extinct, with some of these populations then flourishing again in the spring and summer when water warms (Allee 1919; Stephenson 1935; J. T. Carlton and M. Flenniken, personal observations). In southern latitudes, the reverse occurs where body size increases during the winter and spring and decreases throughout the summer (Ryan 2018). Studies on body sizes indicate that these regional differences are influenced largely by fission and growth reactions to temperature, as an individual will peak in body size at 14 °C (Ryan et al. 2019).

Reproduction in *D. lineata* can occur either sexually or asexually through rapid fissipary involving either pedal laceration or binary longitudinal fission, the latter being the most common method of asexual reproduction in sea anemones (Shick 1991; Bocharova and Kozevich 2011). Asexual proliferation of *D. lineata* can occur very rapidly and extensively (Stephenson 1935; Shick and Lamb 1977). In its native range in Japan, both males and females co-occur, with successful sexual reproduction occurring in the summer, based on the collection of planktonic larvae from externally fertilized gametes (Uchida 1932; Fukui 1991). However, larval settlement and recruitment have not yet been observed outside of laboratory settings (Fukui 1991). Outside of Japan, mixed-sex populations of *D. lineata* were previously seldom reported, having been recorded as typically only female (Hieb 1977; Dunn 1982), male (Shick

1976; Shick and Lamb 1977) or sterile (Dunn 1982). Recent work, however, has revealed sympatric populations with eggs and sperm from Massachusetts to Florida (Ryan and Miller 2019), as well as in Coos Bay, Oregon (Newcomer et al. 2019). Nevertheless, larval production and release, and individuals recruiting as a result of larval settlement, remain unknown in the wild in this species.

The native range of *D. lineata* is from at least Hokkaido, Japan south to Hong Kong (type locality; Fig. 4; see Uchida 1932). It was originally assigned to *Sagartia* (Verrill 1869), and later studied in Japan as *Diadumene luciae* (Uchida 1932). The species was mistakenly redescribed in the Atlantic as a distinct species (*Sagartia luciae*) in 1898 by Verrill, later transferred to the genus *Haliplanella* Hand, 1956, and eventually synonymized with Verrill's own species (*Sagartia lineata*) described 29 years earlier from China (nomenclatural history reviewed by Hancock et al. 2017). There are now populations throughout the world (Fig. 4) except for Africa and Antarctica (Fofonoff et al. 2019a, b, c). Genetic studies will be required to determine whether populations found in Malaysia (Jebram, Selangor), Brazil/Argentina (southeast and northeast, Gusmão et al. 2018), or Indonesia (Dobo, Aru Islands; Dunn 1982; Fig. 4) are (1) native and represent the southern end points of the Asian range of *D. lineata*, (2) introduced, or (3) represent a cryptic tropical sibling species, given that most other global populations occur only in temperate waters. The reasonably well-known timing of appearances of *D. lineata* around the world appears to be episodic, which is a pattern similar to other introduced species in which spread occurs in multiple pulses of invasion (Carlton and Cohen 2003).

Diadumene leucolena (Verrill, 1866)

The ghost anemone *Diadumene leucolena* has a height of 3 cm, with a generally thinner, taller, and paler appearance than *D. lineata* (Hand 1956), always lacking the striking orange or white lines of the latter (Ryan and Kubota 2016). The species inhabits shallow marine and brackish habitats, including artificial substrates such as docks and piers, preferring shaded areas (Field 1949; Hand 1956; Cory 1967; Sassaman and Mangum 1970).

Diadumene leucolena is sensitive to temperatures below 17.5 °C (Sassaman and Mangum 1970). Like its

congener *D. lineata*, *D. leucolena* is euryhaline, being particularly tolerant of low salinities (Pierce and Minasian 1974). The few reports within the native range (e.g. Field 1949) that characterize it as possessing pedal laceration are questionable (see Hand 1956) and have been discounted in later literature to the point that it is believed to be only sexually reproducing (Shick and Lamb 1977; Hand 1956; Fofonoff et al. 2019b).

The native range (Fig. 5) of *D. leucolena* is from New Brunswick, Canada (Fofonoff et al. 2019b) to the Caribbean, the latter including Puerto Rico (material identified by J. C. den Hartog; see Fofonoff et al. 2019a, b, c; perhaps the same as “West Indies” reported by Cuttress, 1977) and Curacao (identified by J. C. den Hartog, *vide* Beneti et al. 2015). *Diadumene leucolena* has been introduced (Fig. 5) to the Eastern Atlantic Ocean and to the Indian and Pacific Oceans. In the Central Eastern Atlantic, populations have been reported from Morocco, the Canary Islands, and Senegal (Ocaña and den Hartog, 2002; Ocaña et al. 2015). Reports of it from Cameroon, Gulf of Guinea were based upon the presumed synonymy with *Diadumene kameruniensis* Carlgren, 1927 (Ocaña and den Hartog 2002), which is retained as a distinct species by Fautin (2016). In the Eastern North Pacific, populations have been reported from Coos Bay, Oregon to the northern Gulf of California (Hand 1956; Carlton 1979a, Wasson et al. 2001), with a perhaps disjunct population on the Pacific coast of Panama in Panama Bay (Reimer 1976, material identified by C. E. Cuttress), although sites south of the Gulf of California have been insufficiently explored. It has been known since the 1950s from O'ahu, Hawaii (Carlton and Eldredge 2009). In the Indian Ocean, it is reported from South Andaman Island in the northwest Indian Ocean (Raghunathan and Choudhury 2017). As with *D. lineata*, its presence both in the tropics and in temperate (to – 1 °C in winter) locations may indicate the presence of cryptic speciation within *D. leucolena* as well.

Diadumene franciscana (Hand, 1956)

Diadumene franciscana is another small *Diadumene* species, with a height of 2–4 cm (Hand 1956). It was originally described from San Francisco Bay (Hand 1956), where it is a well-known component of shallow fouling communities on floats and pilings. Exposure to

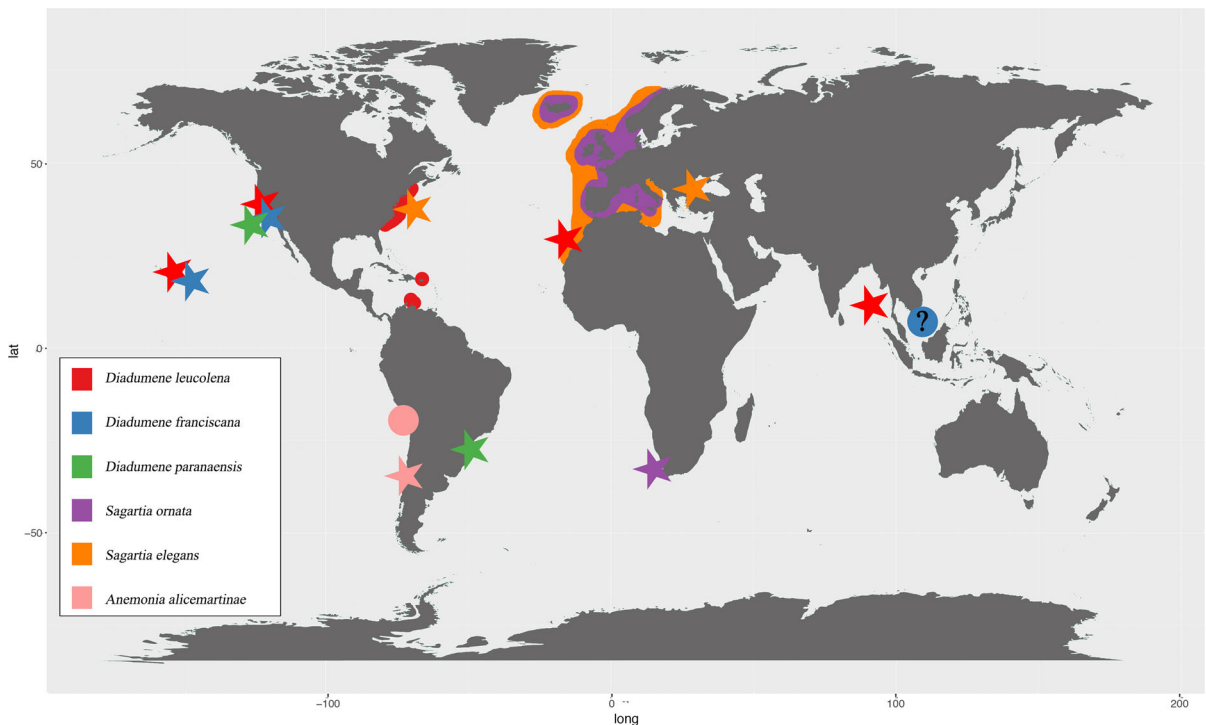


Fig. 5 Map of the native distribution of species of sea anemones (circles or shading) and the approximate locations of established introductions (starred), coded by color for each species according to the map legend. References for distributions are: *Diadumene leucolena* (Field 1949; Hand 1956; Sassaman and Mangum 1970; Carlton 1979a, b; Wasson et al. 2001; Carlton and Eldredge 2009); *Diadumene franciscana*, native range not yet known (Hand 1956; Carlton 1979b; Godwin et al. 2006); *Diadumene paranaensis*, native range not yet

known (Gonzalez-Muñoz et al. 2012; Rodríguez et al. 2012; Beneti et al. 2015); *Sagartia ornata* (Stephenson 1935; Acuña et al. 2004; Mead et al. 2011); *Sagartia elegans* (confirmed but not established; Ates et al. 1998; Pederson et al. 2005; Wells 2013; Grebelnyi and Kovtun 2013; Wells and Harris 2019); *Anemonia alicemartinae*, native range unknown (Häussermann and Försterra 2001, 2005; Canales-Aguirre et al. 2015). In the present paper, the introduced locations of *S. ornata* is referred to as *Sagartia* sp. South Africa

low salinity does not have a negative effect on the species (Hand 1956), and, as it has been found in Hawaii, it can establish in warmer temperatures (Carlton and Eldredge 2009). Since the 1950s, it has been found from Tomales Bay to San Diego, California (reviewed in Fofonoff et al. 2019c).

