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The failed introduction of the sea anemone Sagartia elegans in Salem Harbor, Massachusetts

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THE FAILED INTRODUCTION OF THE SEA ANEMONE *SAGARTIA ELEGANS* IN SALEM HARBOR, MASSACHUSETTS

BY

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Thesis

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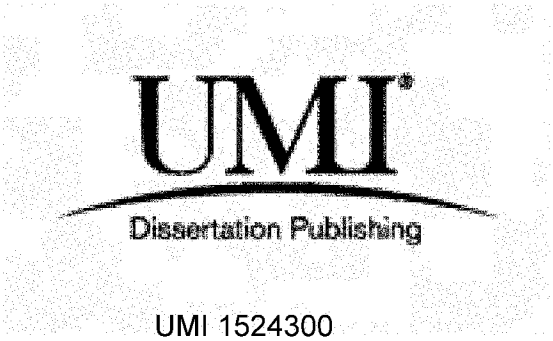

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PREFACE

Recent work by the author, Dr. Adriaan Gittenberger (Acting Director of GiMaRIS), and Dr. James T. Carlton (Professor of Marine Sciences at Williams College), during the 2013 Massachusetts Coastal Zone Management rapid assessment survey, indicates what was originally identified as *Sagartia elegans* (Dalyell, 1848) during the 2000 rapid assessment survey may be a different species of sea anemone. At the time of the publication of this thesis it is still unknown as to what species this anemone is and will therefore be called *S. elegans* until a proper identification can be carried out.

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ABSTRACT

THE FAILED INTRODUCTION OF THE SEA ANEMONE *SAGARTIA ELEGANS* IN SALEM HARBOR, MASSACHUSETTS

by

Christopher D. Wells

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Many studies have reported the arrival and subsequent range expansion of foreign species within the marine ecosystems, but few studies have documented species that arrive and fail to establish. In 2000, the sea anemone *Sagartia elegans* (Dalyell, 1848) was first found in Salem, MA and persisted seasonally until the winter of 2010-2011 after which it has not been found. In both laboratory and field based temperature growth studies, *S. elegans* began regressing in size at 11 °C, stopped asexually reproducing at 9 °C, and died by 4 °C; these temperatures are far above the average winter sea surface temperature in the Gulf of Maine, therefore suggesting that *S. elegans* requires a warm-water refuge. It is still unknown as to what caused the population collapse, but it is likely a combination of both a lack of genetic diversity and an inability to tolerate the cold temperatures during winter.

INTRODUCTION

Introduced species are becoming increasingly recognized as a serious problem and introductions are becoming more and more common (Mooney and Cleland, 2001; Simberloff *et al.*, 2005). Their ability to alter population, community, and ecosystem structure and function as well as cause significant economic damage is well documented (Elton, 1958; Carlton, 1989; Meinesz *et al.*, 1993; Cohen and Carlton, 1995; Cohen *et al.*, 1995; Carlton, 1996b, 2000; Thresher, 2000; Pimentel *et al.*, 2005; Occhipinti-Ambrogi and Sheppard, 2007). Common characteristics of introduced species that increase the success of introductions include: broad native range, wide physiological tolerances, high rates of reproduction, and asexual reproduction (reviewed in Ehrlich, 1989).

Success or failure of biological introductions can be determined at multiple stages in the introduction process as organisms cross major barriers (Blackburn *et al.*, 2011). The first barrier to cross is the geographic barrier: organisms must be able to survive transport from one location to another. Many cannot survive the stress of transport from their native range to their introduced range and will therefore fail (e.g. desiccation, starvation, anoxia). Abiotic factors (e.g. temperature, salinity) and biotic interactions (e.g. predation, competition, parasitism) represent a second barrier to potential introduced species as they attempt to establish a population. Most failed introductions are attributed to either abiotic factors that the introduced species cannot withstand or biotic resistance (Zenni and Nuñez, 2013). Finally, the introduced species must also be able to reproduce within their newly established population and a genetic bottleneck has been argued as a reason for failure at this stage (Simberloff, 2009). The introduction of more individuals

from the native population can help at this stage as novel genotypes can be introduced to the gene pool strengthening the introduced population. This bolstering of the population is called propagule pressure. Propagule pressure is a measurement taking into account the number of individuals and frequency of introductions (Lockwood *et al.*, 2005). After crossing these three barriers (i.e. geographic, abiotic/biotic, and reproductive) the introduced species can be considered established within its new range.

It is expected that most introductions do not succeed (Williamson and Fitter, 1996; Lockwood *et al.*, 2005; Blackburn *et al.*, 2011) and many introductions fail multiple times before becoming successful (Sax and Brown, 2000). Failure is a common outcome of species introductions (Zenni and Nuñez, 2013) and yet the field of invasion biology has focused more strongly on species that have succeeded in establishment in their new range (e.g. Richardson and Pyšek, 2008; MacIsaac *et al.*, 2011; Budy *et al.*, 2013). The few studies on failed introductions have already provided many important insights into invasion biology, particularly in species distribution modeling and analyses of historical factors associated with introductions (Zenni and Nuñez, 2013).

Even sparser than the literature on failed introductions is the documentation of the failure of an introduced species after becoming established (i.e. surviving multiple years in their 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 and therefore lack of genetic input, intentional eradication, or inadvertent anthropogenic intervention such as changing of crop species, habitat destruction, or industrial operation changes (see Table 1 for examples and references).

Table 1: List of 20 species with known failed introduced populations. All species maintained a population for greater than a year. All proposed reasons for failure are included; most are anecdotal and have not been tested quantitatively. **D**: failure due to natural disaster, **I**: failure due to competition, parasitism, or disease from a concurrently or subsequently introduced species, **GD**: failure due to lack of genetic diversity, **A**: failure due to an inadvertent anthropogenic intervention, **E**: failure due to intentional eradication, **U**: unknown reason for failure.

Species (Common name)	**Location of introduction**	**Proposed reason for failure**	**Relevant references**
Dendronephthya sp.	Hawai'i	D	Carlton and Eldredge, 2009
Amandova amandova (Red munia)	Mascarene Islands	D, I	Rountree *et al.*, 1952; Benedict, 1957; Cheke, 1987; Simberloff, 1992
Achatina fulica (Giant African land snail)	Cousine Island, Pacific Islands	D, I, GD	Mead, 1979; Waterhouse and Norris, 1987; Samways *et al.*, 2010
Lonchura oryzivora (Java sparrow)	Mascarene Islands	D, A, E	Meinertzhagen, 1912; Rountree *et al.*, 1952; Benedict, 1957; Cheke, 1987; Simberloff, 1992
Serinus canicollis (Yellow-crowned canary)	Mascarene Islands	D, A, I	Meinertzhagen, 1912; Rountree *et al.*, 1952; Benedict, 1957; Cheke, 1987; Simberloff, 1992; Jones, 1996; Simberloff and Gibbons, 2004
Melopsittacus undulatus (Budgerigar)	Florida	I	Pranty, 2001; Kratter, 2012
Acridotheres cristatellus (Crested myna)	British Columbia	I, A	Johnson and Campbell, 1995; Self, 2003
Aedes aegypti (Yellow fever mosquito)	Spain	I	Juliano, 1998; Eritja *et al.*, 2003; Braks *et al.*, 2004; Kaplan *et al.*, 2010
Cakile edentula (American searocket)	Australia, California	I	Barbour and Rodman, 1970; Rodman, 1986; Boyd and Barbour, 1993

Species (Common name)	Location of introduction	Proposed reason for failure	Relevant references
Ceratitis capitata (Mediterranean fruit fly)	New South Wales, Hawai'i	I	Keiser *et al.*, 1974; Bateman, 1977; Maelzer, 1990
Euproctis chrysorrhoea (browntail moth)	New England	I	Elkinton *et al.*, 2001
Herpestes edwardsii (Indian grey mongoose)	Italy	GD	Carpaneto, 1990; Gaubert and Zenatello, 2009
Bulla sp. (Bubble shell)	Hawai'i	A	Burgess, 1959; Carlton and Eldredge, 2009
Daphnia exilis	New York	A	Hairston *et al.*, 1999
Teredo furcifera (Forked shipworm)	New Jersey, Connecticut	A	Hoagland and Turner, 1980; Hillman, 1985; Carlton, personal communication
Teredo bartschi (Bartsch shipworm)	New Jersey	A	Hoagland and Turner, 1980; Hillman, 1985
Corvus albus (Pied crow)	Mascarene Islands	E	Rountree *et al.*, 1952; Benedict, 1957; Staub, 1976; Cheke, 1987
Ascidiella scabra (Hairy sea squirt)	Japan	U	Nishikawa and Otani, 2004
Wrangelia bicuspidata	Hawai'i	U	Russell, 1992; Carlton and Eldredge, 2009
Mercenaria mercenaria (Northern quahog)	Southern California	U	Burnaford *et al.*, 2011

A recent example of a failed introduction is the European sea anemone *Sagartia elegans* (Dalyell, 1848) in Salem Harbor, Massachusetts. A population of *S. elegans* was found at Hawthorne Cove Marina in Salem, MA (42.5214; -70.8825) during a rapid

assessment survey looking for introduced species in the summer of 2000 (Pederson *et al.*, 2001; Pederson *et al.*, 2005). The species was particularly abundant in 2000 and therefore, is suspected to have been introduced some years prior. It was only found at Hawthorne Cove Marina and has only been documented there since (Pederson *et al.*, 2001; Pederson *et al.*, 2005; Massachusetts Office of Coastal Zone Management, 2013).

The introduced population of *S. elegans* was seasonally abundant; it appeared as early as June (Harris, personal communication) and died back by January. After the winter of 2010-2011, *S. elegans* could not be found in Salem Harbor. The disappearance in the winter as well as its seasonal abundance suggests that winter is particularly stressful for *S. elegans*. Within its northern native range, *S. elegans* is sensitive to winter water temperatures, disappearing completely during extreme winters (1.4 °C) (Ates *et al.*, 1998). Other potential winter stressors include, but are not limited to, variable salinity and heavy wave action due to winter storms, as well as predation by the seasonally abundant, anemone-specialist nudibranch *Aeolidia papillosa* (Linnaeus, 1761).

The main goal of this research was to attempt to explain the disappearance of *S. elegans* through quantitative experimentation. The specific objectives of this thesis are to:

- Determine and quantify important abiotic and biotic factors effecting growth, asexual reproduction, and survival.
- Explore potential reasons for the disappearance of *S. elegans* from Salem Harbor.

In Chapter 1, I discuss methods for culturing and measuring of *S. elegans*. Chapter 1 also explores the effects of temperature, salinity, food, feeding frequency, and substratum on the growth, survival, and asexual reproduction of *S. elegans* in a laboratory

setting. In Chapter 2, I examine the population dynamics and recruitment of *S. elegans* as well as impacts of temperature on growth and reproduction in the field.

CHAPTER I

EFFECTS OF TEMPERATURE, SALINITY, FOOD, FEEDING FREQUENCY, AND SUBSTRATUM ON THE GROWTH, SURVIVAL, AND ASEXUAL REPRODUCTION OF *SAGARTIA ELEGANS* IN THE LABORATORY

Introduction

Benthic marine invertebrates such as gastropods (Paine, 1965), echinoderms (Paine, 1969) and sea anemones (Sebens, 1977, 1982b) often have habitat-dependent body size and indeterminate growth (i.e. ability to increase and decrease in size over a wide range as conditions vary) (Ebert, 1968; Kohn, 1971; Paine, 1976; Bertness, 1977; Levitan, 1988; Ferretti *et al.*, 2009). Body size of sea anemones is more closely related to nutritional history than to polyp age (Stephenson, 1928) as it is determined by the difference between energy intake and metabolic cost (Sebens, 1977, 1979, 1981a, 1982b). Body size changes concurrently as environmental and nutritional conditions change, implying that body size is not genetically defined (Sebens, 1987).

There is an inverse relationship between size and mortality (Ottaway, 1979; Sebens, 1983). Ottaway (1979) found that small individuals of the sea anemone *Actinia tenebrosa* Farquhar, 1898 suffer higher mortality from increased predation, increased desiccation, dislodgement by grazing gastropods, and through interspecific competition. Size also helps in maintenance of space during bouts of intraspecific aggression in *Actinia equina* (Linnaeus, 1758) (Brace and Pavey, 1978) and *Anthopleura xanthogrammica* (Brandt, 1835) (Sebens, 1984). Smaller individuals of *Anthopleura*

elegantissima (Brandt, 1835) and *Anthopleura sola* Pearse and Francis, 2000 are more susceptible to desiccation and burial by sand (Pineda and Escofet, 1989). Stehouwer (1952) and Harris (1973, 1986) found that small individuals of *Metridium senile* (Linnaeus, 1761) attract and are preferentially preyed upon by *A. papillosa*.

Maximum size in benthic invertebrates can be constrained by their ability to capture available prey (Sebens, 1977, 1981a, 1982b, 1983), as well as by size-selective predators (Paine, 1974), refuge size (Kohn, 1971), prey abundance (Paine, 1965, 1976), and prey availability (Vadas, 1977). Physiological stress may also play a role in maximum size (Sebens, 1977, 1981a, 1982b). Asexual reproduction can be a means for a species to control for an optimum size while increasing available surface area for prey capture and biomass for reproduction (Sebens, 1981a, 1982b). Asexual reproduction counters growth by investing excess biomass of the individual into new clones.

In sea anemones, asexual reproduction occurs through vegetative proliferation or apomictic parthenogenesis, and commonly occurs in all major groups of sea anemones (Shick, 1991). Vegetative proliferation can be carried out through pedal laceration, longitudinal or transverse fission, budding, or regeneration from autotomized tentacles (reviewed in Stephenson, 1935; Chia, 1976; Shick, 1991; Bocharova and Kozevich, 2011); few anemones perform asexual reproduction through multiple methods (Stephenson, 1929; Shick, 1991). Asexual reproduction allows for rapid establishment of well adapted clones to local environments (Chia, 1976; Francis, 1976).

Many factors have been documented to either inhibit or stimulate asexual reproduction in sea anemones. These include temperature (Miyawaki, 1952; Johnson and Shick, 1977; Sebens, 1977; Minasian, 1979; Minasian and Mariscal, 1979; Sebens, 1980;

Minasian, 1982; Hunter, 1984), immersion cycles (Johnson and Shick, 1977), rate of water flow (Shick *et al.*, 1979), light (Sebens, 1977, 1980; Hunter, 1984), size (Sebens, 1980; Minasian, 1982), and food (Minasian, 1976; Smith and Lenhoff, 1976; Sebens, 1977; Minasian, 1979; Minasian and Mariscal, 1979; Sebens, 1980; Hunter, 1984), and have been shown to be highly species specific. For example, increased frequency of feedings stimulates asexual reproduction in *Diadumene lineata* (Verrill, 1869) (Minasian, 1976, 1979; Minasian and Mariscal, 1979; Minasian, 1982), but inhibits reproduction in *Aiptasiogeton pellucidus* (Hollard, 1848) (Smith and Lenhoff, 1976), *Aiptasia pallida* (Agassiz in Verrill, 1864) (Hunter, 1984), and *A. elegantissima* (Sebens, 1977, 1980). Factors regulating asexual reproduction therefore need to be examined on a specific level before broader generalizations can be made.

A population of the European sea anemone *S. elegans* was recently found in Salem Harbor, Massachusetts in 2000 (Pederson *et al.*, 2001; Pederson *et al.*, 2005). The population has subsequently failed during the winter of 2010-2011. The introduced population of *S. elegans* was seasonally abundant, disappearing during the winter. Its seasonal abundance as well as its population failure during the winter, suggest that winter is particularly stressful for *S. elegans*. *S. elegans* has been shown to be sensitive to winter water temperatures, disappearing completely during extreme winters in its native range (Ates *et al.*, 1998). Other potential winter stressors include variable salinity and heavy wave action due to winter storms, and predation by *A. papillosa*. *S. elegans* reproduces asexually through pedal laceration, in which small pieces of the pedal disk (i.e. foot) and internal structures break off and regenerate into new anemones.

Releasing from the substratum has been described in a few species of sea anemones and particularly in the genus *Sagartia* (Gosse, 1860; Ashworth and Annandale, 1904). Adult *S. trogolodytes* (Price in Johnston, 1847) and *S. nigropunctata* (Stimpson, 1856) are also known to release from their substrata (Gosse, 1860; Ashworth and Annandale, 1904). This behavior has also been observed in *Epiactis prolifera* Verrill, 1869a in the subtidal (Harris, personal communication). The anemone swells with seawater, releases from the substratum, and then drifts in the current until brushing into an object with its tentacles. The tentacles stick to the object at which point the pedal disk reattaches.

The purpose of this chapter is to explore some of the abiotic factors that may have affected the disappearance of *S. elegans* through quantitative experimentation, as well as explore the unique substratum-releasing behavior observed in *S. elegans*. The specific objectives of this chapter are to:

1. Describe a method for establishing and maintaining permanent *in vitro* cultures of *S. elegans*.
2. Determine the best method for measuring live *S. elegans* accurately without disturbance.
3. Explore the impacts of both decreasing and long-term stable temperature, salinity, different food types, feeding frequency, and substratum texture on growth, asexual reproduction, and survival.
4. Explore potential triggers for the substratum-releasing behavior in *S. elegans*, particularly starvation and temperature stress.

Methods

Site Descriptions

Salem Harbor. Salem Harbor is an embayment on the northern coast of Massachusetts Bay (Figure 1). For the purpose of this study Salem Harbor is defined as the area within a line drawn between Juniper Point, Salem, MA (42.5337, -70.8644) and Fluen Point, Marblehead, MA (42.5215, -70.8522) (Figure 2). Salem Harbor is approximately 24.1 km northeast of Boston, Massachusetts. Surface area within the harbor is approximately 370 hectares ranging in volume from 10.2-20.1 million liters with an average depth of 5.2 m at high tide (Anderson *et al.*, 1975).

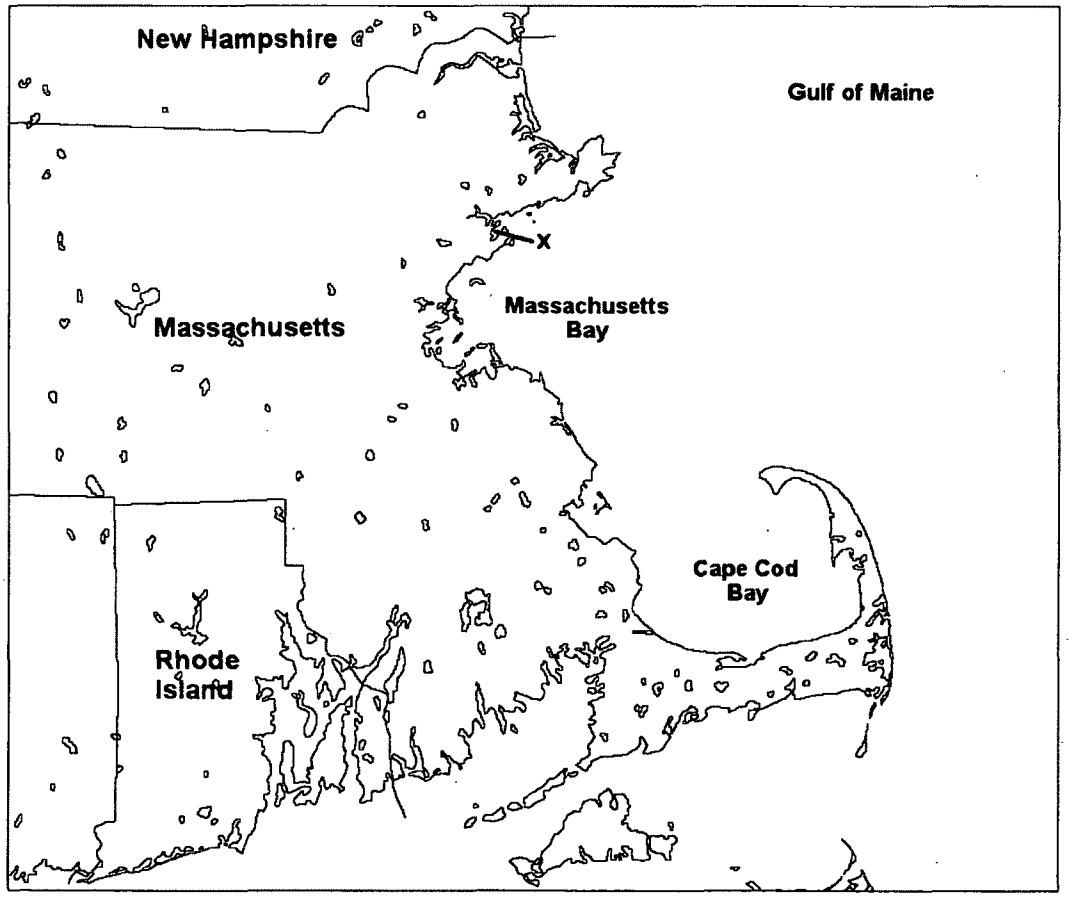

Figure 1: Map of the southern coast of the Gulf of Maine. Salem Harbor (**X**) is an embayment on the northern coast of Massachusetts Bay.

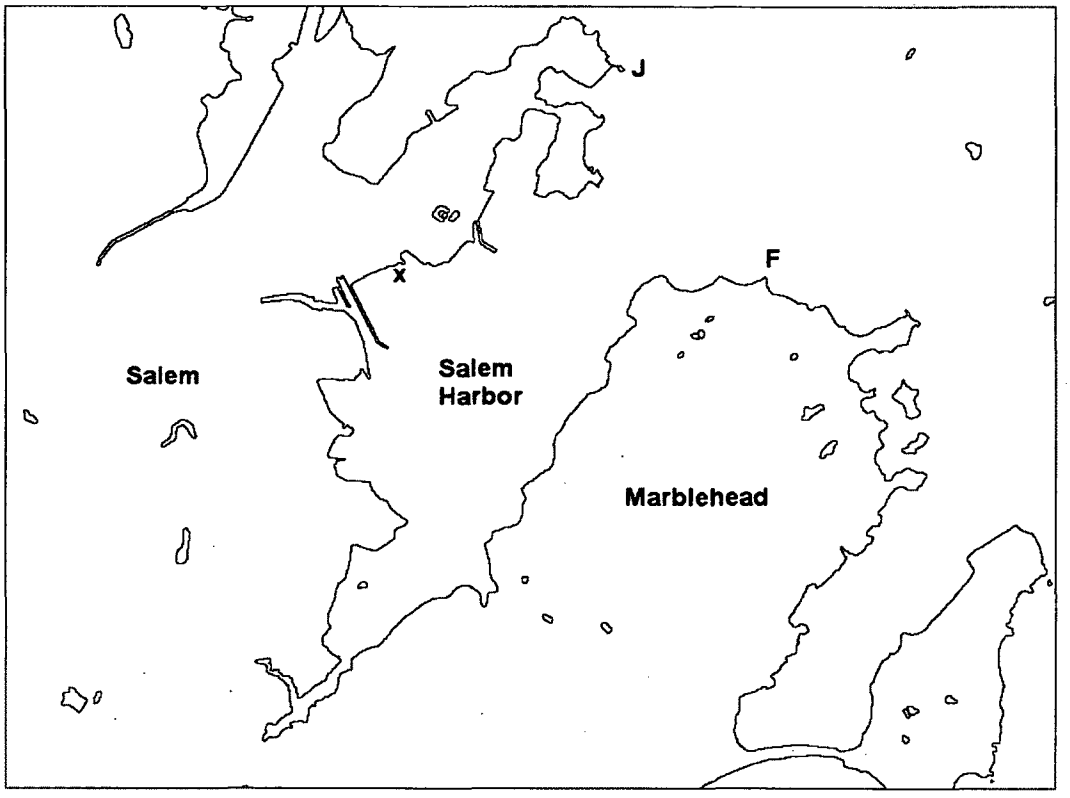

Figure 2: Map of Salem Harbor. For the purpose of this study Salem Harbor is defined as the area within a line drawn between Juniper Point, Salem, MA (**J**) and Fluen Point, Marblehead, MA (**F**). Hawthorne Cove Marina (**X**) is located on the northern shore of Salem Harbor.

