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Chrysaora quinquecirrha Polyps in Barnegat Bay, NJ

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MONTCLAIR STATE UNIVERSITY
SETTLEMENT SURVEY OF
CHRYSAORA QUINQUECIRRHA POLYPS IN BARNEGAT BAY, NJ

by

Monica Katherine Buesser

A Master's Thesis Submitted to the Faculty of

Montclair State University

In partial fulfillment of the requirements

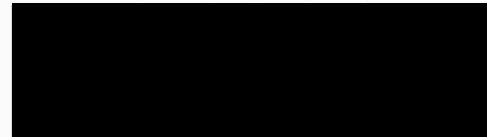
For the degree of Master of Science

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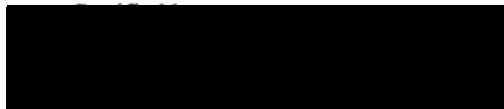
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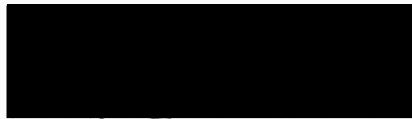
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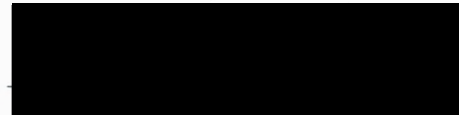
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ABSTRACT

Sea nettles (*Chrysaora quinquecirrha*) have become abundant in the estuaries of the Mid-Atlantic States. Their ample numbers are an indicator of a disturbed ecosystem. Various factors have been attributed to the rise in numbers of sea nettles including eutrophication, overfishing, global warming, construction and species introduction. Barnegat Bay is a highly eutrophic system with excess nitrogen and organic carbon arriving in the bay via runoff and watershed waste inputs. Many commercial fisheries in Barnegat Bay have ceased to exist and the remaining fisheries are dwindling. An overabundance of medusae and polyps will further impact fisheries since jellyfish compete with larval fish when young and prey on planktonic eggs and larvae as they mature.

While observations of the medusa stage indicate a disproportionate abundance in the northern part of the bay, quantification of these differences has not taken place. Information about the life history of the *Chrysaora quinquecirrha* polyp in the field is limited. This research focused on undertaking a settlement survey of polyps from eight sites in Barnegat Bay. Results showed initial settlement in July with continued settlement observed until November. Of the eight sites monitored monthly, only two sites showed settlement and both of these occurred in the northern portion of the bay. Peak settlement was seen at Cattus Island during August with 1,528 polyps collected from that settling plate. Water quality assessment indicated that these sites had lower salinities than all of the other sites except Toms River. Previous research in the Chesapeake Bay has established that *Chrysaora quinquecirrha* polyps are only found in waters of 5-20ppt salinity.

Polyp growth and strobilation will directly determine adult medusa populations. Therefore, the distributions of polyps and medusae are most likely linked and reflect differences in water quality. Other factors may also influence polyp populations including the other species found on the plates with the polyps. With continued research, a count of polyps could be used to predict future medusae populations. This study reports on the temporal and spatial patterns of polyp distribution in Barnegat Bay and the differences in physical characteristics and species composition at the sites where polyps were located.

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A THESIS

Submitted in partial fulfillment of the requirements

For the degree of Master of Science

Biology

By

MONICA KATHERINE BUESSER

Montclair State University

Montclair, NJ

2012

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Chapter 1. A Review of *Chrysaora quinquecirrha*

Taxonomy: Desor 1848

Animalia, Cnidaria, Medusozoa, Scyphozoa, Discomedusae, Semaestomeae,
Pelagiidae, Chrysaora, *Chrysaora quinquecirrha* – sea nettle (Kramp, 1961)



Figure 1. Illustration is by Dale R. Calder (Keys to Marine Invertebrates)

General Description of Medusa

Chrysaora quinquecirrha, as described by Kramp in 1961 (Figure 1), in its medusa form is characterized as being up to 250mm wide, with semicircular or tongue-shaped marginal lappets (lobe-loose fleshy part). The lappet clefts (gaps or division) of the primary and secondary tentacles are deep, while there are only shallow notches in the tertiary tentacles. All stomach pouches are of equal width. Gastric septa (thin partition or membrane in stomach) are straight until well removed from the margin. As the septa move toward the rhopalar (sensory organ) radius (margin) they make an S-like bend. The bell is divided into eight equal sections, in each section there are three large tentacles and two to four smaller ones. These tentacles descend from the subumbrella side of the rhopalar lappets. The color of *Chrysaora quinquecirrha* can be quite variable. They are found pale whitish, yellowish, or pink and occasionally have stripes of color that are radiating up and down the bell (Kramp1961).

