5-2016

Settling Patterns of Chrysaora quinquecirrha Polyps on Common Vinyl Construction Material : Potential Implications for Jellyfish Blooms and Coastal Development in Barnegat Bay New Jersey

Alexander Lawrence Soranno

Settling Patterns of *Chrysaora quinquecirrha* Polyps On Common Vinyl Construction Material: Potential Implications For Jellyfish Blooms And Coastal Development In Barnegat Bay New Jersey.

ABSTRACT

Coastal development in estuaries is altering abiotic and biotic factors that encourage the propagation of populations of *Chrysaora quinquecirrha*. Extensive coastal development results in the proliferation of vinyl bulkheads and plastic floating docks in the Barnegat Bay estuary system. The purpose of this study was to determine if the increase in artificial vinyl substrate can affect density of *C. quinquecirrha* polyp recruitment. Oyster shell and vinyl settling plates were submerged at ten sites in Barnegat Bay for six, two-week periods during the summer of 2014. Polyps showed a greater affinity for settling on vinyl plates (0.337 polyps/cm^2) than oyster shell settling plates (0.179 polyps/cm^2, $P < 0.0248$). Settling density was greater for under hanging surfaces and *C. quinquecirrha* settled more often on vinyl undersides, (0.515 polyps/cm^2) than oyster shell undersides, (0.233 polyps/cm^2, $P < 0.0001$). There was no detectable difference between the settlement on vertical and top surfaces of either substratum. The densities of *C. quinquecirrha* medusa were also measured to determine if the presence of medusae was linked to the presence of polyps. A regression analysis revealed a significant positive relationship between the density of *C. quinquecirrha* medusae in the lagoon and the density of polyps on settling plates ($r = 0.6660$; $P < 0.0187$). Nudibranchs are potential predators of *C. quinquecirrha* polyps and were observed feeding on polyps in a laboratory setting. Nudibranch density was measured for each set of plates to determine if nudibranch predation affected the polyp density. A regression analysis did not show a significant relationship between the density of nudibranchs and the density of

polyps ($r = -0.1263$; $P < 0.8099$), but the negative relationship suggests the potential that they could contribute to polyp reduction in some lagoons. Artificial substratum in the form of vinyl bulkheads and floating docks provides habitat for polyps and this increase in substratum is likely to enhance populations of *C. quinquecirrha* in Barnegat Bay, New Jersey. My results indicate that there are hotspots of polyp recruitment in Barnegat Bay and are related to the presence of reproducing adults in the area. Since the biphasic life history of this species requires hard, non-toxic substrate to overwinter and proliferate, the increasing use of these materials in coastal communities is bound to lead to greater numbers in the future. Potential solutions for limiting their proliferation include improving water quality, which could lead to greater competition for space or the introduction of polyp predators to interrupt the life history cycle leading to fewer adults being generated.

MONTCLAIR STATE UNIVERSITY

Settling Patterns of *Chrysaora quinquecirrha* Polyps On Common Vinyl Construction Material: Potential Implications For Jellyfish Blooms And Coastal Development In Barnegat Bay New Jersey.

by

Alexander Lawrence Soranno

A Master's Thesis Submitted to the Faculty of Montclair State University

In Partial Fulfillment of the Requirements For the Degree of

Master of Science, Biology

May 2016

College/School: College of Science and Mathematics

Department: Biology

Thesis Committee:

[redacted]

Dr. Paul A. X. Bologna
Thesis Sponsor

[redacted]

Dr. John J. Gaynor

[redacted]

Dr. Robert S. Prezant
Committee Member

SETTLING PATTERNS OF *CHRYSAORA QUINQUECIRRHA* POLYPS ON COMMON VINYL CONSTRUCTION MATERIAL: POTENTIAL IMPLICATIONS FOR JELLYFISH BLOOMS AND COASTAL DEVELOPMENT IN BARNEGAT BAY NEW JERSEY.

A THESIS

Submitted in partial fulfillment of requirements

For the degree of Master of Science, Biology

By

Alexander L. Soranno

Montclair State University

Montclair, NJ

2016

ACKNOWLEDGEMENTS

I would like to thank my committee, Dr. Bologna, Dr. Prezant, and Dr. Gaynor, for their guidance and advice during this process. My volunteers, Tara Snyder, Christina Hernandez, and Pat Vojnyk gave up countless hours during their summer to travel up and down Barnegat Bay with me. Christie Barry helped with materials, logistics, and good advice throughout this study. Dr. Bushek and the Haskin Shellfish Laboratory supplied all the oyster shell I needed, and Marine Lumber & Piling lumberyard donated vinyl sheets for settling plates. Last but not least I would like to thank: Dave Daggett, Will Needham, Bruce Hillyer, Rosemary Mason, Rita Carey, Joe Balogh, Marie Talty, Anne Hruza, Dan Hurley, Tom Vannostrand, and the Waretown Marina for graciously allowing me to hang equipment from their docks and wander onto their property every two weeks.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

APPENDIX

INTRODUCTION

The Atlantic sea nettle, *Chrysaora quinquecirrha* Desor 1848, is a scyphozoan jellyfish found along the coast of eastern North America. They inhabit pelagic and coastal habitats, but most human encounters occur in near shore areas. They are known as a nuisance species in shallow, eutrophic estuaries. The life cycle of *C. quinquecirrha,* combined with ecosystems impacted by shoreline construction and eutrophic conditions, enables it to reproduce in large numbers and spread quickly (Purcell et al. 2007; Richardson et. al 2009; Bologna 2011).

The most visible portion of the jellyfish lifecycle is the adult medusa stage. Blooms of scyphozoan medusae have destroyed aquaculture fish stocks, clogged fishing nets, and shut down power plants (Purcell et al. 2007). Large numbers of *C. quinquecirrha* medusae appear in the waters of Barnegat Bay and other mid-Atlantic estuaries each spring (Purcell et al. 1999b; Bologna 2011). Adult medusae are the most recognizable stage in the *C. quinquecirrha* lifecycle, however it is the polyp stage that is critical in maintaining large populations of jellyfish.

C. quinquecirrha polyps are small, sessile, and difficult to find. A polyp has the ability to reproduce through asexual budding. They can also lay down small pedal buds called podocysts, which can survive harsh conditions. Each podocyst has the potential to develop into a new polyp and can live through several generations of medusae. One polyp has the potential to create dozens of the sexually reproducing adult medusae (Cargo & Shultz 1966; Cargo & Rabenold 1980).

The impact of the polyp stage is easy to overlook. *C. quinquecirrha* polyps live on hard surfaces within estuaries along the eastern United States and are the ultimate source of large jellyfish blooms (Arai 2009). Historical data on jellyfish blooms are not sufficient to definitively establish an increase in the frequency of jellyfish blooms worldwide (Purcell 2012). However, the Barnegat Bay estuary seems to be experiencing an increase in density, frequency, and range of *C. quinquecirrha* blooms. Jellyfish blooms impact tourism, fishing, and the overall ecological health of the ecosystems they inhabit (Purcell 1992; Purcell et al. 1994; Pitt et al. 2009; Richardson et al. 2009). Understanding the ecological factors that control *C. quinquecirrha* polyps may be the key to future population control and the ecological restoration of heavily impacted estuaries like Barnegat Bay.

Life Cycle

The spread and recruitment of *C. quinquecirrha* polyps is dependent on the motile medusa stage. Adult *C. quinquecirrha* medusae have a radially symmetrical bell with a single opening in the ventral side (Ford et al. 1997). The mouth is ringed by tentacles and oral arms, which use stinging cells called cnidocytes to catch and incapacitate their prey (Ford et al. 1997). *C. quinquecirrha* medusae swim continuously. The contracting and relaxing motion of the bell creates vortices, which push planktonic prey into the tentacles and oral arms (Ford et al. 1997). Fish eggs, fish larvae, crab larvae, and polychaete worms have all been found in *C. quinquecirrha* gastrovascular cavities, but their primary prey are copepods (Cargo & Shultz 1966; Ford et al. 1997).

The distribution of medusae is determined by temperature and salinity. Medusae can survive between 10°C and 34°C, but are most active between 26°C and 30°C (Decker et al. 2007). Their preferred salinity is between 10 and 16 ppt. As a result, the medusa stage of *C. quinquecirrha* typically appears in late spring in the northeastern United States. As temperatures and salinities rise in August, adult medusae begin to disappear (Decker et al. 2007).

Medusae are dioecious broadcast spawners. They release sperm and egg into the water column and fertilization takes place outside of the body. The zygote forms a motile planula (Cargo & Shultz 1966) that swims until it encounters a suitable hard substratum to attach itself to and metamorphose into the polyp stage. The polyps are most commonly found anchored on the underside of structures (Cargo & Shultz 1996). Planula may be negatively phototropic, which leads them to settle on the sheltered underside of suitable surfaces (Cargo & Shultz 1966).

Hanging upside-down could have several advantages for polyps, such as making *C. quinquecirrha* less visible to predators. Also, the lack of light may limit competition from fast growing algae. Physiological advantages could include less accumulation of sediments and debris and easier removal of waste (Pitt 2000). Discarded or empty oyster shells from the eastern oyster, *Crassostrea virgnica* (Gmelin, 1791), are a common natural settling surface (Cargo & Shultz 1966; Duarte et al. 2012). In at least one scyphozoan species, *Catostylus mosaicus,* (Quoy & Gaimard 1824), the concave shaped shell of another bivalve *Anadara trapezia* (Deshayes 1840) enhanced the polyps' ability to strobilate (Pitt 2000). In addition, many species of scyphozoan planula, including *C. quinquecirrha*, will readily settle on man-made structures such as bulkheads, pilings, and floating docks (Cargo & Shultz 1966; Holst & Jarms 2007; Hoover & Purcell 2009; Duarte et al. 2012).

The settled polyp stage can develop into a scyphostoma (Cargo & Rabenold 1980). Polyps appear as a cup shape and are attached to a hard surface by a short stalk. The cup, or mouth, is surrounded by tentacles, which are used for capturing and ingesting prey. *C. quinquecirrha* polyps feed on zooplankton (Loeb & Blanquet 1973). Their tentacles react to chemical cues produced by their prey (Loeb & Blanquet 1973).

Individual polyps are sessile organisms, but they do have the ability to change location. They can extend an appendage called a pedal stolon, which can be used to anchor the polyp to a new location. This process has been observed to take anywhere between 18 to 35 days and is a response to high polyp density (Cargo & Rabenold 1980).

The polyp stage is asexual, but they can reproduce in several ways. A stolon can break off and create a new individual, a single polyp can divide into two polyps, or polyps can leave behind a disk, about 2 mm in diameter, called a podocyst when they change location (Cargo & Shultz 1966; Cargo & Rabenold 1980; Arai 2009).

Podocysts are instrumental in maintaining populations of polyps. They act as defense against dramatic seasonal change, stochastic events, and predator fluctuations. They are produced in the base of the polyp and constructed from the protoplasm. Podocysts contain significant stores of lipids, proteins, and carbohydrates. Dormant *C. quinquecirrha* in the podocyst stage can tolerate harsh conditions that the polyps and medusae alone could not withstand (Arai 2009). Not only do polyps lay down podocysts in response to harsh conditions, but also when resources are in abundance (Cargo & Rabenold 1980; Arai 2009). Podocysts provide protection from abiotic factors, and are resistant to predatory species of nudibranchs and arthropods (Arai 2009). Under laboratory conditions a single polyp was able to lay down 52 podocysts in ten weeks

(Cargo & Shultz 1966). Polyps typically excyst from their podocysts in the spring when both biotic and abiotic conditions are favorable (Cargo & Rabenold 1980). With a possible two-year lifespan, the ability to lay down dozens of podocysts gives a single polyp a huge asexual reproductive potential (Cargo & Shultz 1966).

The polyps produce jellyfish blooms through strobilation. With warming temperature and abundant food availability, the polyps develop layers of disk shaped, juvenile medusas called ephyra. These ultimately break off and become planktonic. A single polyp usually produces 5 to 6 ephyra per strobilation, but single polyps have been observed producing as many as 16 (Calder 1974). Observations in the Chesapeake Bay reveal the process starting in spring when water temperatures reach 17° C and peaking in the months of May and June. Strobilation continues well into the fall but at a lower rate (Calder 1974). Each polyp has the potential to strobilate several times over the course of a season (Calder 1974; Cargo & Rabenold 1980). The process of strobilation seems to be triggered by a confluence of factors. Temperature and salinity have been tested thoroughly, but other factors including phytoplankton blooms, lunar cycles, and state of overwintering polyps may all play a role (Calder 1974).