Similar to other members of *Diadumene*, *D. franciscana* can reproduce both sexually and asexually by pedal laceration (Hand 1956). There is a possibility that *D. franciscana* is not native to the Eastern Pacific Ocean, but was instead introduced from the Western or Indo-West Pacific Oceans, as suggested by Hand (1956), Carlton (1979a, b) and Carlton and Eldredge (2009), based upon the improbability of it having been historically overlooked in the Eastern Pacific Ocean or being undetected in the Atlantic Ocean, and given the

extent of diadumenid diversity yet to be characterized in the Western Pacific and Indian Oceans (Fig. 5).

Diadumene paranaensis (Beneti et al., 2015)

Diadumene paranaensis is a small (6 mm height), orange-white anemone from shallow-water fouling communities in Brazil. Like its congeners *D. lineata* and *D. leucolena*, *D. paranaensis* reproduces asexually through longitudinal fission and lives attached to hard substrates such as bivalves, rocks, pilings, and dock floats (Beneti et al. 2015). Originally described from an estuary, *D. paranaensis* is resilient to variations in temperature, salinity and desiccation (Beneti et al. 2015).

The Brazilian population was assumed to be non-native because it was found in a harbor and all

individuals collected were interpreted to be clone mates as a result of asexual reproduction (Beneti et al. 2015). In addition, there appear to be no earlier, historical records of this species in Brazil. The description of *D. paranaensis* matches the anatomy and cnidom of a previously unidentified species of *Diadumene* (see Rodríguez et al. 2012, 2014: Fig. 2, *Diadumene* sp.) that had been collected from oil platforms in the Santa Barbara Channel CA (MD, personal observation) and from San Francisco Bay CA (Carlton 1979a; MD, personal observation). Although the individuals in each California population were not obviously clonemates, neither did they have characteristics of a native population, being found only in highly disturbed habitats and being absent from accounts of the anemone fauna before the 1970s (Carlton 1979a). Therefore, although two potential introduced regions have been identified, the native range is unknown (Fig. 5).

Metridium senile (Linnaeus, 1761)

Metridium senile, the fluffy or plumose sea anemone, is among the largest sea anemones, reaching to a meter in height (Stephenson 1935). The taxonomic history of the species has been challenging, as there has been long-term confusion between how to identify and apply the names of *M. senile* and *Metridium dianthus* (Ellis, 1768) of the northeastern Atlantic. For the purposes of this paper and since both descriptions of the species possess the same life history strategies, we treat records of *Metridium senile* and *Metridium dianthus* here under the name *M. senile*. *Metridium senile* occurs from the intertidal zone to depths exceeding 100 m, although their occurrence is limited by the availability of hard substrate such as bivalves, rocks, docks, pilings, and shipwrecks (Carlgren 1933; Hoffmann 1976).

Metridium senile is robust in its responses to changes in water temperature, tolerating short exposures to temperatures up to 24 °C, although it is primarily found in cooler waters (below freezing to 20 °C: Stephenson 1935; Glon et al. 2019). They are also tolerant of a broad range of salinities from 14.8 to 37.5‰, enabling them to thrive in both the open ocean and occasionally in estuarine conditions (Shumway 1978; Glon et al. 2019). At lower latitudes, populations become more patchy and move increasingly into

cooler sublittoral depths (Walsh and Somero 1981; Shick 1991).

Metridium senile exhibits both sexual and asexual reproduction through pedal laceration. The species is an oviparous broadcast spawner, undergoing external fertilization upon release of gametes in late summer to early fall to produce free-swimming planula larvae (Bucklin 1982; Lombardi and Lesser 2010). Although an exact length of time that these larvae are able to exist planktonically is unknown, they are believed to stay in this stage for several months, being readily dispersed or carried over long distances to new habitat (Gemmill 1920; Hoffmann 1987). The more common method of reproduction is asexual reproduction by pedal laceration, which can occur in all individuals, at all times of year, and lead to dense clonal groups (Hand 1956; Hoffmann 1987; Lombardi and Lesser 2010; Glon et al. 2019).

Dispersal may occur via planktonic larvae (Hoffmann 1986; Anthony and Svane 1995), by rafting on marine debris (Goldstein et al. 2014, Carlton et al. 2017, see below) or on detached algae (J. T. Carlton, personal observations, Coos Bay, Oregon). Although sexual reproduction through spawning is considered to be the primary means of dispersal, passive drifting of adults following detachment in response to a disturbance may also occur. Drifting behavior can be triggered by biotic factors such as exposure to the predatory nudibranch *Aeolidia papillosa* (Linnaeus, 1761; Shick et al. 1979) or by abiotic factors such as anoxic conditions which enable drifting through the ballooning of the pedal disc (Shick et al. 1979; Wahl 1985).

Of the six putative species of *Metridium* de Blainville 1824, *M. senile* has the broadest range, with a circumboreal distribution that overlaps with nearly every other species in the genus (Stephenson 1935; Hand 1956; Fautin 2016). *Metridium senile* is considered to be introduced to several regions in the southern hemisphere, with robust established populations in South America, South Africa, and the Falkland Islands (Fig. 6). Additionally, although the range of *M. senile* is circumboreal in the Northern Hemisphere, its status as a native to the Pacific Ocean has been disputed. Despite the endemism of other *Metridium* species in the Pacific, the presence of *M. senile* was not well documented until the mid- to late-1800s, at which time it was noted only in harbors and bays. Originally described by Verrill (1865) as *Metridium fimbriatum*

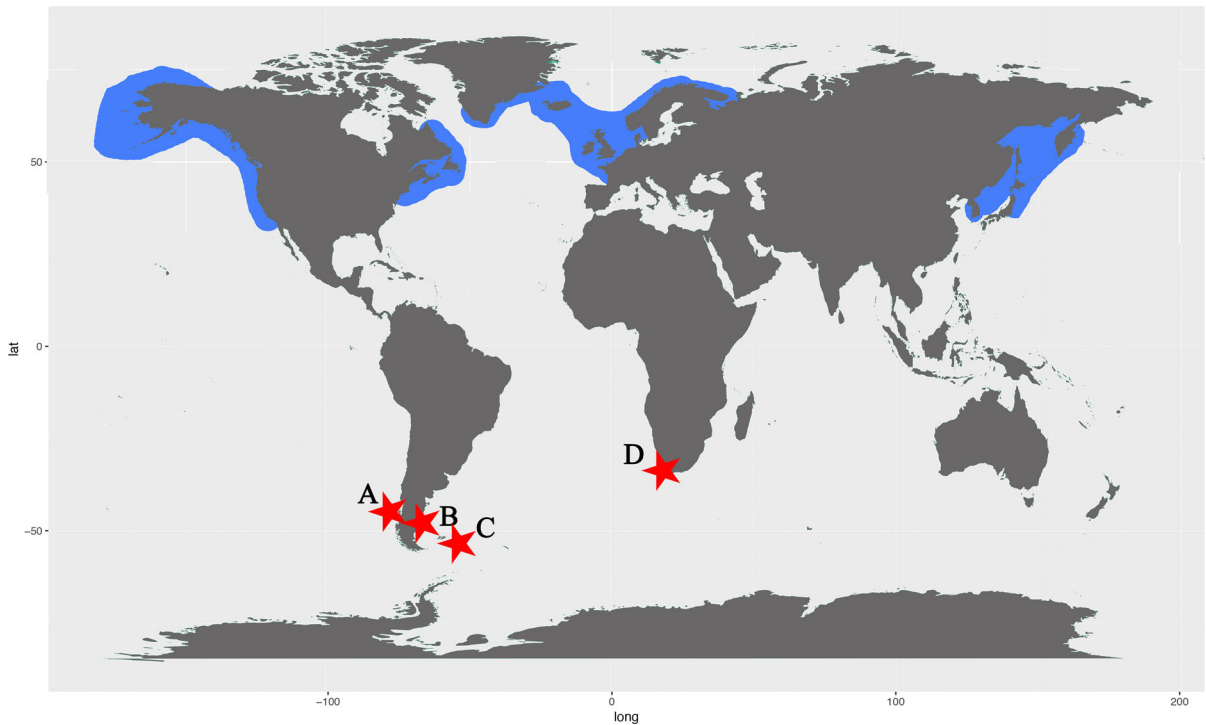


Fig. 6 Map of the native distribution of *Metridium senile* (blue shading). Approximate locations of established introductions are starred, with references including both those of dates of original regional detection and of important distribution information: a Chile (McMurrich 1904; Riemann-Zürneck