Hawthorne Cove Marina, Salem, MA. Hawthorne Cove Marina is a private marina with 110 slips located on the northern shore of Salem Harbor (42.5214; -70.8825) (Figure 2). Float fouling communities are dominated by tunicates and arborescent bryozoans on the vertical surfaces and mussels on the horizontal surfaces. Sides of floats are scraped annually. Depth ranges from 1-4 meters. This is the only location *S. elegans* has been reported on the Western Atlantic.

1.1 Culturing of *Sagartia elegans* and *Artemia franciscana* Nauplii

Polyps of *S. elegans* were collected on floating docks in Hawthorne Cove Marina in Salem, MA, USA during October 2010. Polyps were removed from the shells of the southern blue mussel *Mytilus edulis* Linnaeus, 1758 by hand and placed in shallow dish

pans held at 15 °C on a 12:12 hr light-dark cycle in a temperature- and light-controlled room at the University of New Hampshire. Unless stated otherwise, all animals used in subsequent experiments were from this culture.

Three times weekly, 6-14 g of *Artemia franciscana* Kellogg, 1906 cysts (INVE Aquaculture Inc., Salt Lake City, Utah) was added to 2.5 L of unfiltered seawater. This mixture was heavily aerated and left for 24-72 hr to allow time for the cysts to hatch. *A. franciscana* nauplii were fed to the *S. elegans* culture in concentrations ranging from 3,000 to 24,000 nauplii per mL. Unless otherwise stated, sea anemones were fed from cultures hatched with these methods in all subsequent laboratory experiments.

1.2 Pedal Disk Surface Area as a Measurement of Size for Sea Anemones

To assess whether pedal disk surface area (PDSA) was an accurate indicator of dry mass, the relationship between dry mass and wet mass, average pedal disk diameter (APDD), and PDSA were compared for three species of sea anemone: *S. elegans*, *D. lineata*, and *M. senile*.

1.2.1 Experimental Design. *S. elegans* were collected as described in Section 1.1 from Salem Harbor (n = 50, maximum diameter 2.13-25.69 mm, average diameter 12.61 mm). All individuals are probably from a single genet (i.e. clone) introduced to Salem Harbor prior to 2000. Major (i.e. maximum) and minor (perpendicular to maximum) pedal disk diameters were measured to the nearest 0.01 mm with digital calipers within 24 hr. Animals were dabbed with a dry paper towel then wet mass was determined using a Mettler AC100 scale (Mettler Instrument Co., Highland, NJ) to the nearest 0.1 mg on pre-weighed, aluminum foil dishes. Polyps were preserved in 95% ethanol for 48 hr and then desiccated at 60 °C for 24 hr in a Precision Scientific Thelco Model 17 drying oven

(GCA Co., Chicago, Illinois). Dry mass was determined using a Cahn C31 microscale (Thermo Electron Co., Beverly, MA) to the nearest 0.1 μg on pre-weighed aluminum foil.

D. lineata were collected from an introduced population in Beverly Port Marina, Beverly, Massachusetts in October 2011 off of thalli of *Ulva lactuca* Linnaeus (n = 33, maximum diameter 2.14-10.56 mm, average diameter 5.83 mm). Great effort was taken to collect animals from different areas in the marina to maximize genetic diversity. Major and minor pedal disk diameters were measured to the nearest 0.01 mm with digital calipers 48 hr after being brought into the laboratory. Wet and dry mass was determined as described above for *S. elegans* except polyps were preserved in ethanol for 72 hours.

M. senile were measured and collected by SCUBA at the Coastal Marine Laboratory Pier in Newcastle, New Hampshire in November 2011 on floats and pilings (n = 35, maximum diameter 7-147 mm, average diameter 69 mm). Major and minor pedal disk diameters were measured *in situ* using calipers to the nearest integer. Animals were removed from pilings and floats with a paint scraper and brought into the laboratory. Polyps were dabbed with a dry paper towel then polyps over 80 mm in diameter were bisected with a scalpel; one exceptionally large animal (147 mm diameter) was trisected. Wet mass of anemones and pieces of anemone were immediately measured using a Carolina SLB152-US scale (Carolina Biological Supply Co., Burlington, NC) to the nearest 0.01 g on a pre-weighed plastic dish. Wet masses of pieces from the same anemone were combined. Animals were preserved in 95% ethanol for 72 hr and then desiccated at 60 °C for 24 hr in a Precision Scientific Thelco Model 17 drying oven. Dry mass was determined using a Mettler AC100 scale to the nearest 0.1 mg on pre-weighed

aluminum foil. Pieces of respective anemones were measured separately and combined for a total dry mass for each individual.

Assuming the surface of the pedal disk of a sea anemone is ellipsoid, the PDSA was calculated using the following equation for all individuals of each species:

$$\text{PDSA} = \pi \times \frac{D_{maj}}{2} \times \frac{D_{min}}{2} \quad (1)$$

D_{maj} is the length of the major axis of the pedal disk and D_{min} is the length of the minor axis. To calculate APDD, the major and minor axes were averaged.

To determine if the calculated PDSA was an accurate predictor of actual PDSA, photographs of *S. elegans*, *D. lineata*, and *M. senile* were taken and actual PDSA was measured using the program cellSens Entry (Olympus Corporation, Center Valley, PA) by tracing each anemone. Measurements of the major and minor axis of the pedal disk were also taken with cellSens Entry and used to calculate PDSA. Calculated PDSA was compared with actual PDSA for each species.

1.2.2 Statistical Analysis. All statistical analyses in this section were performed in GraphPad Prism (GraphPad Software, Inc., La Jolla, CA). To determine if wet mass was a good predictor of dry mass, a linear regression was performed for each species. To satisfy the assumption that variances are equal across the variables, the sum of squares was weighted ($1/Y^2$) to take into account the higher variance with larger animals. Similarly, to determine if APDD and PDSA are good predictors of dry mass and if calculated PDSA is a good predictor of actual PDSA, exponential regressions and linear regressions were performed respectively for each species. The sums of squares was weighted ($1/Y^2$) to take account the higher variance with larger animals.

1.3 Effects of Temperature and Salinity on Growth, Asexual Reproduction, and Survival of *Sagartia elegans*

1.3.1 Experimental Design. One hundred twenty *S. elegans* polyps (maximum diameter 1.64-5.01 mm, average diameter 2.78 mm) were spread evenly across twelve 5.7 L Sterilite containers (ten anemones per container). Containers were filled with 4.5 L of water at one of four levels of salinity (3 containers per treatment): 20, 25, 30, or 35 ppt. To achieve these salinities, 500 μm filtered, ultra-violet (UV)-sterilized seawater (average of 31 ppt) was decreased in salinity through the addition of deionized water or increased by the addition of Instant Ocean sea salt (Spectrum Brands, Madison, WI).

The 12 containers were placed within three 39 L Sterilite water baths (4 containers per bath). Water baths were filled with 13 L of freshwater and heated with a 150W JBJ TRUE TEMP Titanium Heating System (Transworld Aquatic Ent., Inglewood, CA) to 15 °C at the beginning of the experiment. To ensure even heat distribution within the water baths one Minijet 404 submersible pump (Spectrum Brands, Madison, WI) was placed in each water bath. The water baths were placed in a temperature-controlled room at 4.0 °C on a 12:12 hr light-dark cycle.

Temperature was decreased 3.0 °C on days 14 and 29, after which temperature was decreased 1.0 °C approximately every 14 days (days 41, 55, 70, 83, and 97) until ambient temperature had been reached. At the start of the experiment and approximately every seven days thereafter, PDSA was determined (see Section 1.2) and pedal lacerates were counted and then discarded.

Animals were fed 1.0 mL (12,000 nauplii per mL) of *A. franciscana* nauplii three times weekly. Water movement and aeration within the containers was provided by two

air pumps connected to a gang-valve system; this allowed two pumps to aerate the twelve containers. Water was changed two days prior to days when temperature was reduced with fresh, unfiltered seawater adjusted to the proper salinity. Containers that had complete mortality within the first few weeks were discarded and not included in analyses.

1.3.2 Statistical Analysis. To determine if all treatments started with the same size animals a one-way analysis of variance (ANOVA) was performed on initial average PDSA. Size, asexual reproduction, and survival were compared between treatments, but could not be tested statistically because of the low number of replicates (n = 3).

1.4 Long-term Effect of Temperature on Size and Asexual Reproduction of *Sagartia elegans*

Twenty polyps of *S. elegans* (maximum diameter 3.72-5.47 mm, average diameter 4.78 mm) were placed in three 37.9 L glass aquaria (20 anemones per aquarium). Tanks were distributed between two temperature-controlled rooms, held at 10 °C and 15 °C, and a wet-laboratory held at room temperature (19-24 °C). Henceforth, the room temperature aquarium will be referred to as the 21.5 °C aquarium. Animals were fed *A. franciscana* nauplii approximately three times weekly. Slow, turbulent water movement and aeration within the aquaria was provided by air pumps. Animals were allowed to grow and proliferate asexually for two years. Many animals from the 15 and 21.5 °C aquarium were used in other experiments reducing the population within these aquaria. Water was changed every two to six weeks with fresh, unfiltered seawater or fresh, 500 μm filtered, UV-sterilized seawater.

After approximately two years (755 days), PDSA of up to 250 adult anemones were measured (see Section 1.2) and number of polyps and pedal lacerates were estimated based on densities within ten 3.0 x 3.0 cm areas (1.5% of total inner surface area of the aquaria).

To estimate total dry biomass of the adult *S. elegans* within each aquarium, the regression equation found in Section 1.2 for converting *S. elegans* PDSA to dry mass was used. The average PDSA was converted into an average dry mass and then multiplied by the number of adults calculated above.

Fission rate (k) was calculated using the equation for exponential increase used by Loomis (1954) and Fulton (1962) to measure asexual reproduction rates in hydroids and Minasian (1976, 1979, 1982), and Minasian and Mariscal (1979) for clonal sea anemones:

$$k = \ln \left(N_t - N_o\right) / t \qquad (2)$$

N_o is the number of sea anemones at the beginning of the experiment and N_t is the number of sea anemones (both adults and pedal lacerates) at time t.

1.5 Effect of Different Forms of Live and Preserved *Artemia spp.* on Growth and Asexual Reproduction of *Sagartia elegans*

1.5.1 Experimental Design. Eighty polyps of *S. elegans* (maximum diameter 3.42-6.81 mm, average diameter 5.10 mm) were spread evenly across 20 1.2 L Sterilite containers (Sterilite Co., Townsend, MA) (4 anemones per container). Containers were filled with 0.7 L of unfiltered seawater. Throughout the experiment, containers were kept in a temperature-controlled room at 15 °C under 24 hr lighting. Animals were fed one of four food items (10 containers per treatment): 24-48 hr old *A. franciscana* nauplii (0.5

mL per feeding), 48 hr old, self-emulsified liquid concentrate (SELCO)-enriched *A. franciscana* nauplii (0.5 mL per feeding), commercially prepared frozen adult *Artemia sp.* (San Francisco Brand, Inc., Newark, CA), or commercially prepared freeze-dried adult *Artemia sp.* (San Francisco Brand, Inc., Newark, CA). SELCO is used to enrich *Artemia spp.* nauplii with polyunsaturated fatty acids and vitamins A, C, D3, and E and is used primarily in fish aquaculture. Both live *A. franciscana* treatments (enriched and non-enriched) were fed to anemones at a concentration of 24,000 nauplii per mL. For more information on the culturing and enrichment protocols see below (Section 1.5.2). Animals fed frozen and freeze-dried adult *Artemia sp.* were fed by placing food directly on the tentacles of the anemones until the animals stopped ingesting food.

Before each feeding, number of pedal lacerates was recorded and lacerates were discarded. Anemones were fed for 1 hr, 3 times weekly. After the feeding, water was filtered through a 100 μm mesh and replaced, except after every third feeding, when water was replaced with fresh, unfiltered seawater. The PDSA of the anemones was measured at the start of the experiment and every 7 days thereafter (see Section 1.2) for 49 days.

1.5.2 *Artemia franciscana* Culture and Enrichment Culture Protocols. Eight grams of *A. franciscana* cysts were placed in 2.5 L of unfiltered seawater. After 24 hr 5-10 mL (24,000 nauplii per mL) of *A. franciscana* nauplii were removed from the culture and placed in 1.0 L of unfiltered seawater along with 0.6 g of INVE Easy SELCO (INVE Aquaculture Inc., Salt Lake City, Utah). Nauplii were allowed to take up nutrients for 24 hr. The remaining cysts and nauplii from the original culture were placed back into 2.5 L of fresh, unfiltered seawater and given an additional 24 hr of hatching and grow-out time.

Both the original culture and the enrichment culture were heavily aerated by 4 air stones attached to two air pumps each. Cultures were kept at room temperature (19-24 °C).

1.5.3 Statistical Analysis. All statistical analyses in this section were performed in GraphPad Prism. To determine if all treatments started with the same size animals, a one-way ANOVA was performed on initial average PDSA. To determine if there was a difference in growth between the polyps fed each treatment, a linear regression was performed on the PDSA measurements. Total asexual reproduction was compared between treatments through a one-way ANOVA with a post-hoc Tukey's multiple comparison test.

1.6 Effect of Different Aged and Enriched *Artemia franciscana* Nauplii on Growth of *Sagartia elegans*

1.6.1 Experimental Design. Sixty polyps of *S. elegans* (maximum diameter 3.09-7.40 mm, average diameter 4.95 mm) were spread evenly across 15 1.2 L Sterilite containers (4 anemones per container). Containers were filled with 0.7 L of unfiltered seawater. Throughout the experiment, containers were kept in a temperature-controlled room at 15 °C under 24 hr lighting. Animals were fed one of three foods (10 containers per treatment): 24 hr old *A. franciscana* nauplii, 48 hr old *A. franciscana* nauplii, or 48 hr old, SELCO-enriched *A. franciscana* nauplii. When anemones were fed, 1.0 mL (24,000 nauplii per mL) of *A. franciscana* was added to each container. For more information on the culturing and enrichment protocols see below (Section 1.6.2).

Before each feeding, pedal lacerates were discarded. Anemones were fed for 1.5 hr, 3 times weekly. After the feeding, water was filtered through a 100 μm mesh and replaced, except every third feeding, after which water was changed for fresh, unfiltered

seawater. The PDSA was measured at the start of the experiment and every 7 days thereafter (see Section 1.2) for 21 days.

1.6.2 *Artemia franciscana* Culture and Enrichment Culture Protocols. Twelve grams of *A. franciscana* cysts was placed in 2.5 L of unfiltered seawater and kept at 27 °C. After 24 hr, 15-30 mL (24,000 nauplii per mL) of *A. franciscana* nauplii were removed from the culture and placed in 2.0 L of unfiltered seawater along with 1.0 g of INVE Easy SELCO. Nauplii were allowed to take up nutrients for 24 hr at room temperature (19-24 °C). The remaining cysts and nauplii from the original culture were placed back into 2.5 L of fresh, unfiltered seawater and given an additional 24 hr of hatching and grow-out time at room temperature (19-24 °C). An additional culture was started 24 hr after the original culture using the same protocol; these nauplii were only allowed to hatch and grow for 24 hr before being fed to the anemones. All cultures were heavily aerated through the use of four air stones attached to two air pumps each.

1.6.3 Statistical Analysis. All statistical analyses in this section were performed in GraphPad Prism. To determine if all treatments started with the same size animals, a one-way ANOVA was performed on initial average PDSA. To determine if there was a difference in growth between treatments, a linear regression was performed on PDSA measurements.

1.7 Effects of Feeding Frequency on Growth, Asexual Reproduction, and Survival of *Sagartia elegans*

1.7.1 Experimental Design for Trial One. Two hundred polyps of *S. elegans* (maximum diameter 1.26-5.90 mm, average diameter 3.04 mm) were spread evenly across 40 1.2 L Sterilite containers (Sterilite Co., Townsend, MA) in 1.0 L of unfiltered

seawater (5 anemones per container). Anemones were starved for 7 days prior to their treatments to remove residual food and to provide a baseline unfed level for feeding experiments. 1.0 mL (24,000 nauplii per mL) of *A. franciscana* nauplii was added to containers in four different treatment schedules: fed daily, every second day, every fourth day, or left unfed. Animals were allowed to feed for 2 hr, much longer than was necessary to feed to repletion. After feeding, all containers were filtered (100 μm) and the water was replaced. Water was exchanged every seventh day with fresh unfiltered seawater. Pedal lacerates were counted daily and removed from the containers. The PDSA of the anemones were measured (see Section 1.2) at the start of the experiment and every seven days thereafter for 35 days. Mortality was also recorded daily. These measurements, when analyzed, will be referred to as trial one results.

1.7.2 Experimental Design for Trial Two. After 35 days, all containers, were reassigned a new feeding regimen. All anemones that were left unfed for the first 35 days were fed daily. Anemones that were fed (daily, every second day, or every fourth) were randomly assigned to being fed daily, every second day, every fourth day, or left unfed to look for convergence of patterns in asexual reproduction. Anemones were subjected to this feeding regimen for an additional 35 days. Feeding, water changes, pedal lacerate counts, PDSA measurements, and notes on mortality were continued throughout the 35 days at the same rate and with the same methods as above (Section 1.7.1). These measurements, when analyzed, will be referred to as trial two results.

1.7.3 Statistical Analysis. All statistics in Section 1.7 were performed within the program JMP Pro 10 (SAS Institute, Inc., Cary, North Carolina). To determine if all treatments started with the same size animals, a one-way ANOVA was performed on

initial average PDSA. To determine the effect of feeding frequency on growth, a linear regression of size was performed. To determine the effect of feeding frequency of trial one and trial two on growth in trial two a multiple linear regression of size was performed. Total pedal lacerates produced per anemone in trial one and trial two were compared between feeding frequencies through the use of a one-way or two-way ANOVA respectively with a post-hoc Tukey's multiple comparison test.

To determine the periodicity of asexual reproduction, a Fourier analysis was performed on the number of pedal lacerates produced per polyp. Fourier analysis isolates individual components of a compound wave or behavior allowing periodicities within the wave to be detected. To satisfy assumptions of a Fourier analysis number of pedal lacerates produced per anemone was square root transformed to make the variance more similar across the trial (i.e. variance is lower at the beginning and higher at the end) followed by a difference transformation to remove any slope (i.e. as animals get larger they produce more).

1.8 Effect of Substratum Texture on the Asexual Reproduction of *Sagartia elegans*

1.8.1 Experimental Design. To determine if *S. elegans* reproduced or grew more in depressions three treatments were used: no depressions, shallow depressions (2 mm deep), and deep depressions (5 mm deep). A 10 mm hole was drilled through the corner of 18 0.0023 m^2 (4.8 x 4.8 x 1.1 cm) tumbled marble tiles. Tiles were strung with monofilament wire through the hole and then the hole was filled with aquarium silicone so anemones could not use the holes as a refuge. Four depressions (either 2 mm deep x 10 mm wide or 5 mm deep x 10 mm wide) were drilled into 12 of the 18 tiles (Figure 3, six tiles per size depression). Tumbled marble tiles have small depressions ranging from

0.1 mm to 4 mm in depth; these depressions were filled with aquarium silicone and allowed to cure for 3 days.

Four polyps of *S. elegans* were placed on each tile; anemones were started in depressions if depressions were present. All tiles were hung in one 37.9 L glass aquarium (Aqueon, Franklin, Wisconsin) filled with approximately 35 L of unfiltered seawater. Counts of polyps in and outside depressions were taken at the start of the experiment and every 7 days thereafter for 56 days. 6 mL (24,000 nauplii per mL) of *A. franciscana* nauplii were fed to the anemones 3 times weekly. After each count, water was exchanged for 35 L of fresh, unfiltered seawater.

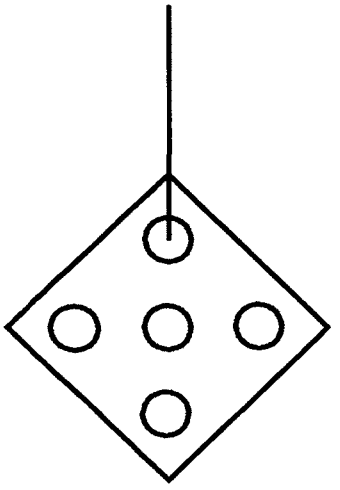

Figure 3: Depression patterning on tiles used to determine how substratum texture affects asexual reproduction of *Sagartia elegans*. Anemones were placed into the four depressions and allowed to grow for 56 days.

Counts were converted to density by dividing by surface area of the treatment (see Table 2). Surface area within the depressions was calculated using the formula for the surface area of an open topped cylinder:

$$\text{Surface area} = 2\pi rh + \pi r^2 \quad (3)$$

where r is the radius of the depression and h is the depth of the depression. The circular surface area (πr^2) of the depressions was subtracted from the surface area of the whole tile to calculate the surface area of the area outside the depressions.

Table 2: Surface area of tiles and depressions within tiles. Surface area within the depressions was calculated using the formula for the surface area of an open topped cylinder.

Treatment	Surface Area (cm^2)
Flat tiles	67.2
2 mm inside depressions	5.7
2 mm outside depressions	64.1
5 mm inside depressions	9.4
5 mm outside depressions	64.1

At the end of the experiment tiles were soaked in a 1% solution of KCl to relax the sea anemones and then subsequently removed from their substrata with a dissecting probe into 95% ethanol, separating anemones that were within depressions those outside depressions. Animals were then desiccated in a Precision Scientific Thelco Model 17 drying oven at 55 °C for 24 hr. Dry mass was determined using a Cahn C31 microscale to the nearest 0.1 μg on pre-weighed aluminum foil.

Dry masses were converted to PDSA using the equation found in the Section 1.2 results, but solving for PDSA. The equation used was:

$$PDSA = 1685\ M_d^{0.787} \quad (4)$$

M_d is the dry mass of a polyp. Using average PDSA and the final density, the amount of space being taken up by anemones was calculated. Amount of area utilized was divided by the total area of the tile to get a percentage of area utilized by anemones.

1.8.2 Statistical Analysis. All statistical analyses in the section were done in GraphPad Prism. To determine if there was a statistically significant difference between the final densities within depressions, outside depressions, and on the tiles without depressions, a one-way ANOVA was performed with a post-hoc Tukey's multiple

comparison test. Final masses were also compared through the use of a one-way ANOVA with a post-hoc Tukey's multiple comparison test.