While medusa may live for several months, polyps have lived up to two years in lab conditions (Arai 2009). Polyps and their podocysts have the ability to survive through winter. It is the density of these polyps and podocysts, together with food availability, which determine the intensity of blooms in the spring (Cargo & Rabenold 1980; Lucas et al. 2012). A settlement experiment with another scyphozoan species, *Cyanea sp.*, found that there was high polyp mortality due to the settlement of barnacle and ascidian larvae (Colin & Kremer 2002). An estuary with good water quality and a healthy benthic community may prevent abundant settlement and growth of *C. quinquecirrha* polyps through competition for substrata. Conversely, an ecosystem that is degraded by input of excess anthropogenic nutrient may have a less robust benthic community and be ideal for *C. quinquecirrha* polyp recruitment. Therefore it is the interactions occurring during planula settlement and polyp stages that is key to understanding, predicting, and possibly altering *C. quinquecirrha* blooms in the future.

Substrata

Polyvinyl chloride, referred to as vinyl for this paper, is currently the most common building material in Barnegat Bay. It is the third most widely produced plastic in the world and has been adapted for use in the production of bulkheads globally. Vinyl is a durable, corrosive resistant plastic that can be molded into interlocking panels. These panels are used to prevent the erosion into the bay, while providing an easily accessible waterfront. It is a cost effective way to replace old wooden bulkheads. This durable material can be found in man made lagoons throughout Barnegat Bay, but it also provides a suitable habitat for the polyp stage of *C. quinquecirrha* . The combination of adult *C. quinquecirrha* and the proliferation of hard substrata create the potential for high levels of polyp recruitment.

The sessile nature of the *C. quinquecirrha* polyp makes the availability of hard substrata an important factor in understanding the magnitude of medusa blooms and a potential for future management. Established colonies of *C. quinquecirrha* polyps require permanent hard surfaces that are not quickly covered by sedimentation. Currently, the natural benthic habitat of Barnegat Bay consists primarily of mud flats, sea grass beds, sand bars, and the edges of salt marshes. None of these habitats have large proportions of hard substrata. Small rocks, and man-made or terrestrial objects washed into the bay are covered in sediment after a short time.

Adult *C. quinquecirrha* medusae are highly fecund with the number of planula likely exceeding the available recruitment space in a natural environment. In the Chesapeake Bay, dramatic reductions in populations of oysters have been accompanied by reductions in populations of *C. quinquecirrha* (Breitburg & Fulford 2006). The available hard substratum of oyster shells act as a limiting factor for *C. quinquecirrha* density. Therefore, the amount of suitable hard substrata may determine the ultimate jellyfish population size (Hoover & Purcell 2009; Duarte et al. 2012).

The construction of docks and bulkheads in estuary lagoons dramatically increases the hard surface areas present in an ecosystem (Richardson et al. 2009; Purcell 2012). If reduction in natural substrata has a negative effect on populations of *C. quinquecirrha*, it seems probable that the introduction of artificial substrata would have the opposite effect. In Barnegat Bay, artificial hard substratum in the form of vinyl bulkheads is widespread (Lathrop & Bognar 2001). The continual coastal development may promote the production of jellyfish blooms.

Recruitment studies that focus on scyphozoan jellyfish show that planula of some species will readily settle on man-made surfaces (Holst & Jarms 2007; Hoover & Purcell 2009). *In situ* experiments with *Aurelia aurelia* (Linnaeus, 1758) planula have shown that they are more likely to settle on high-density plastics over wood (Hoover & Purcell 2009). An experiment provided five different species of scyphozoan with the option of settling on shell, concrete, wood, polyethylene, or glass in a laboratory setting. The polyethylene attracted the highest concentrations of planula for 3 of the 5 species. Only glass had a higher concentration for two of the species tested (Holst & Jarms 2001). Despite neither of these experiments directly testing *C. quinquecirrha*, they do show that there are cases where scyphozoans settle more readily on man-made materials than natural materials and plastics are often more attractive than other common construction materials. One study that did test *C. quinquecirrha* planula *in situ* settling preferences, used oyster shell, steel, and wood in the Chesapeake Bay (Duarte et al. 2012). The oyster shell is the most common natural material where *C. quinquecirrha* polyps are found. Therefore, they provide a frame of reference for the impact of the materials humans add to the bay. The majority of settling specimens of *C. quinquecirrha* were observed on oyster shell instead of steel and wood (Duarte et al. 2012).

New marine construction is becoming increasingly dependent on high-density plastics, yet there are no field studies that indicate how *C. quinquecirrha* recruitment is affected by these materials. Bulkheads, floating docks, and the outer covering of pilings are made of plastics. Polyps have been found on traditional building materials like wood, steel, and concrete, however it is unclear how the switch to plastics will affect future jellyfish blooms (Holst & Jarms 2007; Duarte et al. 2012). Plastics are often preferred by scyphozoan planula to traditional materials or even natural substrata (Holst & Jarms 2007; Hoover & Purcell 2009). If this is the case with *C. quinquecirrha*, then the continual refurbishing of old bulkheads with plastic could be exasperating the jellyfish problem.

Ecological Impacts

The establishment of *C. quinquecirrha* in estuaries like Barnegat Bay is part of a serious shift in ecosystems worldwide. Anthropogenic influences are pushing the balance of ecosystems into an altered state that favors jellyfish (Scheffer et al. 2001; Biesner et al. 2003; Richardson et al. 2009; Purcell 2012). Dissolved oxygen, excess nutrients, overfishing, and construction all play a role in the expansion of jellyfish range and dominance within an ecosystem (Richardson et al. 2009; Purcell 2012). As valuable marine species are overharvested or suffer from habitat degradation, jellyfish are filling in the gaps (Richardson et al. 2009).

Oyster reefs offer a stable, hard surface for polyp recruitment (Breitburg & Fulford 2006). However, in Barnegat Bay the population of oysters collapsed as early as 1925 due to a combination of overfishing and construction of inlets that changed bay circulation (Ford 1997). Therefore, the most prolific and stable hard substrata in Barnegat Bay consists of man-made bulkheads, pilings, and floating docks. A survey published in 2001 determined that 37% of the shoreline in Barnegat Bay was man-made bulkhead (Lathrop & Bognar 2001). These structures are built out of durable materials for the purpose of stabilizing the shoreline for human use. Steel, concrete, creosote and treated wood were common construction materials in Barnegat Bay, but many of those structures are being replaced with lower cost and non-toxic vinyl panels.

The removal of bivalves like oysters can alter conditions in an ecosystem that benefits populations of *C. quinquecirrha*. The eastern oyster *Crassostrea virginica*, are filter feeders and when they are in high abundance, they remove a significant amount phytoplankton and nitrogen from the ecosystems, which in turn limits zooplankton that *C. quinquecirrha* feed on (Purcell et al. 1999a; Nelson et. al 2004).

The complete impact of *C. virginica* density on *C. quinquecirrha* is unclear, because they also provide important substratum for the *C. quinquecirrha* polyp stage (Cargo & Shultz 1966). Therefore, a large population of *C. virginica* could enhance *C. quinquecirrha* polyp population density, but limit their growth (Purcell et al. 1999a). Conversely, the mass removal of *C. virginica* from estuaries through commercial fishing may limit the polyp stage (Breitburg & Fulford 2006). Artificial oyster reefs are created using *C. virginica* shell and aquaculture uses old shell to recruit *C. virginica* spat. Both the process of oyster harvesting and oyster restoration for the purposes of harvesting involves the return of empty oyster shell back into the estuary (Mann & Powell 2007; Schulte et al. 2009). Thus, the oyster fishery continuously removes the benefits of live oysters as ecosystem filters and enhances the available substrata for polyp recruitment through empty shell placement.

A lot of research, funding, and effort are put into habitat restoration in Barnegat Bay and other estuaries around the world. However, once a system is jellyfish dominated, the ecosystem may be centered on jellyfish. Other systems have experienced a shift from large fish biomass to a gelatinous dominated system like the Benguela current in Africa and in the Black Sea (Shiganova 1998; Purcell et al. 2001; Lynam et al. 2006), and removing the practices that created the problem may not change the ecosystem back to its original configuration (Scheffer et al. 2001; Biesner et al. 2003).

Barnegat Bay is heavily impacted by the introduction of anthropogenic nutrients (Kennish et al. 2007). The highly eutrophic conditions of the bay result in low oxygen conditions that benefit *C. quinquecirrha* and are detrimental to fish populations (Breitburg et al. 1997). The excess nutrients promote phytoplankton blooms, boosting the growth of zooplankton, which in turn are fed upon by the polyp, ephyra, and medusa stages of *C. quinquecirrha* (Purcell 1992).

Waste nitrogen and phosphorus from jellyfish can be a significant source of nutrients for phytoplankton, which would serve to intensify the eutrophic conditions that benefited the jellyfish in the first place (Purcell et al. 1999a; Pitt et al. 2009). *C. quinquecirrha* is a voracious predator of zooplankton (Purcell 1992). By feeding on zooplankton, the jellyfish trap nutrients in lower trophic levels. Fish that occupy higher trophic levels are affected in multiple ways by this trophic shift. Hypoxic conditions decrease the ability of fish like *Gobiosoma bosc* (Lacepede, 1800) from escaping medusa stage *C. quinquecirrha* (Breitburg et al. 1997). Predation on ephyra by juvenile *Morone saxatilis* (Walbaum, 1972) is also reduced when oxygen is low (Breitburg et al. 1997).

The link between jellyfish blooms and the problems of eutrophication, overfishing, and coastal development have been well established. The solutions to excessive jellyfish blooms and many other environmental issues are in direct conflict with the most profitable human-based activities that take place in that ecosystem. Anthropogenic nitrogen runoff and building more and more housing developments is common in Barnegat Bay and most estuary systems. Modern construction is not only creating new substrata, but it is replacing old surfaces with new ones that enhance the polyps' ability to settle. However, limiting the number of polyps by reducing available space would create a bottleneck and in turn limit medusa production.

Objectives

The goal of this study is to determine how the continual input of new vinyl substrata into the Barnegat Bay ecosystem will affect jellyfish polyp densities. Specifically:

1 Does vinyl provide a suitable settling surface for *C. quinquecirrha*?

2 If *C. quinquecirrha* does settle on vinyl bulkhead panels, what is the preference for the plastic material when compared to the natural substrata provided by oyster shells?

3 Is there a relationship between the density of common cnidarian predators, specifically nudibranchs, and the density of polyp settlement and is there is a pattern between medusa density and polyp settlement density?

METHODS

To address my research questions, ten sites were chosen within Barnegat Bay, New Jersey (Figure 1, Table 1). Eight sites were located on the Western side of the bay (designated with a 'W'), while the other two were located on the Eastern side of the bay (designated 'E'). All sites were within man-made lagoons comprised of hard substratum including pilings, floating docks, and bulkheads. Sites 1W, 3E, 4W, 9E, and 10W were all located close to the mouth of a lagoon or directly exposed to the main body of Barnegat Bay. Sites 2W, 5W, 6W, 7W, and 8W were deep within a lagoon system with limited tidal flushing. Site 1W was directly across from Barnegat Bay's southern most inlet, and site 4W was directly across from Barnegat Bay's primary inlet (Figure 1).

A series of settling plate arrays were created to assess the settling preference of larval sea nettles within Barnegat Bay (Figure 2). Each array contained three replicates of settling habitat, which consisted of four plates: two plates were constructed from vinyl bulkhead material and two were oyster shells. Each habitat replicate had vinyl plates and oyster shells suspended vertically and horizontally (Figure 3). Settling plates were constructed from vinyl z-shaped retaining wall sheets. These sheets are widely used for the construction of bulkheads in Barnegat Bay. The vinyl sheets were cut into 5cm by 5cm plates.

Oyster shells were selected to represent natural settling substrata and were obtained from the Haskin Shellfish Laboratory located in Bivalve, NJ. All shells were cleaned of living tissue, dried in the sun, and then scrubbed with salt to remove any previous settlers.

Holes were drilled on opposite edges of each vertical plate and they were suspended by stringing monofilament fishing line through the holes, which allowed them to be attached to a frame. Horizontal vinyl plates had two holes in the center that were drilled closely together. The tension of the two monofilaments was adequate to hold the plate steady in a horizontal position. For each horizontal oyster shell, monofilament was strung through a small plastic button, then through the shell, where it was passed through a second button. The same process was repeated in the opposite direction. When the shell was suspended, the opposing forces of the two buttons held the shell steady in the desired horizontal position. They were suspended from a rectangular PVC array in order to limit the transfer of organisms from adjacent colonized surfaces. The monofilament line was attached to the rack with rubber bands to ensure maintenance of their vertical or horizontal position throughout the study period.

Three replicate sets of settling plates were submerged at each location. All except one site were hung beneath docks. Site 6W was hung from the bulkhead due to lack of a suitable dock. Each set was suspended between 10 and 20 cm beneath the low tide line. The first seven sets were placed on June 4, 2014 and the remaining three were placed on June 12, 2014. The sets were left in place for two weeks and collected respectively on June 19th and June 25th. This process was repeated until August 28, 2014 (Table 2).