Chrysaora quinquecirrha is a member of the Scyphozoa class of cnidarians. Scyphozoans have several traits in common with other cnidarians. They usually have tentacles, a radial symmetry, a body wall made up of an outer epidermis, a layer of mesoglea (jelly-like substance), and an inner gastrodermis. The four oral lobes (arms) are long, thin, delicate and translucent (Calder 1972a). There is only a single opening to digestive system and nematocysts (stinging cells) are always present. Medusae of scyphozoans are larger and more structurally refined than the polyp. They can be distinguished from the hydromedusae and cubomedusae because they do not have a velum which is a shelf of tissue projecting inward from the margin of the bell (Pollock 1998).

Chrysaora quinquecirrha is found in warm waters off the Atlantic coast from southern New England down to the Gulf of Mexico (Kramp 1961). They are generally found in waters from 12°C to 35°C. Sea nettles also occur in the western Pacific and Indian Oceans (Balamurugan et al. 2009). Studies of the polyp and ephyra stages have demonstrated that mesohaline waters of 5-20 ppt are the estuarine areas where these stages are most frequently found (Cargo and Schultz 1966). Adult medusa can be found throughout mesohaline (18-30 ppt) and euhaline (30-35 ppt) waters (Calder 1972b). Researchers have studied this jellyfish extensively in the Chesapeake Bay and in the Gulf of Mexico.

Life cycle

Chrysaora quinquecirrha has a complex life cycle. Sea nettles reproduce both sexually and asexually. The familiar medusa is part of the sexual cycle. It can be male, female or hermaphroditic although this is rare (Calder 1972b). Males have bright pink gonads which contain sacs that vary in size and shape and contain spermatozoa

(Littleford 1939). Females have grayish brown or yellowish brown gonads which produce eggs from 0.07 to 0.19mm in size (Littleford 1939). Eggs are initially colorless and become yellow as they mature (Littleford 1939). The medusa produce sperm or eggs once mature, about two months from strobilation. Eggs are shed into gastro vascular cavity where they can be fertilized or into the water column and fertilized externally (Calder 1972). Observation of 51 females, all bearing embryos, suggests that most fertilization occurs in the gastric cavity (Littleford 1939). Eggs develop into planktonic ciliated larva or planula. In the Chesapeake Bay, planulae begin to settle and form polyps in July, settlement of polyps peaks in August or September (Cones and Haven 1969). Therefore you can conclude that settlement of polyps in Barnegat Bay may be slightly delayed because of cooler temperatures in New Jersey, but it should occur within approximately the same timeframe.

A round or oval shaped planulae moves through the water by moving cilia which develop in some cells of the ectoderm (Littleford 1939). The free swimming planula settles within 3-5 days onto the underside of a hard substrate, such as oyster shells or rocks, and develops into a polyp (Cargo and Schultz 1966). An adhesive substance is secreted from the anterior end of the polyp which attaches it to the substrate and forms a disc around the stalk of the polyp (Littleford 1939). Newly set polyps are described as pink buttons with 2-16 tentacles (Cones and Haven 1969). The polyp is very small only 1-4 mm high and 0.6 mm wide (Littleford 1939, Calder 1972b). The body of the polyp is divided into two sections, the stalk and the cup-like body (Littleford 1939). The body of the stalk will vary dependent on the intensity of contraction in the stalk at the time measured (Littleford 1939). The stalk is usually about 1.5mm (Calder 1972b). Tentacles on the polyp are 6mm long and contain nematocysts at regular intervals forming rings around the tentacles (Littleford 1939).

The mouth region of the polyp develops from a small slit into a wide opening within 1-3 hours after attachment (Littleford 1939). The width of the oral disc is from 0.6-1.5mm (Morandini et al. 2004). The mouth of each polyp has a cruciform shape (cross) and oral disc with four peristomal pits (Calder 1972). Tentacles are produced one at a time from the region surrounding the mouth (Littleford 1939). In five days the polyps have four primary tentacles (Littleford 1939). Four secondary tentacles are produced by the 10th day after settlement (Littleford 1939). In fifteen days, the matured polyp has 16 filiform (threadlike) tentacles and is now called scyphistoma. Well fed polyps develop fully in about three weeks (Calder 1972b). Polyps have several types of nematocysts: microbasic heterotrichous euryteles and atrichous isorhizas are found on the tentacles and cnidocils on the base of the polyp (Blanquet and Wetzel 1975). Calder (1971) also observed hototrichous haplonemes in polyps from Chesapeake Bay. Nematocysts may vary dependent on geographical location (Calder 1971). Nematocysts are classified according to their size and shape (Arai 1997).

