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Out of the Blue: The Failure of the Introduced Sea Anemone *Sagartia elegans* (Dalyell, 1848) in Salem Harbor, Massachusetts

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Abstract. Failed invasions can be a key component for understanding and controlling introduced populations because understanding mechanisms behind failures can improve effective controls. In 2000, the non-native sea anemone *Sagartia elegans* was first found in Salem, Massachusetts, and it recolonized each summer. No individuals of *S. elegans* have been found after 2010, despite intensive search efforts. A mismatch between the species' thermal tolerance and winter water temperature is the most likely mechanism for this failed invasion. In both laboratory- and field-based temperature growth studies, *S. elegans* began regressing at 11 °C, stopped asexually reproducing at 9 °C, and died by 4 °C. These temperatures are above the average winter sea surface temperature in the Gulf of Maine, therefore suggesting that *S. elegans* requires a warm-water refuge. Another potential contributor to the disappearance of *S. elegans* is low genetic diversity as a result of establishment of only females (likely clones) and no males.

Introduction

The spread of introduced species has become a global ecological and conservation crisis as invasive organisms are increasingly altering terrestrial and aquatic communities worldwide (Mooney and Cleland, 2001; Gurevitch and Padilla, 2004; Simberloff *et al.*, 2005, 2013; Bellard *et al.*, 2016). Success or failure of biological invasions can be determined at multiple stages in the introduction continuum as organisms cross major invasion barriers (Blackburn *et al.*, 2011). It is expected that most potential introductions do not succeed (Williamson and Fitter, 1996; Lockwood *et al.*, 2005; Blackburn *et al.*, 2011; Zenni and Nuñez, 2013; King and Reed, 2016) and that many invasions may fail multiple times before becoming successful (Sax and Brown, 2000; Dlugosch and Parker, 2008; Simberloff, 2009). Despite this, invasion biology has focused primarily on species that have established successfully (*e.g.*, Richardson and Pyšek, 2008; MacIsaac *et al.*, 2011; Budy *et al.*, 2013). The few studies of failed invasions have provided many important insights into invasion biology, particularly in species distribution modeling and analyses of historical factors associated with invasions (Zenni and Nuñez, 2013). More studies of failed invasion would promote a deeper understanding of the invasion process.

Even sparser than the literature on failed invasions is the documentation of the failure of an introduced species after surviving multiple years in its new environment. Common reasons for the failure of an established population include natural disasters, competition and parasitism by a subsequently introduced species, lack of propagule pressure, intentional eradication, or inadvertent anthropogenic intervention (*e.g.*, Hillman, 1985; Simberloff, 1992; Carlton and Eldredge, 2009; Gaubert and Zenatello, 2009; Kaplan *et al.*, 2010). Understanding the environmental factors leading to the failure of established populations would allow for better management of introduced species.

One notable case of a failed invasion, investigated here, involves the sea anemone *Sagartia elegans* (Dalyell, 1848) in Salem, Massachusetts. A population of *S. elegans* was first found in the summer of 2000 at a single marina in Salem Harbor (Hawthorne Cove Marina [HCM]), during an introduced-species survey (Pederson *et al.*, 2005), where it was identified by Larry Harris and James Carlton by comparing external morphology of the newly found sea anemone to potential source location anemones. It matched the descriptions found in Stephenson (1935), Manuel (1988), and Wood (2013). It was particularly abundant in 2000 and, therefore, was suspected to

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Abbreviations: HCM, Hawthorne Cove Marina; PDSA, pedal disk surface area.

have been introduced some years prior. Subsequent rapid assessment surveys in 2003, 2007, and 2010 also found *S. elegans* at HCM (Pederson *et al.*, 2005; Wells *et al.*, 2014). The introduced population of *S. elegans* in Salem Harbor was seasonally abundant; it appeared as early as June but died back completely by January. Summertime abundance of *S. elegans* did not have an obvious decline or increase over this time. Exhaustive surveys of public spaces in Salem Harbor, including intertidal environments and marshes, failed to find any other populations of *S. elegans* (B. Warren, Salem Sound Coastwatch, pers. comm.).