1.9 Effect of Starvation Stress on the Release from Substrata in *Sagartia elegans*

1.9.1 Experimental Design. Forty five polyps of *S. elegans* (maximum diameter 2.48-8.31 mm, average diameter 5.09 mm) were allowed to attach to nine 0.010 m^2 (10.0 x 10.0 x 0.4 cm) acrylic glass panels (five anemones per panel). Panels were hung in nine 20.8 L glass aquaria (Aqueon, Franklin, Wisconsin) 10 cm from the bottom of the tank (one panel per tank). Aquaria were filled with 20.0 L of 500 µm filtered, UV-sterilized seawater. Aquaria were randomly assigned to one of three feeding frequency treatments (3 tanks per treatment): fed three times weekly (3X), fed one time weekly (1X), or left unfed (0X). Anemones that were to be fed were fed 1.0 mL (3,000 nauplii per mL) of *A. franciscana* nauplii at each feeding. At each feeding the number of anemones on each panel was recorded. Any pedal lacerates produced were discarded three times weekly so as to not compete with adult anemones for food. PDSA was measured (see Section 1.2) at the start of the experiment and every seven days thereafter for 35. Anemones were not measured after releasing from their panels.

1.9.2 Statistical Analysis. All statistics in this section were performed within the program JMP Pro 10 (SAS Institute, Inc., Cary, North Carolina). To determine if all treatments started with the same size animals a one-way ANOVA was performed on initial average PDSA. To determine the effect of feeding frequency on growth and on release rate linear regressions of size were performed.

1.10 Effect of Temperature Stress on the Release from Substrata in *Sagartia elegans*

1.10.1 Experimental Design. One hundred polyps of *S. elegans* (maximum diameter 1.63-4.65 mm, average diameter 2.85 mm) were allowed to attach to ten 0.010 m^2 (10.0 x 10.0 x 0.4 cm) acrylic glass panels (ten anemones per panel). Panels were hung in five 20.8 L glass aquaria 10 cm from the bottom of the tank (two panels per tank). Aquaria were filled with 20.0 L of 500 µm filtered, UV-sterilized seawater. Aquaria were randomly assigned to one of two temperature treatments; the aquaria were either maintained at 15 °C or were started at 15 °C and temperature was decreased slowly. Aquaria maintained at 15 °C were kept in a 15 °C temperature-controlled room on a 12:12 hr light-dark cycle. Aquaria slowly decreasing in temperature were kept in a 4 °C temperature-controlled room on a 12:12 hr light-dark cycle and were heated by 150W JBJ TRUE TEMP Titanium Heating Systems, initially to 15 °C. Water motion was provided by air pumps split between two tanks each. Water was changed once a week with fresh, 500 µm filtered, UV-sterilized seawater. Temperature was held at 15.0 °C for seven days before being decreased 1.0 °C approximately every 4 days. The experiment was carried out until all anemones had released from the panels in the decreasing temperature treatment (29 days).

Anemones were fed 1.0 mL (12,000 nauplii per mL) of *A. franciscana* nauplii three times weekly. At each feeding number of anemones still on panels was recorded. To correct for initial release of animals, proportion of animals on panels were compared after the initial seven days. Any pedal lacerates produced were discarded prior to feeding. PDSA was measured at the start of the experiment and every seven days thereafter for 35 days (see Section 1.2).

Results

1.1 Culturing of *Sagartia elegans* and *Artemia franciscana* Nauplii

Polyps of *S. elegans* were frequently seen floating in the water column and then reattaching elsewhere. Anemones would inflate their body cavity with seawater, release from the substratum, and float in the water column for seconds to hours. When tentacles touched a suitable location they would stick to the substratum and slowly reattach their pedal disk. Sometimes animals would touch multiple surfaces before resettling.

1.2 Pedal Disk Surface Area as a Measurement of Size for Sea Anemones

Wet mass is the best predictor of dry mass for both *S. elegans* and *M. senile* (Table 3, Figure 4-6). For live measuring of *S. elegans* the best measurement protocol is to calculate PDSA (Table 3, Figure 7 and 8). APDD and PDSA are approximately equivalent in their ability to predict dry mass for *D. lineata* and *M. senile* (Table 3, Figure 8, 9, 11, and 12).

Table 3: Weighted R^2 for the relationships between wet mass, APDD, and PDSA with dry mass. Wet mass is the most accurate predictor of dry mass.

Species	Wet Mass	APDD	PDSA
Sagartia elegans	0.98	0.95	0.98
Diadumene lineata	0.85	0.94	0.94
Metridium senile	0.92	0.90	0.90

The method for calculating PDSA is an accurate at predicting the actual PDSA for all species of sea anemone ($R = 0.99$, linear regression, Figure 13-15).

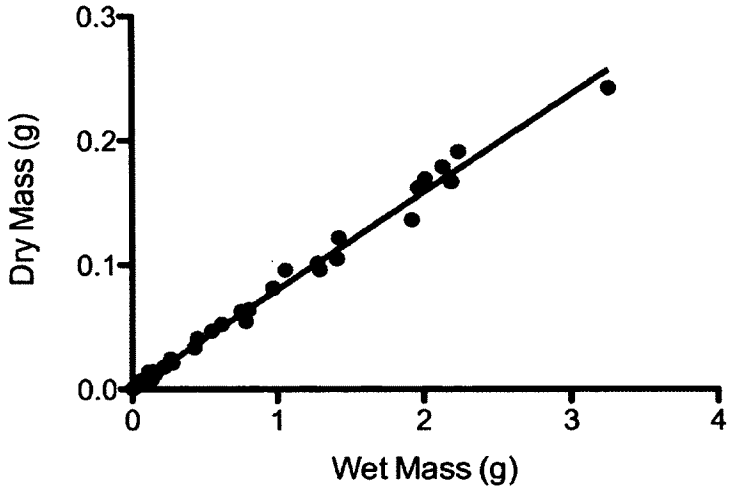

Figure 4: Variation in dry mass with wet mass for *Sagartia elegans* from Hawthorne Cove Marina. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit linear regression ($y = 0.0786\ x + 1.33x10^{-3}$). Wet mass is an excellent predictor of dry mass (Weighted $R^2 = 0.99$).

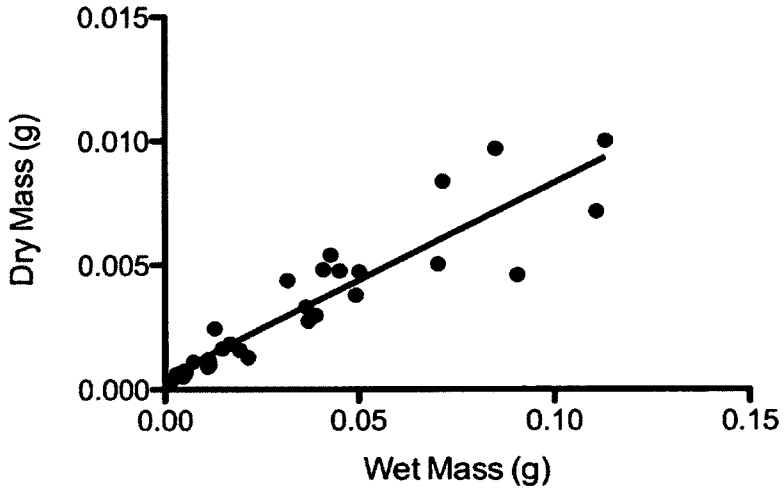

Figure 5: Variation in dry mass with wet mass for *Diadumene lineata* from Beverly Port Marina. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit linear regression ($y = 0.0785\ x + 4.64x10^{-4}$). Wet mass is an excellent predictor of dry mass (Weighted $R^2 = 0.85$).

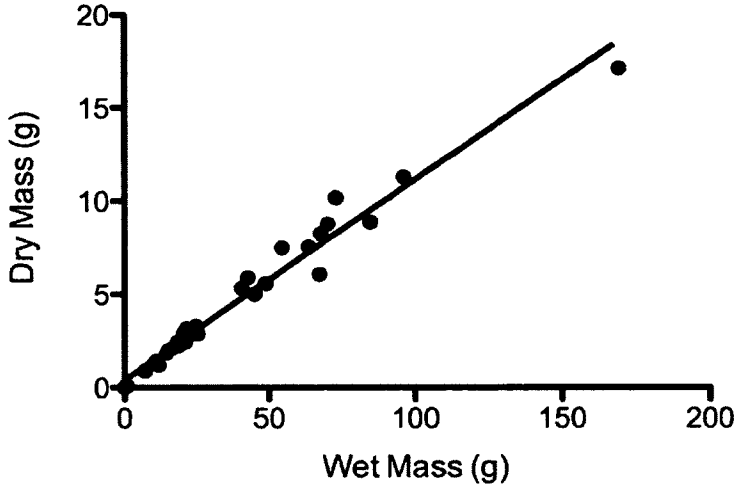

Figure 6: Variation in dry mass with wet mass for *Metridium senile* from the Coastal Marine Laboratory Pier. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit linear regression ($y = 0.1078\ x + 0.387$). Wet mass is an excellent predictor of dry mass (Weighted $R^2 = 0.97$).

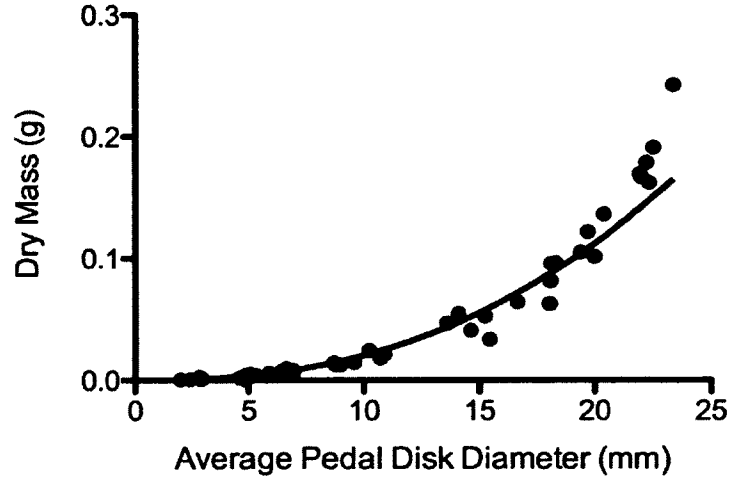

Figure 7: Variation in dry mass with APDD for *Sagartia elegans* from Hawthorne Cove Marina. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit exponential regression ($y = 6.87 \times 10^{-5}\ x^{2.47}$). APDD is an excellent predictor of dry mass (Weighted $R^2 = 0.95$).

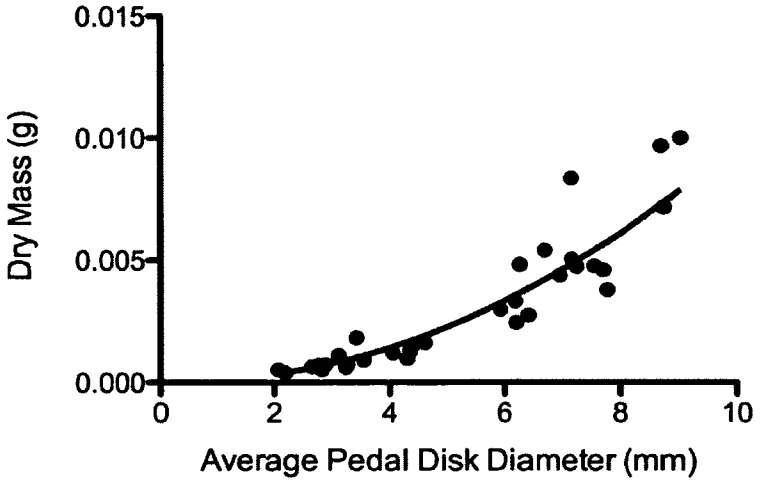

Figure 8: Variation in dry mass with APDD for *Diadumene lineata* from Beverly Port Marina. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit exponential regression ($y = 5.87x10^{-5} x^{2.62}$). APDD is a good predictor of dry mass (Weighted $R^2 = 0.94$).

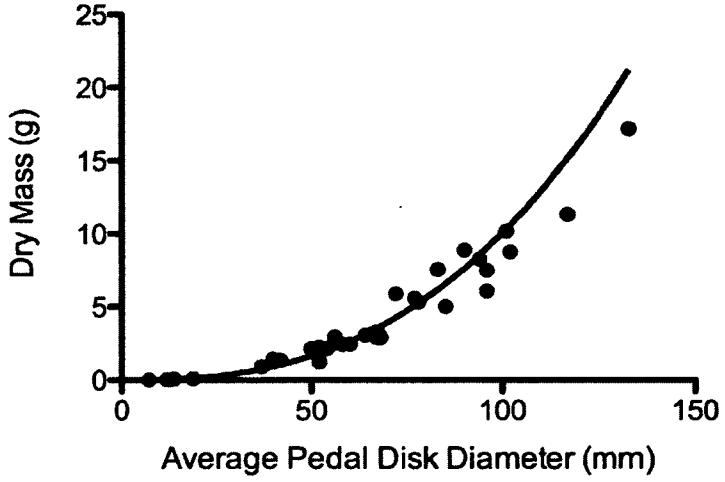

Figure 9: Variation in dry mass with APDD for *Metridium senile* from the Coastal Marine Laboratory Pier. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit exponential regression ($y = 7.73x10^{-5} x^{2.10}$). APDD is a good predictor of dry mass (Weighted $R^2 = 0.90$).

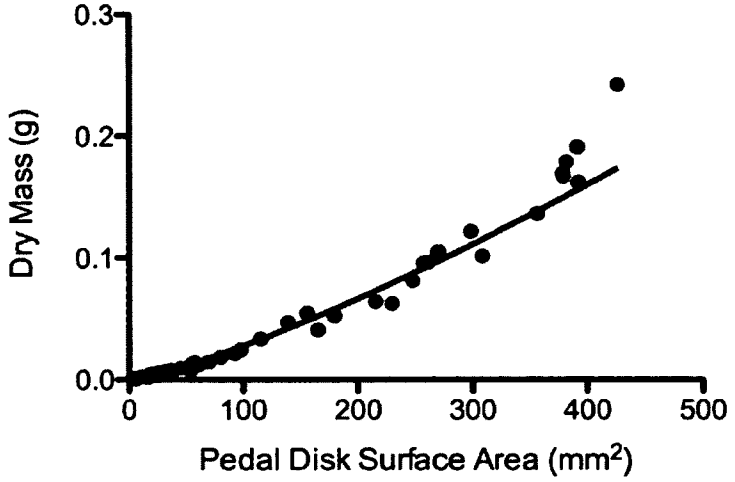

Figure 10: Variation in dry mass with PDSA for *Sagartia elegans* from Hawthorne Cove Marina. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit exponential regression ($y = 7.98x10^{-5}\ x^{1.27}$). PDSA is an excellent predictor of dry mass (Weighted $R^2 = 0.98$), better than average pedal disk diameter.

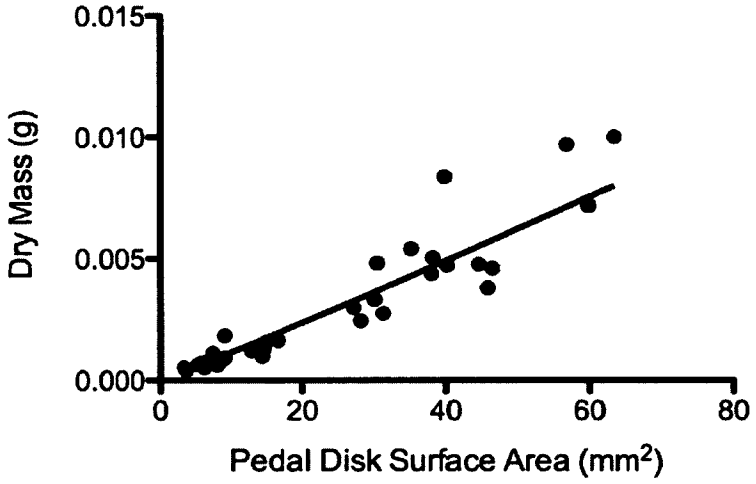

Figure 11: Variation in dry mass with PDSA for *Diadumene lineata* from Beverly Port Marina. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit exponential regression ($y = 0.0348\ x^{1.30}$). PDSA is a good predictor of dry mass (Weighted $R^2 = 0.94$).

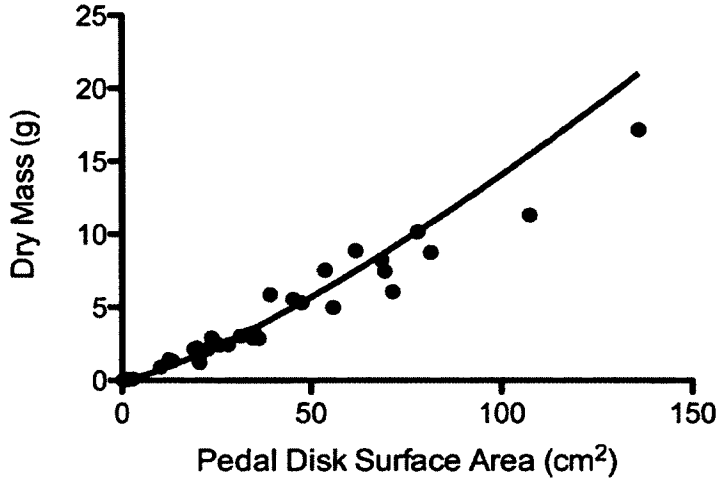

Figure 12: Variation in dry mass with PDSA for *Metridium senile* from the Coastal Marine Laboratory Pier. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit exponential regression ($y = 1.73x10^{-5}\ x^{1.06}$). PDSA is a good predictor of dry mass (Weighted $R^2 = 0.90$).

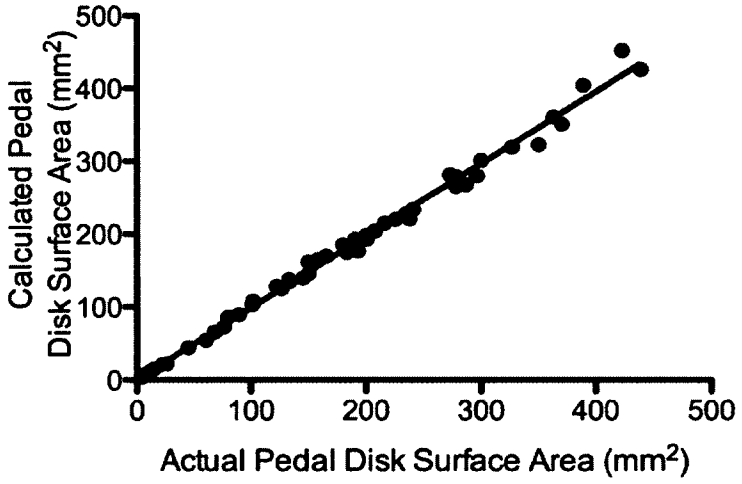

Figure 13: Relationship between actual and calculated PDSA for *Sagartia elegans* collected off the floating docks at Hawthorne Cove Marina. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit linear regression ($y = 0.988x - 0.0340$). Calculated PDSA is a very good predictor of actual PDSA (Weighted $R^2 = 0.99$).

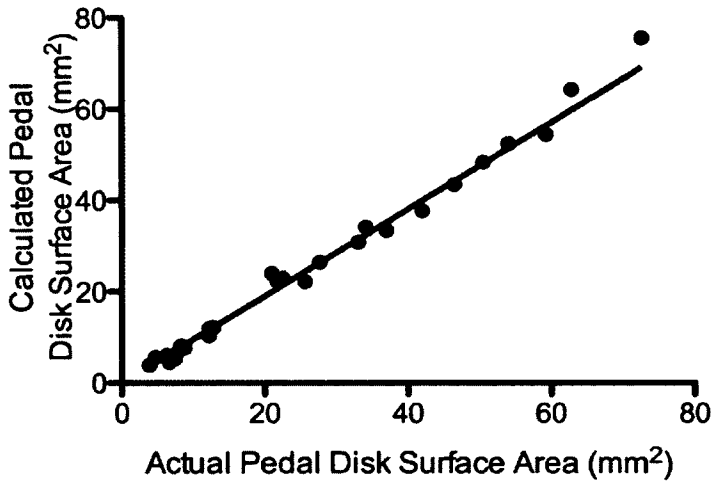

Figure 14: Relationship between actual and calculated PDSA for *Diadumene lineata* collected off the floating docks at Beverly Port Marina. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit linear regression ($y = 0.951x - 0.0461$). Calculated PDSA is a very good predictor of actual PDSA (Weighted $R^2 = 0.98$).

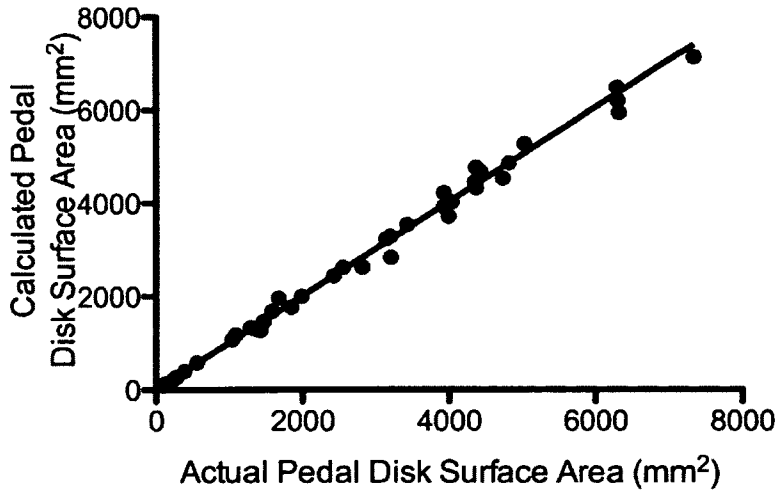

Figure 15: Relationship between actual and calculated PDSA for *Metridium senile* collected off the pier at the University of New Hampshire Coastal Marine Laboratory. The weighted sum of squares ($1/Y^2$) was used in calculating the best-fit linear regression ($y = 1.01x - 0.00611$). Calculated PDSA is a very good predictor of actual PDSA (Weighted $R^2 = 0.99$).

1.3 Effects of Temperature and Salinity on Growth, Asexual Reproduction, and Survival of *Sagartia elegans*

Data from one 25 and one 35 ppt container were discarded due to complete mortality within the first three weeks from unknown causes. Both containers were from the same water bath.

Initial average PDSA did not significantly differ between treatments ($p = 0.081$, ANOVA). *S. elegans* kept at 20 ppt did not grow as fast as those at 25 ppt or above. Anemones in all treatments grew in size until temperature was decreased below 9 °C at which point animals started to decrease in size (Figure 16).

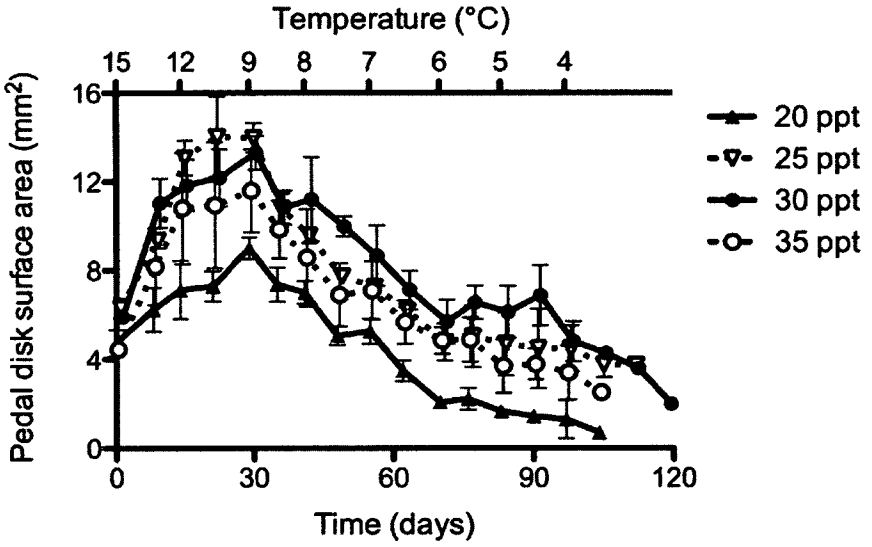

Figure 16: PDSA of *Sagartia elegans* as temperatures decreased over time at different salinity levels (Mean ± 1 SE). Position of the data points were displaced ±1 days along the x-axis so standard error bars would be more visible. *S. elegans* grew until the temperature was changed to 9 °C at which point animals started to decrease in size.