1986; Häussermann and Försterra 2005); b Argentina (Riemann-Zürneck 1975; Martin et al. 2015); c Falkland Islands (Glon 2020); d Table Bay Harbor & Agulhas Bank, South Africa (Griffiths et al. 1996; Laird and Griffiths 2016)

from San Francisco Bay, he soon recognized that it likely belonged to the same highly variable species (*M. senile*) present in the Atlantic Ocean (Verrill 1869). In the early 1900s, Kofoid (1915) suggested it was introduced to San Francisco Bay, with a later statement of it “contaminating” San Diego harbors and other ports through shipping traffic (Kofoid 1915). Carlton (2011) suggested that the reason for Kofoid’s comment may have been because *M. senile* established in Eastern Pacific harbors within the span of human memory at that time. MacGinitie (1935) stated that, “It has been claimed that *Metridium* was introduced from the east coast with oyster spat. This is no doubt a mistake, for it is circumboreal in distribution.” While it would not be impossible for *Metridium* from the United States Atlantic coast to have been transported to the Pacific coast in the late 1800s with commercial oysters, the source of MacGinitie’s reference to such a claim remains unknown (Carlton 1979a).

Sagartia sp. “South Africa”

Acuña et al. (2004) identified *Sagartia* populations first collected in 2001 in South Africa (Fig. 5) as the viviparous European species *S. ornata*, which reaches a height of 14.4 mm (Shaw et al. 1987; Ates et al. 1998). The African populations brood parthenogenic young, reaching densities that exceed 500 individuals/m² in intertidal communities in the region of West Cape (Robinson and Swart 2015). However, Hartog and Ates (2011) and R. Ates (personal communication, 2019), note that the description of the cnidom of South African populations does not match that known for *S. ornata*, and emphasize further that the possession of zooxanthellae in the South African *Sagartia* is anomalous for the genus (but that the closely related *Cereus* is known to be photosymbiotic).

Sagartia ornata in Europe occurs intertidally on hard substrate, with a range that extends farther than other *Sagartia* species into estuaries and other marginal habitats (Stephenson 1935). In contrast,

Robinson and Swart (2015) emphasized that the *Sagartia* living in Langebaan Lagoon on the west coast of South Africa lived in distinctly different habitats—shallow sand, in salt marsh *Spartina maritima* meadows and in eelgrass *Nanozostera capensis* beds, as well as on loose rocks “on fossilized oyster beds.” This habitat divergence may provide an additional clue that a species other than *S. ornata* may be involved, rather than being an example of a habitat shift in an invading species, as proposed by Robinson and Swart (2015).

The restricted occurrence of this presumably alien species has so far limited its impact in South Africa, but where it does occur it is associated with a change in the fauna. This includes an increase in the relative abundances of the tanaid crustacean *Anatanaïs gracilis* (Heller, 1865) and the polychaete worm *Orbinia angrapequensis* (Augener, 1918), in both cases correlated with the anemone’s ability to consolidate sand and trap coarse sediment (Robinson and Swart 2015).

Sagartia elegans

A large population of a non-native *Sagartia*, identified as *S. elegans* (Dalyell, 1848), was discovered in a marina in the Gulf of Maine, in Salem, Massachusetts, in 2000 (Pederson et al. 2005; Wells and Harris 2019); previous to this discovery, no members of the genus *Sagartia* were known from the Northwest Atlantic Ocean. However, the population disappeared by 2010, likely due to the warm water effluent flowing into the marina (which had kept the area warmer than ambient in the winter) ceasing when an adjacent power plant shut down (Wells and Harris, 2019; C. Wells, personal communication). In its native European range, *S. elegans* undergoes boom-and-bust cycles, disappearing following harsh winters or expanding at the range edges during mild winters, with a notable sensitivity to extreme cold (Ates et al. 1998).

Sagartia elegans is a well-known northern European species reaching a height of 4.5 cm, inhabiting coastal and mildly brackish habitats from Scandinavia to North Africa (Fig. 5; Grebelnyi and Kovtun 2013). The species is typically found in the low intertidal to subtidal attached to or in hard substrates, but can also be found at deeper depths to 90 m (Stephenson 1935). Relatively recent reports of large populations in the Black Sea (Grebelnyi and Kovtun 2013) may reflect a range expansion into that more brackish and highly

disturbed system. *Sagartia elegans* reproduces both sexually and through pedal laceration (see Ates et al. 1998; Shaw 1991; Grebelnyi and Kovtun 2013).

As we note later, of interest is that an anemone apparently similar to *Sagartia elegans* has been recorded (as *Sagartia “rosea,”* a submerged invalid name for *S. elegans*; Fautin, 2016) as abundant in fouling communities on offshore structures in China (Yan & Yan 2003). We consider the identity of the *S. elegans* population formerly reported from Massachusetts to be uncertain in the absence of genetic confirmation, and thus it may not be identical with the *S. elegans* known in Europe.

Exaiptasia pallida (Agassiz in Verrill, 1864)

Exaiptasia pallida is often reported under its former name *Aiptasia pallida* or under the name *Exaiptasia diaphana* (Rapp, 1829; see Grajales and Rodríguez 2014, 2019). It has long been reported (under many other names as well, below) from throughout the North and South Atlantic Oceans, including western Europe, the Mediterranean, the west coast of Africa (and St. Helena Island), the west coast of South America, throughout the Caribbean and the Gulf of Mexico (including the Atlantic coasts of Mexico and Panama), and the southwest coast of the United States (Grajales and Rodríguez 2014, 2016). This broad distribution suggests that its highly disjunct distribution in the Pacific Ocean may represent introduced populations. In the Eastern Pacific it is known from southern California to Mexico, Panama, and the Galapagos, in the Central Pacific from the Hawaiian Islands, and in Western Pacific from Australia and Japan, as well as the Red Sea in the Indian Ocean (Mito and Uesugi 2004; Thornhill et al. 2013; Grajales and Rodríguez 2014; Carlton et al. 2019). The broad range obscures its origin, but we suggest below that *E. pallida* may be native to the Western Atlantic.

E. pallida is a noted pest in the aquarium trade (Ram 2013). In the wild, *E. pallida* lives in reef habitats, on mangroves, and on pilings, floats, and other man-made structures, generally growing to an expanded size of 60 cm in height. Because they are prolific asexual reproducers, *E. pallida* tends to form extensive monocultures on suitable hard substrates. The speed with which it covers substrate is a point of concern for aquarists, who note that it grows over corals and other ornamentals and can clog aquarium

filters (Ram 2013). *Exaiptasia pallida* may play a similar fouling role in native environments, as it is often found on shells, coral skeletons, and the roots of mangroves, and this proliferative power makes its appearance of concern in sensitive environments such as isolated marine lakes (Hanzawa et al. 2012; Patris et al. 2019), in Madeira (Canning-Clode et al. 2013; Wirtz 2014) and in the Galapagos Islands (Carlton et al. 2019), although the quantified effects of *E. pallida* in these systems so far has either not been studied or is minimal (Patris et al. 2019). Experimental competitive interactions between *E. pallida* and native European species indicate that it is competitively matched by ecologically similar native species and thus unlikely to become dominant (Escribano-Álvarez and López-González 2018). However, its broad ecological tolerance, ability to thrive in acidic waters (Hoadley et al. 2015), and its introduction into regions with novel suites of anemone species may provide advantage to *E. pallida* in new regions.

Although it is most commonly found in tropical environments that experience a relatively narrow range of temperatures and salinities, *E. pallida* shows broad physiological tolerance. Unlike many photosymbiotic cnidarians, *E. pallida* maintains its symbiosis under thermal and salinity stress, and shows enhanced thermal tolerance when under salinity stress (Gegner et al. 2017). Although *E. pallida* associates with symbiotic dinoflagellates (Symbiodinaceae), this symbiosis is more flexible than in many other cnidarians: *E. pallida* can harbor symbionts from the genera *Symbiodinium*, *Breviolum*, and *Cladocopium* (see Thornhill et al. 2013; LaJeunesse et al. 2018), and can also survive without them. *Exaiptasia pallida* exhibits remarkable plasticity in reproduction. It is capable of asexual reproduction via longitudinal fission to generate two similarly-sized, feeding daughters, via pedal laceration to produce smaller daughters, and can also produce tentacle-less polyps under stress, described as a “wurst” form (Hunter 1984; Shick 1991; Rädcker et al. 2019). Although generally gonochoric, clonally produced offspring can mature into adults that differ in sex from their parent and some individuals switch from gonochoric to hermaphroditic, with self-fertilization possible in hermaphrodites (Schlesinger et al. 2010). This biological plasticity is one reason that *E. pallida* has become an important emerging model for anthozoan biology and genetics (reviewed by Rädcker et al. 2018).