Sagartia elegans is native to the European coast and can be found in subtidal habitats from the Adriatic Sea to Scandinavia, to depths of 60 meters, attached to hard substrata (Manuel, 1988; Ates *et al.*, 1998; Grebelnyi and Kovtun, 2013) and artificial substrata (Coolen *et al.*, 2018). Within this range, *S. elegans* may experience temperatures ranging from 1 °C, in its northeastern range during the coldest months, to 26 °C, in the Mediterranean during the warmest months (Kennedy, 2019). In the Netherlands, *S. elegans* was present only after mild winters with relatively high minimum sea temperature (>5 °C), and it disappeared during especially cold winters (Braber and Borghouts, 1977; Ates *et al.*, 1998). Typical of sea anemones, *S. elegans* is gonochoristic; it sexually reproduces through broadcast spawning (Stephenson, 1929), and it does not have a resting stage. The only method of asexual reproduction observed in *S. elegans* is pedal laceration (Stephenson, 1929; Manuel, 1988; Shaw, 1991), in which small pieces of the pedal disk and internal structures break off and regenerate into new daughter anemones. Within its native range, *S. elegans* is preyed upon by the nudibranch *Aeolidia papillosa* (Linnaeus, 1761) (Mollusca, Gastropoda); but it is not the preferential prey species, possibly because of its cnidome (*i.e.*, cnidae complement) and the presence of acontia used in defense (Edmunds *et al.*, 1974). *Sagartia elegans* has been reported outside of its native range in Salem Harbor (Pederson *et al.*, 2005) and the northwestern Black Sea (Grebelnyi and Kovtun, 2013).

In the present study, we exhaustively surveyed for *S. elegans* in Salem Harbor and quantified important abiotic factors affecting growth, asexual reproduction, and survival. We use these factors to explore potential reasons for the disappearance of *S. elegans* from Salem Harbor. Impacts of temperature and salinity were determined in field and laboratory experiments.

Materials and Methods

Site description

On the western Atlantic, *Sagartia elegans* (Dalyell, 1848) has been found within Salem Harbor only at a single site (HCM, described below). Salem Harbor is an embayment on the northern coast of Massachusetts Bay. For the purpose of this study, Salem Harbor is defined as the area bound by a line drawn between Juniper Point, Salem, Massachusetts (GPS coordinates: 42.5337, −70.8644), and Fluen Point, Marblehead, Massachusetts (42.5215, −70.8522) (Fig. 1). Salem Harbor is about 24 km northeast of Boston. Surface area within the harbor is about 370 hectares, ranging in volume from 10.2 to 20.1 megaliters, with an average depth of 5.2 m at high tide (Anderson *et al.*, 1975). Harbor surface water temperature ranged from 1 °C to 24 °C, with peak temperatures in early August and lowest temperatures in January and February (CDW, unpubl. data). Salinity ranged from 23.5 to 34.5 ppt during an environmental impact assessment (Anderson *et al.*, 1975), although current ranges are unknown. During the time

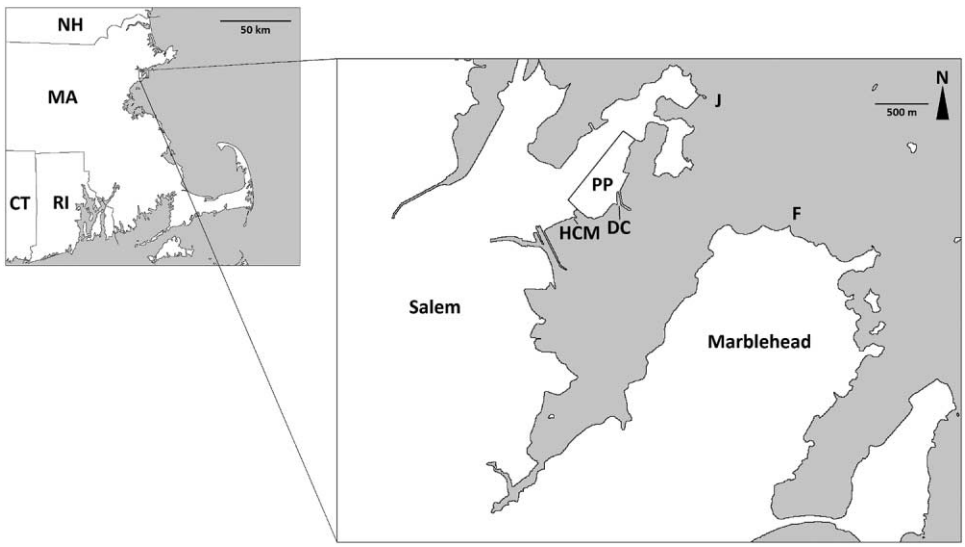

Figure 1. Map of the southern coast of the Gulf of Maine with an inlay of Salem Harbor. DC, effluent discharge channel of the power plant; F, Fluen Point; HCM, Hawthorne Cove Marina; J, Juniper Point; PP, coal- and oil-fired power plant.