Anemones at 20 ppt had very low rates of asexual reproduction compared to those at or above 25 ppt. Asexual reproduction stopped after temperature reached 9 °C for all treatments (Figure 17).

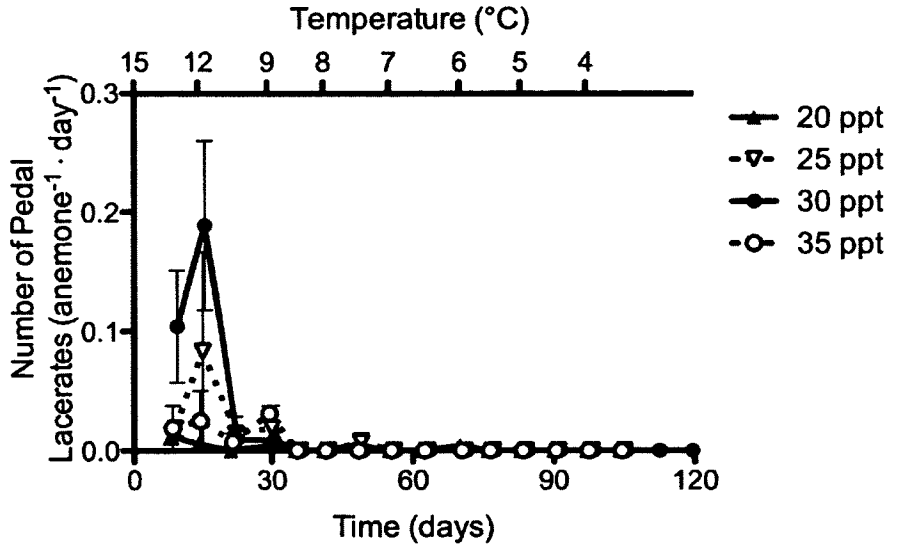

Figure 17: Number of pedal lacerates produced per *Sagartia elegans* polyp per day as temperature was decreased over time at different salinity levels (Mean ± 1 SE). Position of the data points were displaced ±1 days along the x-axis so standard error bars would be more visible. Asexual reproduction stopped after 9 °C.

Polyps of *S. elegans* died below 6 °C. After the third week at 4 °C all polyps in all treatments, except for two polyps in the 30 ppt treatment, had died. Polyps still alive at 4 °C were heavily discolored and would likely have died within another week. Anemones at 20 ppt sustained heavier mortality at higher temperatures (Figure 18).

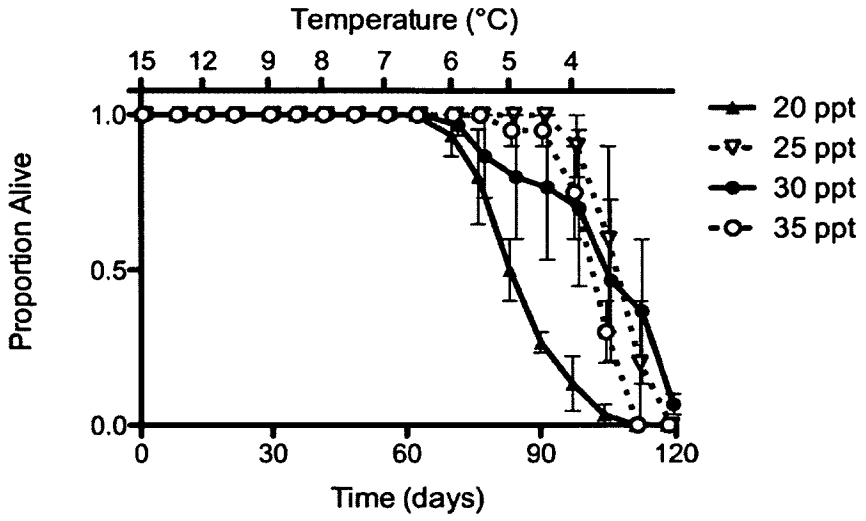

Figure 18: Proportion of *Sagartia elegans* alive as temperature was decreased over time at different salinity levels (Mean ± 1 SE). Position of the data points were displaced ±1 days along the x-axis so standard error bars would be more visible. *S. elegans* started to die after temperatures were changed to 6 °C.

1.4 Long-term Effect of Temperature on Size and Asexual Reproduction of *Sagartia elegans*

Average PDSA of adult *S. elegans* was inversely related to temperature (Table 4, Figure 19). Number of adults, pedal lacerates, and total adult dry biomass are directly related to temperature (Table 4). Polyps of *S. elegans* were frequently seen floating in the water column and then reattaching elsewhere (see Section 1.1 results).

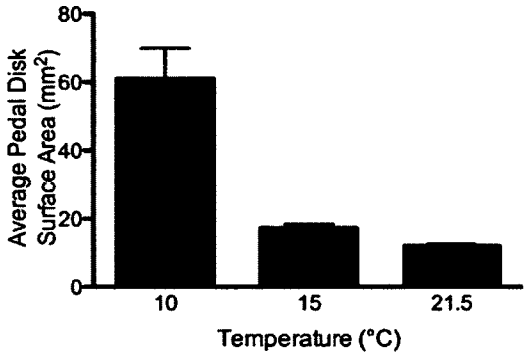

Figure 19: Average PDSA of polyps of *Sagartia elegans* held at 10, 15 or 21.5 °C for two years (Mean ± 1 SE). Error bars denote variation within individual size in each culture. Average PDSA was inversely related to temperature.

Table 4: Average PDSA, number of adults and pedal lacerates, and total adult dry biomass of *Sagartia elegans* in aquaria kept at differing temperatures for two years. Number of adults, pedal lacerates, total dry biomass, and fission rate are directly related to temperature whereas average PDSA was inversely related. Number of adults and pedal lacerates for aquaria held at 15 and 21.5 °C were estimated.

Temperature (°C)	Average PDSA (mm^2)	Number of Adults	Number of Pedal Lacerates	Total Adult Dry Biomass (g)	Fission Rate
10	60.9	45	2	0.77	0.0050
15	17.3	15000*	1900*	51.0	0.0089
21.5	11.9	41000*	3800*	86.4	0.0102

1.5 Effect of Different Forms of Live and Preserved *Artemia spp.* on Growth and Asexual Reproduction of *Sagartia elegans*

During the experiment one polyp of *S. elegans* being fed frozen adult *Artemia sp.* died between days 20 and 26. Between days 40 and 42 one polyp being fed frozen adult *Artemia sp.* and one being fed SELCO-enriched *A. franciscana* nauplii died. It is unknown as to why the anemones died as all other anemones within all treatments were visually healthy and consuming food readily.

Initial size of anemones was not significantly different ($p = 0.513$, ANOVA). Growth was not significantly affected by different food treatments ($p = 0.151$, linear regression, Figure 20).

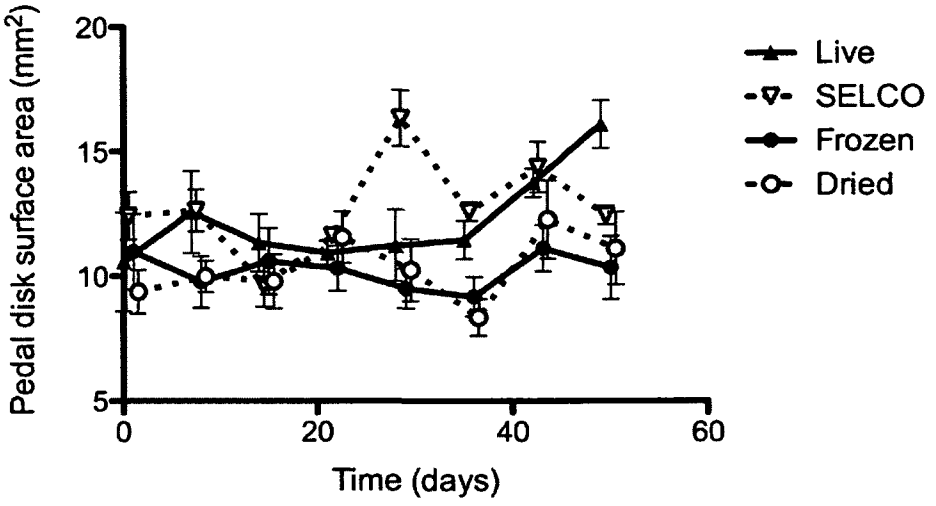

Figure 20: PDSA of polyps of *Sagartia elegans* being fed varying diets (Mean ± 1 SE). Position of the data points were displaced ±1 days along the x-axis so standard error bars would be more visible. Growth of *S. elegans* was not significantly affected by the diets ($p = 0.151$, linear regression).

Total number of pedal lacerates produced per polyp of *S. elegans* per day was affected by food treatment. Anemones fed live *A. franciscana* or SELCO-enriched *A. franciscana* nauplii produced significantly more pedal lacerates than those fed frozen or dried adult *Artemia sp.* ($p < 0.05$, Tukey's test, Figure 21). There was no statistically significant difference between the number of pedal lacerates produced by animals fed live or SELCO-enriched *A. franciscana* nauplii or between those fed frozen or

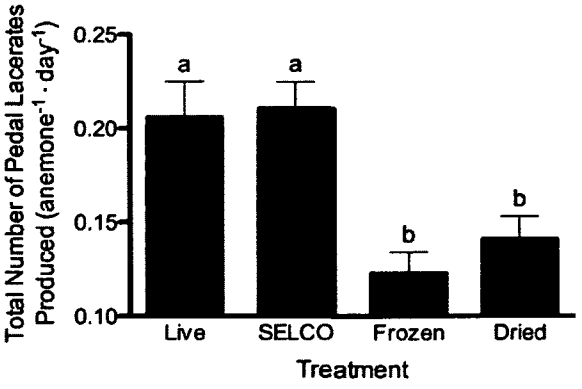

Figure 21: Total number of pedal lacerates produced per polyp of *Sagartia elegans* (Mean + SE). Those anemones fed live or SELCO-enriched *Artemia franciscana* reproduced more than those fed frozen or dried adult *Artemia spp.* ($p < 0.05$, Tukey's test). Different letters denote statistical differences ($p < 0.05$, Tukey's test).

dried adult *Artemia sp.* ($p > 0.05$, Tukey's test, Figure 21).

1.6 Effect of Different Aged and Enriched *Artemia franciscana* Nauplii on Growth of *Sagartia elegans*

Initial size of the anemones was not significantly different ($p = 0.917$, ANOVA). Age of nauplii and use of SELCO did not impact growth or asexual reproduction ($p = 0.425$, ANOVA).

1.7 Effects of Feeding Frequency on Growth, Asexual Reproduction, and Survival of *Sagartia elegans*

1.7.1 Trial One. There was no difference in initial size between treatments ($p = 0.051$, ANOVA). Growth of *S. elegans* between feeding frequencies was significant between all treatments ($p \leq 0.0002$, ANOVA, Figure 22). Anemones fed more frequently grew at a faster rate than those fed less frequently and anemones left unfed shrank. Anemones only died in the treatment left unfed (21 of 50). Anemones either died on days four and five or after day 19, but no replicates lost all of the anemones (Figure 23).

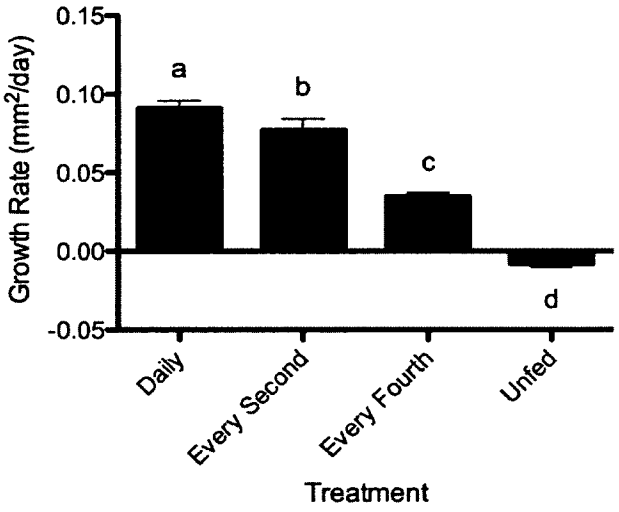

Figure 22: Growth rate of *Sagartia elegans* being fed at varying frequencies (Mean ± 1 SE). Growth rate of *S. elegans* was statistically significant between all treatments as is denoted by the different letters ($p \leq 0.0002$, ANOVA). Anemones fed more frequently grew at a faster rate than those fed less frequently and anemones left unfed shrank.

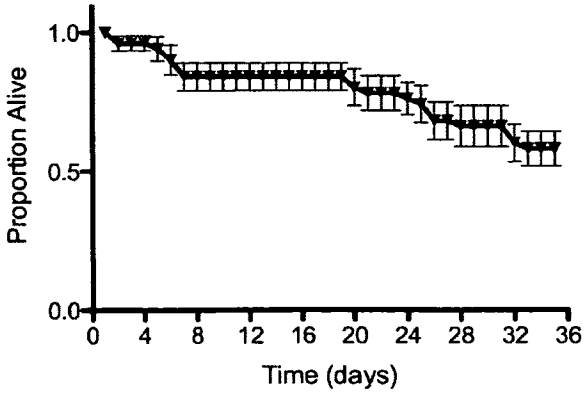

Figure 23: Proportion of unfed *Sagartia elegans* alive in each container (Mean ± 1 SE). *S. elegans* died either between days 4 and 5 or after day 20. 21 of the original 50 anemones died during the 35 day period.

Total reproduction per anemone per day was significantly different between only anemones fed (daily, every second, or every fourth day) and unfed ($p < 0.05$, Tukey's test, Figure 24). Size of pedal lacerate was qualitatively larger as anemones were fed more frequently. Reproductive capacity diminished for animals that were left unfed (Figure 25D). *S. elegans* formed distinct patterns when fed every two or four days; pedal laceration was inhibited within the first 24 hr after feeding (Figure 25B and C). When fed every two days *S. elegans* had a reproductive pattern with a period of two days ($p = 0.0004$, Fourier analysis, Figure 26B). When fed every four days *S. elegans* had a

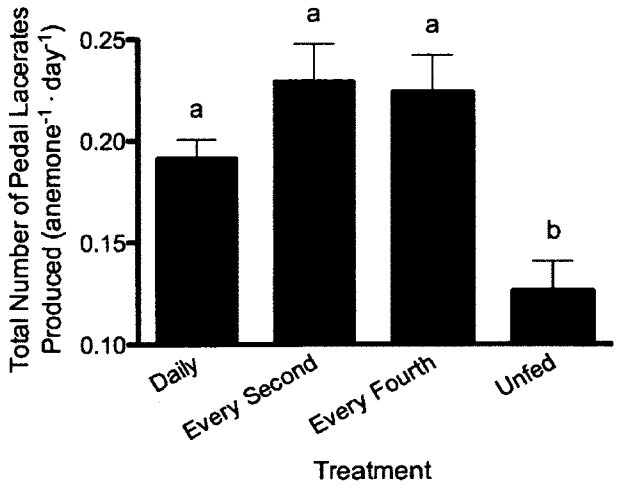

Figure 24: Total number of pedal lacerates produced per polyp of *Sagartia elegans* fed at different feeding frequencies (Mean + SE). There was a significant difference in total reproduction of anemones that were fed compared to left unfed ($p < 0.05$, Tukey's test). Frequency of feeding did not affect growth; rather growth was dependent on whether or not *S. elegans* was fed. Different letters denote statistical differences ($p < 0.05$, Tukey's test).

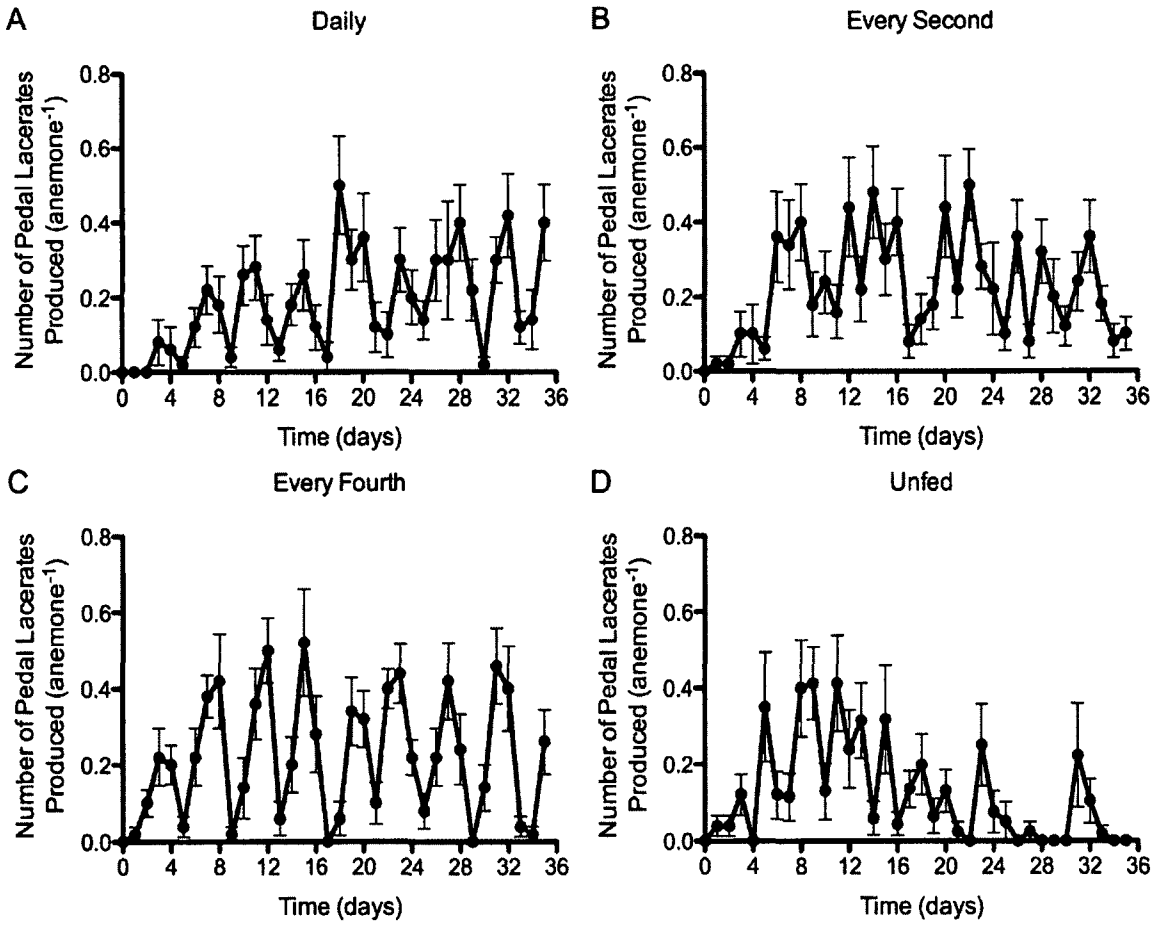

Figure 25: Number of pedal lacerates produced per anemone by *Sagartia elegans* when fed *Artemia franciscana* (A) daily, (B) every second day, (C) every fourth day, or (D) when left unfed. Distinct patterns were formed in treatments fed every second or every fourth day; asexual reproduction was inhibited the day after feeding in animals fed every second (0, 2, 4...) and fourth day (0, 4, 8...).

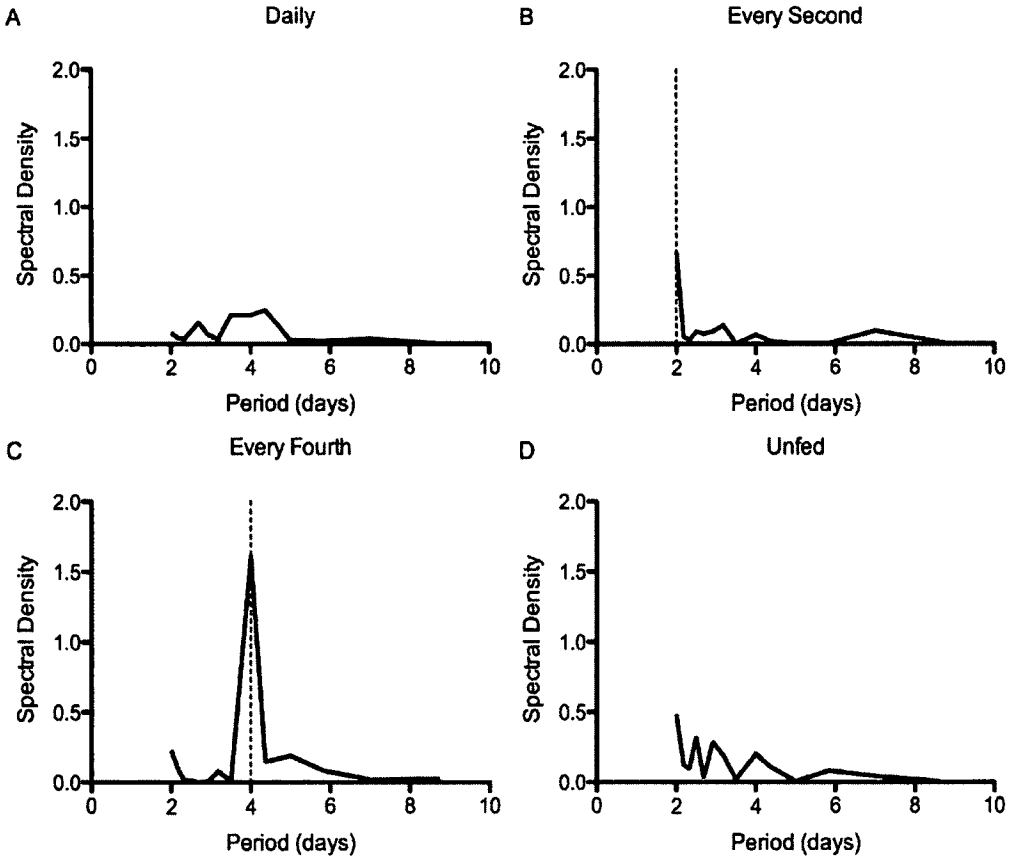

Figure 26: Periodogram of number of pedal lacerates produced daily by *Sagartia elegans* when fed *Artemia franciscana* (A) daily, (B) every second day, (C) every fourth day, or (D) when left unfed. Peaks represent a detected periodocity with significant periodocities being highlighetd by dashed vertical lines. Fourier analysis dectected no periodocity in the asexual reproduction of anemones fed daily ($p = 0.483$) or left unfed ($p = 0.236$). *S. elegans* that were fed every second day followed a two day reproduction cycle ($p = 0.0004$) and *S. elegans* fed every four days followed a four day reproduction cycle ($p < 0.0001$).

reproductive pattern with a period of four days ($p < 0.0001$, Fourier analysis, Figure 26C). No periodicity could be detected for animals fed every day or left unfed ($p \geq 0.236$, Fourier analysis, Figure 26A and D).