As in *M. senile*, the taxonomic history of *E. pallida* is complex. The taxon as currently recognized includes concepts associated with nine nominal species (see Grajales and Rodríguez 2014). Both *Aiptasia pallida* and *A. pulchella* had been recognized as introduced species in the Pacific, but with more limited ranges (Okey et al. 2003; Mito and Uesugi 2004; reviewed by Grajales and Rodríguez 2014); the synonymy of these with several more species with narrow ranges partly explains the global distribution of *E. pallida*. The type locality of *E. pallida* is the North American Atlantic coast. The type locality of *A. diaphana* (Rapp, 1829) is Naples, Italy, while further synonyms include *A. inula* (Duchassaing and Michelotti, 1864), *A. mimosa* Duchassaing and Michelotti, 1864, and *A. tagetes* (Duchassaing and Michelotti, 1864), all described from the Caribbean. *Aiptasia minuta* (Verrill, 1867) was described from Japan, but its identity is controversial, as there are no type specimens and some authors have considered it to belong to *Aiptasiomorpha*, rather than *Aiptasia* (see Uchida and Soyama 2001; Grajales and Rodríguez 2014). Records from the mid-Atlantic came later (Fig. 7), with the earliest record being that of *A. insignis* (Carlgren 1941) from St. Helena. Records from the tropical Pacific (as *Aiptasia pulchella* Carlgren 1943) and from the eastern Pacific (as *Aiptasia californica* Carlgren, 1952) were described within the next decade.

The complexity of this taxonomic history complicates the effort to reconstruct a clear invasion history at this time of *E. pallida*. For example, it is considered as a “non-indigenous” species in France (Ardura and Planes 2017), as it is assumed to have been introduced by mariculture of the imported Japanese oyster *Crassostrea gigas* (Grizel and Heral 1991). However, it was first identified as the Pacific *Aiptasia pulchella*, a name now placed in the synonymy of *E. pallida*, which was present in Europe before Japanese oyster culture began in France in the 1970s.

Molecular analyses of *E. pallida* have identified three narrowly-restricted genetic populations and one widespread genetic population. The narrowly-restricted populations are from Florida (Thornhill et al. 2013, Bellis et al. 2016), Brazil (Grajales and Rodríguez 2016), and Atlantic Panama (Bellis et al. 2018); the Brazilian species has been described (as *Exaiptasia brasiliensis* Grajales and Rodríguez 2016) but the Floridian and Panamanian populations have

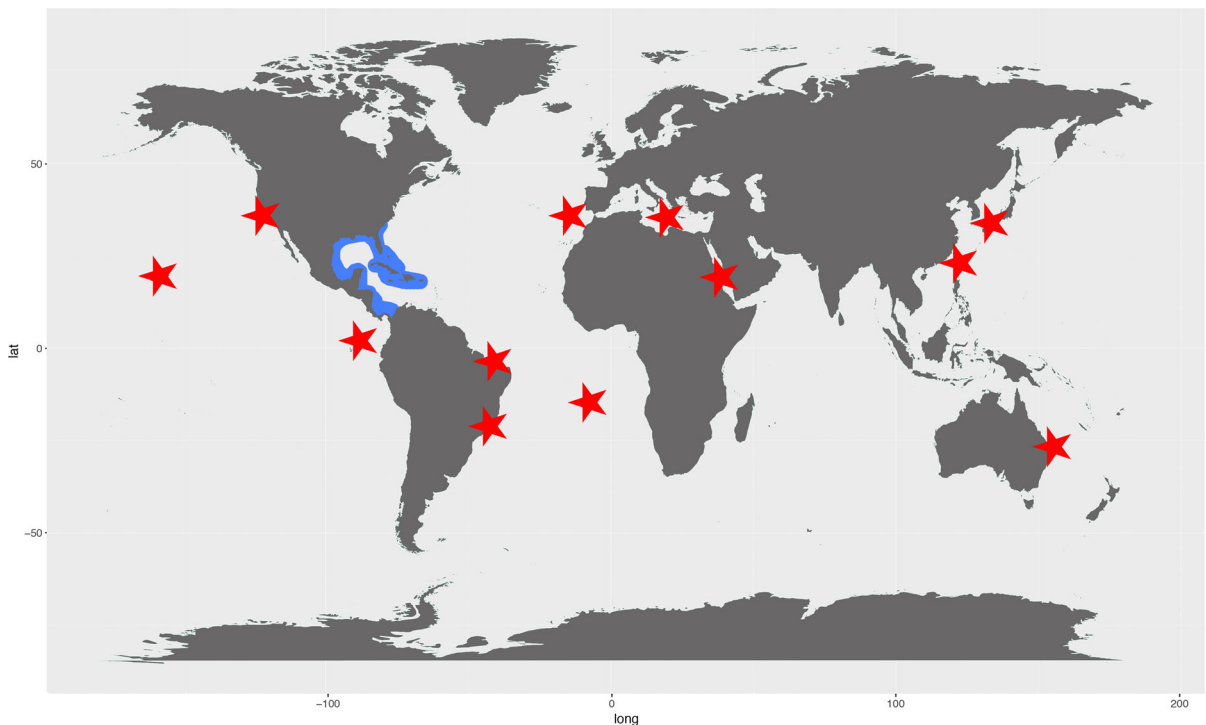


Fig. 7 Map of the presumed native distribution of *Exaiptasia pallida* (blue shading). Approximate general locations of established introductions are starred, with references including

those of dates of original regional detection and/or of important distribution information included in the text and as noted in Grajales and Rodríguez (2014)

not been taxonomically differentiated from *E. pallida*. The widespread populations encompasses all other locations, spanning oceans and continents and co-occurring with the more narrowly distributed populations (Thornhill et al. 2013; Grajales and Rodríguez 2016; Bellis et al. 2018). The genetic markers that have been used to elucidate relationships within this widespread clade are insufficiently variable to discern points of origin, but the existence of apparently endemic clades in the broader Tropical West Atlantic might be a clue as to its origin: *E. pallida* may have split from *E. brasiliensis* and from the unnamed Floridian and Panamanian populations before it was introduced elsewhere, which suggest that it originated in the Caribbean or Tropical West Atlantic.

Anemonia alicemartinae (Häussermann and Försterra, 2001)

Anemonia alicemartinae is a bright red anemone with a height of generally less than 25 mm. It appears to be a habitat generalist, being found commonly on rocks from the intertidal to 16 m over a range of 13–23 °C in

normal open ocean salinities (33–36‰), as well as living on macroalgae, stones, marine debris, and crabs (Häussermann and Försterra 2001). It also occurs in fouling communities in Chile (J. T. Carlton, personal observations). Reproduction occurs through frequent longitudinal fission, and although fertile specimens have been recorded, these have all been female, which suggests clonal populations (Häussermann and Försterra 2001). In light of the single sex populations and its ability for quick attachment and reattachment of the pedal disc, *A. alicemartinae* is inferred to spread only as adult anemones.

The species was first described from Chile, but is presumed to have been introduced to Chile from elsewhere because it was not recorded in surveys until 1975 (Fig. 5; see Häussermann and Försterra 2001). Population genetics support the hypothesis that the single-sex Chilean populations of *A. alicemartinae* originated from a small population to the north, in the south of Peru, from which individuals may have then been transported southward in ship hull biofouling (Canales-Aguirre et al. 2015).

The absence of this colorful, conspicuous, relatively large, easily accessible and abundant intertidal sea anemone from the historical literature of South American west coast anemones, including in Peru (Häussermann and Försterra 2001), as well as the absence of any other species of *Anemonia* in the Eastern Pacific Ocean (and thus the improbability of a short-range ancient endemic existing only in southern Peru) strongly suggest that *A. alicemartinae* has been introduced from either the Indo-West Pacific or from the Atlantic Ocean. A phylogeny of known *Anemonia* species may thus place *A. alicemartinae* with Eastern Atlantic-Mediterranean, Western Atlantic, or Indo-West Pacific clades.