S. elegans was present at HCM, a coal- and oil-fired power plant was present; but it has since been decommissioned and replaced with a natural gas-fired power plant (Sedor, 2014).

HCM is a private marina with 110 slips, located on the northern shore of Salem Harbor (42.5214, −70.8825). Float fouling communities are dominated by ascidians and arborescent bryozoans on the vertical surfaces and by mussels and clonal anemones (*Metridium senile* (Linnaeus, 1761)) on the horizontal surfaces. Sides of floats are scraped annually by marina staff for maintenance purposes. Depth at HCM ranges from 1 to 4 m. HCM is known for its exceptionally high load of introduced species compared to other sites in the Gulf of Maine (Pederson *et al.*, 2005; Wells *et al.*, 2014).

Laboratory culture and measurement methods

Polyps of about 250 *S. elegans* individuals were collected from several different locations on the floating docks in HCM during October 2010 in order to create cultures for use in the following experiments. Polyps were removed from the shells of the mussel *Mytilus edulis* Linnaeus, 1758 by hand and were placed in shallow dish pans held at 15 °C on a 12h : 12h light : dark cycle in a temperature- and light-controlled room at the University of New Hampshire. Cultures were fed brine shrimp *Artemia franciscana* Kellogg, 1906 three times weekly. Anemones were allowed to asexually reproduce, and the asexual products were used in the subsequent experiments. Cultures were not maintained as clonal lines.

Wells (2013) found that the best method for accurately measuring the growth of anemones, without disturbing and removing them from their substratum, was to measure the pedal disk surface area (PDSA), assuming that the pedal disk was ellipsoid. The following equation for an ellipsoid was used to calculate pedal disk surface area for *S. elegans*:

$$\mathrm{PDSA} = \pi \times \frac{D_{\mathrm{maj}}}{2} \times \frac{D_{\mathrm{min}}}{2},$$

where D_{maj} is the length of the major axis of the pedal disk (*i.e.*, maximum diameter) and D_{min} is the length of the minor axis (*i.e.*, perpendicular to the maximum).

Field density

Field surveys were conducted to explore the seasonal population dynamics of *S. elegans* in its introduced range and to find any remnant populations. Because *S. elegans* was expected to maintain an annual population at HCM, surveys in 2009 and 2010 were originally conducted for other purposes; and their methods differ slightly from the more extensive 2011–2013 surveys.

On October 23, 2009, during a pilot study, the density of *S. elegans* was approximated by counting all polyps on haphazardly chosen vertical sides of 15 floats (about 0.40 m^2) at HCM. In the late summer to early winter of 2010, the density of *S. elegans* was approximated by counting all polyps on haphazardly chosen vertical sides of 20 floats at HCM. Counts were done from August to December monthly (four surveys). From June 2011 to January 2013, every 1–4 weeks (48 surveys), the density of *S. elegans* was approximated by counting polyps within 0.06-m^2 (0.25 × 0.25-m) polyvinylchloride (PVC) quadrats laid haphazardly on a vertical side of 30 floats at HCM. A scuba survey was performed in November 2011 to determine whether *S. elegans* was on the underside of the floats. The bottoms of 54 floats were examined for *S. elegans* polyps. In November and December 2012, floating docks and other structures were examined for polyps of *S. elegans via* kayak (Table 1).

Field survival and growth study

Temperature is highly variable within Salem Harbor, and temperature is frequently indicated as the major reason for established populations failing (Zenni and Nuñez, 2013). Laboratory-cultured anemones were allowed to attach to panels; and the panels were hung off HCM in two separate years to explore the relationship between temperature and *S. elegans* growth, asexual reproduction, and survival. In June 2011, 10 sanded but otherwise clean acrylic glass panels (0.01 m^2, 10.0 × 10.0 × 0.4 cm) with 5 polyps of *S. elegans* were hung. Panels were hung so that they were isolated from the floats at HCM to prevent predation. Floating structures, such as

Table 1

Georeferenced sites examined for Sagartia elegans *during kayak surveys in November and December 2012*