Environmental conditions such as change in temperature, salinity, or food availability will cue the polyp to become a strobila which will divide horizontally by transverse segmentation (Cargo and Rabenold 1980). Strobilation forms ephyra which are juvenile medusa that are about 0.84 mm in diameter (Littleford 1939). Usually strobilation begins in late spring and continues through the summer. Ephyra have eight pairs of lappets (projecting lobe like structure or loose flaps) and eight rhopalia (or tentaculocyst-auditory/sensory organ) (Littleford 1939). The rhopalar clefts split the ephyral arms more than half way down (Calder 1972a). Ephyra initially have no tentacles, they do however have aggregations of nematocysts on ephyral arms (Littleford 1939). Tentacles develop 4-5 days after separation (Littleford 1939). When small the ephyra swim upside down with subumbrellar side up, but as it develops tentacles it begins to swim in the normal fashion (Littleford 1939).

The juvenile medusa grows into an adult and once mature can shed thousands of eggs daily to perpetuate the cycle. When cold weather cools the temperature of the water to 10°C the adult medusa will die, but the polyps will form a cyst and overwinter (Purcell et al. 1999). Polyps encyst when conditions are not favorable and have been recorded to survive up to four years in laboratory conditions (Littleford 1939). Warm temperatures in the spring will cause the polyp to excyst. In other species of jellyfish it was found that polyps will divide to form more polyps if adequate food is present or go through strobilation forming ephyra if food is limited (Hoover and Purcell 2009).

Polyp Stage

Although the medusa may shed hundreds or thousands of gametes daily, it is usually only seasonal in appearance. The polyp stage of *Chrysaora quinquecirrha* life cycle has several methods of reproduction which can create colonies of polyps that survive for years and produce many generations of juvenile medusae.



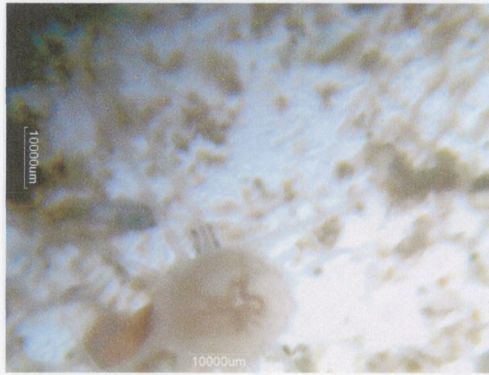


Figure 2. Polyps found on Cattus Island settlement plate in August.

Preferred settlement

Fertilized eggs of *Chrysaora quinquecirrha* quickly form into planulae, a free swimming larval form that will eventually settle on a hard substrate and develop into polyps. Sea nettle polyps are small and cryptic. Researchers determined that in the Chesapeake Bay, polyps were most commonly found on oyster shells and the underside of other hard substrates (Cargo and Schultz 1966). The polyps probably settle underneath objects to prevent sediments from covering them. By being on the underside of objects, polyps would also avoid the typical marine fouling found on upper surfaces. Other Scyphozoa planulae (*Aurelia aurita*, *Cyanea capillata*, *Cyanea lamrckii*, *Chrysaora hysoscella*, *Rhizostoma octopus*) have also been shown to strongly favor the underside of settlement plates in laboratory experiments (Holst and Jarms 2006). *Chrysaora quinquecirrha* polyps are found in shallower waters and were not found below 11 meters (Cargo and Schultz 1966). The planula may use light to orient themselves on the darker side of substrate although this is not evident in the lab studies (Cargo and Schultz 1966).

Consequently, overwintering *Chrysaora quinquecirrha* polyps in the Chesapeake Bay were also primarily found on oyster shells (Brietburg and Fulford 2006). This relationship is mutually beneficial because *Chrysaora quinquecirrha* medusae consume large quantities of *Mnemiopsis leidyi* ctenophores which prey on oyster larvae and *Chrysaora quinquecirrha* does not consume oyster larvae (Brietburg and Fulford 2006). Restoration of oysters may coincide with higher population numbers of sea nettles (Breitburg and Fulford 2006).

Bulkheads have traditionally been made of chemically treated wood which has been shown to harbor a reduced number of species (Weis and Weis 1992). Plastic bulkheads have begun to replace wooden bulkheads in many areas due to recent changes in regulations forbidding the use of chemically treated wood. The plastic bulkheads may give *Chrysaora quinquecirrha* polyps a new hard non-toxic surface to attach and grow. A recent study found that plastics were a preferred over rubber and treated wood as a settling substrate for *Aurelia labiata* polyps (Hoover and Purcell 2009). Another study

on settlement preferences of five different Scyphozoan planulae indicated that all tested species preferred to settle on the underside of settlement plates 80-100% of the time and also preferred plastic and glass over shells, wood, or concrete as a substrate (Holst and Jarms 2006). *Chrysaora quinquecirrha* polyps are generally not found on plants (Cones and Haven 1969).