Nematostella vectensis (Stephenson, 1935)

The starlet sea anemone *Nematostella vectensis* is a small species (4–6 mm height) which burrows into the fine, often anoxic sediments within marsh pools or creek banks, and frequently occurring in intertidal mats of the yellow-green alga *Vaucheria* (Stephenson 1935; Hand and Uhlinger 1992, 1994). Populations generally are found in brackish habitats within coastal saltmarshes, and are resilient to extremes of salinity (9–51.5‰) and temperature (–1° to 28 °C) (Hand and Uhlinger 1992). The broad thermal (Bleakney and Meyer 1979; Kneib 1988; Reitzel et al. 2013a, b) and salinity (Hand and Uhlinger 1992) tolerances of *N. vectensis* likely aid in its invasion success.

Although much is known about the genetics and physiology of *N. vectensis* because of its adoption as a model biological system (Hand and Uhlinger 1994; Darling et al. 2005; Layden et al. 2016) relatively little is known about its ecology or about the impact it might have in the regions into which it has been introduced. In its native range, *N. vectensis* is prey for small crustaceans and probably for bottom-feeding fish (Kneib 1988, 1991; Posey and Hines 1991); in turn, it eats small arthropods, worms, and molluscs (Lindsay 1975; Frank and Bleakney 1976; Williams 1983; Posey and Hines 1991; Sheader et al. 1997). As these general classes of prey are broadly available, the diet of *N. vectensis* is likely conserved across its range, although the specific identity and relative composition of the diet predictably fluctuates at spatial and temporal scales. While we have found no studies of the ecology of *Nematostella* in its introduced range (below), Posey and Hines (1991), in experimental

studies conducted in Chesapeake Bay, found that *N. vectensis* significantly reduced the abundance of certain benthic prey species.

The species can undergo both sexual and asexual reproduction by transverse fission (Shick 1991; Hand and Uhlinger 1994). In their native range, *N. vectensis* is a dioecious seasonal reproducer in late summer (Frank and Bleakney 1976; Hand and Uhlinger 1992), although they can be induced to spawn more frequently in captivity (Hand and Uhlinger 1992). Because they are small, live in sediments, and are translucent, they are not easily detected and are likely more widespread than reported (Hand and Uhlinger 1994). Although some populations are quite large (Hand 1957; Williams 1975; Hand and Uhlinger 1992), others are small or ephemeral (Bleakney and Meyer 1979; Williams 1983, 1987; Sheader et al. 1997).

First described from the Isle of Wight (Stephenson, 1935), the species was subsequently identified in salt marshes on the east and west coasts of North America and elsewhere in England (Fig. 8; reviewed by Hand and Uhlinger 1994; Reitzel et al. 2008). The relatively small size of the population in England led to the listing of the species as vulnerable to extinction due to habitat loss (Williams 1983) and the subsequent development of a conservation plan (reviewed in Sheader et al., 1997). Because of its broad and disjunct range, *N. vectensis* was initially assumed to represent multiple species (Crowell 1946). After the uniformity of individuals across the range was determined (Hand 1957; Williams 1975), a human-mediated, rather than natural, mechanism for dispersal became plausible (Hand and Uhlinger 1994). Early genetic assays of the populations in the UK showed that those populations consisted of single clonal genotypes (Pearson et al. 2002), and studies of the populations in the Eastern United States failed to find any correspondence between geographic and genetic distance (Darling et al. 2004). Fine-scale, range wide studies (Reitzel et al. 2008, 2013a, b; Darling et al. 2009) revealed that populations from the UK and from Pacific coast of North America had the closest affinity to populations from the American Atlantic coast, suggesting introduction from the American Atlantic to both the Pacific Ocean and to Europe. The split between the UK and North American populations is a relatively deep one (Reitzel et al. 2008). At the time of the study, all studied populations in the UK represented a single

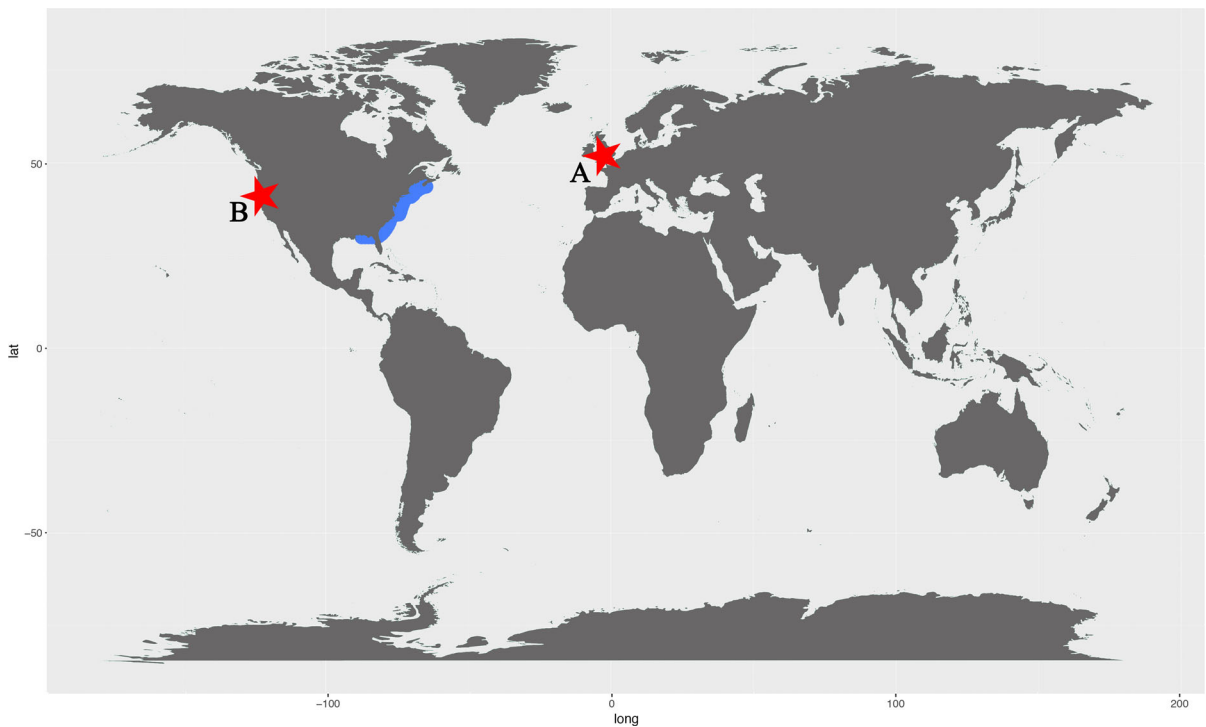


Fig. 8 Map of the native distribution of *Nematostella vectensis* (blue shading), based on Hand and Uhlinger 1994. Approximate locations of established introductions are starred, with references including those of dates of original regional detection and/

or of important distribution information. a Three locations in the U.K. (Stephenson, 1935; reviewed by Hand and Uhlinger 1994; Reitzel et al. 2008); b Pacific Coast of Oregon, Washington and California south to San Francisco

genetic cluster, as did each population in Western North America (Reitzel et al. 2008), suggesting a single founding invasion for each. As patterns of genetic similarity and diversity in North Eastern North America suggest that this is the native range of *N. vectensis* (see Reitzel et al. 2008, 2013a, b), its protected status in the UK is ironic.

Factors and strategies leading to successful introduction

The probabilities of completing each of the four main stages of introduction (Fig. 1) are heavily influenced by the life history strategies of each of the species considered here. Nearly all of the species examined in this review have completed all the stages to become introduced species, with the exception of *Sagartia elegans*, but other anemone species have traits which readily lend themselves to potential invasion success.

Transport stage

Active dispersal by sea anemones is limited to crawling or floating of adults, dispersal of gametes into the water column, and swimming larvae. Although long-lived gametes and larvae are possible, and may explain some broadly distributed species, long-distance transoceanic and interoceanic dispersal is typically mediated by rafting or by human mechanisms.

Anthropogenic debris resulting from the 2011 Japanese tsunami has traveled eastward over a span of more than eight years through the North Pacific carrying living Asian animal and plant communities that have landed in North America and the Hawaiian Islands (Carlton et al. 2017; JTC, personal observations). Several of these arriving communities contained *M. senile*, *D. lineata*, *Anthopleura* sp., and several unidentified anemone species (Carlton et al. 2017; JTC personal observations). Such rafts are much slower (travelling at 1–2 knots) compared to commercial vessels (20–25 + knots; Kaluza et al. 2010), and

thus the effects on sessile biofouling species differ significantly from ship-mediated transport: potential acclimatization time to changing environments would be beneficially longer, reduced water flow pressure may lead to less dislodgment, and the much greater transoceanic travel times (months and years for rafts versus days or weeks for vessels) means that much longer times are available for recruitment through asexual reproduction (Coutts et al. 2010). In addition, rafted objects that successfully land after an ocean crossing become potentially permanent landed “craft,” as opposed to vessels that may spend only hours at a destination. In comparison with natural materials, anthropogenic (plastic) materials do not degrade as easily, creating a more stable, long-lasting substrate for transport (Carlton et al. 2017). Goldstein et al. (2014) reported finding anemones identified as *Metridium* sp., *Calliactis* sp., *Anthopleura* sp., Actiniidae, and Hormathiidae from rafting debris in the North Pacific Ocean.