Date of survey	Site	Type	GPS coordinates
November 2012	Salem Harbormaster floating dock	Floating dock	42.5255, −70.8693
November 2012	Floats in Cat Cove	Floating structure	42.5257, −70.8736
November and December 2012	Power plant water discharge channel	Floating structures	42.5231, −70.8763
November and December 2012	Salem Ferry floating dock	Floating dock	42.5214, −70.8796
December 2012	*Friendship of Salem*	Full-rigged ship	42.5201, −70.8865
December 2012	Pickering Wharf	Floating dock	42.5194, −70.8872
December 2012	Palmer Cove Yacht Club	Floating dock	42.5137, −70.8869

fouling panels, have reduced predation because of their isolation from habitats with predators (Dumont *et al.*, 2011). At the start of the experiment and about every two weeks thereafter, we noted PDSA, number of pedal lacerates (*i.e.*, asexual offspring) produced, and whether or not animals had visibly ripe gonads, until all animals had released from the panels or died, in January 2012. Animals that had released from the panels were assumed to have died because there are few suitable habitats for hard-bottom anemones such as *S. elegans* underneath HCM and because there is a substantial population of their predator, the nudibranch *Aeolidia papillosa* (Linnaeus, 1761) (Wells, 2013). Pedal lacerates were discarded so that daughter anemones would not compete for space with the original anemones and to facilitate tracking of adult survival. Temperature was measured concurrently using a HOBO Pendant temperature and light data logger 64K (Onset Computer Corporation, Bourne, MA) set to measure temperature every 20 minutes. From June 2012 to January 2013, the experiment was repeated with 10 polyps of *S. elegans* per panel. Measurements of PDSA were taken every one to two weeks, but pedal lacerates were not counted. Panels were removed in January 2013. Linear regressions comparing size (both years) and asexual reproduction (2011 only) to temperature were performed. Size measurements from 2011 and 2012 were pooled. Because animals died or fell off the panels and because panels fell off as a result of wave action throughout the experiment, sample size varied across time.

Laboratory temperature and salinity study

Within its native range, *S. elegans* is sensitive to salinity and does not survive in brackish conditions in estuaries (Ates *et al.*, 1998). Salinity within Salem Harbor can range from 23.5 to 34.5 ppt, frequently dropping below full-strength seawater (Anderson *et al.*, 1975); and it is, therefore, a possible reason for *S. elegans'* disappearance. The effect of salinity on growth, asexual reproduction, and survival was quantified through laboratory experiments. We spread 120 *S. elegans* polyps evenly across 12 Sterilite containers (Sterilite, Townsend, MA) (1.7 L; 10 anemones per container). Anemones were chosen haphazardly from culture tanks. Containers were filled with 1.0 L of water at 1 of 4 levels of salinity (3 replicate containers per treatment): 20, 25, 30, or 35 ppt. Ultraviolet (UV)-sterilized seawater (500-μm filtered, average of 31 ppt) was decreased in salinity through the addition of deionized water or was increased in salinity by the addition of Instant Ocean sea salt (Spectrum Brands, Madison, WI) to achieve these salinities. Salinities were measured with a refractometer. The 12 containers were placed within 3 Sterilite water baths (39 L; 4 containers per bath). Water baths were filled with 13 L of freshwater and were heated with a 150-W JBJ (Inglewood, CA) True Temp Titanium Heating System to 15 °C at the beginning of the experiment, in order to emulate October temperatures, just before temperatures precipitously drop (CDW, unpubl. data). The heating systems have internal temperature monitors with an accuracy of ±0.3 °C. One Minijet 404 submersible pump (Spectrum Brands Pet, Blacksburg, VA) was placed in each water bath to ensure even heat distribution within the water baths. The water baths were placed in a temperature-controlled room at 4.0 °C on a 12h : 12 h light : dark cycle. Temperature was decreased by 3.0 °C on days 14 and 29, after which temperature was decreased by 1.0 °C every 2 weeks (days 41, 55, 70, 83, and 97) until ambient temperature had been reached. This drop in temperature resembled the temperature drop measured in Salem Harbor between October and January (CDW, unpubl. data). At the start of the experiment and approximately every seven days thereafter, size was measured, and pedal lacerates were counted and then discarded. Animals were fed 1.0 mL (12,000 nauplii per mL) of *A. franciscana* nauplii 3 times weekly. This amount of food completely satiated anemones at the time of feeding, and digestion of this amount of *A. franciscana* took approximately 24 hours. Water movement and aeration within the containers were provided by two air pumps connected to a gang-valve system. Water was changed with fresh seawater adjusted to the proper salinity two days prior to days when temperature was reduced. Containers that had complete mortality within the first three weeks were discarded and were not included in analyses because anemones were within temperatures and salinities found to be acceptable in initial pilot studies. Anemones that died were not replaced because there was concern that starting some containers at different temperatures would affect their growth, reproduction, or mortality. In addition, 4 containers with 10 anemones per tank were kept in a separate temperature-controlled room at 15 °C on a 12h : 12h light : dark cycle. Water changing, feeding regime, and sampling followed the same methods as the experimental treatments. Linear regressions were performed comparing growth and shrinkage rates for *S. elegans*.