At the end of each two-week period, plates were cut from the racks and new plates were suspended in place. Photos were taken of each plate with a Canon EOS 30D camera and a 18-55mm macro lens. Plates were then brought back to the lab in seawater and suspended in a tank with a temperature of 22°C and a salinity of 20 ppt. *Chrysaora quinquecirrha* recruitment was measured within five days back in the laboratory under a dissecting microscope.

All vinyl plates had an area of 25 cm^2. The area of oyster shell settling plates was determined by placing a clear grid composed of square centimeters over the plate and counting the number of cm^2 that contained oyster shell. Squares that were partially full were counted as 0.5 cm^2. The number of *C. quinquecirrha* polyps was counted for each side of the plate. The number of nudibranchs per plate was counted. The mobility of the nudibranchs made it difficult to distinguish between any of the four plates on one rack since they could easily move from one plate to another while they were being transported or stored in the lab prior to quantification.

To approximate density of medusae of *C. quinquecirrha*, 0.84 m^2 lift nets were used to take ten samples along the shoreline for each sample day at each site. The 10 lift net samples were spaced evenly along the waterfront of each site, allowing for man-made and natural obstacles. The nets were allowed to sink to the bottom and were submerged for a minimum of 30 seconds before retrieval. The number and size of medusae of *C. quinquecirrha* were recorded for each sample. The depth of each sample was recorded to determine total water volume. A regression analysis was done for the density of adult *C. quinquecirrha* per site per day the polyp density for that site on the same day.

The average density of nudibranchs, *Cuthona* sp. and cf *Eubranchus* spp., was recorded for each site and collection date was plotted against the density of polyps. A regression analysis was done to determine if there was an inverse relationship between the distributions of these two organisms.

To establish if there is a possible predator-prey relationship between nudibranchs and *C. quinquecirrha* they were recorded interacting in the laboratory. Polyps were collected from settling plates using a pipette. The end of the pipette was cut at an angle to create a spatula like tool. The polyps were gently scraped off of the surface and sucked up with the pipette. They were then transferred to a plastic petri dish and left undisturbed for one week in order to let them attach. The dishes were then moved to a larger tank where they were fed newly hatched brine shrimp twice a week. The nudibranchs were collected from settling plates, placed in small tank with oyster shell for substratum, and were not fed for 3 to 5 days prior to filming experiments. Several nudibranchs were placed into the petri dishes containing the polyps. The petri dishes were placed under a dissecting microscope until feeding behavior concluded, or one hour had passed with no apparent feeding behavior. Video was recorded using a video camera held up to the eyepiece of a dissecting microscope.

RESULTS

Substrates and Orientation

During the course of the study at each site where recruitment was observed, individuals were recorded on both oyster shells and on vinyl bulkhead material. At no point during the study was there evidence of overgrowth from the rack onto the plates. The arrays were observed under conditions of fast moving current, chop, and boat wake and in each instance, the plates maintained their orientation relative to the array, and the array to the structure it was attached to. Recruitment of *C. quinquecirrha* was detected at five of the study sites 2W, 5W, 6W, 7W, and 8W. Overall, the average density of polyps when recruitment was detected was 1,791 polyps/m^2 for oyster plates and 3,371 polyps/m^2 for vinyl plates. ANOVA results showed significant differences among sites for settling density ($F_{9,1335} = 15.4$, $P < 0.0001$). Results from the 2-Way ANOVA completed on material and orientation indicate a significant difference in polyp settlement on vinyl compared to oyster shell (Figure 4) and significantly greater settlement on the underside of settling plates compared to surface and vertical orientations ($F_{2,1335} = 36.28$, $P < 0.0001$; Figure 5).

While the mean settling density ranged between 195-390 polyps/m^2 for the vertical sides or tops of plates, the average density for vinyl bottom plates was 5154 polyps/m^2. Maximum settling densities for bottom plates exceeded 32,000 polyps/m^2 at site 6W on August 14, 2014. This suggests that substantial recruitment was occurring during this study and that the cumulative settlement in some regions is extremely high. It also suggests that even a small increase in new vinyl substrata could have a large impact on the local jellyfish populations.

Spatial and Temporal Settling Patterns

The first polyps of *C. quinquecirrha* appeared on the plates collected on July 2, 2014, but the highest densities of recruits were found on plates collected on August 14, 2014 (Figure 6). Of the five study sites showing recruitment, three consistently had recruitment throughout the summer, which ranged between an average of 33 polyps/m^2 to 4600 polyps/m^2 (Figure 6). These three sites 5W, 6W, and 8W are all located on the west side of the bay spaced approximately evenly between the middle inlet and northern most point in Barnegat Bay. All three sites are located deep within a man-made lagoon systems. The remaining two sites, 2W and 7W, had less frequent detection of polyps and lower densities. Site 2W had a maximum average of 32 polyps/m^2 and Site 7W had a maximum average of 238 polyps/m^2 (Figure 6).

Recruitment of polyps was detected four weeks after the start of the study at site 8W and 6W. Recruitment was detected at six weeks at site 7W and 5W. Finally recruitment was detected at eight weeks for site 2W. This indicates a possible north to south pattern in the appearance of polyps of *C. quinquecirrha*. (Figure 6).

Medusae Distributions

Medusae were initially observed at study site 8W in week two, 6W in week four, 5W in week six, and 2W in week 8. This indicates a possible north to south pattern of in the appearance of *C. quinquecirrha* medusae in Barnegat Bay (Figure 7). Three study sites (5W, 6W, & 8W) had consistent presence of *C. quinquecirrha* medusae in densities high enough to be measured by lift nets (Figure 7). Medusae were observed visually as early as June 19th, but densities were too low to appear in any of the lift nets. When adults were present, mean densities per site ranged from 0.1 medusae/m^3 to a maximum of 4.13 medusae/m^3. Sites 2W had much lower densities of medusae with an average of $1.7*10^{-5}$ medusae/m^3, and Site 7W had no adult medusae captured and no visual observations. Medusae were detected in two sites were no recruitment was detected. Medusae appeared in lift nets at study site 4W and were visually spotted at Site 9E, although they never occurred in the lift net samples.

A regression analysis showed there was a significant relationship between the presence of adult *C. quinquecirrha* medusae and the presence of recruited polyps on plates collected two weeks later ($r = 0.6660$; $P < 0.0187$; Figure 8).

Potential Predators

The presence of nudibranch predators is another factor that could have affected polyp density at different sites. Observing native nudibranchs, *Cuthona* sp. and cf *Eubranchus* spp., feeding on polyps in-situ is extremely problematic and was not accomplished during this study. However, nudibranchs were observed feeding on *C. quinquecirrha* polyps in laboratory conditions. Some individuals did not approach the polyps while other nudibranchs immediately moved towards the polyps and initiated feeding. It was the *Cuthona sp.* that was observed interacting with the polyps. In one case, the nudibranch appeared to be repelled each time it came into contact with a polyp tentacle. In another trial a large polyp was partially eaten and in a third trial the nudibranch ingested an entire small polyp. While feeding preference of nudibranchs for *C. quinquecirrha* polyps is still unclear, they demonstrated a clear ability to feed on them given the opportunity.

The density of nudibranchs on settling plates was measured at the same time as polyp density (Figure 9). Initial observations indicate that there is a possible interaction between these organisms during the polyp stage of *C. quinquecirrha* (Figure 10). The high mobility of nudibranchs and the design of the arrays made it impossible to separate the nudibranch densities on individual plates or arrays from a particular site/date collection trip. Therefore, the densities for the 12 plates from a particular site were pooled together and compared to nudibranch abundance. When a regression analysis was applied to the presence of nudibranchs on settling plates against the density of polyps on those plates, there was not a significant relationship ($r = -0.1263$; $P < 0.8099$; Figure 10).

DISCUSSION

Dense populations of *C. quinquecirrha* medusae are a common occurrence in Barnegat Bay (Crum et al. 2014). They disrupt recreational activities, depress populations of commercially valuable fish and invertebrates, and retard the progress of conservation and restoration efforts in other systems (Purcell 1992; Purcell 1994; Richardson et al. 2009). Managing populations of *C. quinquecirrha* is particularly challenging because they seem to be able to reproduce faster and tolerate harsher conditions than other dominant species in the bay (Breitburg et al. 1997). The key to understanding jellyfish blooms and managing them within the estuary is identifying the limiting factor that determines the maximum reproductive potential of the species. Adult medusae can survive the low oxygen eutrophic waters of Barnegat Bay, so they thrive long after other species have been driven away or killed by hypoxia (Breitburg et al. 1997; Richardson et al. 2009). They can feed on planktonic organisms that can live in eutrophic estuaries, so they can continue to maintain their energy intake after fish like striped bass, *Morone saxatilis*, or the naked goby, *Gobiosoma bosc* would be negatively impacted (Purcell 1992; Breitburg et al. 1997). They can produce tens of thousands of eggs a day, so they can readily take advantage of any reproductive opportunity. Healthy ecosystems maintain competitors and produce predators of *C. quinquecirrha*. Striped bass, anchovies, sardines, all feed on the same zooplankton that *C. quinquecirrha* feeds on (Detwyler & Houde 1970; Peebles et al. 1996), while the butterfish, *Peprilus triacanthus* Peck 1804, is a potential predator of *C. quinquecirrha*. Healthy populations of the above mentioned species could have the potential to hold adult populations of this species in check. Other ecosystems have experienced shifts in trophic interactions toward jellyfish dominated food webs (Purcell et al. 2001; Lynam et al. 2006) and Barnegat Bay may be headed in that direction (Crum et al. 2014).

Another aspect that pushes this system farther towards a gelatinous dominated ecosystem is that the poor water quality and oxygen content limits the recruitment of other sessile organisms to hard surfaces (Colin & Kremer, 2002). Not only do polyps have ample recruitment surface, but the organisms that might outcompete them for space are limited by the ecosystem health as well.

It is important to determine what aspects of *C. quinquecirrha* lifecycle and ecology limit their population in the Barnegat Bay ecosystem. The temperature and salinity tolerances have been well established and certainly affect the reproductive success of *C. quinquecirrha* each year and could be a potential limiting factor for the population of *C. quinquecirrha* (Purcell et al. 1999b; Decker et al. 2007). However, prior to Hurricane Sandy there haven't been any major changes in the inlets of the bay to affect these factors. Populations of *C. quinquecirrha* have been spreading despite the lack of change; therefore it seems likely that temperature and salinity are not limiting factors. It is important to consider other factors that could be controlling populations of *C. quinquecirrha*.

It is the polyp stage of the *C. quinquecirrha* lifecycle that is likely the most critical for maintaining large perennial populations (Cargo & Rabenold 1980; Breitburg & Fulford 2006; Arai 2009). Polyps have somewhat limited opportunities when it comes to recruitment. They need a hard surface, space that is not already occupied, and they thrive in areas that are sheltered from direct sunlight (Cargo & Shultz 1966). Oyster shell is a native and common polyp settling surface (Breitburg & Fulford 2006). Studies have shown a positive correlation between the amount of oyster shell present and populations of *C. quinquecirrha* (Breitburg & Fulford 2006). It is also the substratum where polyps can most reliably be found (Cargo & Shultz 1966; Duarte et al. 2012). In Barnegat Bay, the vast majority of the population of oysters has either been harvested or died from disease (Ford 1997). Naturally occurring hard objects on the soft bottom of Barnegat

Bay are rare, but strongly competed for. This provides a potential bottleneck for populations of *C. quinquecirrha* if alternate substrata are not available. However, coastal development represents a continuous input of new hard surfaces into the bay (Lathrop & Bognar 2001).

New and refurbished bulkheads are primarily constructed with vinyl panels. Bulkheads are by far the most abundant source of settling surface area currently in the bay. Another application of vinyl in Barnegat Bay is floating docks. Floating docks are used because they move up and down with tidal flux. The underside of these docks provides an ideal settling surface for *C. quinquecirrha* planula. Floating docks are more varied in their construction and are made from a greater variety of materials than bulkheads, but many of them use vinyl.

In order to understand the impact of coastal development on jellyfish, it is essential to understand how planula and polyps interact with recruiting surfaces. The vinyl bulkhead settling plates simulate the increasing abundance of this material in coastal lagoons, while the oyster shell settling plates serve as a useful comparison for natural settling substrata. Dramatic reductions in oyster reefs have been linked to crashes in populations of jellyfish in the Chesapeake Bay (Breitburg & Fulford 2006). This indicates that there is an important relationship between available settling substrata and populations of *C. quinquecirrha*. It is essential to establish if vinyl surfaces provide an equal or greater settling surface than oyster shell. If it does, then the presence of bulkheads and floating docks will fill the gap in space from reduced oyster stocks, while providing none of the ecological services.

During this study, *C. quinquecirrha* planulae significantly settled in higher densities on vinyl settling plates than oyster settling plates (Figure 4). In previous studies, *C. quinquecirrha* planulae have shown a much higher preference for oyster shell over wood (Duarte et al. 2012). Since wood is the most common building material that is being replaced by vinyl, there is potential for new construction to have a strong impact on populations of *C. quinquecirrha*.