1.7.2 Trial Two. There was a statistical difference in initial size between treatments ($p < 0.0001$). Anemones that were fed more frequently in trial one were initially larger. Growth of *S. elegans* was dependent on trial one ($p < 0.0001$, two-way ANOVA, Figure 27A) and trial two treatment ($p \leq 0.0001$, two-way ANOVA, Figure 27B). Anemones that were being fed every fourth day in trial one increased in size in trial two, whereas those that were fed daily or every second day in trial one did not grow significantly or shrank in size in trial two (Figure 27A). *S. elegans* that were fed daily or every second day in trial two grew in size whereas animals that were fed every fourth day or left unfed shrank in size on average (Figure 27B). There was no interactive effect

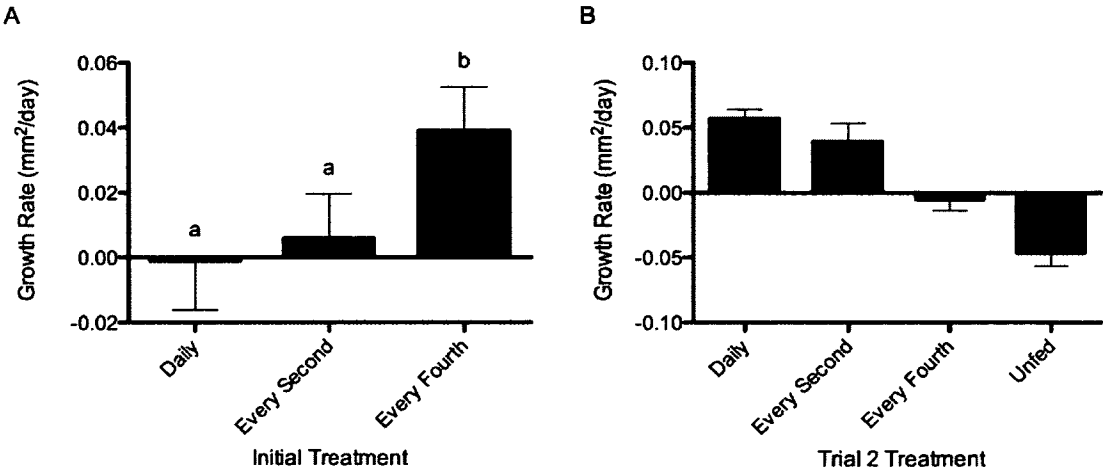

Figure 27: Growth rate of *Sagartia elegans* fed at varying feeding frequencies in trial two (Mean ± 1 SE). (A) Anemones that were being fed every fourth day in trial one increased in size in trial two, whereas those that were fed daily or every second day in trial one did not grow significantly or shrank in size in trial two. Different letters denote statistical significance ($p < 0.05$, Tukey's test). (B) There was a statistically significant difference between the growth rates of all treatments with respect to the feeding frequency in trial two ($p < 0.05$, Tukey's test).

between trial one and trial two ($p = 0.065$, two-way ANOVA). There was no mortality in trial two.

In respect to asexual reproduction, there was an interactive effect between the feeding frequency of the animals in trial one and trial two ($p = 0.004$, two-way ANOVA). Animals that were fed more in trial one reproduced more if the frequency of feeding was reduced in trial two; those that were fed more in trial two reproduced less (Figure 28). Previous asexual reproductive patterns from trial one were lost immediately for anemones that changed treatment and replaced by patterns similar to those found in trial one for the feeding frequency they changed to (Figure 29). Reproductive capacity did not reduce over time for animals left unfed in trial two. When fed every two days *S. elegans* had a reproductive pattern with a period of two days ($p \leq 0.025$, Fourier analysis, Figure 29B). When fed every four days *S. elegans* had a reproductive pattern with a period of four days ($p \leq 0.037$, Fourier analysis, Figure 29C). No periodicity could be detected for anemones fed every day or left unfed ($p \geq 0.066$, Fourier analysis, Figure 29A and D).

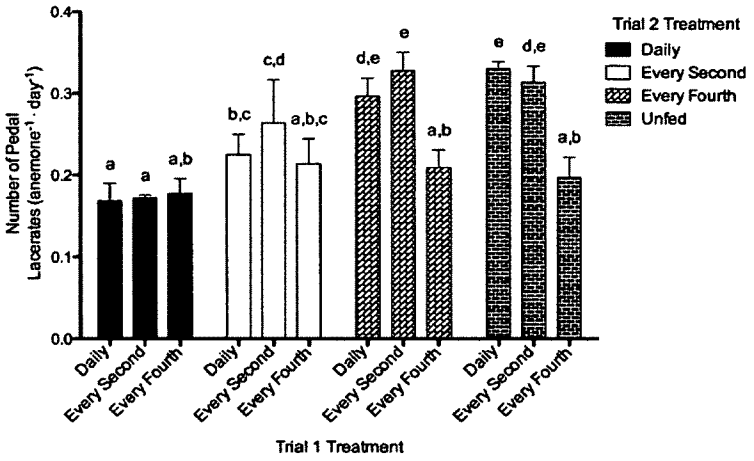

Figure 28: Total number of pedal lacerates produced per polyp of *Sagartia elegans* fed at different feeding frequencies (Mean + SE). Animals that were fed more in trial one reproduced more if the frequency of feeding was reduced in trial two; those that were fed more in trial two reproduced less. Different letters denote statistical differences ($p < 0.05$).

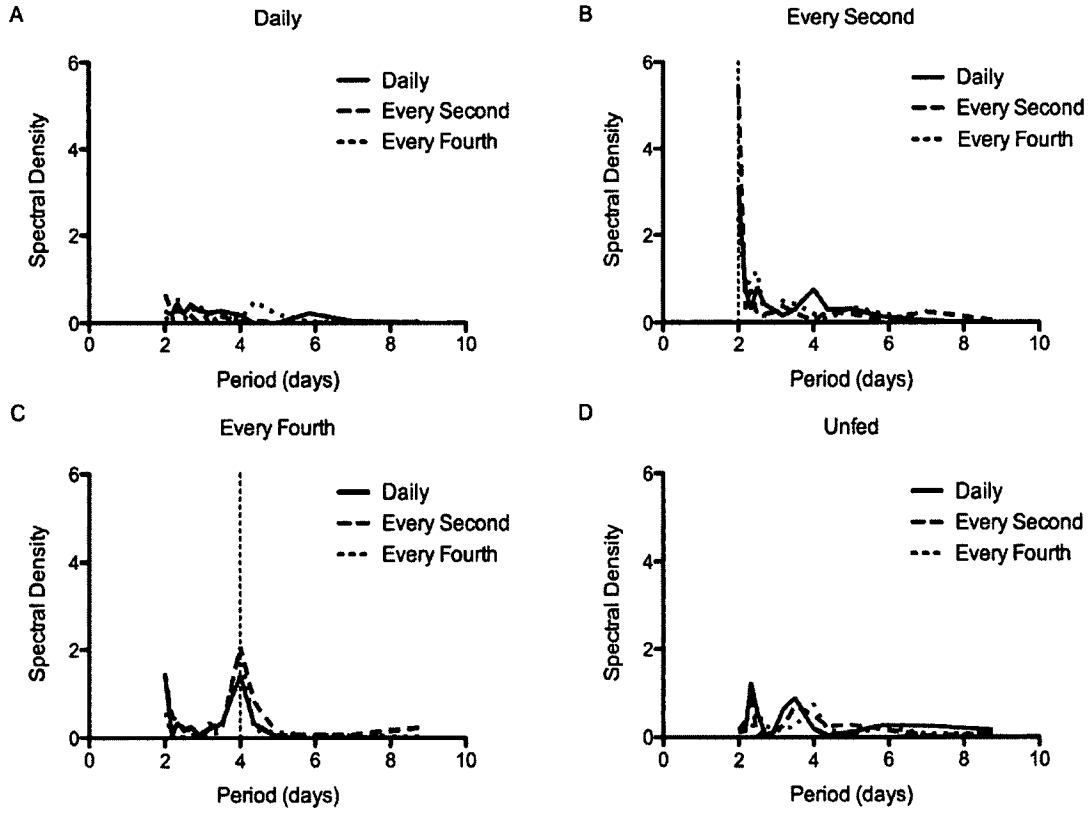

Figure 29: Periodogram of number of pedal lacerates produced daily by *Sagartia elegans* when fed *Artemia franciscana* (A) daily, (B) every second day, (C) every fourth day, or (D) when left unfed. Animals were initially fed at one of three frequencies for 35 days: daily, every second day or every fourth day (represented by different line patterns). Peaks represent a detected periodocity with significant periodocities being highlighted by dashed vertical lines. Fourier analysis dectected no periodocity in the asexual reproduction of anemones fed daily ($p \geq 0.066$) or left unfed ($p \geq 0.134$). *S. elegans* that were fed every second day followed a two day reproduction cycle ($p \leq 0.025$) and *S. elegans* fed every four days followed a four day reproduction cycle ($p \leq 0.037$) no matter the initial treatment.

1.8 Effect of Substratum Texture on the Asexual Reproduction of *Sagartia elegans*

Final densities of *S. elegans* differed significantly between all treatments ($p = 0.0003$, ANOVA, Figure 30A-B) and were highest inside depressions ($p < 0.05$, Tukey's test, Figure 30B). Anemones within depressions maintained a higher density than anemones outside of the depression and on flat tiles. Final dry masses were statistically significant between treatments ($p < 0.0001$, ANOVA) and largest within the depressions ($p < 0.05$, Tukey's test, Figure 30C). Animals seemed to be crowding one another out of depressions after day 28 and as the amount of space became limited density started to decrease after day 35 (Figure 30A) especially inside the 5 mm deep depressions. The anemones in depressions for both 2 and 5 mm deep depressions took up approximately 37.6% of the surface area at the end of the experiment. Anemones were only utilizing between approximately 5.2 to 7.5 % of the surface area outside the depressions.

Throughout the experiment, sea anemones were constantly releasing from their substratum and floating around the tank (see Section 1.1 results). In all likelihood, animals were attaching to other tiles affecting the densities of other treatments. Large anemones infrequently left the depressions or released from the substratum; there may be a relationship between size and ability to release from the substratum. Depressions may be a more desirable location. Anemones that attached to the bottom and sides of the glass aquarium after releasing from the tiles were small in size; it is suspected that their small size was maintained through pedal laceration.

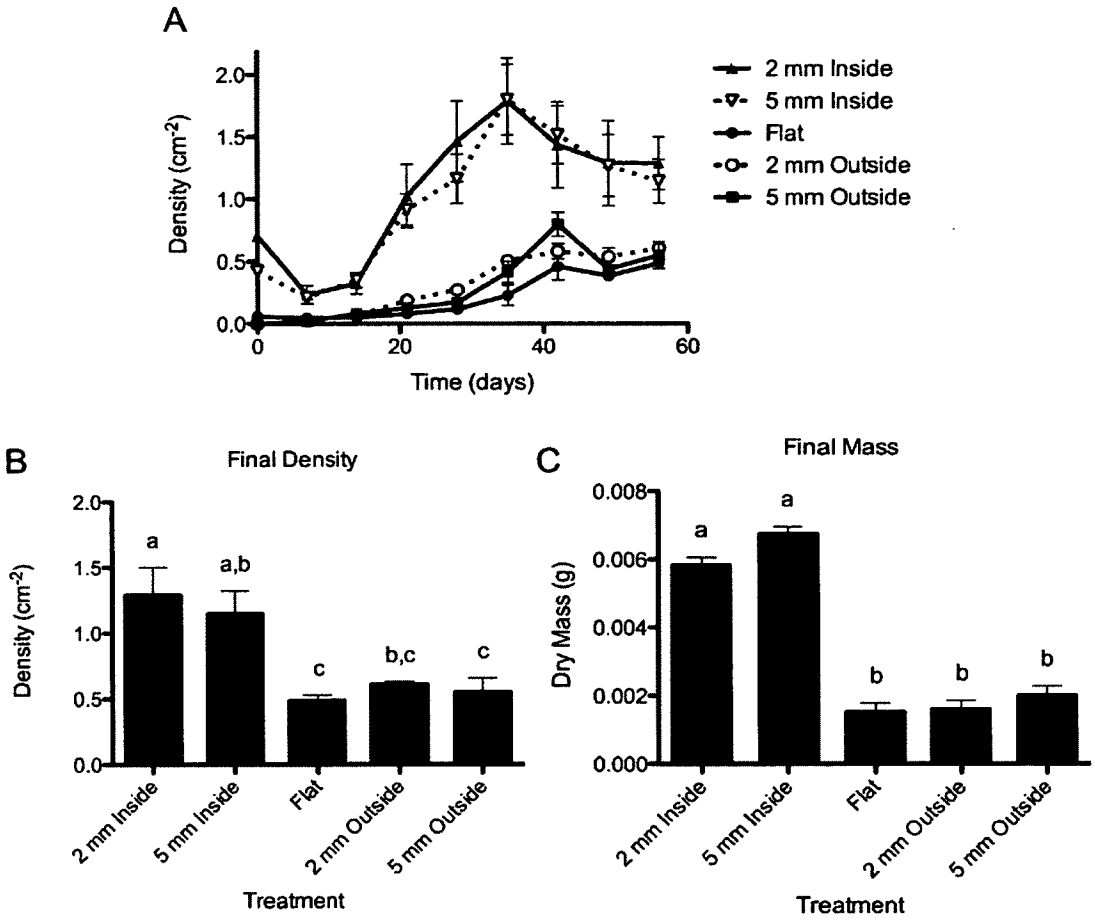

Figure 30: (A) Density of *Sagartia elegans* inside and outside depressions or on flat tiles over time (Mean ± 1 SE). Animals increased in density inside depressions until day 35 at which time animals started crowding each other out. (B) Final density of *S. elegans* inside and outside depressions or on flat tiles (Mean + SE). Density was highest within the depressions. Different letters denote statistical differences ($p < 0.05$). (C) Final mass of *S. elegans* inside and outside depressions or on flat tiles (Mean + SE). Different letters denote statistical differences ($p < 0.05$).

1.9 Effect of Starvation Stress on the Release from Substrata in *Sagartia elegans*

Initial sizes of polyps of *S. elegans* did not differ ($p = 0.953$, ANOVA). Feeding frequency was positively related to *S. elegans* growth rate ($p < 0.0001$, ANOVA, Figure 31). Animals fed three times weekly grew in size whereas animals fed once weekly or left unfed shrank in size (Figure 31). At the end of 35 days, only two polyps being fed

three times weekly and one polyp being fed once weekly were left on the panels. All animals left unfed released before day 21 (Figure 32A). Release rate was significantly

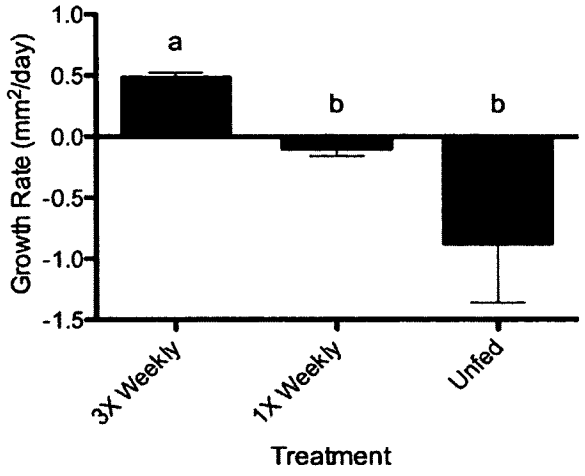

Figure 31: Growth rate of *Sagartia elegans* still on panels being fed at different frequencies (Mean ± 1 SE). Animals fed three times weekly grew in size, whereas animals fed once weekly or left unfed shrank in size. Different letters denote statistical differences ($p < 0.05$, Tukey's test).

higher with anemones left unfed ($p < 0.0001$, Tukey's Test, Figure 32B); there was no difference between those fed once and fed three times weekly ($p = 0.765$, Tukey's Test, Figure 32B).

1.10 Effect of Temperature Stress on the Release from Substrata in *Sagartia elegans*

Within the first week, 70% of the animals, from all treatments, released from all panels. After the initial seven days, no animals released from the panels maintained at 15.0 °C. Anemones exposed to decreasing temperatures start to release after temperatures decreased below 13.0 °C. All anemones released from the panels after the temperature had reached 10.0 °C (Figure 33). Anemones maintained at 15.0 °C grew whereas those exposed to decreasing temperature shrank.

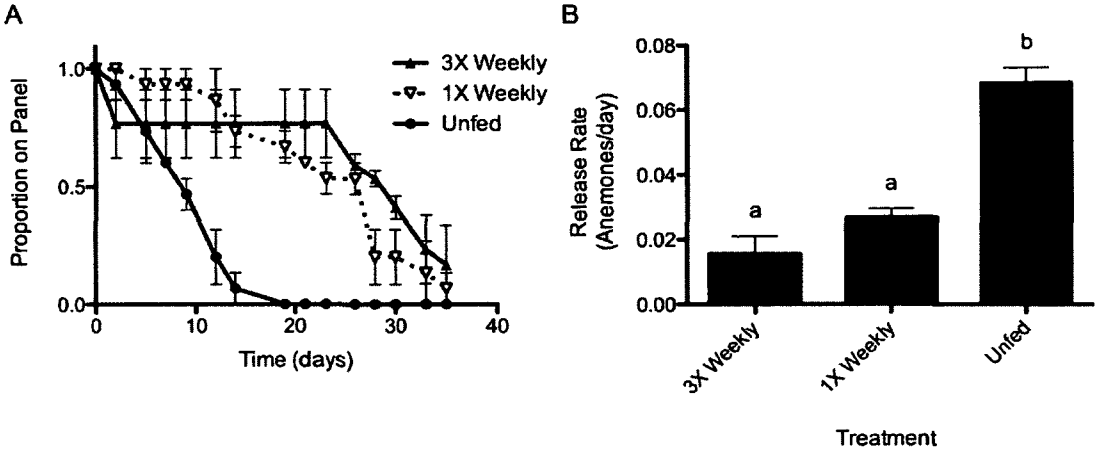

Figure 32: (A) Proportion of *Sagartia elegans* remaining on panels and (B) release rate for polyps being fed differing feeding frequencies (Mean ± 1 SE). All animals being left unfed released before day 21. Different letters denote statistical differences ($p < 0.05$, Tukey's test).

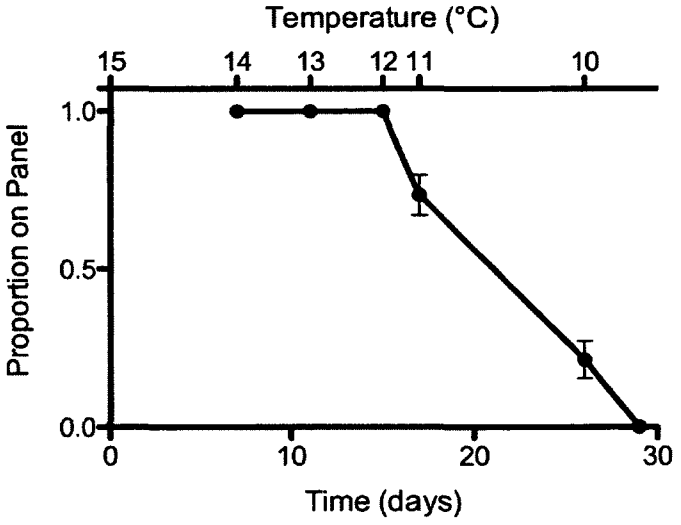

Figure 33: Proportion of *Sagartia elegans* remaining on panels as temperature decreased over time (Mean ± 1 SE). After temperature was decreased below 13 °C anemones started to release from the panels with all anemones off the panels at 9 °C.

Discussion

When *S. elegans* was kept at a constant temperature and allowed to proliferate, growth was counteracted by asexual reproduction. When temperature was high (15 and 21.5 °C), *S. elegans* was extremely proliferous, increasing in population over four orders of magnitude in the course of two years at the cost of individual size (Table 4). Populations may have been even higher in number if food was not a limited resource. Populations held at 10 °C were just above the temperature limit for asexual reproduction; asexual reproduction was very infrequent. The decreased incidence of asexual reproduction allowed the anemones grown at 10 °C to grow much larger than those grown at 15 and 21.5 °C (Table 4, Figure 19). Total clonal biomass was similar in magnitude between cultures at 15 and 21.5 °C, but two orders of magnitude larger than anemones kept at 10 °C (Table 4). It seems *S. elegans* slows down metabolically at these temperatures only just maintaining its clonal biomass. This is odd as *S. elegans* is known to maintain populations at temperatures far below this in their northern native range (Ates *et al.*, 1998).

Growth of *S. elegans* was not affected by the preparation of the food, although asexual reproduction was higher for those fed live nauplii (Figure 21). It could not be determined whether the higher asexual reproduction was a product of the food being live or of the differing nutritional value in nauplii compared to adult brine shrimp. Newly hatched brine shrimp have a higher ratio of fat to protein than adults (Léger *et al.*, 1987). Age of nauplii and use of SELCO did not impact growth or asexual reproduction. SELCO is used to enrich *Artemia spp.* nauplii with polyunsaturated fatty acids and vitamins. Increasing the fat to protein ratio through the use of SELCO was not

beneficial. Soaking adult brine shrimp in SELCO may elicit an asexual reproduction response similar to feeding the anemones nauplii through an adjustment of the ratio of fat to protein.

Although preparation of *Artemia spp.* did not significantly affect growth, frequency of feeding did have a significant effect. The more frequently *S. elegans* was fed, the larger the individuals grew (Figure 22). The growth rate did not scale with the amount of food available; it would be expected that an animal that was fed twice as frequently, and therefore twice as much, would grow twice as fast. There seems to be a maximal growth rate hindering the growth of animals fed more frequently (daily and every second day). Anemones fed more frequently in the second trial than what they were fed in the first trial continued to increase in size; those fed less frequently shrank (Figure 27). This indicates that the anemones were near their maximal size for the amount of food they were consuming in the first trial. Animals that were fed at any frequency produced more pedal lacerates than animals left unfed (Figure 24). Also, those fed more frequently seemed to produce larger pedal lacerates. This would allow for a greater ability to respond to blooms of food. *S. elegans* that were fed more frequently in the second trial reproduced less and those fed less frequently reproduced more (Figure 28). This is likely due to their initial sizes being larger, but also due to the increased suppression of asexual reproduction by feeding.