Results

Field density

In 2009, *Sagartia elegans* was present in October (average 4.2 polyps m^{-2}, Fig. 2). Anemones were primarily found within dead *Mytilus edulis* shells and attached to live *M. edulis*, although many sea anemones were also found attached to the floats and as epibionts on other fouling organisms. No *S. elegans* individuals were sexually mature, and all were of the same color.

In 2010, *S. elegans* was present from September to December. Densities were highest in early October (average 210 polyps m^{-2}) and were dropping precipitously by December (Fig. 2). Temperature was the highest in September (21.2 °C), and it slowly decreased until December (7.4 °C) (Massachusetts Bay Buoy, Northeastern Regional Association of Coastal Ocean Observing Systems, 2019). The highest abundance of sea anemones was on primary space on the vertical surfaces of the floats within the first 10 cm below the

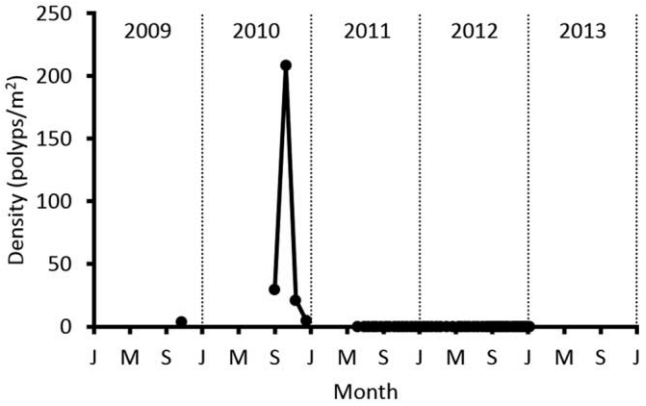

Figure 2. Density of *Sagartia elegans* on the vertical surfaces of floats at Hawthorne Cove Marina in Salem, Massachusetts, from October 2009 to February 2013. Dotted vertical lines delineate years. Density was sampled 1 time in 2009, 4 times in 2010, and 48 times between 2011 and 2013. J, January; M, May; S, September.

water surface. Sea anemones were also epibiotic on *M. edulis, Ciona intestinalis* (Linnaeus, 1767), *Steyla clava* Herdman, 1881, *Ostrea edulis* Linnaeus, 1758, *Ulva lactuca* Linnaeus, 1753, *Saccharina latissima* (Linnaeus) C.E.Lane, C.Mayes, Druehl & G.W.Saunders, 2006, and *Chondrus crispus* Stackhouse, 1797. In addition, they were found attached to free-floating *Ascophyllum nodosum* (Linnaeus) Le Jolis, 1863, which were tangled with the floats. Most polyps were 14 mm in diameter and larger, and all polyps above 20 mm had female gonads visible through their oral disk. All *S. elegans* individuals were of the same color.

From June 2011 to January 2013, we failed to detect *S. elegans* through all methods, including the repeated surveys of the vertical sides of floats (Fig. 2), kayak surveys, and the scuba survey.

Field survival and growth study

Both the size of *S. elegans* (Fig. 3A, $R^2 = 0.913$, $F_{1,24} = 250.79$, $P < 0.001$, linear regression) and the number of pedal lacerates being produced (Fig. 3B, $R^2 = 0.929$, $F_{1,6} = 78.82$, $P < 0.001$, linear regression) were strongly correlated with temperature. Size and asexual reproduction decreased with temperature. Asexual reproduction stopped after temperature fell below 9.3 °C. Three of the 10 panels in 2011 were dislodged from HCM during Hurricane Irene on August 27, 2011. On panels still attached, many of the anemones were heavily damaged, with some subsequently disappearing in September. After the losses during and directly after Hurricane Irene, anemones were not lost until November. While the hurricane had a major initial impact, after the hurricane the rate of disappearance from the panels was similar between years. After temperature dropped below 11 °C, anemones disappeared at an accelerated rate; and all anemones had disappeared prior to temperatures decreasing to 6 °C.