Sea anemones may be transported as part of mariculture operations. Early awareness of this vector as an interprovincial phenomenon is found in the suggestion by Verrill (1898) that the intentional transport of oysters (*Crassostrea virginica*) from “the south” (meaning primarily at that time Chesapeake Bay) to Long Island Sound for commercial purposes may have transported *Diadumene lineata* to New England (even though the anemone was not yet known from southern waters). While numerous workers have invoked the commercial oyster industry as a likely vector for sea anemone introductions, actual records of sea anemones on transported and relaid oysters appear to be rare. Carl and Guiguet (1958) found *D. lineata* on newly imported Japanese oysters (*Crassostrea gigas*) arriving in British Columbia. Grizel and Heral (1991) found the anemone *Aiptasia pulchella* (now recognized as *Exaiptasia pallida*) on oysters (*Crassostrea gigas*) imported from Japan to France, and reported that it had survived and become established on the French Atlantic coast. The transplantation of shellfish and marsh grasses also may have mediated the introduction of *N. vectensis* to England and the Pacific coast of North America (Reitzel et al. 2008). In addition to their direct association with bivalves and marsh plants, anemones may be vectored by equipment such as fishing nets (Zabin et al. 2004) and boat fenders, hulls, rope, and gear (personal observations). The association of *E.*

pallida with the ornamental aquarium industry, a vector typically linked to other non-native species invasions (Antoniadou and Chintiroglou 2007), suggest additional pathways for introductions.

Commercial shipping and cruise liners are instrumental in the movement of species in three significant ways: hull fouling, transport in ballast water, and attachment in sea-chests. Biofouling organisms on the hull of ships must be able to withstand sharp fluctuations in temperatures and salinity, as well as current depending on the speed of the ship (Coutts et al. 2010). Records of sea anemones surviving long-distance travel on ships’ hulls have likely been under-reported, although reports of anemones on local and moored vessels are not uncommon (for example, Orton 1930, *Sagartiogeton viduatus* (Muller, 1776) (as *Sagartia viduata*) in England; Marine Biological Association 1957, *Diadumene lineata* (as *Aiptasiomorpha lineata*), in England; Farrapeira et al. 2007, *Aiptasia pallida* and *Diadumene lineata*, in Brazil; J. T. Carlton and M. Flenniken, *Diadumene lineata* in Connecticut; Spano et al. 2018, *Anthothoe* sp. in Australia). Visscher (1928) recorded *Metridium* sp. and *Diadumene lineata* (as *Sagartia luciae*) from unspecified ships’ hulls. The first live observation of *D. lineata* as a passenger on the hull of an interoceanic ship was by Gollasch and Riemann-Zurneck (1996), who found it on a car-carrier vessel that had traversed around the globe from the Mediterranean to the Pacific Ocean and back to Europe; multiple *D. lineata* had attached to the live Japanese oyster, *Crassostrea gigas*, also on the hull. If a species is unable to persist in a high-flow area, a sea-chest (cavity-like structure on the hull of a ship providing a water intake for the ship) is a protected low-flow environment for producing extensive fouling communities (Frey et al. 2014). These have been found to successfully carry sea anemones across bodies of water (Coutts & Dodgshun 2007).

Ballast water from ships acts as an ecologically non-selective vector, particularly for organisms with a pelagic life history stage. In San Francisco Bay, for example, many contemporary invasions are believed to result from ballast water (Carlton and Geller 1993). Carlton & Geller (1993) were able to rear *Metridium senile* from larvae in ballast water from a Japanese ship that arrived in Coos Bay, Oregon (JTC, unpublished observations). Although *N. vectensis* also produces planula larvae, these live only a week before settling (Hand and Uhlinger 1992), and the species

inhabits brackish, shallow pool habitats that are not likely sources of ballast water. However, since ballast water, when taken up, contains sediments which are not necessarily expelled when the ballast is released in the arrival port (Maglić et al. 2017), sediments can build up over time within the ballast tank or ballasted hold that can potentially provide suitable soft substrate suitable for some anemone species (Bailey et al. 2005; Briski et al. 2010, 2012). Modern ballast water management, which by the 2020s requires all ships at sea to have ballast treatment systems installed, may result in fewer ballast-mediated invasions (Batista et al. 2017; Campara et al. 2019; Davidson et al. 2017). This may perhaps mean that the longest-term ship-related vector, hull biofouling, may return proportionally as the major vessel-related vector for global species transport.

In turn, one of the most common artificial substrates that introduced sea anemones inhabit are docks and piers in harbors. These serve as an immediate, available suitable substrate for species arriving on or in ships and can also serve as a source pool for the local area through both natural vectors and secondary anthropogenic-mediated dispersal. Both *M. senile* and *Sagartia* sp. South Africa have been introduced to South Africa (Figs. 5 and 6). In a harbor such as Table Bay where *M. senile* has established, shipping traffic is high and is assumed to have contributed either through fouling or ballast water to the introduction of many other introduced and cryptogenic species (Mead et al. 2011). The presence of *M. senile* in Argentina, particularly in fouling communities, corresponds with an increase in commercial shipping traffic since the 1980s (Martin et al. 2015), including possible transport from Chile around the tip of South America, where it has been well established since at least 2005 (Häussermann and Försterra 2005). Though *A. alicemartinae* has been highly influenced by changes in sea surface temperature and salinity, the expansion of the southernmost point of distribution is more likely due to the high maritime traffic present in the area (Pinochet et al. 2019). Cruise ships are also a large potential source of species movement: over 1.1 million tourists visited Alaska in 2018 via cruise ships, having increased from less than a million visitors 15 years prior (Ringer 2006; McDowell Group 2019). Alaska appears to be primed for transport and introduction of sea anemone species such as *M. senile* and *D. lineata*, as heavily frequented source ports are rich with

potential invaders, the more so with climate change leading to warming polar and subpolar waters. Thus, the August 2019 discovery of *D. lineata* in Sitka, Alaska (<https://www.inaturalist.org/observations/30146032>) may reflect such newer invasion pattern scenarios.

The introduction of new species may correspond to events that result in increased ship-based travel. The California Gold Rush of 1848–1850, which brought many ships from around the world to the Pacific Coast, was responsible for new invasions in San Francisco Bay (Carlton 1996). Japan re-entered into global trade in the 1860s, and increased shipping exports a century later in the 1970s; these events align with the timing of the appearance of *D. lineata* in the northern (1890s) and southern (1970s) hemispheres (Table 1). Additionally, the added transport activity and new vessel routes during wartime have resulted in numerous introductions coinciding with world wars (see Carlton 1996 for review). The abundance of *M. senile* in California appeared to increase based on comments in the literature after the Gold Rush, World War II and the Korean War (Light 1941; Hand 1956; Purcell 1977; Purcell and Kitting 1982). Carlton (1979a) made the first speculation that *M. senile* from the Atlantic may have been introduced during the Gold Rush period in San Francisco in ship fouling biota; whether this was a new species introduction or a mixing of native Pacific populations with Atlantic populations remains unknown. Relative to *E. pallida*, the oldest records are in the 1800s from Europe, the Caribbean, and the Southeastern United States; as argued above, the probable native range for the species is the Tropical West Atlantic. These facts suggest that interoceanic and transcontinental trade, which was increasing at that time through the Caribbean, was the route by which *E. pallida* spread from the Tropical West Atlantic to Europe and the Pacific Ocean.

The three species *M. senile*, *D. lineata*, and *E. pallida* have been observed to detach and float in response to unsuitable conditions, and then to reattach and proliferate when conditions are more favorable (Davenport 1903; Wahl 1985; Bedgood et al. 2020). Similarly, *A. alicemartinae* has been observed to passively roll along the substrate or drift in the current (Häussermann and Försterra 2001). Since adults are potentially more tolerant to extremes than juveniles or gametes, the strategy of movement when adults may be beneficial to the species. The ease of detachment

and reattachment to a substrate would increase the potential for colonizing a ship's hull, or conversely, detach from a ship's hull and colonize a new surface. Although toxic antifouling paints are commonly used on ships, some organisms (bryozoans and algae) are known to have tolerance to such paints, and can in turn provide a non-toxic substrate for the attachment of other species (Floerl et al. 2004; Briski et al. 2018).