When orientation is considered as a factor, there is a clear propensity for settling on vinyl bottom surfaces. However there is not a detectable difference in settling propensity for vertical and top surfaces for either substratum. A consistently vertical surface made of oyster shell is likely to be a rare occurrence in nature. Due to the curved nature of most oyster shells, the oyster settling plates were never perfectly vertical. The complex surface of the shell can offer horizontal surfaces for settlement even when the shell is held vertically. Despite this, there was no clear difference between mean densities of vertical oriented plates of either material, or the top surface of horizontal settling plates (Figure 5). In both vertical and top facing surfaces, vinyl still provides a suitable settling surface equal to oyster shell for *C. quinquecirrha* polyps. Consequently, newly constructed vinyl bulkheads will provide potential habitat for *C. quinquecirrha* polyps.

The undersides of horizontal surfaces, which are most commonly found in the form of floating docks, have a significant potential for planula recruitment. For example at site 8W, one float built to accommodate two personal watercraft has an area of 9 m^2. The average polyp recruitment density for bottom surfaces at site 8W was 4,110 polyps/m^2; which translates into a maximum recruitment potential of 37,000 polyps for this single floating dock during a two-week period. If projected throughout the summer and polyp asexual reproduction after settlement is considered, the absolute abundance of polyps on these surfaces is dramatically greater. As such, the act of installing a new floating dock could have a major affect on polyp settlement, which in turn, could increase adult medusa density for the surrounding area.

Vertical settling surfaces most often take the form of bulkheads and pilings. At the same site, 8W, the waterfront has a bulkhead area of 30 m^2. Average recruitment to vertical vinyl plates was 430 polyps/m^2. Therefore, maximum polyp recruitment potential for a new or refurbished bulkhead at that site would be 12,900 polyps. In this case the recruitment potential is almost triple for a floating dock versus the bulkhead for one building lot. Considering that the 8W site was one of 40 similar sized lots in the same man-made lagoon, bulkheads can also have a significant potential to affect adult medusa densities. More than 37% of Barnegat bay is lined with bulkheads (Lathrop & Bognar 2001), which creates a large well of polyp habitat.

All of the sites that consistently had recruitment (5W, 6W, & 8W) were in highly structured man-made lagoon systems. Site 5W was 785 meters from the bay, 6W was 1,230 meters from bay, and site 8W was 393 meters from the bay. Each site had one or more turns between the settling plates and the beginning of the lagoon system. The sites had limited tidal exchange and no flow through. The structure and poor flow of these environments may enhance the impacts of eutrophication (Kennish et al. 2007). The high density of housing developments along these lagoons means there was runoff of chemicals like nitrogen and phosphorus. The majority of nutrient loading in Barnegat

Bay comes from surface runoff (Kennish et al. 2007). The limited tidal flushing means that the nutrient filled water was not replaced with cleaner water from the bay or ocean.

The low flow, eutrophication, and high structural availability of man-made lagoons make ideal *C. quinquecirrha* recruitment areas. These sites have the potential to act as *C. quinquecirrha* medusa reservoirs, producing an excess of medusae that can be carried to other parts of the bay or self seed. The relative stability of an isolated lagoon can thus protect polyps through conditions that are not favorable for other organisms.

All of the sites where no recruitment was observed were either on the bay or had little shelter from the bay. Two of these sites were directly across from inlets. Sites 4W and 9E had sightings of adult *C. quinquecirrha* medusae, but no recruitment was detected. The sites without recruitment were consistently in areas that were more exposed to bay, and the sites where polyps were observed were sheltered within lagoons. It is possible that these sites vary in the physical oceanographic features such that larvae are not delivered to those regions. In this case, swimming adults might occur, but recruiting larvae are advected from the sites.

In a laboratory setting, nudibranchs *Cuthona* sp., were observed feeding on *C. quinquecirrha* polyps. In some cases small polyps were eaten entirely, while in other instances larger polyps were partially ingested, leaving some parts of the polyp remaining. Is the presence of nudibranchs in high density enough to be a check on polyp recruitment? Also, are newly settled planula particularly vulnerable to grazing by nudibranchs? Results indicated that the highest nudibranch densities were present at sites with the lowest polyp density and vice versa. The data were not sufficient to establish a definite relationship (Figure 10). However, future research has the potential to establish a connection between the populations of these two organisms with increased sample size.

It does seem that there are more nudibranchs in areas when there was low polyp recruitment density. It is unclear if the presence of nudibranchs is limiting polyp recruitment or if the areas where polyps are successful are not favorable for nudibranchs. The highest nudibranch densities occurred at the beginning of the study prior to any observed polyp recruitment (Figure 10). It is possible that the apparent pattern is temporal and the two species are not found in high densities at the same time due to some other abiotic or biotic factor.

Conclusions

The main purpose of this study was to determine the settling substrate selection between natural substrate (oyster shells) and artificial (vinyl). However, other settling factors play an important role in site selection in many invertebrates. The majority of previous research in scyphozoan settling behavior has dealt specifically with substrate material (Pitt 2000; Holst & Jarms 2007; Hoover & Purcell 2009; Duarte et al. 2012). Extensive research into the settlement behavior of barnacles has shown that at least some invertebrates are capable of using a number of physical and chemical cues to make settling choices. These include, surface topography, sheer stress, presence of conspecifics and potential predators, as well as light and orientation (Hudson et al. 1983; Wethey 1986; Le Tourneux & Bourget 1988; Johnson & Strathmann 1989).

Over the course of this study a potential pattern was revealed from the photo documentation of each plate as it was collected. The settlement of other organisms appears to be low at sites and time periods with the highest *C. quinquecirrha* polyp recruitment (Figure 11). Conversely, any site that experienced dense recruitment of other sessile species, including various tunicates, bryozoans, and hydroids, saw no recruitment of *C. quinquecirrha* (Figure 12). A second possible pattern that emerged was that oyster shells had a denser settlement of other fouling organisms than the vinyl plates (Figure 13). The results of this study indicate that *C. quinquecirrha* planulae are more likely to settle on vinyl plates. A possible explanation for this could be that vinyl surfaces are less likely to be settled by other species competing for limited space. A third pattern was that every plate where recruitment of *C. quinquecirrha* was detected over the course of the study was in a sheltered, man-made lagoon on the west side of the Bay and far from an inlet. Sites that consistently showed dense growth of other invertebrate species were located closer to inlets and exposed to the main body of Barnegat Bay.

The next important question is what chemical, physical, and biological factors lead to the selection of substratum like vinyl for *C. quinquecirrha*. Further research is necessary to fully understand the impact of construction on population of sea nettles. The role of water quality could be an important factor in recruitment patterns for competing species. If other sessile species are affected by water quality, then cleaner water could mean more competition for space, despite construction. This information could allow environmental managers and policy makers to target specific locations when trying deal with jellyfish problems. Another unknown is the rate of recruitment to established encrusting communities versus new surface. There is constant construction going on in Barnegat Bay, however the vast majority of hard surfaces have been in the bay for longer than one year. The settling arrays from this study were left submerged in the bay all summer. There was consistently lower density of visible settling organisms on arrays at sites where polyps were present. The relative contribution of older material is unclear. Does new construction put an area at dramatically increased risk of sea nettle blooms or are all areas with bulkheads and docks at equal risk? Could limiting new construction to fall and winter months give other organisms time to settle and prevent a large jellyfish bloom the following summer? The results of this study indicate that coastal development in Barnegat Bay provides a superior settling surface for *C. quinquecirrha* polyps in the form of vinyl bulkheads and floating docks. It seems likely that the *C. quinquecirrha* blooms will continue to increase in frequency and intensity while construction continues.

LITERATURE CITED

Arai, M. N. (2009). The potential importance of podocysts to the formation of scyphozoan blooms: a review. Hydrobiologia, 616(1), 241-246.

Beisner, B. E., Haydon, D. T., & Cuddington, K. (2003). Alternative stable states in ecology. Frontiers in Ecology and the Environment, 1(7), 376-382.

Bologna, P. (2011). Sea Nettle (*Chrysaora quinquecirrha*) Polyps in Barnegat Bay, NJ. Barnegat Bay Partnership, a Pilot Assessment.

Breitburg, D. L., & Fulford, R. S. (2006). Oyster-sea nettle interdependence and altered control within the Chesapeake Bay ecosystem. Estuaries and Coasts, 29(5), 776-784.

Breitburg, D. L., Loher, T., Pacey, C. A., & Gerstein, A. (1997). Varying effects of low dissolved oxygen on trophic interactions in an estuarine food web. Ecological Monographs, 67(4), 489-507.

Calder, D. R. (1974). Strobilation of the sea nettle, *Chrysaora quinquecirrha*, under field conditions. The Biological Bulletin, 146(3), 326-334.

Cargo, D. G., & Rabenold, G. E. (1980). Observations on the asexual reproductive activities of the sessile stages of the sea nettle *Chrysaora quinquecirrha* (Scyphozoa). Estuaries, 3(1), 20-27.

Cargo, D. G., & Schultz, L. P. (1966). Notes on the biology of the sea nettle, *Chrysaora quinquecirrha*, in Chesapeake Bay. Chesapeake Science, 7(2), 95-100.

Colin, S. P., & Kremer, P. (2002). Population maintenance of the scyphozoan *Cyanea* sp. Settled planulae and the distribution of medusa in the Niantic River, Connecticut, USA. Estuaries, 25(1), 70-75.

Crum, K. P., Fuchs, H. L., Bologna, P. A., & Gaynor, J. J. (2014). Model-to-data comparisons reveal influence of jellyfish interactions on plankton community dynamics. Marine Ecology Progress Series, 517, 105-119.

Decker, M. B., Brown, C. W., Hood, R. R., Purcell, J. E., Gross, T. F., Matanoski, J. C., Bannon, R. O., Setzler-Hamilton, E. M. (2007). Predicting the distribution of the scyphomedusa *Chrysaora quinquecirrha* in Chesapeake Bay. Marine Ecology Progress Series, 329, 99-113.

Detwyler, R., & Houde, E. D. (1970). Food selection by laboratory-reared larvae of the scaled sardine *Harengula pensacolae* (Pisces, Clupeidae) and the bay anchovy *Anchoa mitchilli* (Pisces, Engraulidae). Marine Biology, 7(3), 214-222.

Duarte, C. M., Pitt, K. A., Lucas, C. H., Purcell, J. E., Uye, S. I., Robinson, K., Brotz, L., Decker, M. B., Sutherland, K. R., Malej, A. M., Madin, L., Mianzan, H., Gili, J., Fuentes, V., Atienza, D., Pages, F., Breitburg, D., Malek, J., Graham, W. M., Condon, R. H. (2012). Is global ocean sprawl a cause of jellyfish blooms? Frontiers in Ecology and the Environment, 11(2), 91-97.

Ford, M. D., Costello, J. H., Heidelberg, K. B., & Purcell, J. E. (1997). Swimming and feeding by the scyphomedusa *Chrysaora quinquecirrha*. Marine Biology, 129(2), 355-362.

Ford, S. E. (1997). History and present status of molluscan shellfisheries from Barnegat Bay to Delaware Bay. *The history, present condition, and future of the molluscan fisheries of North and Central America and Europe*, NOAA Technical Report NMFS, 127 (*1*) 119-140.

Holst, S., & Jarms, G. (2007). Substrate choice and settlement preferences of planula larvae of five Scyphozoa (Cnidaria) from German Bight, North Sea. Marine Biology, 151(3), 863-871.

Hoover, R. A., & Purcell, J. E. (2009). Substrate preferences of scyphozoan *Aurelia labiata* polyps among common dock-building materials. In Jellyfish Blooms: Causes, Consequences, and Recent Advances. Hydrobiologia 616, 259-267.

Hudon, C., Bourget, E., & Legendre, P. (1983). An integrated study of the factors influencing the choice of the settling site of *Balanus crenatus* cyprid larvae. Canadian Journal of Fisheries and Aquatic Sciences, 40(8), 1186-1194.

Johnson, L. E., & Strathmann, R. R. (1989). Settling barnacle larvae avoid substrata previously occupied by a mobile predator. Journal of Experimental Marine Biology and Ecology, 128(1), 87-103.

Kennish, M. J., Bricker, S. B., Dennison, W. C., Glibert, P. M., Livingston, R. J., Moore, K. A., Noble, R. T., Paerl, H. W., Ramstack, J. M., Seitzinger, S., Tomasko, D. A., Valiela, I. (2007). Barnegat Bay-Little Egg Harbor Estuary: case study of a highly eutrophic coastal bay system. Ecological Applications, 17(5), S3-S16.

Lathrop, R.G. and J.A. Bognar. (2001). Habitat Loss and Alteration in the Barnegat Bay Region. Journal of Coastal Research Special Issue 32, 212-228.

Le Tourneux, F., & Bourget, E. (1988). Importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides*. Marine Biology, 97(1), 57-66.