Laboratory temperature and salinity study

Anemones in all treatments grew until temperature was decreased below 9 °C, at which point animals started to shrink (Fig. 4A). Anemones in the control group continued to grow throughout the experiment. There was no significant difference between growth rates ($F_{3,6} = 2.95$, $P = 0.120$, ANOVA) and shrinkage rates ($F_{3,6} = 0.19$, $P = 0.901$, ANOVA) in the four salinity treatments, although the sample size was very small ($n = 2-3$). The pooled mean growth rate before the temperature decreased below 9 °C was 0.21 $mm^2\ day^{-1}$; and after decreasing below 9 °C, the shrinkage rate was 0.11 $mm^2\ day^{-1}$. Beyond 9 °C, asexual reproduction stopped, except for one pedal lacerate produced at 8 °C and 6 °C (Fig. 4B). Control anemones produced a mean of 0.07 pedal lacerates per day throughout the experiment. Polyps of *S. elegans* in the experimental treatments started dying once temperature decreased below 7 °C (Fig. 4C). Anemones were considered dead when tissue started to visibly degrade, which was preceded by loss of color and release from the substratum. After the third week at 4 °C, all polyps in all treatments, except for 2 polyps in the

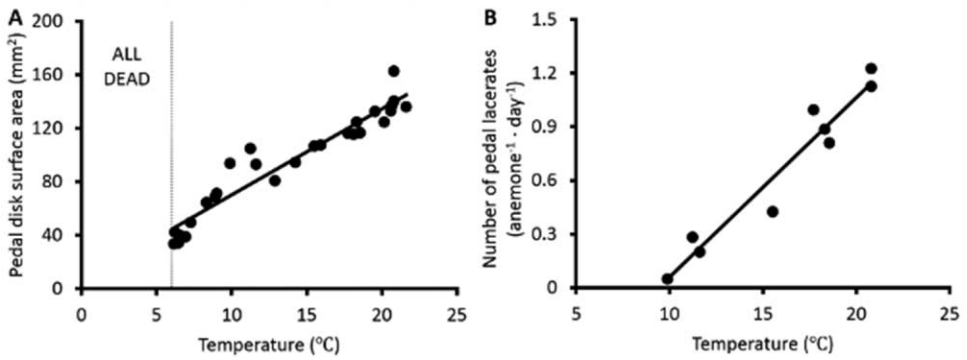

Figure 3. Relationship between temperature and (A) pedal disk surface area and (B) asexual reproduction of *Sagartia elegans* polyps at Hawthorne Cove Marina in Salem, Massachusetts (mean ± SE). All anemones died after temperatures decreased below 6 °C. Both size ($n = 27$) and number of pedal lacerates ($n = 8$) were strongly correlated with temperature ($R^2 > 0.913$, $P < 0.001$).