Strobilation

Calder (1974) studied the strobilation of *Chrysaora quinquecirrha* from March 1972-Feb 1973. Strobilation was first observed in April when the water temperature was 16.8°C. His studies indicated that strobilation rapidly increased after this date through June. On June 5, 25% of the polyps were strobilating. After June very few polyps were observed to be producing ephyra. October was the latest date that strobilating polyps were observed. Several peaks of strobilation were observed and they seemed to coincide with tidal cycle. Scyphistoma can strobilate several times during the season producing anywhere from 1-16 ephyra each time. Under experimental conditions it was shown that elevating the water temperature will cue strobilation in polyps that have been maintained in cold conditions. Other scyphozoans have been observed to produce ephyra in response to changes in food availability, salinity, oxygen concentration, iodine availability, light, pH, symbiotic zooxanthellae and chemical treatments (Arai 1997, Calder 1974).

Two separate processes are undertaken during strobilation, segmentation and metamorphosis. During the segmentation process several ephyrae are made and released, but a portion of the polyp remains that can completely regenerate itself, possibly several times a season (Calder 1974). More ephyra are produced by polyps when there is abundant food increasing the numbers of medusa (Purcell et al. 1999). However, there is no increase in the number of polyps with an increase in food, possibly because polyp production is a long term strategy and ephyra production is a quicker response to current environmental conditions (Purcell et al. 1999).

Cyst production

If conditions are not acceptable for continued growth or strobilation, polyps will form cysts around themselves and go dormant until conditions improve. *Chrysaora quinquecirrha* polyps are able to encyst and overwinter and live for more than one year. Researchers have cultured polyps that have lived for four years in the lab, continually forming cysts in the fall and strobilating each summer (Arai 2009). Some studies have shown that adverse conditions cause encystment. In the lab conditions causing encystment include: oxygen depletion, water temperature below 4°C, and salinity below 5‰ or above 30‰ (Cargo and Schultz 1966). Heavy bacterial fouling also caused polyps to encyst (Cargo and Schultz 1966). Cysts also are thought to protect polyps from predators such as nudibranchs (Arai 2009). The cysts will reform a thinner chitin shell if

the original one is removed (Arai 2009). Some polyps will not form a cyst in colder water if other conditions are not limiting and therefore, they will be the first to strobilate in the spring when water temperatures reach 19-20°C (Cargo and Schultz 1967). Other studies have shown that good conditions will increase the amount of cysts produced while poor conditions of no food and no water exchange will cause a reduction in polyp size and no encystment or cyst production (Arai 2009). Extremely poor conditions may not allow the polyp enough time and/or energy to create a cyst.

Cysts can be formed by polyps in several ways, from the pedal (basal) disc, at the end of a stolon, and on the stalk itself (Cargo and Rabenold 1980). Planulae can also form planulocysts; they are usually larger than podocysts and form slightly different plano-convex shape when they settle (Arai 2009). Polyps will produce cysts several times a year and some will produce large numbers of cysts (Cargo and Schultz 1967). This asexual form of reproduction not only increases survival during adverse conditions, but this natural part of the lifecycle enables *Chrysaora quinquecirrha* polyps to create blooms of medusae as the polyps excyst and begin to strobilate when the water warms in the spring (Cargo and Schultz 1967).

Podocysts

Podocysts are formed underneath the pedal discs which is a thin plate of tissue that attaches to the substrate. Pedal discs are located opposite the mouth on scyphozoan polyps. When forming a cyst, the foot of the polyp spreads into two or more parts up to 2-3 mm apart. As the polyp divides, cysts will form at points of contact with the substrate (Cargo and Schultz 1966). Podocysts are covered in chitin and form at the foot of the polyp (Arai 2009). The chitin is created from the ectodermal and endodermal layers which still contain the nematocysts (Cargo and Schultz 1966). Viable *Chrysaora quinquecirrha* podocysts are generally opaque to start with and turn reddish brown in color with a diameter of 0.35-0.45 mm (Morandini et al. 2004). The interior of the podocysts contains carbohydrate, lipids, and proteins (Arai 2009). Typically they are irregularly shaped discs with a depression in the middle (Arai 2009).