Asexual reproduction was inhibited within the first 24 hr after feeding. Those fed on a two- and four-day cycle had a two- and four-day cycle of asexual reproduction respectively (Figure 25, 26 and 29). This periodicity was immediately lost when anemones were transferred to a new feeding regime in the second trial. New periodicities

reflecting their second trial feeding regime were started immediately. These periodicities were similar to what was found in the first trial for the same treatments. This pattern of inhibition within the first 24 hr is also found with *A. pellucidus* (Smith and Lenhoff, 1976). *A. pallida* and *A. elegantissima* also are asexually inhibited after feeding (Sebens, 1977, 1980; Hunter, 1984) although *D. lineata* is asexually stimulated by increases in feeding frequency (Minasian, 1976, 1979; Minasian and Mariscal, 1979; Minasian, 1982). How feeding frequency affects asexual division is highly species-specific and likely adapted to the conditions over the range occupied by a particular species. With *S. elegans*, it may be possible that food cannot be digested while asexually reproducing. During pedal laceration, parts of the gastrovascular cavity, column, and pedal disk are torn from the mother anemone to form new daughter anemones. Tears within the gastrovascular cavity may hinder digestion. It may be more important for the mother anemone to continue to exploit limited food resources when available instead of investing energy into asexual reproduction. This is the case with *A. elegantissima*; anemones do not asexually reproduce until food is highly limited as time is needed for the necessary internal reorganization (Sebens, 1977, 1980). Particular care should be taken when comparing asexual behaviors of *S. elegans* and *A. elegantissima* as they do not share the same mode of asexual reproduction (i.e. pedal laceration as compared to longitudinal fission).

S. elegans grew largest and reached highest densities within depressions on the tile substrata (Figure 30). Similarly, individual size of *A. elegantissima* increased from exposed to protected microhabitats in the intertidal (Sebens, 1982a). *S. elegans* seems to prefer to have its pedal disk inserted into depressions, probably for protection from

predators or heavy currents; Manuel (1981, 1988) observed similar behavior in *S. elegans* in its native range. Many anemones are only observed in the wild with their pedal disk within a depression, crevice, or shell. Examples include *Condylactis gigantea* (Weinland, 1860), *Ragactis lucida* (Duchassaing de Fonbressin and Michelotti, 1860), and *Lebrunia neglecta* (Duchassaing de Fonbressin and Michelotti, 1860) in holes in coral reefs (Sebens, 1976); *A. sola* in crevices in the intertidal (Harris, 1991); and *Bartholomea annulata* (Le Sueur, 1817) in shells and coral rubble (personal observation). Anemones seemed to wander more when outside the depressions, perhaps searching for a suitable refuge for their pedal disk. The closely related *S. trogolodytes* rarely changes its location once settled in a suitable cavity (Ashworth and Annandale, 1904). Anemones were frequently observed releasing from their substratum and floating around the tank. Soon after releasing they attached to a new location through the use of their tentacles. Tentacles stuck to the new substratum and the pedal disk flipped down and reattached; sometimes individuals touched multiple surfaces before reattaching.

It is unknown as to what determines where *S. elegans* resettles, but it has been shown that many anemones prefer an organic substratum (Shick, 1991) particularly of the family Hormathiidae (Manuel, 1988). The sea anemone *Calliactis parasitica* (Couch, 1842) releases from an inorganic substratum when it encounters the periostracum of the common whelk *Buccinum undatum* Linnaeus, 1758 (Ross and Sutton, 1961); commonly the empty shells of *B. undatum* are inhabited by the hermit crab *Pagurus bernhardus* Linnaeus, 1758. When the shell touches the tentacles of *C. parasitica* the anemone's tentacles stick to the shell and the pedal disk is transferred over, unaided by the hermit crab (Ross, 1960; Ross and Sutton, 1961). In the wild, *C. parasitica* is always found on

shells occupied by hermit crabs (Ross, 1960). The sea anemone *Stomphia coccinea* (Müller, 1776) is highly attracted to an organic compound in the shell of *Modiolus modiolus* (Linnaeus, 1758) and will actively transfer itself from other inorganic surfaces (Ross, 1965).

Starvation stress through reduced feeding was found to elicit the substratum-releasing behavior in other experiments. Anemones left unfed released from their substratum within a few weeks (Figure 32A). Those fed once and three times weekly had a reduced release rate (Figure 32B). When there is no food, releasing from the substratum may allow *S. elegans* the opportunity to find a new location where food is more abundant while also allowing for increased clonal dispersal. Decreasing temperature also elicited a releasing behavior. At temperatures below 12 °C, some anemones released from their substratum and at 10 °C all anemones had detached (Figure 33). This substratum-releasing behavior seems to be stress-induced, and has been previously described in *Sagartia*. Adult *S. trogolodytes* and *S. nigropunctata* are known to release from their substratum in culture (Gosse, 1860; Ashworth and Annandale, 1904). This allows for great dispersal potential and the ability to colonize new environments (Jokiel, 1989; Martel and Chia, 1991; Helmuth *et al.*, 1994). Suspension in the water column may increase the chances of encountering floating debris, which could greatly enhance long distance, adult dispersal (Arnaud *et al.*, 1976; Highsmith, 1985; Jackson, 1986).

Although *S. elegans* does appear to have many of the characteristics of a successfully introduced species (i.e. asexual reproduction, ability for long distance dispersal), the anemone does not seem to be well adapted to survival in Salem Harbor. *S.*

elegans is particularly sensitive to temperatures which are highly variable within Salem Harbor. The temperature-induced releasing from the floats would expose *S. elegans* to elevated levels of predation by *A. papillosa*. As temperatures reached 9 °C asexual reproduction stopped and animals started to decrease in size (Figure 16 and 17). Reduction in size indicates a high level of stress (Sebens, 1979). *S. elegans* is normally proliferous when its needs are satisfied. After 6 °C mortality was high and by 4 °C all individuals had died (Figure 18). All the aforementioned temperatures are well above the average winter temperature for the Gulf of Maine. I have recorded temperature within Salem Harbor below 2 °C for weeks during winter. For *S. elegans* to survive these winters in the wild, a warm-water temperature refuge is required. This topic will be further explored in Chapter 2.

CHAPTER II

RECRUITMENT, SURVEYS, AND THE IMPACT OF TEMPERATURE ON *SAGARTIA ELEGANS* IN SALEM HARBOR, MASSACHUSETTS

Introduction

Introduced species have the potential to alter ecosystems and cause significant economic costs (Meinesz *et al.*, 1993; Cohen and Carlton, 1995; Carlton, 1996b, 2000; Thresher, 2000; Occhipinti-Ambrogi and Sheppard, 2007). The annual economic cost incurred from managing the approximately 50,000 introduced species in the United States is over $120 billion alone (Pimentel *et al.*, 2005). Introduced species are increasingly recognized as a serious problem as introductions become more and more common (Mooney and Cleland, 2001; Simberloff *et al.*, 2005).

The field of invasion biology has increased in size rapidly since the mid-1980s (Kolar and Lodge, 2001). Most of the research has focused on successful introductions and what makes the introduction successful, and yet it is expected that most introductions will fail (Williamson and Fitter, 1996; Lockwood *et al.*, 2005; Blackburn *et al.*, 2011); it is equally important to understand the reasoning behind failed introductions (Kolar and Lodge, 2001; Zenni and Nuñez, 2013). The few studies on failed introductions have already provided a large amount of important information, particularly in species distribution modeling and analyses of historical factors associated with introductions (Zenni and Nuñez, 2013). For example, Miller *et al.* (2007) compared failed and successful mollusk introductions and found that local abundance in their native habitat,

tolerance to low salinity, and developmental mode were good predictors of introduction success or failure.

An introduction failure can happen at any stage in the introduction continuum (Blackburn *et al.*, 2011). An introduced species must first cross the geographic barrier. Usually this is aided, either deliberately (e.g. crops, erosion control, biological control) or unintentionally (e.g. within shipping material, ballast, hull fouling), by some anthropogenic means. After arriving in the new location the newly introduced species must be able deal with the present abiotic forces and biotic resistance, while attempting to establish a population. Failures during these intermediate steps are difficult to observe directly. Most studies that do so are anecdotal with a lack of quantitative experimentation. Here, I quantitatively look at factors that may have affected the disappearance of the sea anemone *S. elegans*.

S. elegans was found in Salem Harbor, Massachusetts in 2000 on a rapid assessment survey (Pederson *et al.*, 2001; Pederson *et al.*, 2005). It was particularly abundant when it was found in 2000 and is therefore suspected to have been introduced some years prior. The population has subsequently disappeared and cannot be found. It was only found at one marina in Salem Harbor: Hawthorne Cove Marina.

The introduced population of *S. elegans* was seasonally abundant; it appeared as early as June (Harris, personal communication) and died back by January. This cycle repeated itself annually. After the winter of 2010-2011, *S. elegans* could not be found in Salem Harbor. The disappearance in the winter as well as its seasonal abundance suggests that winter is particularly stressful for *S. elegans*. Within its northern native range, *S. elegans* is sensitive to winter water temperatures, disappearing completely

during extreme winters (Ates *et al.*, 1998). *S. elegans* collected from their introduced range in Salem Harbor were found to release from their substrata in the laboratory as temperature reached 10 °C, a sign of stress in sea anemones (Figure 33). This behavior in Salem Harbor would expose *S. elegans* to elevated levels of predation by *A. papillosa*. As temperatures reached 9 °C asexual reproduction stopped and animals started to decrease in size (Figure 16 and 17). Reduction in size and lack of asexual reproduction in *S. elegans* indicates a high level of stress. After 6 °C mortality was high and by 4 °C all individuals had died (Figure 18). *S. elegans* is also negatively impacted by salinity; particularly below 20 ppt (Figure 16-18). The aforementioned temperatures are well above the average winter temperature for the Gulf of Maine. Temperature seems to be particularly important to the survival and maintenance of introduced populations of *S. elegans*.

In this chapter I examine the population dynamics and recruitment of *S. elegans*, as well as impacts of temperature on growth and reproduction in the field. The specific objectives of this chapter are to:

1. Document the disappearance of *S. elegans* from Hawthorne Cove Marina through surveys and a recruitment study.
2. Explore the impacts of temperature on the growth and asexual reproduction of *S. elegans* in the field.

Methods

Site Descriptions

For site descriptions of Salem Harbor and Hawthorne Cove Marina in Salem, MA see Chapter 1.

Beverly Port Marina, Beverly, MA. Beverly Port Marina is located on the northern shore of Beverly Harbor (42.5402, -70.8828) approximately 1.5 km north of Hawthorne Cove Marina. It is a private marina with approximately 215 slips. Floats are dominated by mussels and colonial and solitary tunicates. Depth ranges from 2-9 meters. *S. elegans* has never been documented at Beverly Port Marina.

Jodrey State Fish Pier, Gloucester, MA. Jodrey State Fish Pier is located in the northeastern shore of Gloucester's inner harbor (42.6127, -70.6530) approximately 17.1 km northeast of Hawthorne Cove Marina. It is a commercial fishing wharf with 54 slips and 3 berths. Floats are dominated by mussels and arborescent bryozoans. Minimum depth is 3 meters. *S. elegans* has never been documented at Jodrey State Fish Pier.

2.1 Surveys for *Sagartia elegans*, *Diadumene lineata*, and *Aeolidia papillosa* in Salem Harbor

2.1.1 2009 Field Density. On October 23, 2009, during a pilot study, density of *S. elegans* was approximated by counting all polyps on haphazardly chosen vertical sides of 15 floats (approximately 0.40 m^2) at Hawthorne Cove Marina in Salem, MA.

2.1.2 2010 Field Density. Density of *S. elegans* was approximated by counting all polyps on haphazardly chosen vertical sides of 20 floats (approximately 0.40 m^2) at Hawthorne Cove Marina in Salem, MA. Counts were done from August to December

monthly. During the same time, on the same floats, presence or absence of the introduced sea anemone *D. lineata* was also recorded.

2.1.3 2011-2013 Field Density. Density of *S. elegans* was approximated by counting polyps within a 0.0625 m^2 (0.25 x 0.25 m) polyvinylchloride (PVC) quadrat laid haphazardly on a vertical side of 30 floats at Hawthorne Cove Marina in Salem, MA. Quadrats were laid starting in June of 2011 and approximately every 1-4 weeks thereafter until January 2013. During the same time, on the same floats, the number of *A. papillosa* and presence or absence of *D. lineata* was recorded.

To determine if *S. elegans* was on the underside of the floats, a SCUBA survey was performed in November of 2011. The bottoms of over 50 floats were examined for *S. elegans* polyps. During the same dive, 15 0.625 m^2 (0.25 x 0.25 m) PVC quadrats were laid on the bottom haphazardly to quantify the density of *A. papillosa.*

In November and December of 2012, floating docks and other structures were examined for polyps of *S. elegans* via ocean kayak (Table 5).

2.2 Recruitment of *Sagartia elegans* in Gloucester, Beverly, and Salem, Massachusetts

Ten 0.010 m^2 (10.0 x 10.0 x 0.4 cm) acrylic glass panels were hung at Jodrey State Fish Pier, Beverly Port Marina, and in Hawthorne Cove Marina in June 2011. Panels were randomly assigned to one of two treatments: scraped cleaned every 3-6 weeks or left alone. Number of polyps of *S. elegans* settling was enumerated prior to cleaning. Digital photographs were taken prior to cleaning to document fouling community succession; this data will not be reported on in this thesis. Panels were removed from their respective sites in October of 2012.

Table 5: Georeferenced sites examined for *Sagartia elegans* during kayak surveys in November and December of 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	42.5214, -70.8796
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

2.3 Growth, Asexual Reproduction, and Survival of *Sagartia elegans* at Hawthorne Cove Marina

2.3.1 2011 Experimental Design. In June of 2011 10 0.010 m^2 (10.0 x 10.0 x 0.4 cm) acrylic glass panels with 5 polyps of *S. elegans* were hung off the floating docks of Hawthorne Cove Marina in Salem, MA. At the start of the experiment and approximately every 2 weeks thereafter, PDSA (see Section 1.2), number of pedal lacerates produced, and whether or not animals had visibly ripe gonads was noted until all animals had released from the panels or died. Pedal lacerates were discarded so daughter anemones would not compete for space with the original anemones. Temperature was measured concurrently through the use of a HOBO Pendant temperature and light data logger 64K (Onset Computer Corporation, Inc., Bourne, MA) set to measure temperature every 20 minutes.

In June of 2012 the above experiment was repeated with 10 polyps of *S. elegans* per panel. PDSA measurements were taken every 1-2 weeks (see Section 1.2), but pedal lacerates were not counted. Pedal lacerates were discarded so daughter anemones would not compete with the original anemones for space.

2.3.3 Statistical Analysis. Linear regressions comparing size and asexual reproduction to temperature were performed. Size was separated by year and compared.

Results

2.1 Surveys for *Sagartia elegans*, *Diadumene lineata*, and *Aeolidia papillosa* in Salem Harbor

2.1.1 2009 Field Density. In 2009, *S. elegans* was present in October, but not in high density. Average density was approximately 4.2 polyps per m^2. Anemones were primarily found within dead southern blue mussel (*M. edulis*) shells and attached to live mussels, although many animals were also found attached to the floats and as epibionts on other fouling animals and algae. All *S. elegans* were of the same color. None of the *S. elegans* found were sexually mature.

2.1.2 2010 Field Density. In 2010, *S. elegans* was present from September to December. Densities were highest in early October (average density 210 polyps per m^2, maximum density 980 polyps per m^2, Figure 34). The highest abundance of sea anemones were found taking up primary space on the vertical surfaces of the floats within the first 10 cm below the water. Animals were also epibiotic on live and dead *M. edulis*, the solitary tunicates *Ciona intestinalis* (Linnaeus, 1767) and *Steyla clava* Herdman, 1881, the European oyster *Ostrea edulis* Linnaeus, 1758, as well as the thalli of *Ulva lactuca*, *Saccharina latissima* (Linnaeus) C.E. Lane, C. Mayes,

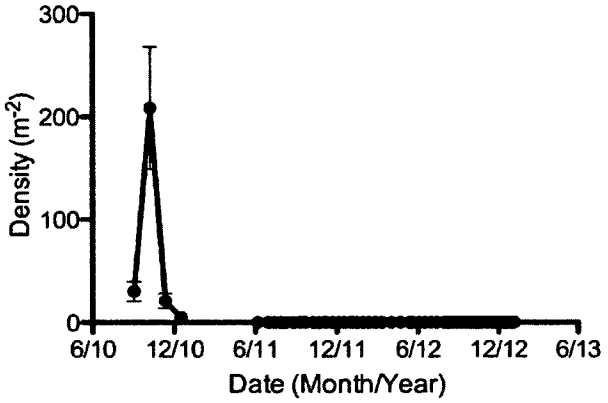

Figure 34: Density of *Sagartia elegans* on the vertical surfaces of floats at Hawthorne Cove Marina in Salem, MA from September 2010 to January 2013 (Mean ± 1 SE). Animals were present in 2010, but could not be found in 2011 through 2013.

Druehl & G.W. Saunders, *Chondrus crispus* Stackhouse, and drift *Ascophyllum nodosum* (Linnaeus) Le Jolis. Most polyps 14 mm in diameter and larger, and all polyps above 20 mm, had female gonads attached to their mesenteries visible through their oral disk (Figure 35). All *S. elegans* were of the same color.

Figure 35: Close-up photograph of a sexually mature female *Sagartia elegans* collected in October of 2010. Female gonads (**G**) can be seen attached to the mesenteries through the translucent oral disk. The mouth (**M**) has been labeled as a frame of reference. *Artemia fransicana* cysts and nauplii can be seen around the mouth. Color was edited with the program GIMP 2 (Free Software Foundation, Boston, MA) to reflect a more accurate representation of true colors.

D. lineata were present at all sampling dates, but decreased in occurrence as fall progressed (Figure 36). *D. lineata* was commonly found attached to primary space, *U. lactuca*, *S. clava*, and drift *A. nodosum*, as well as on and amongst clumps of *M. edulis*.

2.1.3 2011-2013 Field

Density. *S. elegans* were never found from June 2011 to January 2013 (Figure 34). *S. elegans* were not found while kayaking at any of the sites nor during the SCUBA survey.

Densities of *A. papillosa* peaked during winter months on vertical surfaces of floats at Hawthorne Cove Marina (Figure 37). Density of nudibranchs was highest during early December of 2012 (3.2 nudibranchs per m^2). *A. papillosa* was frequently found amongst clonal aggregations of *M. senile* and *D. lineata* as well as within clumps of *M. edulis*. Densities of *A. papillosa* on the mud below the floats at Hawthorne Cove Marina were qualitatively higher than on the floats. *A. papillosa* could be seen on the

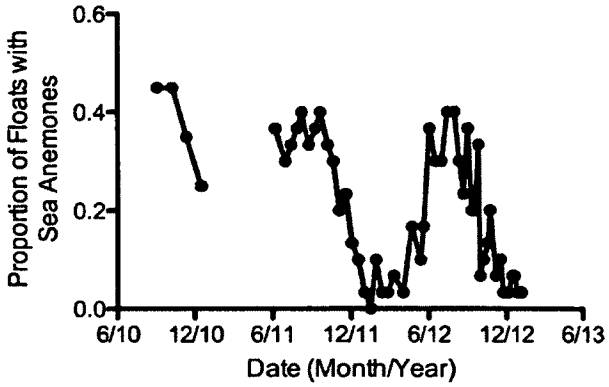

Figure 36: Proportion of floats with *Diadumene lineata* on their vertical surfaces at Hawthorne Cove Marina in Salem, MA from September 2011 to January 2013. *D. lineata* populations peaked in fall and were rare during the winter months when their predator *Aeolidia papillosa* was present in significant numbers.

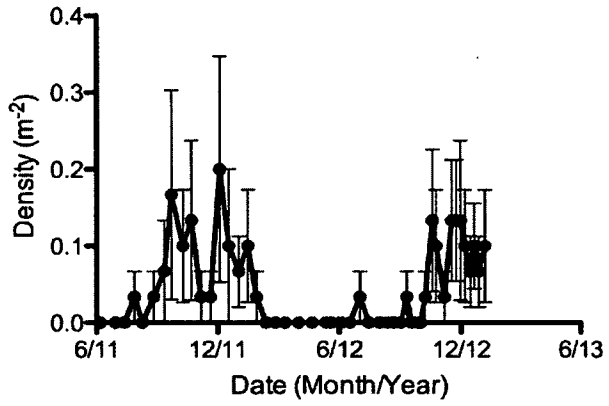

Figure 37: Density of *Aeolidia papillosa* on the vertical surfaces of floats at Hawthorne Cove Marina in Salem, MA from June 2011 to January 2013 (Mean ± 1 SE). *A. papillosa* populations peaked in winter and were rare during the summer months.

bottom throughout most of the year during times of low turbidity. During the SCUBA survey, *A. papillosa* were at a mean density of approximately 14.9 nudibranchs per m^2 (maximum density 48 nudibranchs per m^2). *A. papillosa* were found moving towards and on clumps of *M. edulis* consuming *M. senile*; one anemone was being consumed by six nudibranchs simultaneously! No *A. papillosa* were found while kayaking at any of the sites.

D. lineata was present at all sampling periods between June 2011 and January 2013 except for in January 2012. Densities of *D. lineata* appeared to be negatively correlated with the abundance of *A. papillosa* although temperature is a compounding factor.

2.2 Recruitment of *Sagartia elegans* in Gloucester, Beverly, and Salem, Massachusetts

S. elegans never settled on any panels at any of the sites between June 2011 and October 2012. Many other groups of introduced, native, and cryptogenic organisms (see Carlton, 1996a for definitions) settled on the panels including solitary and colonial ascidians, gastropods, bivalves, polychaetes, hydrozoans, actiniarians, rhodophytes, phaeophytes, and chlorophytes.

2.3 Growth, Asexual Reproduction, and Survival of *Sagartia elegans* at Hawthorne Cove Marina

In both field seasons, temperature was directly related to both size of animals and amount of pedal lacerates being produced ($p < 0.0001$, linear regression, Figure 39-39). There was a similar relationship between temperature and size in 2011 and 2012 ($p = 0.599$, linear regression, Figure 39). As temperature decreased so did average size of *S. elegans*. Asexual reproduction stops at 9.3 °C.

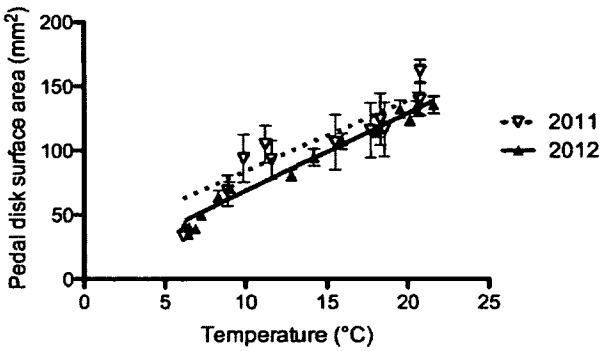

Figure 39: Relationship between temperature and size of polyps in the 2011 and 2012 field seasons (Mean ± 1 SE). There was no difference in the relationship between size and temperature between years ($p = 0.599$, linear regression).

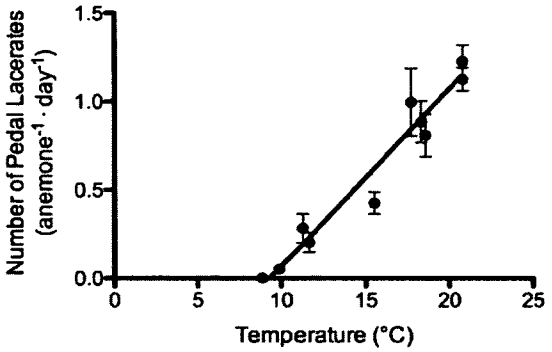

Figure 38: Relationship between temperature and asexual reproduction in the 2011 field season (Mean ± 1 SE). Both size and asexual reproductive output are directly related to temperature ($p < 0.0001$, linear regression). Asexual reproduction stops at 9.3 °C.