Not surprisingly, most successful introductions of sea anemones have occurred in cases where the salinity and temperature are similar between the novel and native habitat, particularly when the putative native ranges cover large and ecologically diverse regions which likely allows for a high level of pre-existing diversity and phenotypes readily able to acclimate. However, many of the successfully introduced species possess broad tolerances for salinity and temperature, and many are intertidal and thus tolerant of exposure to air. These traits may enable such species to survive the physiological challenges of long-distance transport. Species known to have broad tolerances to both temperature and salinity include *M. senile*, *D. lineata*, *E. pallida*, and *N. vectensis*. Those also tolerant to estuarine (brackish) water include *D. paranaensis*, *D. leucolena*, *D. franciscana*, and *Sagartia* species. The only species not currently known to have a broad tolerance to temperature or salinity extremes is *A. alicemartinae*. Additionally, *M. senile* has been observed surviving in anoxic conditions for 5 days to 3 weeks, and up to 6 weeks for some individuals (Sassaman and Mangum 1972; Wahl 1984). *Diadumene lineata* has long been known to exhibit high physiological versatility, adaptable to both euryhaline and eurythermal conditions (Verrill 1898; Parker 1902; Uchida 1932; Miyawaki 1951; Sassaman and Mangum 1970; Shick 1976, 1991; Dunn 1982). The attributes of physiological flexibility may explain the phylogenetic clustering of introduction-prone species, with more than half of the known invaders belonging to Diadumenidae or its sister family Metridiidae.

Rafting on natural substrates is possible, and anemones have been recorded from drifting algae, sea grass blades and rhizomes, and on shells (Cohen et al. 2005; Robertson 1962) as well as on pumice (Bryan et al. 2012). However, as introductions have consistently increased alongside historic rises in anthropogenic activity, human-mediated vectors are likely the mechanisms by which movement has been

enabled across physical barriers or vast distances (Carlton 2003). As an individual is moved via one of these vectors, the tolerance to sharp fluctuations in temperature and salinity, depending on stage (larvae or polyp), is what determines the success of moving through the filter of transport to the introduction stage.

Introduction stage

Factors contributing to successful post-transport survival and introduction include basic physiological accommodation (reviewed above), traits of local dispersal capacity, individual behavior, and individual mobility, and the outcome of ecological interactions with the resident community (Cardeccia et al. 2018). Adaptations to the potentially temporarily harsh conditions that characterize long-distance transport may further facilitate the survival of a species upon arrival in a new location. Short-term behavioral responses (below) are likely more important in the Introduction phase than in the Transport phase, but faster, modern means of long distance transport may make Transport more similar to, and an extension of, the Introduction phase, rather than acting as a distinct, separate stage.

Behavioral responses of sea anemones to ecological stress include retracting tentacles, constricting the body column to reduce the surface area, and secreting copious amounts of mucus (Sassaman and Mangum 1970; Kiener 1972; Podbielski et al. 2016). In unfavorable environmental conditions, including decreasing salinity or exposure to air, sea anemones contract and produce mucus that “insulates” their bodies from those conditions (Sassaman and Mangum 1970; Shumway 1978; Häussermann and Försterra 2001). In *D. lineata*, this mucus hardens into a remarkable protective capsule, enabling it to withstand environmental extremes for unknown lengths of time (Kiener 1972; Carlton 1979a; Gollasch and Riemann-Zurneck 1996). The ability to enter into an encapsulated resting stage (encystment) allows *D. lineata* especially able to withstand physiological extremes, including desiccation and freshwater exposure (Uchida 1932; Kiener 1972; Carlton 1979a; Gollasch and Riemann-Zurneck 1996; Podbielski et al. 2016). Moving a ship into freshwater has been used to reduce biofouling (and *inter alia*, the potential transport of non-native species) but would likely be ineffective for *D. lineata*. The behavioral response of *M. senile* to

freshwater is to detach and float away (Brock et al. 1999), which may also short circuit the efficacy of freshwater treatment and potentially facilitate introductions by the release of anemones into a region where tidal currents could transport them back into salt water.

Sea anemones have relatively low metabolic demands and generally diverse diets (Shick 1991), which facilitates both the Transport and Introduction phases of invasion. Encystment in *D. lineata* is accompanied by a metabolic slowdown, and *M. senile* can partially regulate metabolic rate in response to lowering temperatures, salinity changes, and oxygen availability (Sassaman and Mangum 1970, 1973; Shumway 1978).

Establishment stage

Anthropogenic activities and structures can create suitable environmental conditions that facilitate the introduction and establishment of non-native species. Artificial habitat within a suitable temperature regime or salinity zone may provide suitable substrate that otherwise may not naturally be present, and thus enable either direct colonization or serve to extend the range of a species and connect isolated metapopulations.

The broad range of habitat needs of many generalist sea anemones enables them to establish upon introduction. In addition to a wide range of anthropogenic surfaces, the habitat generalist *D. lineata* has been found on a wide range of natural substrates, including barnacles (*Amphibalanus* spp.), sea squirts (*Molgula manhattensis*), slipper limpets (*Crepidula fornicata*), spider crabs (*Libinia emarginata*), and wood (Z. Currimjee and M. Flenniken 2013, personal observation). Similarly, low substrate selectivity by the anemone *Anemonia alicemartinae* has been identified as one of the important traits leading to its invasion success (Thiel and Gutow 2005; Lopez et al. 2013).

Multiple cycles of introduction, survival and reproduction may be critical to the eventual establishment of a viable population, as well as the number of initially introduced individuals (Casties and Briski 2019). Numerous biotic pressures, including competition, predation, and disease (Alonso and Castro-Díez 2012) in a new region may influence the success of a species in establishment. Genetic characterization of *D. lineata* has revealed a potentially high diversity of

unique clones among introduced populations, which indicates that multiple introductions may play an important role in the invasion success and spread of this species (Ting and Geller 2000). The introduction and retention of multiple genotypes would increase the long-term stability of a population, as genotype frequency might fluctuate over time. Competitive success, especially in highly disturbed environments, is a hallmark of successful invaders (e.g. Bando 2006) and is an attribute of at least some introduced anemones (Escribano-Álvarez and López-González 2018).

Spread stage

Physio-chemical tolerances, multiple modes of reproduction, broad habitat preference, and behavioral plasticity equip a species to succeed through the multiple steps in the invasion process, but these factors need to work in concert for a species to persist or spread in its introduced range. Characteristics such as propagule supply, quality and/or density of propagules, and the dispersal of propagules through an area over time, greatly affects both establishment and successful spread (Ruiz et al. 2000; Casties and Briski 2019). The longer a species persists in a region, the more propagules may be spread, increasing the chances of long-term persistence and of an even greater range in the introduced region (Milbau and Stout 2008).

Anthropogenic alteration of habitat such as subsea structures and shipwrecks serve to connect and extend populations by providing hard substrate in a naturally soft bottom area, enabling sea anemones that inhabit subtidal and deeper depths to extend their range. Offshore petroleum platforms, which rank among the largest artificial structures in the marine environment, are typically placed over soft-sediment substrate that normally would be inhospitable to hard substrate-dwelling species. These structures provide an artificial reef habitat suitable for attachment, potentially serving as a “stepping stone” for both native and non-native species (Wolfson et al. 1979; Page et al. 2006); in China, an anemone referred to as *Sagartia rosea* (an invalid name for the European *Sagartia elegans*; see Fautin 2016) is a common species on offshore platforms (Yan and Yan 2003; Li et al. 2011), while “Actiniaria” were documented as common on a fixed oil platform in the northern Beibu Gulf of China (Yan

et al. 2006), and *Bunodosoma caissarum* Corrêa in Belém, 1987 as common on drilling ships (Ferreira et al. 2006). As these offshore structures may be moved after use, not only do they provide a stepping stone, but they can also introduce a well-established community to a new location.

In the Southern California Bight, *M. senile* is a common fouling species on oil and gas platforms, with particular dominance in the platform invertebrate assemblages despite its relative rarity in the nearshore environment (Page et al. 2006, 2015). Pipelines in the North Sea cross and intersect a large geographic area, forming a 45,000 km “subway system” of hard substrate habitat across a shelf region characterized by soft sediments. *Metridium senile* has been noted as occurring on pipelines in the North Sea (< 200 m) and along pipelines (115 m) on the Agulhas Bank at the tip of South Africa, having colonized either through planktonic larval dispersal, dislodgment from ship fouling communities, or by slow movement along the pipeline itself (Laird and Griffiths 2016; Lacey and Hayes 2019). The presence of it on oil rigs in South Africa has encouraged the citation of ship fouling as the most probable vector of introduction (Mead et al. 2011). Although *M. senile* is not as prevalent south of Massachusetts on the North American Atlantic coast, artificial habitats including the shipwrecks in New Jersey provide fragmented hard substrate habitat that may assist in extending the southward limit of their natural range by increasing habitat availability and complexity.

Both sexual and asexual reproducers are represented in these ten species. Species that solely undergo sexual reproduction include *D. leucolena* and *S. ornata*, while species that are able to undergo both asexual and sexual reproduction include *D. franciscana*, *D. lineata*, *E. pallida*, *M. senile*, *N. vectensis* and *S. elegans*. Additionally, two species, *D. paranaensis* and *A. alicemartinae*, are only known from monosexual populations inferred to solely exhibit asexual reproduction based on the absence of individuals of the opposite sex. Asexual reproduction enables a species to establish potentially long-lived single sex populations with a single inoculation, with population size expanding regardless of the presence of sexual reproduction. The ability to reproduce through both asexual and sexual means in the non-native range, along with the lack of senescence, contributes to a species’ ability to be durable invaders (Frank and

Bleakney 1976; Hand and Uhlinger 1992; Stefanik et al. 2013), and those species that are able to reproduce asexually and sexually based on the presence of both sexes are indeed the more widespread of the introduced sea anemones (Figs. 5, 6, and 7).