The polyp can move across a substrate surface with a help of a stolon leaving a trail of podocysts (Arai 2009). Stolons bud from the side of the polyp stalks and once they reach the substrate, they can form a new polyp or a cyst (Cargo and Schultz 1966). Each podocysts can develop into a polyp and produce ephyra increasing the productivity of the original polyp. These new polyps can also make more podocysts increasing the numbers in a polyp colony. In several species, encystment creates many more individuals than strobilation (Arai 2009). Experimental studies have found colonies of polyps with a population of more than one hundred polyps and cysts. One polyp kept in optimal conditions at 21-23 °C formed 52 cysts and 6 polyps during the summer (Cargo and Schultz 1966). This added ability of the polyp to reproduce itself may increase the

possibility of jellyfish blooms (Arai 2009). The capacity of one polyp to clone itself many times has the ability to pass along mutations almost as well as in sexual reproduction (Adler and Jarms 2009). Interestingly, in another *Chrysaora* species it has been observed that the cysts created produce a larval form that is ciliated and will swim to a new location, attach, and produce a new polyp (Littleford 1939).

Other asexual reproductive strategies

In addition to releasing ephyra, creating podocysts, and stolon budding, there are several other documented asexual processes that Scyphozoan polyps undergo. In *Sanderia malayensis*, several different types of asexual reproduction were observed, they included: Sanderia-type budding, stolons, bud like particles, tentacles tips/pieces, longitudinal fission, and gastric constriction (Adler and Jarms 2009).

Sanderia-type budding begins with a protrusion becoming visible at the junction between the calyx and the stalk. Another protrusion develops on the opposite side of the polyp which develops a stolon. The initial bud develops a mouth opening and tentacles and by the fourth day is able to feed itself. The mother and daughter polyp then begin to separate. The connecting tissue between the two becomes thinner and mother polyp pulls itself away with the stolon. Sometimes the daughter polyp creates a stolon and pulls away from the mother polyp (Adler and Jarms 2009).

Stolons that form and attach near the stalk of the polyp can pull the entire polyp away from the old stalk and create a new polyp. Sometimes the stolons are severed from the polyp and create new polyps. The detachment of the mother polyp from the stolons is gradual as the tension increases between the mother and daughter polyp (Adler and Jarms 2009).

Bud-like particles are released from some *Sanderia malayensis*. These particles are released from the intersection of the calyx and the stalk. These tissue pieces varied in size from 0.24-1.10mm. The shape of the bud-like particles was also highly variable. Some particles rotate and floated over the bottom of the lab dish. After 3-7 days the ball-like pieces attached to the substrate. Within two days of attachment the mouth and tentacles of the new polyp develop and the polyps grew and fed normally. Buds that were separated from the mother polyp developed without settling on substrate (Adler and Jarms 2009).

Sanderia malayensis polyps have another unique method of division. Sometimes club shaped swelling can be found on the tentacle tips of full grown polyps. These swollen regions appear opaque and often bend down to touch the substrate. The tentacle pieces break off and are variable in size and shape, averaging 0.32 in diameter. These pieces are free swimming and move like planula and develop into polyps within 4-12 weeks

depending on substrate availability. This type of reproduction has been noted in *Chrysaora* species (Adler and Jarms 2009).

Longitudinal fission can start with the tentacular end creating a two headed polyp. A stolon will develop to pull one head away from the other. Fission from top to bottom is rare and considered a rupture. The rupture occurs when a stolon pulls the stalk apart and the mouth disc and tentacles are split between the two daughter polyps (Adler and Jarms 2009).

Gastric constriction is a very rarely observed method of asexual division. *Sanderia malayensis* polyps were observed to completely evert. Gastric tissue created a short stolon. The stolon was constricted from the polyp and eventually settled on substrate and produced a new polyp. This strategy was similar to bud like particles, but it accelerated the regeneration time (Adler and Jarms 2009).

An alternative reproductive method utilized by the hydrozoan *Turritopsis nutricula* includes a medusa stage that can settle and convert into polyps (Fautin 2002). Immature medusae of this species were shown to revert to polyp stage after encysting due to unfavorable environmental conditions. Mature medusae were also observed to spontaneously degenerate into polyps and stolons (Piraino et al. 1996). Although this form of regeneration has not been documented in scyphozoan species, considering all the other methods of reproduction employed and the fact that the medusa is genetically identical to polyps, it is a good candidate for further study.