Three of the ten 2011 panels were dislodged from Hawthorne Cove Marina during Hurricane Irene on August 27, 2011. On panels still attached, many of the anemones were heavily damaged with some subsequently disappearing in September (Figure 40). Anemones were not subsequently lost until November, after temperatures reached below 11 °C at which point animals started to release from the panels at an accelerated rate (Figure 40-42). All polyps in both years had disappeared prior to temperatures decreasing to 6 °C.

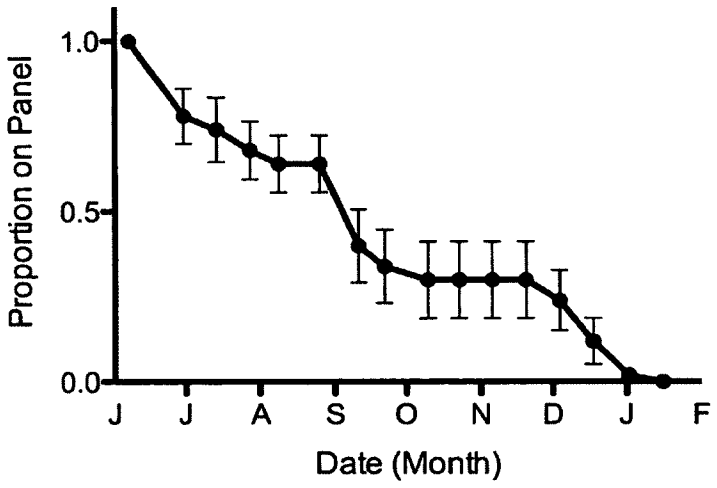

Figure 40: Proportion of *Sagartia elegans* on panels from June 2011 to January 2012. A portion of the animals released from the panel within the first few weeks, probably due to the difference in temperature and other abiotic factors differing between their source culture and the field. In August Hurricane Irene removed three panels and damaged many of the anemones which subsequently released from the panels. Below 11 °C animals started to release from the panels quickly and were gone before temperatures reached 6 °C.

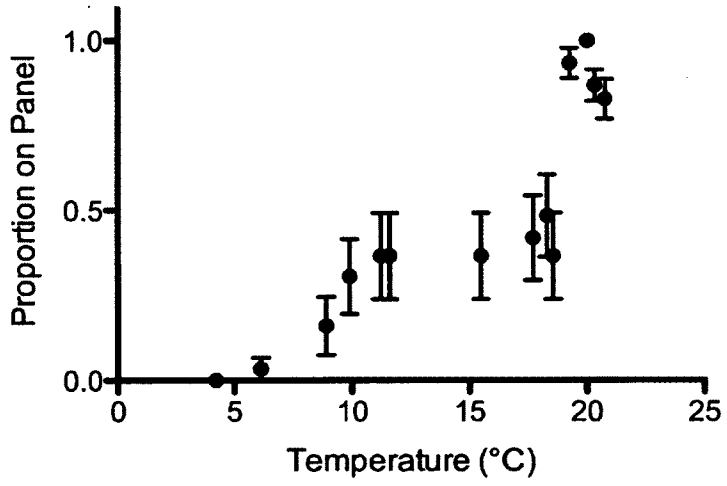

Figure 41: Proportion of *Sagartia elegans* on panels from June 2011 to January 2012 compared with water temperature including data points before Hurricane Irene. Anemones started to release in great numbers during Hurricane Irene and after temperatures fell below 11 °C.

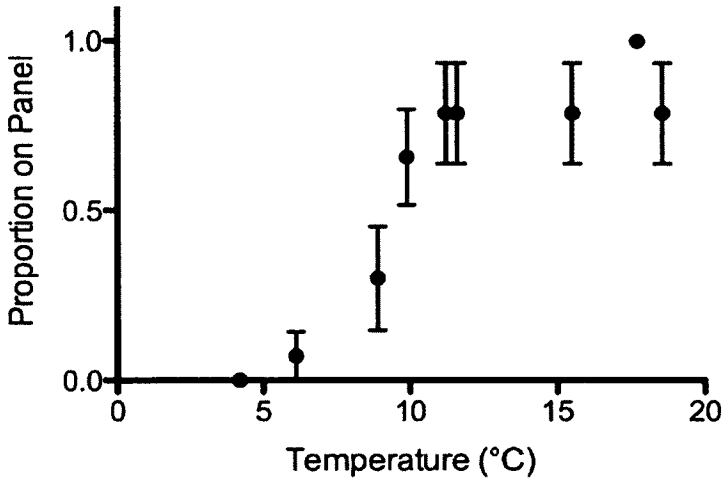

Figure 42: Proportion of *Sagartia elegans* on panels from June 2011 to January 2012 compared with water temperature without data points before Hurricane Irene. Anemones did not release until temperatures fell below 11 °C.

Discussion

S. elegans was present every year prior to the winter of 2010-2011 at Hawthorne Cove Marina in Salem Harbor, MA (Pederson *et al.*, 2001; Pederson *et al.*, 2005; Harris, personal communication). After the winter of 2010-2011 *S. elegans* could not be found in Salem Harbor including via SCUBA surveys and on remote flocking docks. The species did not recruit after the winter of 2010-2011 indicating that the source population(s) must have disappeared.

The disappearance of *S. elegans* may have to do with its inability to tolerate the temperature present in Salem Harbor. I have recorded temperature within Salem Harbor below 2 °C during the winters of 2011 and 2012. This is much lower than the temperature *S. elegans* was found to release from it substratum: 11 °C (Figure 41 and 42). Asexual reproduction was found to stop at 9.3 °C (Figure 38) and animals were dead in both laboratory experiments (Section 1.3, Figure 18) and in the field (Figure 39) at temperatures below 6 °C.

For *S. elegans* to survive the winter, the population must have a temperature refuge. One potential temperature refuge within the harbor is the discharge channel of a coal and oil-fired power plant. This plant is located less than 100 meters from Hawthorne Cove Marina (Figure 43). The power plant is allowed to withdraw 2.53 billion liters of seawater daily and discharge that water up to 15.8 °C warmer than ambient temperature (Anderson *et al.*, 1975). Within the discharge channel, temperatures may rise up to 9.6 °C (Anderson *et al.*, 1975). An increase of only a few degrees during the winter would be enough to ensure survival of *S. elegans* throughout the winter months. It is possible that *S. elegans* could overwinter in the discharge channel and then recruit at Hawthorne

Cove Marina when temperature becomes more appropriate. This would explain the cyclical nature of the population at Hawthorne Cove Marina.

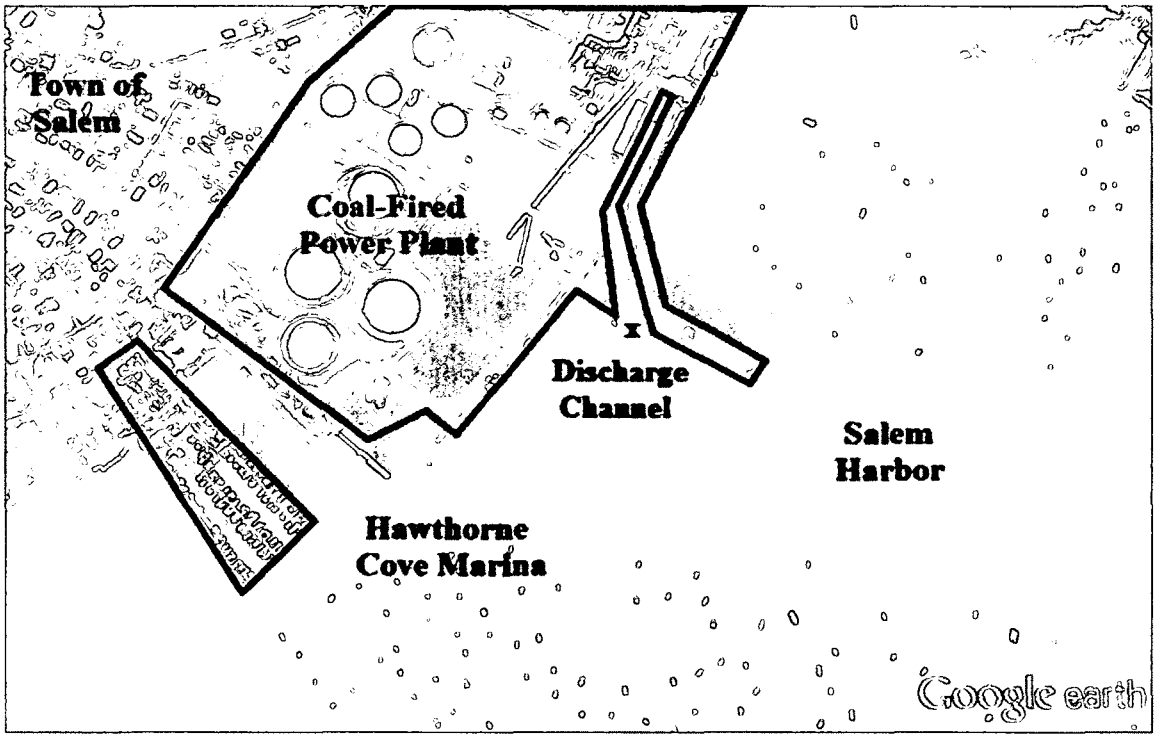

Figure 43: Aerial view of part of Salem Harbor. Nearly adjacent to Hawthorne Cove Marina is a coal-fired power plant which could have been used as a warm-water refuge during times when sea surface temperature was too low for survival of *Sagartia elegans*. The x denotes the exit of the discharge channel for the power plant.

DISCUSSION

One possible reason for the disappearance of *S. elegans* is heavy precipitation during the winter reducing the salinity to levels detrimental to *S. elegans* survival. Survival is negatively impacted when salinities decrease below 20 ppt (Figure 18). Precipitation in the area (Logan Airport, Boston, MA) in January of 2011 was approximately 40 mm higher than the average of the previous three years (NOAA, 2013). This elevated precipitation may have lowered the salinity to unsuitable levels for the introduced population, but impacts of precipitation on Salem Harbor salinity have not been studied. Salinities during an environmental impact assessment were not found to be highly variable within the harbor, ranging from 23.5 to 34.5 ppt (Anderson *et al.*, 1975) and it is therefore unlikely that *S. elegans* failed due to salinity alone.

Temperature probably played the largest role in the disappearance of *S. elegans*. Temperatures below 6 °C were found to be detrimental to *S. elegans* survival in both culture (Figure 18) and in the field (Figure 39). This temperature was higher than the average daily meteorological winter temperature (i.e. December through February) of seven of the nine years prior to its failure (Figure 44A; NOAA, 2013). This temperature was lower than all the average daily temperatures for the month of February during the previous nine years (Figure 44B; NOAA, 2013). For *S. elegans* to survive the winter, the population must have a temperature refuge. One such refuge within the harbor is a coal and oil-fired power plant. The plant is located less than 100 meters from Hawthorne Cove Marina (Figure 43) and is allowed to withdraw 2.53 billion liters of seawater each day and discharge that water up to 15.8 °C warmer than ambient temperature for

thermoelectric cooling (Anderson *et al.*, 1975). Within the discharge channel temperatures may rise up to 9.6 °C (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.

Transport from the power plant to Hawthorne Cove Marina may simply involve individuals releasing from the substratum, as has been seen in culture (Section 1.1), and reattaching to floats. *S. elegans* could also attach to floating debris and algae to get to Hawthorne Cove Marina. *S. elegans* was frequently observed releasing from its substrata and floating in the culturing tank when stressed. This behavior seems to be a common behavior within the genus. Adult *S. trogolodytes* and *S. nigropunctata* have also been observed releasing from their substrata in the same fashion (Gosse, 1860;

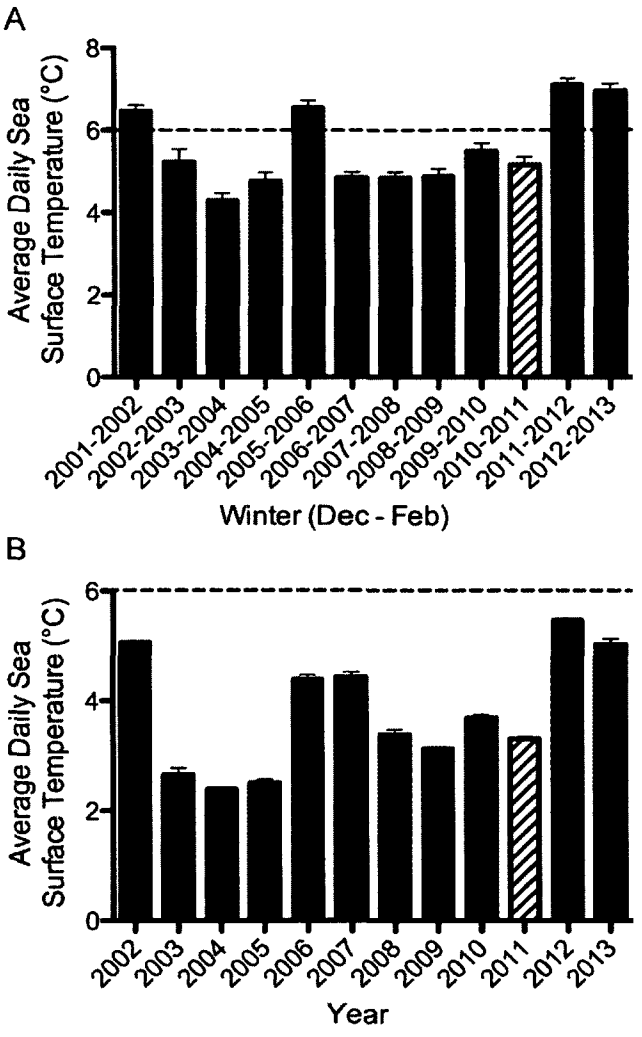

Figure 44: Average daily sea surface temperature for (A) December through February and in (B) February in the winters from 2001-2002 to 2012-2013 in Massachusetts Bay (Mean ± 1 SE). The hashing denotes the year of the disappearance of *Sagartia elegans* from Salem Harbor, MA. Temperatures below the hashed line indicate fatal temperatures. Average daily winter sea surface temperature in the winter *S. elegans* disappeared falls within temperatures of previous years *S. elegans* overwintered.

Ashworth and Annandale, 1904). Harris (personal communication) has also observed this behavior with *E. prolifera*. This ability to move relatively great distances for normally sedentary adults allows for greater dispersal and colonizing ability (Jokiel, 1989; Martel and Chia, 1991; Helmuth *et al.*, 1994) and may occur more frequently than expected (Johannesson, 1988; Worcester, 1994). Suspension in the water column, through releasing from the substratum, would increase the chances of encountering floating and rafting debris, which could greatly enhance long distance, adult dispersal (Arnaud *et al.*, 1976; Highsmith, 1985; Jackson, 1986).

Many aquatic organisms use warm-water effluent to survive in locations that would normally be too cold. Thermal enrichment of an Arkansas lake greatly increased the growth rate of largemouth bass *Micropterus salmoides* (Lacepède, 1802) (Galloway and Kilambi, 1988). Growth rate and survival during winter was also increased with introduced Nile tilapia *Oreochromis niloticus* (Linnaeus, 1758) using the thermal effluent from a tilapia aquaculture facility (Peterson *et al.*, 2005). Introduced tilapia (redbelly tilapia *Tilapia zilli* (Gervais, 1848) and blue tilapia *O. aureus* (Steindachner, 1864)) have also been described utilizing the warm-water effluent from a nuclear power plant in North Carolina (Crutchfield, 1995). The introduced Asian clam *Corbicula fluminea* (Müller, 1774) survives in the warm-water effluent during the cold winter months in the St. Lawrence River (Simard *et al.*, 2012). Study sites were repopulated each year by *C. fluminea* by August by passive downstream movement from populations in refuges from winter stresses (discharge of Middleton and South Meadow power stations) (Morgan *et al.*, 2004).

It is probable that the introduced population of *S. elegans* was all one clone. All animals were of one color morph with olive columns and pedal disks, translucent olive oral disks, and magenta tentacles. This is in contrast to the variety of color morphs in their native range; there are at least five fairly distinct color morphs with intergrading forms common (Stephenson, 1935; Manuel, 1981, 1988). Although *S. elegans* is dioecious, all sexually mature *S. elegans* had female gonads, indicative of a clonal population. Unisexuality has been observed in populations of the sea anemones *D. lineata* (Shick, 1976; Shick and Lamb, 1977; Dunn, 1982), *Anthopleura asiatica* Uchida and Muramatsu, 1958 (Fujii, 1987), and *Nematostella vectensis* Stephenson, 1935 (Harris, personal communication). Sex change has rarely been observed in sea anemones (Carter and Funnell, 1980; Ayre, 1988; Carter and Miles, 1989, but see Schlesinger *et al.*, 2010) and within a normal, sexually reproducing population of sea anemones the sex ratio is commonly 1:1 (Gemmill, 1920; Carter and Thorpe, 1981; Jennison, 1981; Sebens, 1981b; Shaw *et al.*, 1987; Hunt and Ayre, 1989). If the introduced population consisted of one clone then adaptation, through genetic recombination during sexual reproduction, would be absent. Genetic recombination, particularly chromosomal crossover, is important in creating new combinations of genes from the parents. *S. elegans* would not have had a chance to adapt to the Gulf of Maine environment and therefore was likely to fail at some point.

One possible method for controlling the spread of some introduced species may be to briefly shut down or reduce the output of a power plant. This assumes that the introduced species could not live without the power plant and that the cost of keeping a

power plant off for the required amount of time to kill the introduced species is less than the damages that the introduced species would incur on the local ecosystem.

It is still unclear as to why the introduced population of *S. elegans* failed. It is likely a combination of both a lack of genetic diversity and an inability to tolerate the cold temperatures present in the Gulf of Maine during winter. Increased effort in detecting introduced species immediately or shortly after introduction will be important in both eradication efforts and collecting data on failed introductions. More data on failed introductions will only promote a deeper understanding of the introduction process.

LIST OF REFERENCES

Anderson, C.O., Jr., Brown, D.J., Ketschke, B.A., Elliott, E.M., and Rule, P.L. 1975. *The effects of the addition of a fourth generating unit at the Salem Harbor Electric Generation Station on the marine ecosystem of Salem Harbor.* Massachusetts Division of Marine Fisheries, Boston.

Arnaud, F., Arnaud, P.M., Intès, A., and Le Loeuff, P. 1976. Transport d'invertébrés benthiques entre l'Afrique du Sud et Sainte Hélène par les laminaires (Phaeophyceae). *Bulletin du Muséum National d'Histoire Naturelle* 384: 49-55.

Ashworth, J.H., and Annandale, N. 1904. Observations on some aged specimens of *Sagartia troglodytes*, and on the duration of life in coelenterates. *Proceedings of the Royal Society of Edinburgh* 25: 295-308.

Ates, R.M.L., Dekker, R., Faasse, M.A., and den Hartog, J.C. 1998. The ocurrence of *Sagartia elegans* (Dalyell, 1848) (Anthozoa: Actiniaria) in the Netherlands. *Zoologische Verhandelingen* 323: 263-276.

Ayre, D.J. 1988. Evidence for genetic determination of sex in *Actinia tenebrosa*. *Journal of Experimental Marine Biology and Ecology* 116: 23-34.

Barbour, M.G., and Rodman, J.E. 1970. Saga of the west coast sea-rockets: *Cakile edentula* ssp. *californica* and *C. maritima*. *Rhodora* 72: 370-386.

Bateman, M.A. 1977. Dispersal and species interaction as factors in the establishment and success of tropical fruit flies in new areas. *The Proceedings of the Ecological Society of Australia* 10: 106-112.

Benedict, B. 1957. The immigrant birds of Mauritius. *Avicultural Magazine* 63: 155-157.

Bertness, M.D. 1977. Behavioral and ecological aspects of shore-level size gradients in *Thais lamellosa* and *Thais emarginata*. *Ecology* 58: 86-97.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson, J.R.U., and Richardson, D.M. 2011. A proposed unified framework for biological invasions. *Trends in Ecology & Evolution* 26: 333-339.

Bocharova, E.S., and Kozevich, I.A. 2011. Modes of reproduction in sea anemones (Cnidaria, Anthozoa). *Biological Bulletin* 38: 849-860.

Boyd, R.S., and Barbour, M.G. 1993. Replacement of *Cakile edentula* by *C. maritima* in the strand habitat of California. *American Midland Naturalist* 130: 209-228.

Brace, R.C., and Pavey, J. 1978. Size-dependent dominance hierarchy in the anemone *Actinia equina*. *Nature* 273: 752-753.

Braks, M.A.H., Honório, N.A., Lounibos, L.P., Lourenço-De-Oliveira, R., and Juliano, S.A. 2004. Interspecific competition between two invasive species of container mosquitoes, *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae), in Brazil. *Annals of the Entomological Society of America* 97: 130-139.

Budy, P., Thiede, G.P., Lobón-Cerviá, J., Fernandez, G.G., McHugh, P., McIntosh, A., Vøllestad, L.A., Becares, E., and Jellyman, P. 2013. Limitation and facilitation of one of the world's most invasive fish: an intercontinental comparison. *Ecology* 94: 356-367.

Burgess, C.M. 1959. Where did this shell come from? *Hawaiian Shell News* 7: 73-74.

Burnaford, J.L., Henderson, S.Y., and Pernet, B. 2011. Assemblage shift following population collapse of a non-indigenous bivalve in an urban lagoon. *Marine Biology* 158: 1915-1927.

Carlton, J.T. 1989. Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. *Conservation Biology* 3: 265-273.

Carlton, J.T. 1996a. Biological invasions and cryptogenic species. *Ecology* 77: 1653-1655.

Carlton, J.T. 1996b. Marine bioinvasions: the alteration of marine ecosystems by nonindigenous species. *Oceanography* 9: 36-43.

Carlton, J.T. 2000. *Quo vadimus exotica oceanica*? Marine bioinvasion ecology in the twenty-first century. Pp. 6-23 in *Marine bioinvasions: first international conference*, Pederson, J., ed. MIT Sea Grant College Program, Cambridge.

Carlton, J.T., and Eldredge, L.G. 2009. Marine bioinvasions of Hawai'i: the introduced and cryptogenic marine and estuarine animals and plants of the Hawaiian archipelago. Bishop Museum, Honolulu.

Carpaneto, G.M. 1990. The Indian grey mongoose (*Herpestes edwardsi*) in the Circeo National Park: a case of incidental introduction. *Mustelid and Viverrid Conservation* 2: 10.

Carter, M.A., and Funnell, M. 1980. Reproduction and brooding in *Actinia*. Pp. 17-22 in *Developmental and cellular biology of coelenterates*, Tardent, P. and Tardent, R., eds. North-Holland Biomedical Press, Amsterdam.

Carter, M.A., and Miles, J. 1989. Gametogenic cycles and reproduction in the beadlet sea anemone *Actinia equina* (Cnidaria: Anthozoa). *Biological Journal of the Linnean Society* 36: 129-155.

Carter, M.A., and Thorpe, J.P. 1981. Reproductive, genetic and ecological evidence that *Actinia equina* var. *mesembryanthemum* and var. *fragacea* are not conspecific. *Journal of the Marine Biological Association of the United Kingdom* 61: 71-93.