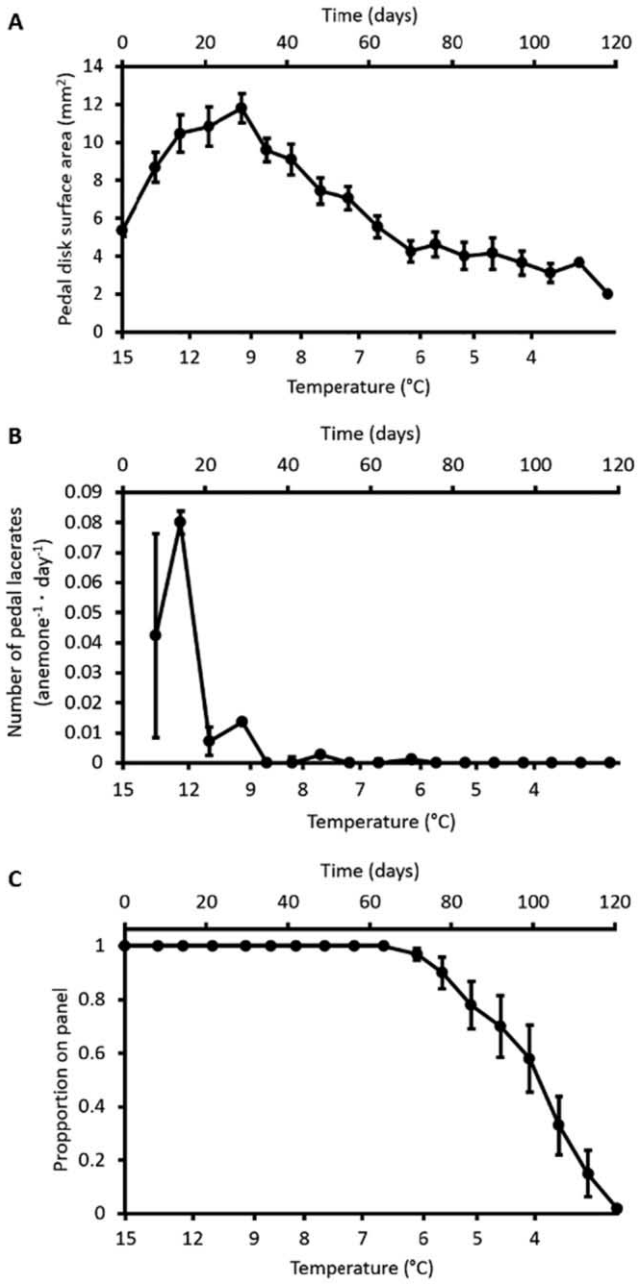

Figure 4. (A) Pedal disk surface area, (B) asexual reproduction, and (C) proportion of polyps alive for *Sagartia elegans* as temperature was decreased in a laboratory setting (n = 12, mean ± 1 SE). Salinity treatments were pooled because no difference was found.

30-ppt treatment, had died. Polyps still alive at 4 °C were heavily discolored and unattached.

Discussion

Sagartia elegans disappeared from Salem Harbor sometime between December 2010 and June 2011. Extensive surveys of the only location where *S. elegans* had been found failed to detect any individuals. Wider searches, including kayak and scuba surveys (this study) and intertidal and benthic surveys, also failed to locate any remnant populations (B. Warren, Salem Sound Coastwatch, pers. comm.). Additional surveys in 2013 and 2018 did not locate any *S. elegans* individuals at HCM (Wells *et al.*, 2014; A. Pappal, Massachusetts Coastal Zone Management, pers. comm.).

We conclude that temperature likely played the largest role in the disappearance of *S. elegans*. Temperatures below 6 °C were found to be detrimental to *S. elegans*' survival both in culture and in the field (Figs. 3A, 4C). This is higher than the minimum temperature (5 °C) found by Braber and Borghouts (1977) and Ates *et al.* (1998) in the field. Within the species' native range, certain populations of *S. elegans* may experience temperatures as low as 1 °C (Kennedy, 2019). It seems that the source population of the original colonization of *S. elegans* was from its southern native range.

In the 9 years prior to the disappearance of *S. elegans*, winter sea surface temperature was below 6 °C for a minimum of 76 consecutive days and, on average, for 97.3 consecutive days. In the winter of 2011, there were 112 consecutive days of below 6 °C sea surface temperature (Massachusetts Bay Buoy, Northeastern Regional Association of Coastal Ocean Observing Systems, 2019). For *S. elegans* to survive winter temperatures, there must have been a temperature refuge in Salem Harbor. It is highly unlikely that a new invasion was occurring every year, because the vector for sea anemone introduction is typically hull fouling (Carlton, 2003). The only plausible refuge in Salem Harbor was a coal- and oil-fired power plant located less than 100 meters from HCM (Fig. 1). This power plant used Salem Harbor water for thermoelectric cooling and discharged water back into the harbor through a discharge channel that opened toward HCM (Anderson *et al.*, 1975). The plant was allowed to discharge water up to 15.8 °C warmer than ambient temperature, and temperatures within the discharge channel could have risen up to 9.6 °C (Anderson *et al.*, 1975). On average, winter effluent temperatures were 12.6 °C (US Department of Energy, 1982), more than sufficiently warm for *S. elegans* to survive the cold winters; and the power plant had been under significantly more use since 1982 (Mooney and Kawa, 2008). Water within Salem Harbor was not significantly warmed outside of the discharge channel (Anderson *et al.*, 1975). An increase of only several degrees during the winter would be enough to keep *S. elegans* alive throughout the winter months in this channel. A change in power plant procedures, such as cleaning the discharge channels during winter (*i.e.*, directly killing fouling organisms) or a short reduction in boiler service (*i.e.*, a reduction in discharge temperature), could have massive impacts on a refuge population already stressed by New England winter temperatures. There are no public records of the power plant changing its power plant procedures in the winter of 2010 and 2011.