Loeb, M. J., & Blanquet, R. S. (1973). Feeding behavior in polyps of the Chesapeake Bay sea nettle, *Chrysaora quinquecirrha* (Desor, 1848). Biological Bulletin, 150-158.

Lucas, C. H., Graham, W. M., & Widmer, C. (2012). Jellyfish life histories: Role of polyps in forming and maintaining scyphomedusa populations. Advances in Marine Biology, 63, 140-166.

Lynam, C. P., Gibbons, M. J., Axelsen, B. E., Sparks, C. A., Coetzee, J., Heywood, B. G., & Brierley, A. S. (2006). Jellyfish overtake fish in a heavily fished ecosystem. Current Biology, 16(13), 492-493.

Mann, R., & Powell, E. N. (2007). Why oyster restoration goals in the Chesapeake Bay are not and probably cannot be achieved. Journal of Shellfish Research, 26(4), 905-917.

Nelson, K. A., Leonard, L. A., Posey, M. H., Alphin, T. D., & Mallin, M. A. (2004). Using transplanted oyster (*Crassostrea virginica*) beds to improve water quality in small tidal creeks: a pilot study. Journal of Experimental Marine Biology and Ecology, 298(2), 347-368.

Peebles, E. B., Hall, J. R., & Tolley, S. G. (1996). Egg production by the bay anchovy *Anchoa mitchilli* in relation to adult and larval prey fields. Marine Ecology Progress Series. 131(1), 61-73.

Pitt, K. A. (2000). Life history and settlement preferences of the edible jellyfish *Catostylus mosaicus* (Scyphozoa: Rhizostomeae). Marine Biology, 136(2), 269-279.

Pitt, K. A., Welsh, D. T., & Condon, R. H. (2009). Influence of jellyfish blooms on carbon, nitrogen and phosphorus cycling and plankton production. In Jellyfish Blooms: Causes, Consequences, and Recent Advances. Hydrobiologia, 616, 133-149.

Purcell, J. E. (1992). Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. Marine Ecology-Progress Series, 87, 65-65.

Purcell, J. E. (1994). Predation mortality of bay anchovy *Anchoa mitchilli* eggs and larvae due to scyphomedusae and ctenophores in Chesapeake Bay. Marine Ecology-Progress Series, 114, 47-58.

Purcell, J. E. (2012). Jellyfish and ctenophore blooms coincide with human proliferations and environmental perturbations. Annual Review of Marine Science, 4, 209-235.

Purcell, J. E., Malej, A., & Benović, A. (1999a). Potential links of jellyfish to eutrophication and fisheries, Ecosystems at the Land-Sea Margin: Drainage Basin to Coastal Sea (eds T. C. Malone, A. Malej, L. W. Harding, N. Smodlaka and R. E. Turner) American Geophysical Union, 241-263.

Purcell, J. E., Shiganova, T. A., Decker, M. B., & Houde, E. D. (2001). The ctenophore *Mnemiopsis* in native and exotic habitats: US estuaries versus the Black Sea basin. In Jellyfish Blooms: Ecological and Societal Importance. Hydrobiologia 451, 145-176

Purcell, J. E., Uye, S. I., & Lo, W. T. (2007). Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. Marine Ecology-Progress Series, 350, 153-174.

Purcell, J. E., White, J. R., Nemazie, D. A., & Wright, D. A. (1999b). Temperature, salinity and food effects on asexual reproduction and abundance of the scyphozoan *Chrysaora quinquecirrha*. Marine Ecology-Progress Series,180, 187-196.

Richardson, A. J., Bakun, A., Hays, G. C., & Gibbons, M. J. (2009). The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends in Ecology and Evolution, 24(6), 312-322.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C., & Walker, B. (2001). Catastrophic shifts in ecosystems. Nature, 413(6856), 591-596.

Schulte, D. M., Burke, R. P., & Lipcius, R. N. (2009). Unprecedented restoration of a native oyster metapopulation. Science, 325(5944), 1124-1128.

Shiganova, T. A. (1998). Invasion of the Black Sea by the ctenophore Mnemiopsis leidyi and recent changes in pelagic community structure. Fisheries Oceanography, 7(3-4), 305-310.

Wethey, D. S. (1986). Ranking of settlement cues by barnacle larvae: influence of surface contour. Bulletin of Marine Science, 39(2), 393-400.

TABLES AND FIGURES

Tables

Table 1: Site names and coordinates in Barnegat Bay, New Jersey, summer 2014. Sites are numbered in order starting with the lowest number corresponding to the southern most site and moving north to the highest numbers. Each site has either a W for the west side of the bay, or an E for the east side of the bay. Three sets of settling plates were placed at each site.

SITE NAME	LATTITUDE°	LONGITUDE°
10W	40.063201	-74.057537
9E	40.04202	-74.050451
8W	40.015945	-74.100434
7W	39.937617	-74.156017
6W	39.911297	-74.138498
5W	39.844828	-74.151856
4W	39.78775	-74.183918
3E	39.695199	-74.141468
2W	39.665653	-74.221435
1W	39.58066	-74.335744

Table 2: This table displays collection dates for settling plate arrays. Each "Week #" designation represents a round of placements and the number of weeks the experiment has been running. The dates are the day that each set of arrays was removed from the bay after 2 weeks of soaking. The start date of the experiment was June 4, 2014. Three sites were visited on alternating weeks due to time constraints and were started on June 12, 2014.

Period of Plate Placement and Collection	Collection Date	Sites Visited
Week 2	June 19, 2014	1W, 3E, 5W, 6W, 8W, 9E, 10W
	June 25, 2019	2W, 4W, 7W
Week 4	July 2, 2014	1W, 3E, 5W, 6W, 8W, 9E, 10W
	July 9, 2014	2W, 4W, 7W
Week 6	July 16, 2014	1W, 3E, 5W, 6W, 8W, 9E, 10W
	July 23, 2014	2W, 4W, 7W
Week 8	July 31, 2014	1W, 3E, 5W, 6W, 8W, 9E, 10W
	August 6, 2014	2W, 4W, 7W
Week 10	August 14, 2015	1W, 3E, 5W, 6W, 8W, 9E, 10W
	August 20, 2014	2W, 4W, 7W
Week 12	August 28, 2014	1W, 3E, 5W, 6W, 8W, 9E, 10W

Figures

Figure 1: Map of site locations in Barnegat Bay New Jersey, Summer 2014. Sites are numbered moving from South to North and have an E (East), or W (West) to indicate which side of Barnegat Bay they are on. Inlets to Barnegat Bay are located across from site 1W and 4W, and near site 10W.

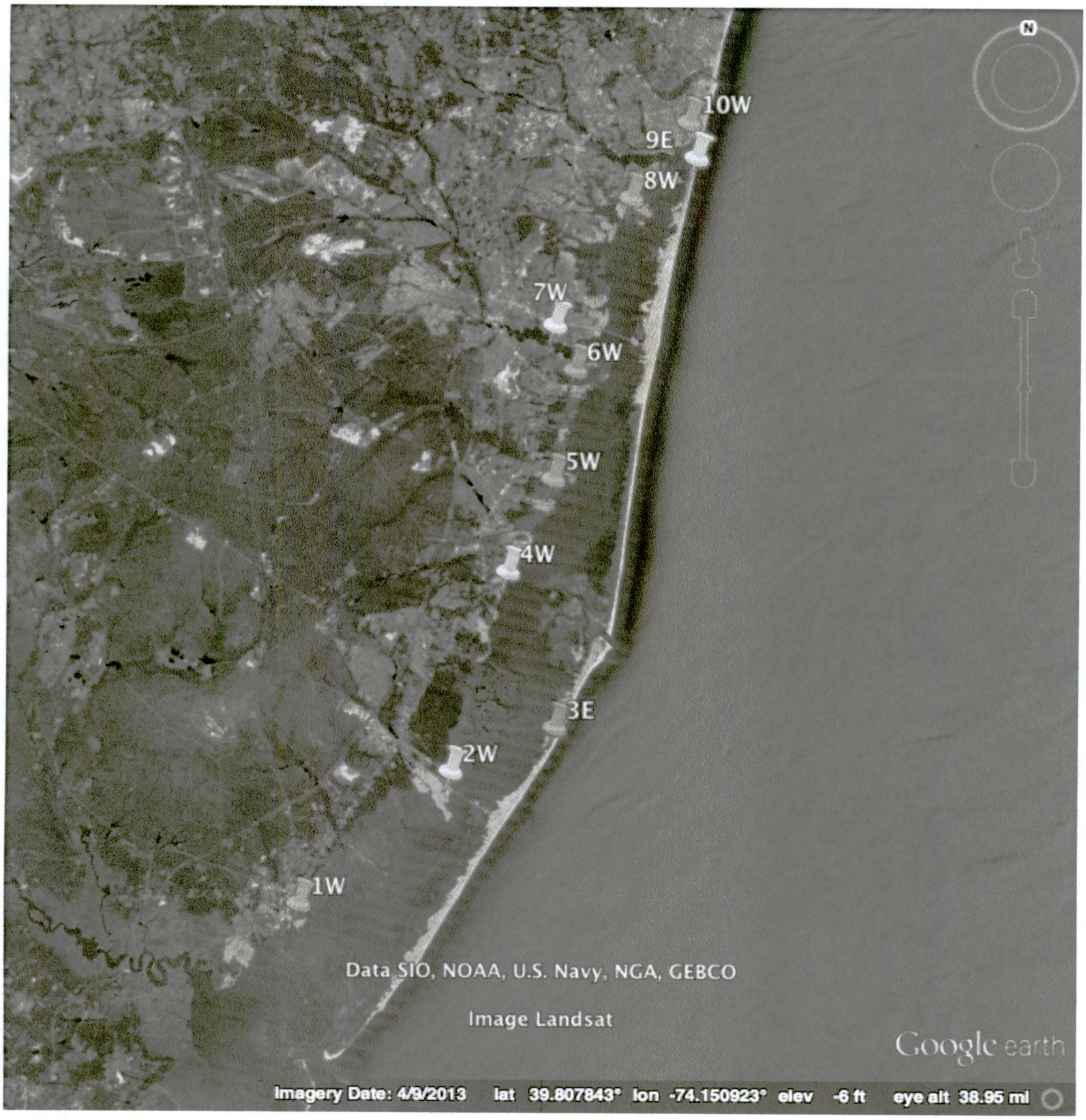


Figure 2: A newly placed array of settling plates in Barnegat Bay NJ, Summer 2014. Three of these arrays were placed at each study site.

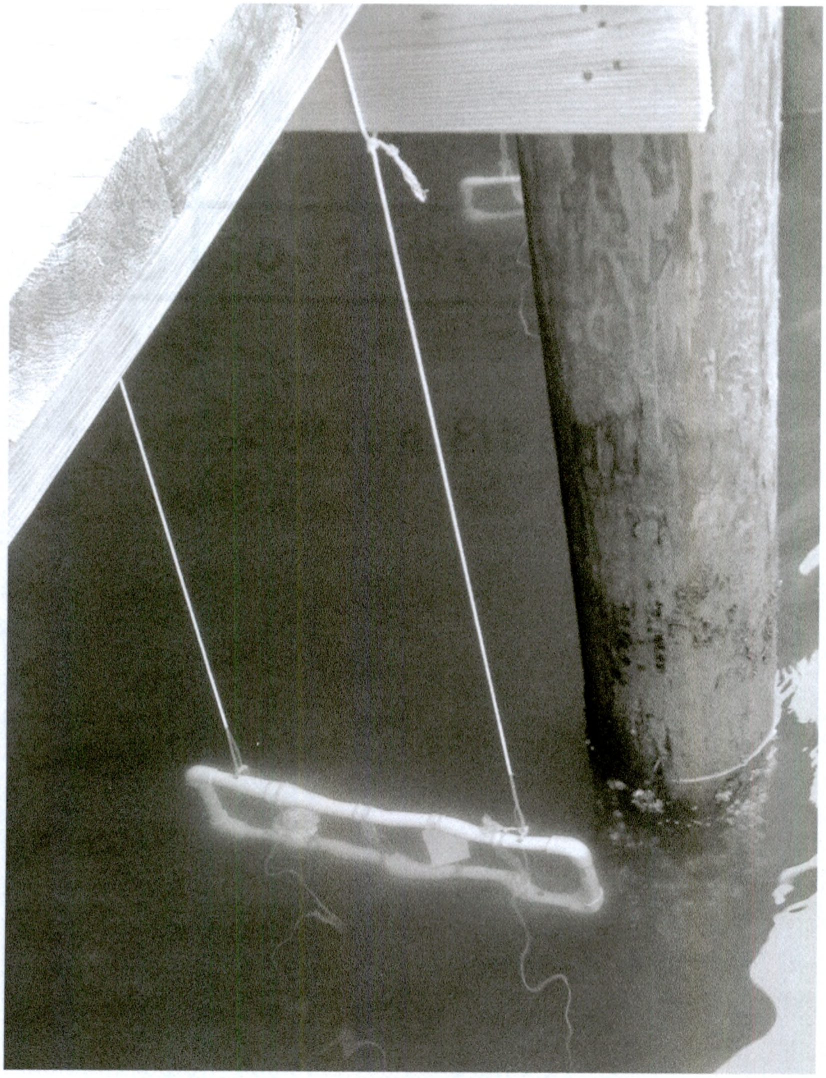


Figure 3: An array retrieved after being submerged for two weeks. Plates were suspended with monofilament to isolate the plates from possible overgrowth by organisms on the rack. They were attached to the rack with rubber bands to maintain tension and plate stability.