Of the two modes of reproduction, for anemones, asexual reproduction appears to be the most important in invasion success. For example, although capable of sexual reproduction, *D. lineata* is regarded as foregoing sexual reproduction throughout its global introduced range (Shick 1976; Shick and Lamb 1977; Minasian and Mariscal 1979; Ting and Geller 2000), although there may potentially be some sexual reproduction (yet to be demonstrated) in regions that have undergone multiple introductions and where male and female anemones occur in the same population (Newcomer et al. 2019; Ryan and Miller 2019). Species may display unique reproductive responses to stress, which shows variation in trade-offs between types of reproduction. Both *N. vectensis* and *M. senile* are more likely to undergo asexual and sexual reproduction in favorable conditions than under stress, with the difference in output more pronounced for sexual rather than asexual reproduction (Hand and Uhlinger 1992, Glon et al. 2019). However, the increase in the fission rate of *D. lineata* particularly when temperatures are higher may be more beneficial in increasing the surface area to volume ratio, as there is higher biomass accumulation (Ryan and Miller 2019; Ryan et al. 2019).

Introduced populations that are a single sex (e.g., *D. lineata*, *D. paranaensis*, *N. vectensis*) can only spread within their introduced habitat by crawling, floating, or rafting. In addition to having limited means of spreading, these populations have limited genetic variation and may be more susceptible to ecological fluctuations. Ephemerality of populations, such as in the case of *Sagartia elegans*, limits successful establishment; however, multiple introductions, as can occur in a harbor with high shipping activity can increase genotypic variation and may over time lead to establishment and subsequent spread. The limitations of solely asexual reproduction may appear to be a detriment to invasion success, but it may instead create more possibilities. Despite the presence of specialized predators (e.g. the nudibranch *Aeolidia* sp.) in some introduced areas (Kienberger et al. 2016) the ability to quickly reproduce asexually to form dense clonal groups decreases the impact of predation.

Furthermore, for numerous introduced species, the reproductive strategies in the introduced range vary from those in the native range, and often manifest as an increase in the frequency of asexual reproduction (Johnson and Shick 1977; Meinesz et al. 1993; Jokela et al. 1997; Alonso and Castro-Díez 2012; Krueger-Hadfield et al. 2016). This shift towards asexual reproduction in the non-native range has been exploited by numerous species (Platt and Jeschke 2014). The phenomenon may be partially explained by the “invasive queens hypothesis”, which postulates that when species are transported to a new environment they are released from their natural enemies, which in turn makes sexual reproduction less advantageous due to its high costs (Platt and Jeschke 2014).

Discussion: assessing the risk of introduction and successful establishment

Ports with intense shipping routes, particularly long-established older routes, have the most introduced sea anemones (See Figs. 4, 5, 6, and 7). Such ports can also act as hubs for subsequent introductions (Carlton 2003). All of the *Diadumene* species discussed here have been introduced to San Francisco Bay, presumably because of the high rates of shipping traffic (and other vectors, such as historical commercial oyster industries) to that bay. The potential risk for ports for the introduction of non-native sea anemones (and other species) can be assessed by examining the salinity, temperature, voyage time, and voyage route, and comparisons of donor and recipient regions (Jóźwiak and Barańska 2014). A longer voyage decreases the potential of a successful introduction, whereas short voyages between harbors may result in more likely introductions (Jóźwiak and Barańska 2014). How a species is able to cope within a stressful environment, even short term, affects how important each of these factors are in determining introduction potential.

Life history traits common among members of lineage may also indicate the potential of successful introductions (Fig. 2). Based on the species that have had successful introductions as compared with those that have remained in their native ranges, the combination of tolerance to environmental extremes with flexibility in reproductive strategy assists in the introduction process. As noted above, the majority of

successful introductions are within the Acuticulate group of Metridioidea (*Metridium*, *Diadumene*, *Sagartia*, *Exaiptasia*), while *A. alicemartinae* is the only representative of the Actinioidea clade, and *N. vectensis* is the sole representative of the Edwardioidea. The lineage-specific nature of the primary anemone invaders highlights an ancestral proclivity and rise of traits encouraging survival and thriving after transplantation, suggesting that potential additional invaders may be found within these lineages as global connectivity continues to increase and as the climate and ocean conditions change.

For example, *Aiptasiogeton eruptaurantia* (Field, 1949), normally ranging from Louisiana to Chesapeake Bay, has now been detected in Rhode Island in both summer 2013 and 2019 surveys, as well as in New York in the summer of 2019 (Wells et al. 2014; J. T. Carlton, M. I. McCuller, and J. Pederson, August 2019 personal observations). This may indicate a potential range expansion. In warm waters, *Bartholomea annulata* (Le Sueur, 1817), a species native to the Caribbean that undergoes both sexual and asexual reproduction to form aggregations (Jennison 1981), is commonly harvested and thus moved via the aquarium trade (O'Reilly et al. 2018, Legore et al. 2005). The combination of life history strategies encourage the potential for introduction and invasion if released into a non-native body of water from an aquarium. Additionally, the dominant presence of *Sagartia “rosea”* [= *S. elegans*, above] in fouling communities on offshore platforms in China (Li et al. 2011) implies that if this is a native member of the *Sagartia* lineage, it is prime for introduction to new locations.

Several closely related species have been suggested as introduced to other parts of the world, but have not been confirmed, needing further study beyond what is included in this review. *Diadumene cincta* Stephenson, 1925 has been argued as introduced to Europe, though whether it was an introduction from another continent or a range expansion is unknown (see Hartog and Ates 2011 for full account). In Peru, the presence of another metridioidean, *Gonactinia prolifera* (Sars, 1835), peaked the interest of Carlgren (1959) as having been introduced from Europe on ships, although this has not been confirmed despite the propensity for asexual reproduction via transverse fission (Stephenson 1935).

Cereus pedunculatus (Pennant, 1777) of the North-east Atlantic, also a member of the Acuticulate clade

of anemones, is a temperate, shallow (< 25 m) water species that inhabits sand and mud (Manuel 1981). It is reproductively facile, exhibiting oviparity, or is hermaphroditic or parthenogenetic with prolific viviparity (Stephenson 1929; Rossi 1975; Schäfer 1981; Shick 1991). Although it does employ symbioses with zooxanthellae, it has the potential to acclimate to different environments by being flexible with the specific photosymbiont (Davy et al. 1997). In the family Actiniidae, *Actinia equina* (Linnaeus, 1758) also reproduces both sexually and asexually (Perrin et al. 1999), prefers rocky substrate, and has a distribution extending across the temperature extremes from the cold northeast Atlantic, northern and southern Africa, Japan, and Israel (Chomsky et al. 2009). It has long proven a taxonomic issue with its high morphological and genetic variability and “cosmopolitan” distribution indicating a species complex (e.g. Monteiro et al. 1997; Chomsky et al. 2009; Wilding and Weedall 2019). Whether the wide, highly variable distribution is indicative of an adaptable lineage is unknown, as it could indicate a potentially successful invader.

Several of these species (*D. franciscana*, *D. paranaensis*, *E. pallida*, *A. alicemartinae*) have unknown or hypothesized native ranges presumably due to understudied research areas or the early nature of their invasion history. Baseline surveys of areas-at-risk are vital, both to understand and record native diversity and to track the spread of non-natives. On the US east coast for example, several collaborative initiatives, such as the Marine Invader Monitoring and Information Collaborative (MIMIC) and New England Rapid Assessment Surveys are undertaking surveys for marine non-natives, focusing on fouling communities where most alien sea anemones have first appeared. These data will be essential moving forward to identify both when and where alien species appear as a first response. In particular, cold polar regions are becoming increasingly vulnerable to introduced species due to rapid effects of climate change and increased boat traffic (e.g. McCarthy et al. 2019; Ware et al. 2015), necessitating routine surveys and identification of potential risk factors.

Our knowledge of sea anemone introductions and invasiveness remains far from complete. Sea anemone biology and life history, including reproductive behavior and dispersal potential, as well as distributions must be further researched particularly in

understudied taxa. There are numerous opportunities for molecular studies, from examining the regulation of genes in native and introduced ranges to population genetic diversity and the identification of potential source populations. These investigations can address potential cryptic diversity revealing finer-grained patterns to add to our understanding of invasion patterns across all marine taxa, particularly from a regional perspective. Understanding how life history strategies of sea anemone species and active vectors work together in the twenty-first century will aid in prioritizing survey locations as well as invasions and vector management.

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