Many aquatic organisms use warm-water effluent to survive in locations that would normally be too cold (*e.g.*, Langford

et al., 1972; Galloway and Kilambi, 1988; Crutchfield, 1995; Peterson *et al.*, 2005; Simard *et al.*, 2012; Lukas *et al.*, 2017). Thermally influenced systems are hotspots for introduced species, providing habitat for animals outside of their normal temperature range (reviewed in Lukas *et al.*, 2017). Growth rate and survival during winter were increased in introduced tilapia *Oreochromis niloticus* (Linnaeus, 1758) using the thermal effluent from an aquaculture facility (Peterson *et al.*, 2005) and a nuclear power plant (Crutchfield, 1995). The introduced Asian clam *Corbicula fluminea* (O. F. Müller, 1774) survived in warm-water effluent during the cold winter months in the St. Lawrence River (Simard *et al.*, 2012), and then it subsequently repopulated sites downstream during warmer months (Morgan *et al.*, 2004). The widely introduced bryozoan *Bugula neritina* (Linnaeus, 1758) had large populations on a dock heated by power plant effluent in south Wales, and it disappeared only after the power plant was decommissioned (Ryland *et al.*, 2011). Similarly, *S. elegans* was absent from HCM during the winter and spring before its failure, and it repopulated HCM from a refuge population each summer. This may have been facilitated by the ability of *S. elegans* to travel short distances *via* ballooning, where polyps fill with seawater, release from their substratum, and then reattach *via* use of their tentacles (Wells, 2013), a behavior also seen in congeners (Gosse, 1860; Ashworth and Annandale, 1904).

Salinity was likely not responsible for *S. elegans* failure in Salem Harbor. Laboratory experiments found that the introduced population of *S. elegans* was not sensitive to salinities ranging from 20 to 35 ppt, which completely covers the range of salinities observed in Salem Harbor (Anderson *et al.*, 1975).

In addition to temperature stress, the introduced population of *S. elegans* was likely one clone. All animals were of one color morph, in contrast to the variety of color morphs in their native range; there are at least five fairly distinct color morphs (Stephenson, 1935; Manuel, 1988; Wood, 2013). Although *S. elegans* is gonochoristic, all sexually mature *S. elegans* individuals had female gonads, indicative of a clonal population. Within a sexually reproducing population of sea anemones, the sex ratio is commonly 1:1 (Gemmill, 1920; Carter and Thorpe, 1981; Jennison, 1981; Sebens, 1981; Shaw *et al.*, 1987; Hunt and Ayre, 1989). The possibility of there being more than one female clone of the same color cannot be excluded; however, our data strongly support that there was not a sexually reproducing population reducing adaptive potential. *Sagartia elegans* would not have had a chance to adapt to the Gulf of Maine environment and, therefore, was likely to fail at some point. Failure of clonal populations of another introduced sea anemone, *Diadumene lineata* (Verrill, 1869), is apparently common (Shick *et al.*, 1979); yet there have been no studies focusing on these ephemeral populations.

One possible method for controlling the spread of introduced species that have invaded regions beyond their thermal tolerance may be to briefly shut down or reduce the activity of industry providing a thermal refuge. This assumes that the introduced species could not live without the thermal refuge and that the cost of temporarily discontinuing industry for the required amount of time to kill the introduced species is less than the damage that the introduced species would inflict on the local ecosystem. Another possibility is modifying the temperature of effluent leaving the facility. As of June 2012, the coal- and oil-fired power plant in Salem Harbor was decommissioned; and it is being replaced by a natural gas-fired power plant (Ailworth, 2012), which will eliminate impact on local water temperatures because the natural gas boilers being built will be air cooled (Buttaro *et al.*, 2014). It would be informative to do a comparative study of the fouling community at HCM before and after shutdown of the power plant, because HCM is a highly invaded site compared to other nearby sites (Pederson *et al.*, 2005; Wells *et al.*, 2014).

Increased effort in detecting introduced species immediately or shortly after invasion will be imperative to both eradication efforts and the collection of data on failed invasions. More data on failed invasions will promote a deeper understanding of the invasion process because little work has been focused on failed introduced species. Particular effort in detecting and understanding the special cases where an introduced species becomes established and then subsequently fails will be especially helpful in introduced species management because these reasons could be developed into possible management skills for the eradication of newly invaded species.

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