Ephyra to Medusa

According to Calder (1972a) the ephyra of *Chrysaora quinquecirrha* goes through six stages of development to become a mature adult medusa (Fig.3). The first stage of development starts with the newly detached ephyra. They are approximately 2.0 – 3.5 mm in diameter. One to three days after release, during Stage 2 of development, ephyra gain eight primary tentacles which appear simultaneously and grow at the same rate. The oral arms begin to develop at each corner of the enlarging manubrium. The oral arms are relatively distinct and move independently. As the lappets fold under in Stage 3 the ephyra begin to look like medusa. This stage occurs approximately 10-14 days after release. The oral arms are now well developed. During Stage 4 medusa develop secondary tentacles between the primary tentacles and rhopalia. At about 25 days after liberation, one new tentacle emerges from each corner of the tentacular pouches of the gastrovascular cavity. Each of the original 16 lappets becomes divided in two to create 32 tongue shaped lappets. Oral arms are now becoming frilly. Gonads develop and at this stage the medusa is considered sexually mature.

In Stage 5, 16 tertiary tentacles appear on the lateral sides of the secondary tentacles making a total of 40 tentacles. Lappets next to tertiary tentacles divide in two creating a

total of 48 lappets. This stage is also referred to as the Dactylometra stage. Stage 6 culminates in a medusa with seven or more tentacles per octant (56+) and eight or more lappets per octant (64+) (Calder 1972a).

The age of development into different stages of *Chrysaora quinquecirrha* is variable. Classification of this species was originally based on juvenile morphology. The varying number of lappets and tentacles confused taxonomists. Eventually scientists discovered the various stages of the adult medusa were not separate species, but *Chrysaora quinquecirrha* in its various forms. Some individuals of *Chrysaora quinquecirrha* do not reach stage 5 or 6, because they sexually mature at stage 4 (Calder 1972a). Earlier sexual maturity allows this jellyfish to spawn earlier and more often possibly leading to more blooms.

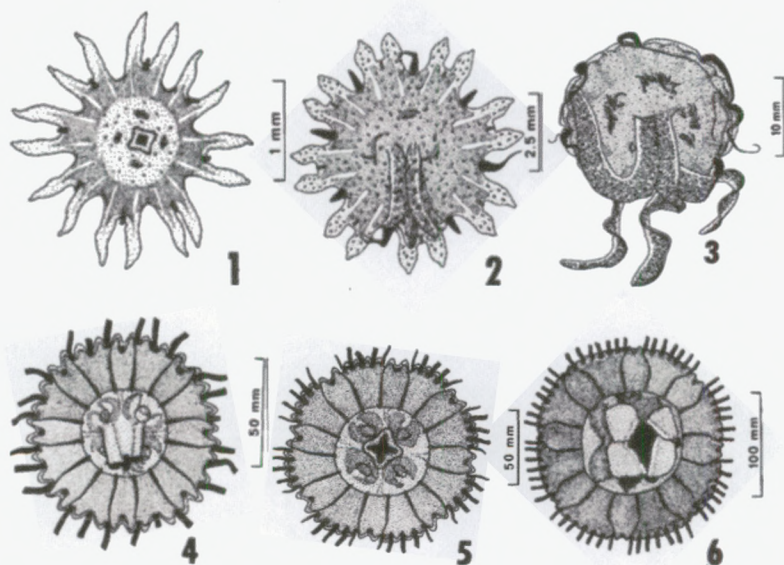


Figure 3. Ephyra to Medusa

Illustration by Dale R. Calder, Development of the Sea Nettle, *Chrysaora quinquecirrha* 1972a (oral arms and tentacles are not illustrated stage 4-6)

Range of physical conditions

Chrysaora quinquecirrha is found in coastal areas of the eastern Atlantic, western Pacific and Indian Oceans. It is classified as a mesohaline and euhaline species. Researchers have studied this scyphozoan extensively in estuarine conditions. There are physical conditions which seem to limit distribution of this species in the mesohaline environment. Previous studies have indicated that changes in salinity, temperature, and oxygen concentration can have a substantial impact on *Chrysaora quinquecirrha* polyps and medusae influencing their ability to reproduce and survive (Condon et al. 2001,

Mangum et al. 1972, Purcell et al. 1999). Other physical factors such as light and availability of prey also influence the behavior of this scyphozoan (Loeb 1973, Matanoski et al. 2001).

Oxygen concentration

Areas of low dissolved oxygen are found in many coastal areas due to the anthropogenic effects of eutrophication. Hypoxic waters (<2mg oxygen/l) also form in estuaries because of the water stratification due to density differences created by salinity and temperature (Wu 2002). Fish and other organisms cannot survive in hypoxic waters and their distribution and behavior will be altered. Marine organisms can often detect and avoid areas of low oxygen. Hypoxia has been linked to a decrease in species diversity and the elimination of some sensitive species (Wu 2002).