Cheke, A.S. 1987. An ecological history of the Mascarene Islands, with particular reference to extinctions and introductions of land vertebrates. Pp. 5-89 in *Studies of Mascarene island birds*, Diamond, A.W., ed. Cambridge University Press, Cambridge.

Chia, F.-S. 1976. Sea anemone reproduction: patterns and adaptive radiations. Pp. 111-116 in *Coelenterate ecology and behavior*, Mackie, G.O., ed. Plenum Press, New York.

Cohen, A.N., and Carlton, J.T. 1995. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. United States Fish and Wildlife Services, Washington DC and the National Sea Grant College Program, Washington DC.

Cohen, A.N., Carlton, J.T., and Fountain, M.C. 1995. Introduction, dispersal and potential impacts of the green crab *Carcinus maenas*; in San Francisco Bay, California. *Marine Biology* 122: 225-237.

Crutchfield, J.U., Jr. 1995. Establishment and expansion of redbelly tilapia and blue tilapia in a power plant cooling reservoir. *American Fisheries Society Symposium* 15: 452-461.

Dunn, D.F. 1982. Sexual reproduction of two intertidal sea anemones (Coelenterata: Actiniaria) in Malaysia. *Biotropica* 14: 262-271.

Ebert, T.A. 1968. Growth rates of the sea urchin *Strongylocentrotus purpuratus* related to food availability and spine abrasion. *Ecology* 49: 1075-1091.

Ehrlich, P.R. 1989. Attributes of invaders and the invading processes: vertebrates. Pp. 315-328 in *Biological invasions, a global perspective*, Drake, J.A., Mooney, H.A., diCastri, F., Groves, R.H., Kruger, F.J., Rejmenek, M. and Williamson, M., eds. John Wiley and Sons, London.

Elkinton, J.S., Parry, D., and Boettner, G. 2001. Introduced tachinids explain decline of invasive browntail moth. *The ESA 2001 Annual Meeting.*

Elton, C.S. 1958. *The ecology of invasions by animals and plants.* Methuen and Co., London.

Eritja, R., Escosa, R., Lucientes, J., Marquès, E., Molina, R., and Ruiz, S. 2003. Esabliecimiento en Europa por importación accidental de mosquitos vectores de enfermedades humanas. Pp. 85-87 in *Contribuciones al conocimiento de las especies exóticas invasoras en España*, Capdevila-Argüelles, L., Zilletti, B. and Pérez Hidalgo, N., eds. Grupo Especies Invasoras, León.

Ferretti, C., Vacca, S., De Ciucis, C., Marengo, B., Duckworth, A.R., Manconi, R., Pronzato, R., and Domenicotti, C. 2009. Growth dynamics and bioactivity variation of the Mediterranean demosponges *Agelas oroides* (Agelasida, Agelasidae) and *Petrosia ficiformis* (Haplosclerida, Petrosiidae). *Marine Ecology* 30: 327-336.

Francis, L. 1976. Social organization within clones of the sea anemone *Anthopleura elegantissima. Biological Bulletin* 150: 361-376.

Fujii, H. 1987. The predominance of clones in populations of the sea anemone *Anthopleura asiatica* (Uchida). *The Biological Bulletin* 172: 202-211.

Fulton, C. 1962. Environmental factors influencing the growth of *Cordylophora. Journal of Experimental Zoology* 151: 61-78.

Galloway, M.L., and Kilambi, R.V. 1988. Thermal enrichment of a reservoir and the effects on annulus formation and growth of largemouth bass, *Micropterus salmoides. Journal of Fish Biology* 32: 533-543.

Gaubert, P., and Zenatello, M. 2009. Ancient DNA perspective on the failed introduction of mongooses in Italy during the XXth century. *Journal of Zoology* 279: 262-269.

Gemmill, J.F. 1920. The development of the sea-anemones *Metridium dianthus* (Ellis) and *Adamsia palliata* (Bohad). *Philosophical Transactions of the Royal Society of London* 209: 351-375.

Gosse, P.H. 1860. *Actinologia britannica: a history of the British sea-anemones and corals.* Van Voorst, London.

Hairston, N.G., Jr., Perry, L.J., Bohonak, A.J., Fellows, M.Q., Kearns, C.M., and Engstrom, D.R. 1999. Population biology of a failed invasion: paleolimnology of *Daphnia exilis* in upstate New York. *Limnology and Oceanography* 44: 477-486.

Harris, L.G. 1973. Nudibranch associations. Pp. 213-315 in *Current topics in comparative pathobiology*, Cheng, T.C., ed. Academic Press, New York.

Harris, L.G. 1986. Size-selective predation in a sea anemone, nudibranch, and fish food chain. *The Veliger* 29: 38-47.

Harris, L.G. 1991. Comparative ecology of subtidal actiniarians from the coasts of California and the Gulf of Maine, USA. *Hydrobiologia* 216/217: 271-278.

Helmuth, B., Veit, R.R., and Holberton, R. 1994. Long-distance dispersal of a subantartic brooding bivalve (*Gaimardia trapesina*) by kelp-rafting. *Marine Biology* 120: 421-426.

Highsmith, R.C. 1985. Floating and algal rafting as potential dispersal mechanisms in brooding invertebrates. *Marine Ecology Progress Series* 25: 169-179.

Hillman, R.E. 1985. Pathology of shipworms in Barnegat Bay - a model system. *American Malcological Union* Special Edition 1: 101-109.

Hoagland, K.E., and Turner, R.D. 1980. Range extensions of teredinids (shipworms) and polychaetes in the vicinity of a temperate-zone nuclear generating station. *Marine Biology* 58: 55-64.

Hunt, A., and Ayre, D.J. 1989. Population structure in the sexually reproducing sea anemone *Oulactis muscosa*. *Marine Biology* 102: 537-544.

Hunter, T. 1984. The energetics of asexual reproduction: pedal laceration in the symbiotic sea anemone *Aiptasia pulchella* (Carlgren, 1943). *Journal of Experimental Marine Biology and Ecology* 83: 127-147.

Jackson, J.B.C. 1986. Modes of dispersal of clonal benthic invertebrates: consequences for species' distributions and genetic structure of local populations. *Bulletin of Marine Science* 39: 588-606.

Jennison, B.L. 1981. Reproduction in three species of sea anemones from Key West, Florida. *Canadian Journal of Zoology* 59: 1708-1719.

Johannesson, K. 1988. The paradox of Rockall: why is a brooding gastropod (*Littorina saxatilis*) more widespread than one having a planktonic larval dispersal stage (*L. littorea*)? *Marine Biology* 99: 507-513.

Johnson, L.L., and Shick, M.J. 1977. Effects of fluctuating temperature and immersion on asexual reproduction in the intertidal sea anemone *Haliplanella luciae* (Verrill) in laboratory culture. *Journal of Experimental Marine Biology and Ecology* 28: 141-149.

Johnson, S.R., and Campbell, R.W. 1995. Crested myna (*Acridotheres cristatellus*). in *The birds of North America*, Poole, A. and Gill, F., eds. The Acadamy of Natural Sciences, Philadelphia.

Jokiel, P.L. 1989. Rafting of reef corals and other organisms at Kwajalein Atoll. *Marine Biology* 101: 483-493.

Jones, C.G. 1996. Bird introductions to Mauritius: status and relationships with native birds. Pp. 113-123 in *The introduction and naturalisation of birds*, Holmes, J.S. and Simons, J.R., eds. HMSO, London.

Juliano, S.A. 1998. Species introduction and replacement among mosquitoes: interspecific resource competition or apparent competition? *Ecology* 79: 255-268.

Kaplan, L., Kendell, D., Robertson, D., Livdahl, T., and Khatchikian, C. 2010. *Aedes aegypti* and *Aedes albopictus* in Bermuda: extinction, invasion, invasion and extinction. *Biological Invasions* 12: 3277-3288.

Keiser, I., Kobayashi, R.M., Miyashita, D.H., Harris, E.J., Schneider, E.L., and Chambers, D.L. 1974. Suppression of mediterranean fruit flies by oriental fruit flies in mixed infestations in Guava. *Journal of Economic Entomology* 67: 355-360.

Kohn, A.J. 1971. Diversity, utilization of resources, and adaptive radiation in shallow-water marine invertebrates of tropical oceanic islands. *Limnology and Oceanography* 16: 141-154.

Kolar, C.S., and Lodge, D.M. 2001. Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution* 16: 199-204.

Kratter, A.W. 2012. Twenty-first report of the Florida Ornithological Society Records Committee: 2011. *Florida Field Naturalist* 40: 85-100.

Léger, P., Naessens-Foucquaert, E., and Sorgeloos, P. 1987. International study on *Artemia* XXXV. Techniques to manipulate the fatty acid profile in *Artemia* nauplii, and the effect on its nutritional effectiveness for the marine crustacean *Mysidopsis bahia* (M.). Pp. 411-424 in *Artemia research and its applications*, Sorgeloos, P., Bengtson, D.A., Decleir, W. and Jaspers, E., eds. Universa Press, Belgium.

Levitan, D.R. 1988. Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi. *Oecologia* 76: 627-629.

Lockwood, J.L., Cassey, P., and Blackburn, T. 2005. The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution* 20: 223-228.

Loomis, W.F. 1954. Environmental factors controlling growth in *Hydra*. *Journal of Experimental Zoology* 126: 223-234.

MacIsaac, H.J., Tedla, R.A., and Ricciardi, A. 2011. Patterns and rate of growth of studies in invasion ecology. Pp. 51-60 in *Fifty years of invasion ecology: the legacy of Charles Elton*, Richardson, D.M., ed. Blackwell Publishing Ltd., Oxford.

Maelzer, D.A. 1990. Fruit-fly outbreaks in Adelaide, S.A., From 1948-49 to 1986-87 1. Demarcation, frequency and temporal patterns of outbreaks. *Australian Journal of Zoology* 38: 439-452.

Manuel, R.L. 1981. *British Anthozoa.* The Linean Society, London.

Manuel, R.L. 1988. *British Anthozoa (Coelenterata: Octocorallia & Hexacorallia): keys and notes for the identification of the species.* Linnean Society of London and the Estuarine and Brackish-water Sciences Association, London.

Martel, A., and Chia, F.-S. 1991. Drifting and dispersal of small bivalves and gastropods with direct development. *Journal of Experimental Marine Biology and Ecology* 150: 131-147.

Massachusetts Office of Coastal Zone Management. 2013. Report on the 2010 rapid assessment survey of marine species at New England floating docks and rocky shores. Massachusetts Office of Coastal Zone Management, Boston.

Mead, A.R., ed. 1979. *Ecological malacology: with particular reference to Achatina fulica.* Academic Press, London.

Meinertzhagen, R. 1912. On the birds of Mauritius. *Ibis* 6: 82-108.

Meinesz, A., de Vaugelas, J., Hesse, B., and Mari, X. 1993. Spread of the introduced tropical green alga *Caulerpa taxifolia* in northern Mediterranean waters. *Journal of Applied Phycology* 5: 141-147.

Miller, A.W., Ruiz, G.M., Minton, M.S., and Ambrose, R.F. 2007. Differentiating successful and failed molluscan invaders in estuarine ecosystems. *Marine Ecology Progress Series* 332: 41-51.

Minasian, L.L., Jr. 1976. Characteristics of asexual reproduction in the sea anemone, *Haliplanella luciae* (Verrill), reared in the laboratory. Pp. 289-298 in *Coelenterate ecology and behavior*, Mackie, G.O., ed. Plenum Press, New York.

Minasian, L.L., Jr. 1979. The effect of exogenous factors on morphology and asexual reproduction in laboratory cultures of the intertidal sea anemone, *Haliplanella luciae* (Verrill) (Anthozoa: Actiniaria) from Delaware. *Journal of Experimental Marine Biology and Ecology* 40: 235-246.

Minasian, L.L., Jr. 1982. The relationship of size and biomass to fission rate in a clone of the sea anemone, *Haliplanella luciae* (Verrill). *Journal of Experimental Marine Biology and Ecology* 58: 151-162.

Minasian, L.L., Jr., and Mariscal, R.N. 1979. Characteristics and regulation of fission activity in clonal cultures of the cosmopolitan sea anemone, *Haliplanella luciae* (Verrill). *Biological Bulletin* 157: 478-493.

Miyawaki, M. 1952. Temperature as a factor influencing upon the fission rate of the orange-striped sea anemone, *Diadumene luciae*. *Journal of the Faculty of Science of Hokkaido University* 10: 123-126.

Mooney, H.A., and Cleland, E.E. 2001. The evolutionary impact of invasive species. *Proceedings of the National Academy of Sciences of the United States of America* 98: 5446-5451.

Morgan, D.E., Keser, M., Swenarton, J.T., and Foertch, J.F. 2004. Effect of Connecticut Yankee Power Plant on population dynamics of Asiatic clams and their interactions with native bivalves. *American Fisheries Society Monograph* 9: 419-439.

Nishikawa, T., and Otani, M. 2004. Occurrence of the European ascidian *Ascidiella scabra* (Müller, 1776) in the 19 century in Nagasaki, Japan, probably as an ephemeral alien species. *Contributions from the Biological Laboratory, Kyoto University* 29: 401-408.

NOAA. 2013. National Weather Service Forecast Office. National Oceanic and Atmospheric Administration, Washington.

Occhipinti-Ambrogi, A., and Sheppard, C. (Eds). 2007. Marine bioinvasions: a collection of reviews. *Marine Pollution Bulletin* 55: 299-401.

Ottaway, J.R. 1979. Population ecology of the intertidal anemone *Actinia tenebrosa* III. Dynamics and environmental factors. *Australian Journal of Marine and Freshwater Research* 30: 41-62.

Paine, R.T. 1965. Natural history, limiting factors and energetics of the opisthobranch *Navanax inermis*. *Ecology* 46: 603-619.

Paine, R.T. 1969. The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. *Ecology* 50: 950-961.

Paine, R.T. 1974. Intertidal community structure - experimental studies on the relationship between a dominant competitorand its principal predator. *Oecologia* 15: 93-120.

Paine, R.T. 1976. Size-limited predation: an observational and experimental approach with the *Mytilus-Pisaster* interaction. *Ecology* 57: 858-873.

Pederson, J., Bullock, R., Calder, D., Carlton, J.T., Chapman, J.W., Cohen, A.N., Dean, H., Dyrynda, P., Harris, L.G., Lambert, C., Lambert, G., Mathieson, A., Tyler, S., and Winston, J.E. 2001. Draft rapid assessment survey of Massachusetts, August 7-11, 2000. Massachusetts Institute of Technology Sea Grant Program College Program, Cambridge.

Pederson, J., Bullock, R., Carlton, J.T., Dijkstra, J.A., Dobroski, N., Dyrynda, P., Fisher, R., Harris, L.G., Hobbs, N., Lambert, G., Lazo-Wasem, E., Mathieson, A., Miglietta, M.-P., Smith, J., Smith, J., III, and Tyrrell, M. 2005. Marine invaders in the northeast. Massachusetts Institute of Technology, Cambridge.

Peterson, M.S., Slack, W.T., and Woodley, C.M. 2005. The occurrence of non-indigenous Nile tilapia, *Oreochromis niloticus* (Linnaeus) in coastal Mississippi, USA: ties to aquaculture and thermal effluent. *Wetlands* 25: 112-121.

Pimentel, D., Zuniga, R., and Morrison, D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. *Ecological Economics* 52: 273-288.

Pineda, J., and Escofet, A. 1989. Selective effects of disturbance on populations of sea anemones from northern Baja California, Mexico. *Marine Ecology Progress Series* 55: 55-62.

Pranty, B. 2001. The budgerigar in Florida: rise and fall of an exotic psittacid. *North American Birds* 55: 389-397.

Richardson, D.M., and Pyšek, P. 2008. Fifty years of invasion ecology – the legacy of Charles Elton. *Diversity and Distributions* 14: 161-168.

Rodman, J.E. 1986. Introduction, establishment and replacement of sea-rockets (Cakile, Cruciferae) in Australia. *Journal of Biogeography* 13: 159-171.

Ross, D.M. 1960. The association between the hermit crab *Euparugus bernhardus* (L.) and the sea anemone *Calliactis parasitica* (Couch). *Proceedings of the Zoological Society of London* 134: 43-57.

Ross, D.M. 1965. Complex and modifiable behavior patterns in *Calliactis* and *Stomphia*. *American Zoologist* 5: 573-580.

Ross, D.M., and Sutton, L. 1961. The response of the sea anemone *Calliactis parasitica* to shells of the hermit crab *Pagurus berhardus*. *Proceedings of the Royal Society of London* 155: 266-281.

Rountree, F.R.G., Guérin, R., Pelte, S., and Vinson, J. 1952. Catalogue of the birds of Mauritius. *Mauritius Institute Bulletin* 3: 155-217.

Russell, D.J. 1992. The ecological invasion of Hawaiian reefs by two marine red algae, *Acanthophora spicifera* (Vahl) Boerg. and *Hypnea musciformis* (Wulfen) J. Ag., and their association with two native species, *Laurencia nidifica* J. Ag. and *Hypnea cervicornis* J. Ag. *ICES Marine Science Symposium* 194: 110-125.

Samways, M., Hitchens, P., Bourquin, O., and Henwood, J. 2010. *Tropical island recovery: Cousine Island, Seychelles*. John Wiley & Sons, Chichester.

Sax, D.F., and Brown, J.H. 2000. The paradox of invasion. *Global Ecology and Biogeography* 9: 363-371.

Schlesinger, A., Kramarsky-Winter, E., Rosenfeld, H., Armoza-Zvoloni, R., and Loya, Y. 2010. Sexual plasticity and self-fertilization in the sea anemone *Aiptasia diaphana*. *PLoS ONE* 5: e11874.

Sebens, K.P. 1976. The ecology of Caribbean sea anemones in Panama: utilization of space on a coral reef. Pp. 67-77 in *Coelenterate ecology and behavior*, Mackie, G.O., ed. Plenum Press, New York.

Sebens, K.P. 1977. Habitat suitability, reproductive ecology, and the plasticity of body size in two sea anemone populations (*Anthopleura elegantissima* and *A. xanthogrammica*), University of Washington, Seattle, Washington.

Sebens, K.P. 1979. The energetics of asexual reproduction and colony formation in benthic marine invertebrates. *American Zoologist* 19: 683-699.

Sebens, K.P. 1980. The regulation of asexual reproduction and indeterminate body size in the sea anemone *Anthopluera elegantissima* (Brandt). *Biological Bulletin* 158: 370-382.

Sebens, K.P. 1981a. The allometry of feeding, energetics, and body size in three sea anemone species. *Biological Bulletin* 161: 152-171.

Sebens, K.P. 1981b. Reproductive ecology of the intertidal sea anemones *Anthopleura xanthogrammica* (Brandt) and *A. elegantissima* (Brandt): body size, habitat, and sexual reproduction. *Journal of Experimental Marine Biology and Ecology* 54: 225-250.

Sebens, K.P. 1982a. Asexual reproduction in *Anthopleura elegantissima* (Anthozoa: Actiniaria): seasonality and spatial extent of clones. *Ecology* 63: 434-444.

Sebens, K.P. 1982b. The limits to indeterminate growth: an optimal size model applied to passive suspension feeders. *Ecology* 63: 209-222.

Sebens, K.P. 1983. Population dynamics and habitat suitability of the intertidal sea anemones *Anthopleura elegantissima* and *A. xanthogrammica. Ecological Monographs* 53: 405-433.

Sebens, K.P. 1984. Agonistic behavior in the intertidal sea anemone *Anthopleura xanthogrammica. The Biological Bulletin* 166: 457-472.

Sebens, K.P. 1987. The ecology of indeterminate growth in animals. *Annual Review of Ecology and Systematics* 18: 371-407.

Self, B. 2003. Vancouver crested mynas gone. *Winging It* 15: 7.

Shaw, P.W., Beardmore, J.A., and Ryland, J.S. 1987. *Sagartia troglodytes* (Anthozoa: Actiniaria) consists of two species. *Marine Ecology Progress Series* 41: 21-28.

Shick, J.M. 1976. Ecological physiology and genetics of the colonizing actinian *Haliplanella luciae*. Pp. 137-146 in *Coelenterate ecology and behavior*, Mackie, G.O., ed. Plenum Press, New York.

Shick, J.M. 1991. *A functional biology of sea anemones*. Chapman & Hall, London.

Shick, J.M., Hoffman, R.J., and Lamb, A.N. 1979. Asexual reproduction, population structure, and genotype-environment interactions in sea anemones. *American Zoologist* 19: 699-713.

Shick, J.M., and Lamb, A.N. 1977. Asexual reproduction and genetic population structure in the colonizing sea anemone *Haliplanella luciae*. *Biological Bulletin* 153: 604-617.

Simard, M.A., Paquet, A., Jutras, C., Robitaille, Y., Blier, P.U., Courtois, R., and Martel, A.L. 2012. North American range extension of the invasive Asian clam in a St. Lawrence River power station thermal plume. *Aquatic Invasions* 7: 81-89.

Simberloff, D. 1992. Extinction, survival, and the effects of birds introduced to the Mascarenes. *Acta Oecologica* 13: 663-678.

Simberloff, D. 2009. The role of propagule pressure in biological invasions. *Annual Review of Ecology, Evolution, and Systematics* 40: 81-102.

Simberloff, D., and Gibbons, L. 2004. Now you see them, now you don't! – population crashes of established introduced species. *Biological Invasions* 6: 161-172.

Simberloff, D., Parker, I.M., and Windle, P.N. 2005. Introduced species policy, management, and future research needs. *Frontiers in Ecology and the Environment* 3: 12-20.

Smith, N., III, and Lenhoff, H.M. 1976. Regulation of frequency of pedal laceration in a sea anemone. Pp. 117-125 in *Coelenterate ecology and behavior*, Mackie, G.O., ed. Plenum Press, New York.

Staub, F. 1976. *Birds of Mascarenes and St. Brandon.* Mauritius: Organisation Normale des Entreprises, Port Louis.

Stehouwer, H. 1952. The preference of the slug *Aeolidia papillosa* (L.) for the sea anemone, *Metridium senile* (L.). *Archives Neerlandaises de Zoologie* 10: 161-170.

Stephenson, T.A. 1928. *The British sea anemones.* Ray Society, London.

Stephenson, T.A. 1929. On methods of reproduction as specific characters. *Journal of the Marine Biological Association of the United Kingdom* 16: 131-172.

Stephenson, T.A. 1935. *The British sea anemones.* Ray Society, London.

Thresher, R.E. 2000. Key threats from marine bioinvasions: a review of current and future issues. Pp. 24-36 in *Marine bioinvasions: first international conference*, Pederson, J., ed. MIT Sea Grant College Program, Cambridge.

Vadas, R.L. 1977. Preferential feeding: an optimization strategy in sea urchins. *Ecological Monographs* 47: 337-371.

Waterhouse, D.F., and Norris, K.R. 1987. *Achatina fulica* Bowdich. Mollusca: Achatinidae giant African Snail. in *Biological control*, Waterhouse, D.F. and Norris, K.R., eds. Inkata Press, Melbourne.

Williamson, M., and Fitter, A. 1996. The varying success of invaders. *Ecology* 77: 1661-1666.

Worcester, S.E. 1994. Adult rafting versus larval swimming: dispersal and recruitment of a botryllid ascidian on eelgrass. *Marine Biology* 121: 309-317.

Zenni, R.D., and Nuñez, M.A. 2013. The elephant in the room: the role of failed invasions in understanding invasion biology. *Oikos* 122: 801-815.