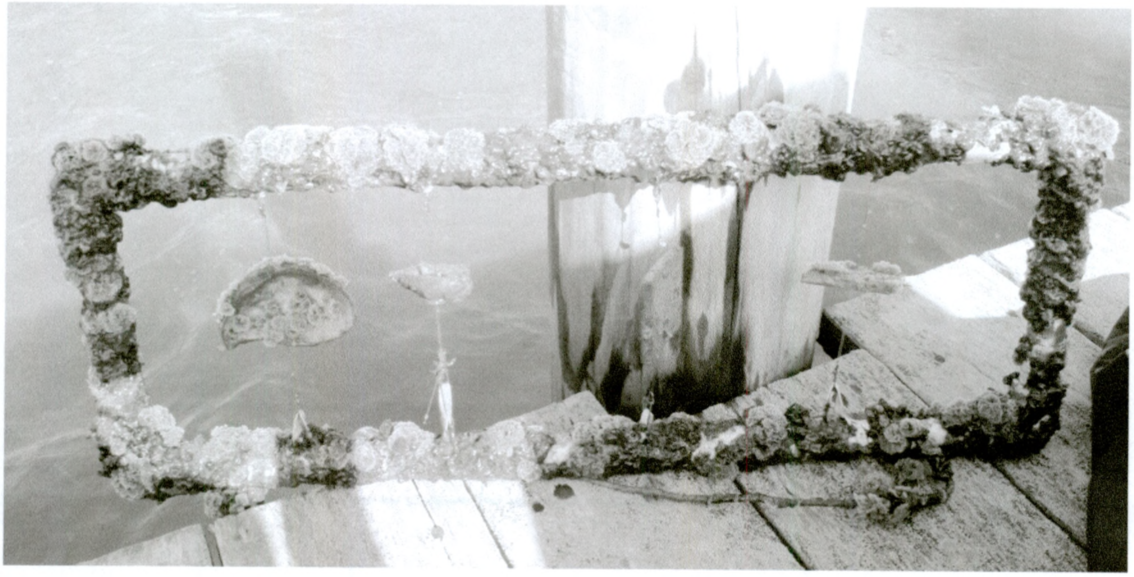


Figure 4: Mean difference in recruitment of *C. quinquecirrha* planulae on oyster and vinyl settling plates in Barnegat Bay NJ in the summer of 2014. This graph shows that there is a significant increase in the density of polyps on vinyl settling plates ($P = 0.0248$).

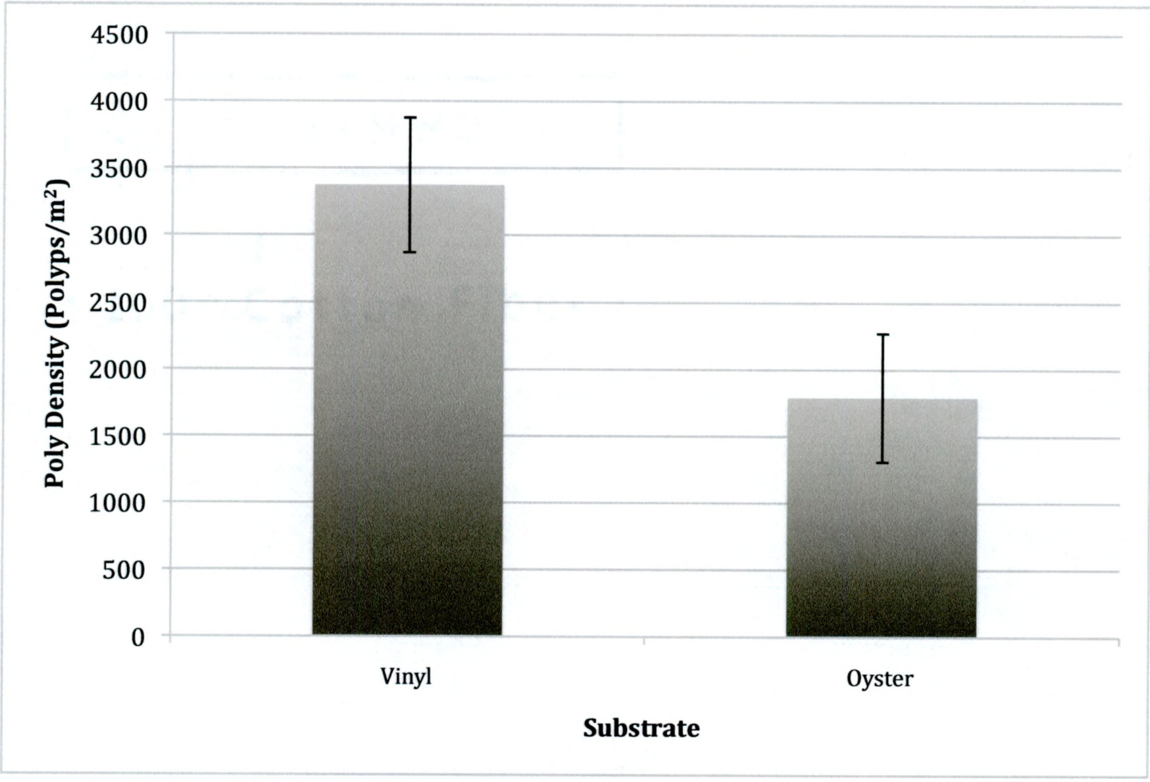


Figure 5: Mean density of *C. quinquecirrha* polyps on each orientation and substrate type for settling plates in Barnegat Bay NJ in the summer of 2014. This shows a significant increase in polyp recruitment for the bottom surface of vinyl plates and then the bottom of oyster plates. All of the other substrate orientation combinations showed no significant differences in recruitment of polyps. Substrate-Orientation combinations that are significantly different are labeled with different letters. The three different groups are A ($P < 0.0001$), B ($P < 0.0001$), and C ($P < 0.0001$).

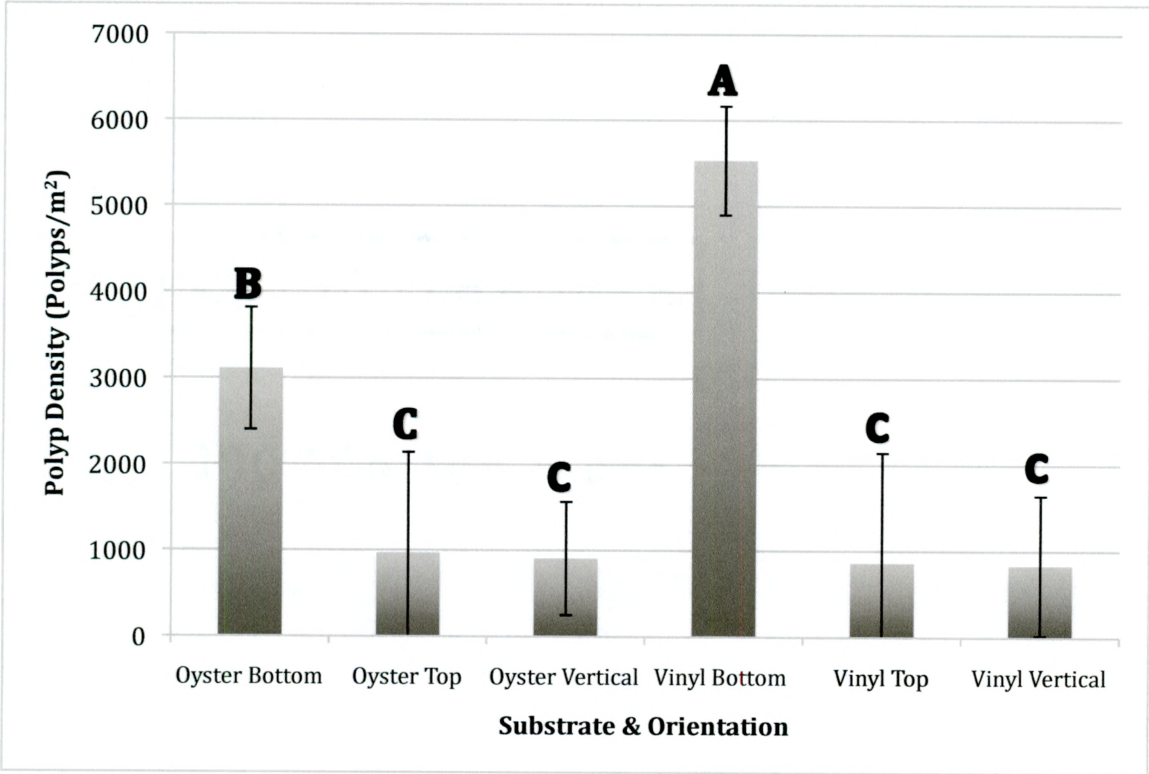


Figure 6: Average *C. quinquecirrha* polyp recruitment on vinyl and oyster settling plates in Barnegat Bay New Jersey between June 19, 2014 and August 28, 2014. Each site consisted of 3 sets of settling plates. Each set had two oyster shell plates and two vinyl plates.

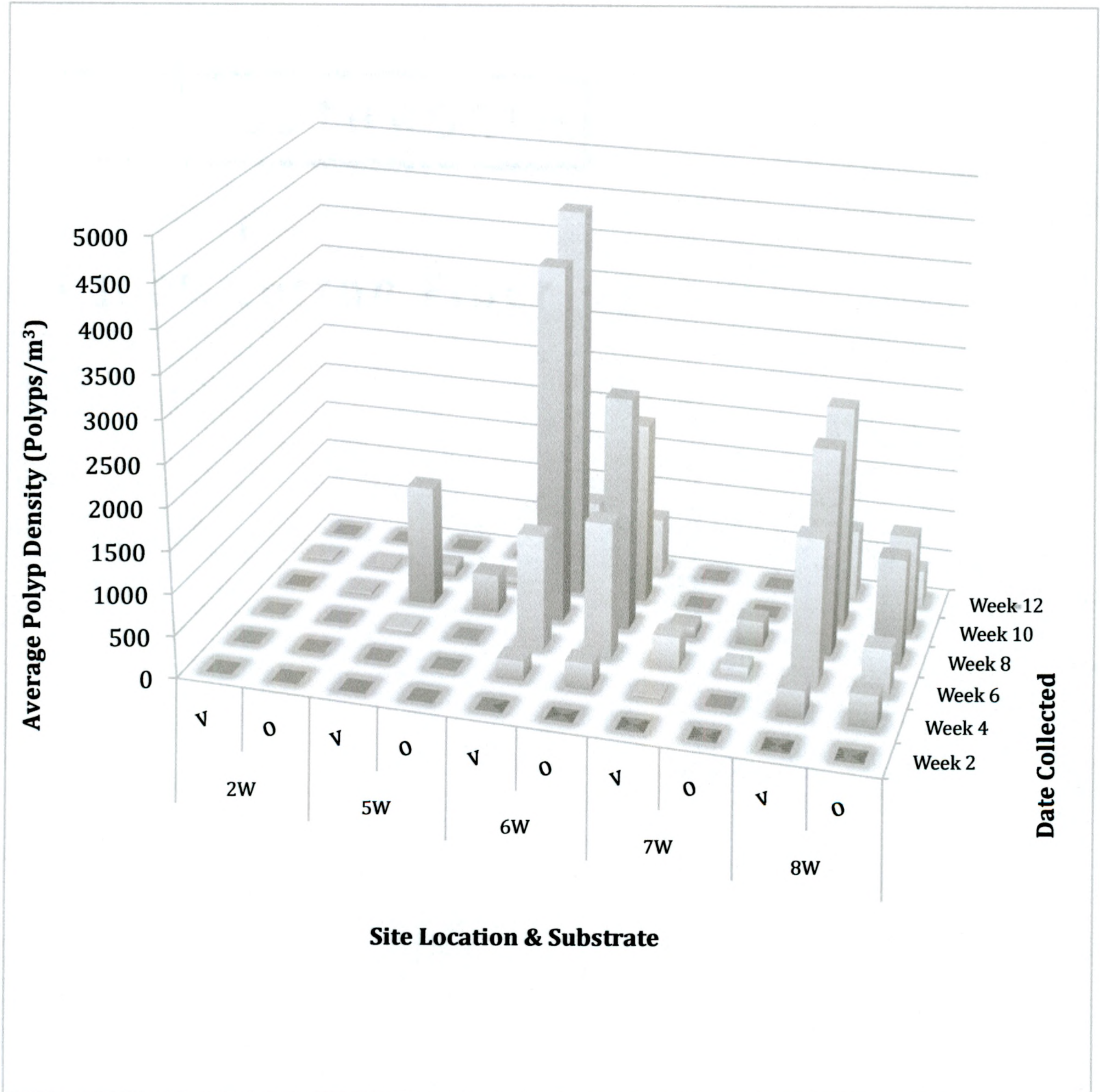


Figure 7: Average *C. quinquecirrha* density of polyp stage versus medusa stage in Barnegat Bay New Jersey between June 19, 2014 and August 28, 2014 at sites where recruitment was detected. The polyp density is displayed in polyps/cm^2 and the medusae density is in liters for the sake of presenting the variables in the same scale.