Polyps of *Chrysaora quinquecirrha* are generally found in shallow (<11 m) waters (Cargo and Schultz 1966). Shallower water is more likely to be mixed and therefore have more favorable dissolved oxygen concentrations, but shallow waters are also subject to fluctuations in oxygen concentrations that may cause temporary anoxic or extreme hypoxic conditions (Condon et al. 2001). Researchers tested the ability of *Chrysaora quinquecirrha* polyps to tolerate hypoxic conditions. Polyps were placed in dissolved oxygen concentrations of 3.5 mg/l – 0.5 mg/l. High polyp survival was seen in all concentrations for the first five days, even after 24 days of extremely hypoxic conditions (0.5 mg/l) over 40% of the polyps still survived. None of the polyps in this experiment formed cysts, but polyps in all oxygen concentrations formed strobila. (Condon et al. 2001). The capacity of this species to tolerate extremely hypoxic conditions may allow it to compete more effectively than other more sensitive benthic fauna.

The medusa of *Chrysaora quinquecirrha* has the ability to survive in extremely hypoxic conditions (0.5mg oxygen/l) for up to 48 hours (Condon et al. 2001). In the northern Gulf of Mexico, populations of *Chrysaora quinquecirrha* medusae are associated with areas of hypoxia along the Louisiana shelf (Graham 2001). Trawls of areas in the Gulf of Mexico recorded catching *Chrysaora quinquecirrha* in areas with significantly lower dissolved oxygen (Graham 2001). Hypoxic waters (<2mg/l) tend to benefit jellyfish by reducing competition from other less tolerant species and making *Chrysaora quinquecirrha* a more efficient predator (Graham 2001). Researchers admit the relationship between hypoxia and *Chrysaora quinquecirrha* is not clear, but this species has taken advantage of its ability to survive in this hostile environment (Graham 2001).

A study was done on how low levels of dissolved oxygen effect trophic interactions within an estuarine environment. Several aspects of predator-prey interactions are impacted by hypoxia. Shifts in vertical distribution of organisms will alter encounter

rates and time spent foraging and the location of foraging (Breitburg et al. 1997). Alternate trophic pathways were observed as the predator-prey relationship changed when oxygen concentrations fell (Breitburg et al. 1997). Significant increases in predation on fish larvae by *Chrysaora quinquecirrha* were recorded at reduced dissolved oxygen concentrations of 2.5 and 1.5 mg/L (Breitburg et al. 1997). Medusa did not change their position (depth or nearest neighbor distance) in mesocosms at differing oxygen concentrations (Breitburg et al. 1997). Striped bass assayed in the same way behaved differently. As the oxygen concentration decreased, the striped bass captured fewer fish larvae at all prey densities tested (Breitburg et al. 1997). Lower oxygen levels change the dynamics of this trophic system and favor *Chrysaora quinquecirrha* over one of its competitors, the striped bass.

Salinity

Chrysaora quinquecirrha medusae are found in estuarine areas with salinity from 5-25 ppt (Wright and Purcell 1997). This species is atypical compared to other cnidarians because it can tolerate such low salinities (Purcell et al. 1999). Polyps have been detected in waters between 5 and 20 ppt salinity (Cargo and Schultz 1966). Scyphistomae (mature polyps) flourish in waters of 10-25 ppt salinity and are not found in salinities below 7 ppt (Purcell et al. 1999).

One experiment demonstrated that most polyps died or encysted at salinities of 5 ppt and below and at salinities higher than 25 ppt (Cargo and Schultz 1966). Transferring medusae from 20 ppt to 5 ppt salinities caused all animals to fall to the bottom of lab beakers and half of these medusae died within 36 hours (Wright and Purcell 1997). *Chrysaora quinquecirrha* may not be able to control buoyancy or regulate volume at extremely low salinities (Wright and Purcell 1997). Survival was best at 10, 15, and 20 ppt salinities (Cargo and Schultz 1966).

Changes in salinity were shown to cause the polyps to strobilate even when the temperature of the water was lowered (Cargo and Schultz 1966). Some studies indicate that since iodide is required for strobilation, and salinity is directly correlated with iodide concentration, changes in salinity will affect strobilation (Purcell et al. 1999). Ephyra production has been found to be highest at salinities of 20 ppt (Purcell et al. 1999). *Chrysaora quinquecirrha* does not produce ephyra at high salinities (35 ppt) and polyps encysted above 35.5 ppt (Purcell et al. 1999). The physiological cost of salinity regulation in this typically mesohaline species may be the cause of limited reproduction in very low or very high salinities (Wright and Purcell 1997).