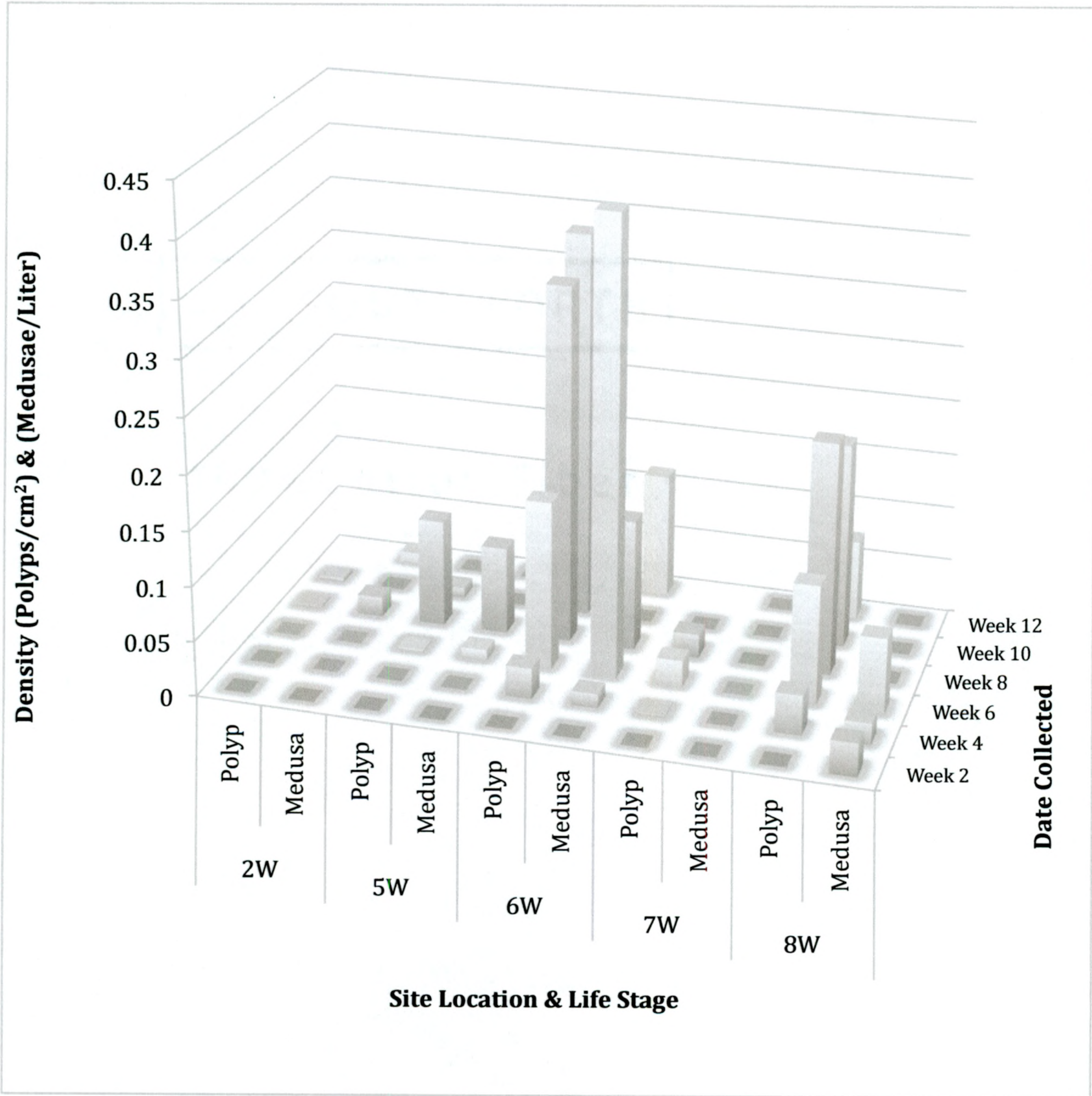


Figure 8: The medusa stage density plotted against the polyp stage density of *C. quinquecirrha*. A regression analysis shows significant relationship between the density of medusae and the density of polyp stage recruitment (r = 0.6660, P = 0.0187).

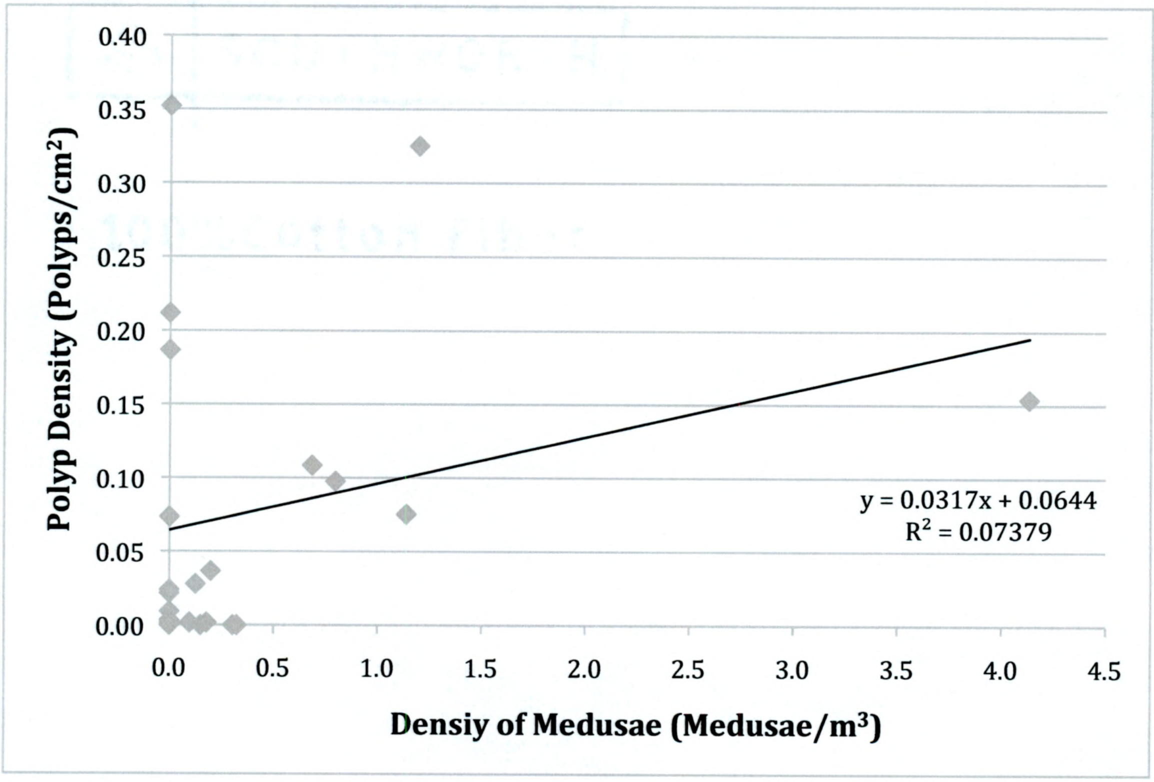


Figure 9: Average *C. quinquecirrha* polyp density versus nudibranch density in Barnegat Bay New Jersey between June 19, 2014 and August 28, 2014.

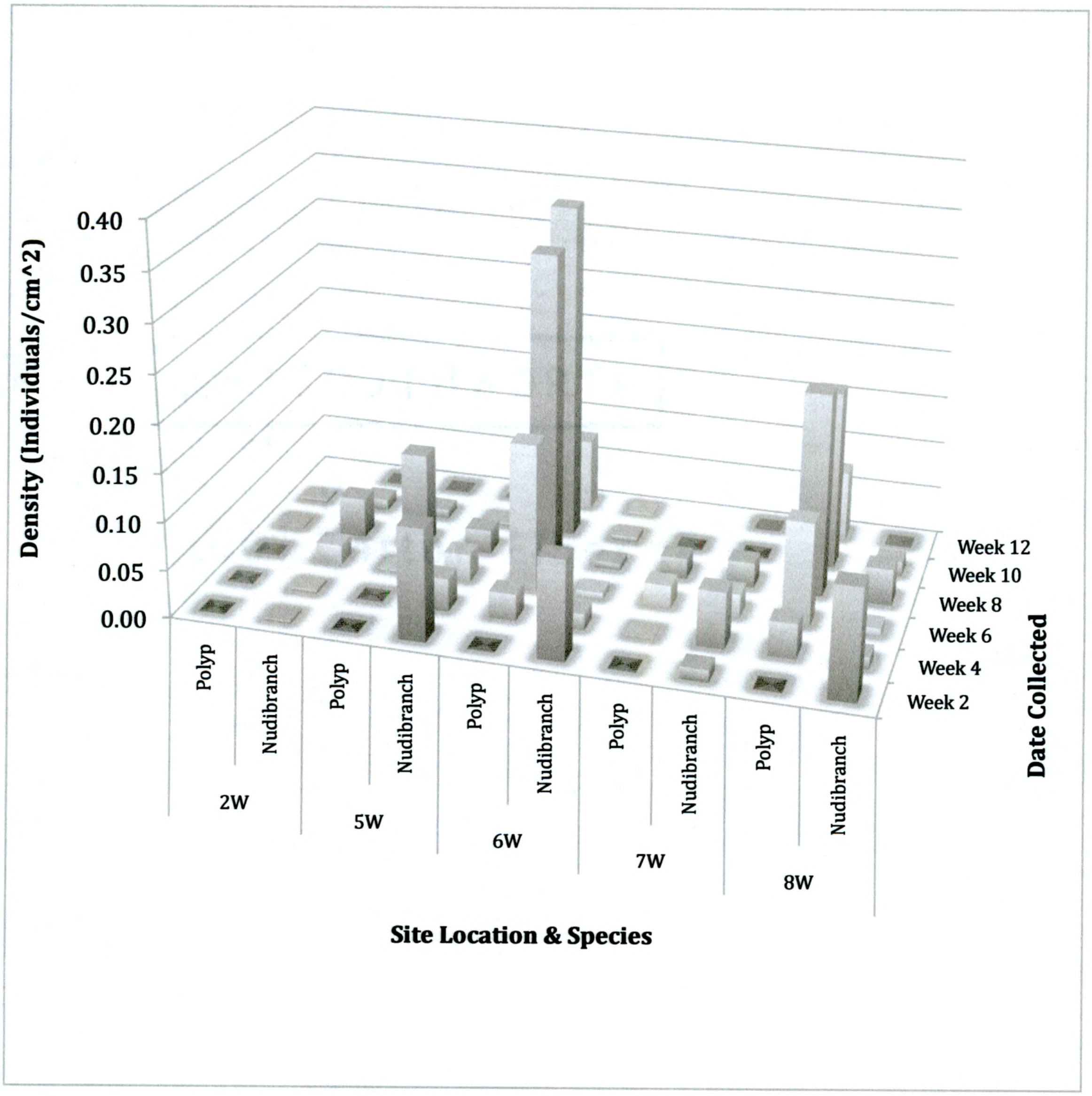


Figure 10: Density of nudibranchs and the polyp stage of *C. quinquecirrha*. A regression analysis shows that there is a relationship between nudibranchs and the polyp stage recruitment (r = -0.1263, P = 0.8099).

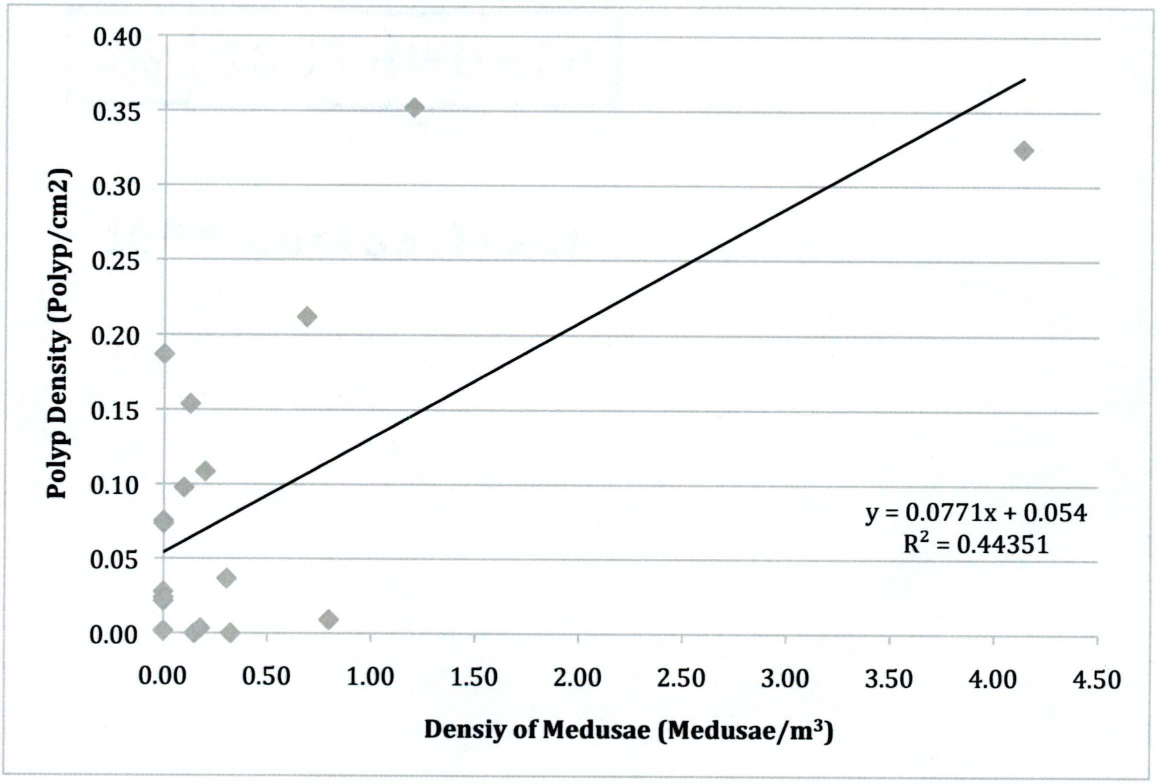


Figure 11: A plate for site 6W where polyps were commonly found.

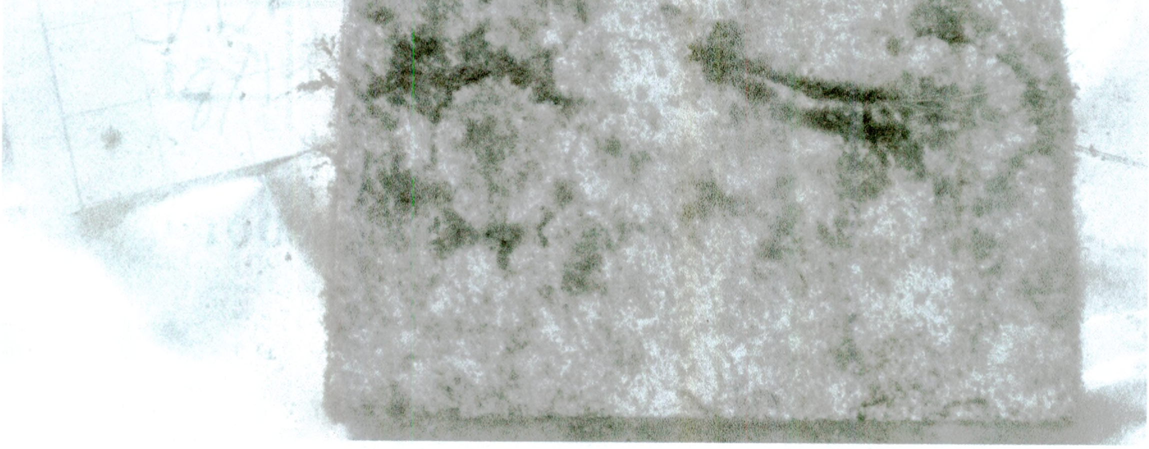


Figure 12: A vinyl settling plate from site 3E where no polyps were found during the study.

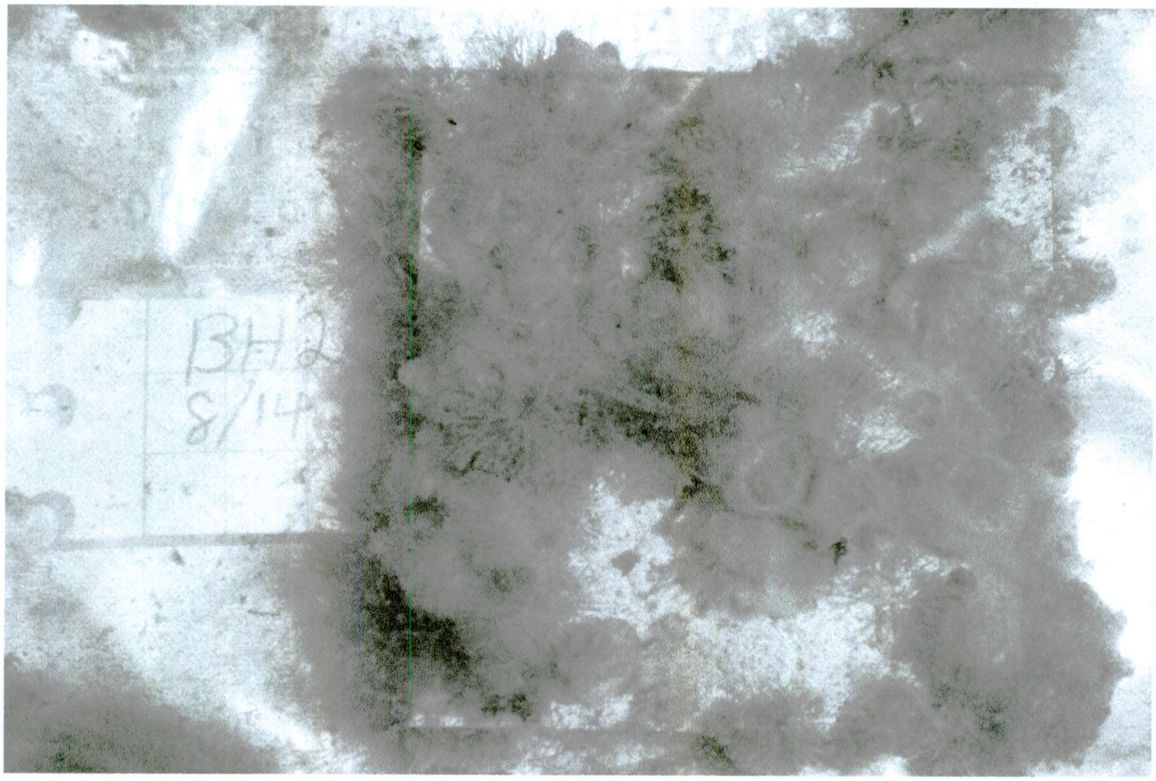
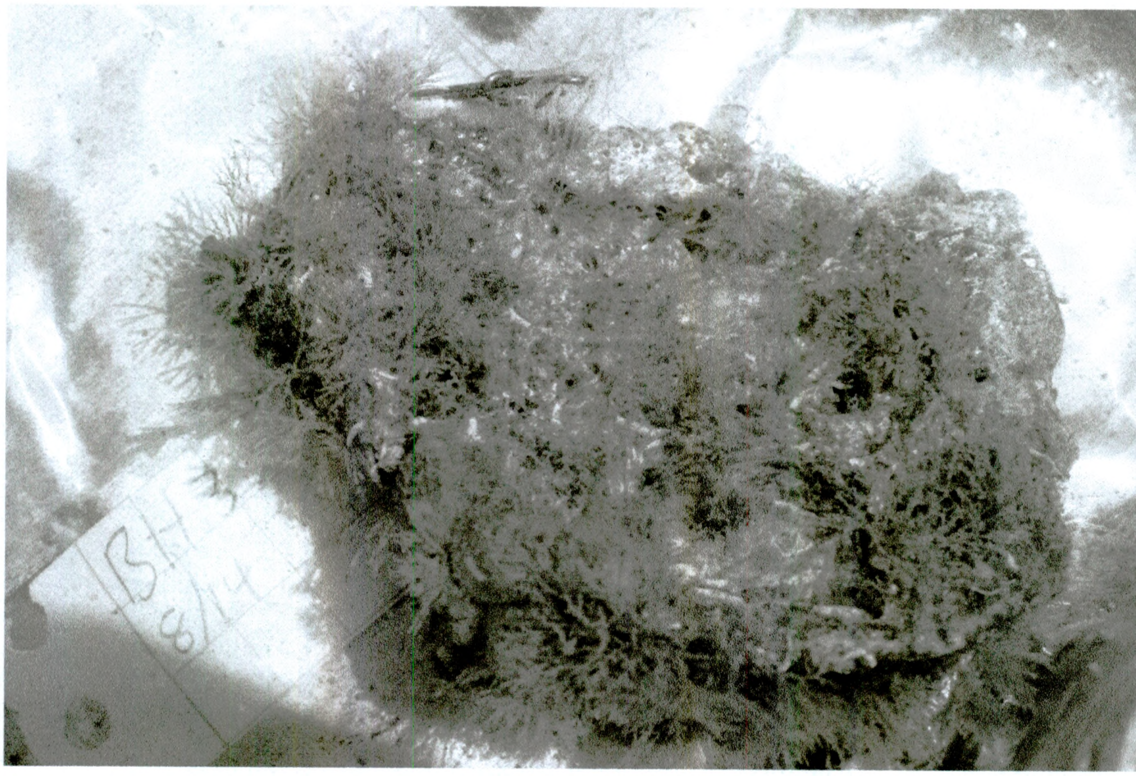


Figure 13: A oyster shell settling plate from site 3E where no polpys were found during the study.



APPENDIX

Appendix 1: Temperature, salinity, and dissolved oxygen data beginning with the first placement of settling plates through the final collection of the summer. Cells containing NA were field days when the YSI was not available.

SITE	Water Quality	Week 0	Week 2	Week 4	Week 6	Week 8	Week 10	Week 12
1W	Temperature (C°)	23.0	NA	26.0	NA	NA	24.0	24.3
	Salinity (ppt)	27.9	NA	26.8	28.0	NA	26.0	23.7
	Dissolved Oxygen (mg/L)	7.3	NA	3.5	NA	NA	NA	5.6
2W	Temperature (C°)	23.2	26.4	NA	NA	26.7	26.7	NA
	Salinity (ppt)	23.2	26.1	26.0	27.5	26.2	23.0	NA
	Dissolved Oxygen (mg/L)	3.4	4.7	NA	NA	7.9	6.3	NA
3E	Temperature (C°)	21.6	NA	26.5	NA	NA	22.6	24.6
	Salinity (ppt)	25.8	NA	28.2	28.0	NA	22.5	24.6
	Dissolved Oxygen (mg/L)	6.8	NA	5.4	NA	NA	NA	6.9
4W	Temperature (C°)	23.3	26.0	NA	NA	25.6	25.7	NA
	Salinity (ppt)	24.6	26.3	25.0	25.0	26.9	24.3	NA
	Dissolved Oxygen (mg/L)	2.5	2.8	NA	NA	4.0	4.4	NA
5W	Temperature (C°)	24.3	NA	28.4	NA	NA	25.3	27.0
	Salinity (ppt)	22.9	NA	24.4	26.0	NA	16.0	20.6
	Dissolved Oxygen (mg/L)	5.8	NA	4.9	NA	NA	NA	5.8
6W	Temperature (C°)	25.7	NA	29.4	NA	NA	26.3	28.3
	Salinity (ppt)	13.6	NA	16.6	26.0	NA	15.0	14.8
	Dissolved Oxygen (mg/L)	8.0	NA	7.9	NA	NA	NA	6.8
7W	Temperature (C°)	22.7	24.8	NA	NA	24.1	23.6	NA
	Salinity (ppt)	8.0	10.3	15.0	11.0	12.4	8.5	NA
	Dissolved Oxygen (mg/L)	6.2	4.1	NA	NA	6.5	6.4	NA
8W	Temperature (C°)	24.6	NA	27.3	NA	NA	25.3	28.4
	Salinity (ppt)	16.7	NA	16.1	26.0	NA	14.0	17.0
	Dissolved Oxygen (mg/L)	6.0	NA	6.5	NA	NA	NA	7.7
9E	Temperature (C°)	22.7	NA	27.2	NA	NA	24.8	26.6
	Salinity (ppt)	21.3	NA	17.3	17.0	NA	14.0	19.9
	Dissolved Oxygen (mg/L)	8.9	NA	6.8	NA	NA	NA	7.9
10W	Temperature (C°)	24.0	NA	27.5	NA	NA	24.3	26.8
	Salinity (ppt)	22.1	NA	19.3	16.0	NA	24.0	23.8
	Dissolved Oxygen (mg/L)	7.4	NA	5.2	NA	NA	NA	7.1