The low tolerance and reduced asexual reproduction reported at high salinities is confusing because this species is reported to occur in high salinity waters off the Atlantic, Pacific, the Gulf of Mexico and Indian coasts (Graham 2001, Kramp 1961, Purcell et al.

1999). *Chrysaora quinquecirrha* medusa from high salinity waters have a different appearance than *Chrysaora quinquecirrha* found in mesohaline estuarine waters (Purcell et al. 1999). Medusae found in the Chesapeake Bay (and Barnegat Bay-personal observation) are milky white, while *Chrysaora quinquecirrha* found in coastal waters have reddish brown stripes on the bell and oral arms (Purcell et al. 1999). Some researchers have concluded that there are two distinct populations of *Chrysaora quinquecirrha*, the high salinity red, and the low salinity white. In estuarine areas, the red medusa could be carried into the bays by high salinity bottom waters and the white presumably washed down the bay in the upper level low salinity surface waters (Purcell et al. 1999). Bayha (2005) has genetically analyzed populations of *Chrysaora quinquecirrha* from several areas of the world and determined that estuarine populations of *Chrysaora* are a separate species. He has also determined that each estuary has its own genetically isolated species of *Chrysaora quinquecirrha* (Bayha 2005).

Extremely low salinities could negatively affect ionic regulation of polyps and medusa (Wright and Purcell 1997). Wright and Purcell (1997) performed several experiments on the ionic changes that occur in *Chrysaora quinquecirrha* with changes of salinity. They found *Chrysaora quinquecirrha* actively regulates the concentrations of sodium, potassium, calcium, magnesium, and sulfate. Medusae were transferred from a concentration of 20ppt salinity to 8ppt and 12ppt. In experimental concentrations, tissue and mesogleal fluid sodium concentrations fell to a level approximating concentrations in the surrounding water within six hours. In the 8ppt concentration, sodium levels recovered within a week becoming higher than the surrounding water demonstrating the ability of this species to regulate sodium (Wright and Purcell 1997).

Potassium concentrations were tested in the same manner. Medusae kept at a concentration of 20 ppt salinity contained tissue potassium concentrations twice that of the surrounding medium (Wright and Purcell 1997). When *Chrysaora quinquecirrha* was transferred from 20 ppt to 8 ppt salinity, mesogleal potassium levels fell to those approximating levels found in waters of 20 ppt salinity. Medusae transferred from 20 ppt to 12 ppt concentrations showed no significant change in potassium levels (Wright and Purcell 1997).

Calcium and magnesium levels were tested in the same way and showed similar results. Individuals transferred from 20 ppt to 8 ppt showed an initial decrease of calcium in mesogleal fluid and tissue within 6 hours. Mesogleal fluid maintained a higher calcium concentration than tissue or surrounding water. Magnesium levels stayed higher in both tissue and mesogleal fluid compared to levels in 8 ppt and 12 ppt solutions. Tissue levels of magnesium were higher than mesogleal fluid levels. This regulation was observed for one week. Sulfate concentrations were also measured and shown to be significantly lower than the surrounding medium (Wright and Purcell 1997).

Changes in salinity causes rapid changes in weight due osmosis related to tissue hydration (Wright and Purcell 1997). A decrease in salinity from 16 ppt to 8 ppt caused weight increases of 10-15%. This represents a body weight over 30% higher than control animals (Wright and Purcell 1997). Medusae transferred to lower salinities had a water influx that approximated 10% to 20% of original body weight in the first day after transfer (Wright and Purcell 1997).

The osmolality of *Chrysaora quinquecirrha* mesogleal fluid was measured in medusae in 5, 12, 15, and 20 ppt salinities. All medusae tested between 12-20ppt had osmolalities comparable to the surrounding water. Individuals tested at 5ppt and 12ppt had significantly higher osmolalities when compared to the surrounding medium (Wright and Purcell 1997). Researchers determined that between 15ppt and 12ppt salinities *Chrysaora quinquecirrha* switches from being hypo-osmolar to hyperosmolar. In the range of salinities between 12ppt and 20ppt, *Chrysaora quinquecirrha* operates as an osmoconformer (Wright and Purcell 1997).

In the lab polyps were found to tolerate salinities of 30-40 ppt (Cargo and Schultz 1966, Cones and Haven 1969). In the field polyps have not been found in areas where salinities are over 25 ppt. The reason for this difference could be that larvae will not settle in areas that have high salinity, but polyps may be able to adapt to higher salinity if conditions change (Cones and Haven 1969). Lab grown *Chrysaora quinquecirrha* polyps were observed to grow and form stolons at salinities of 40 ppt (Cones and Haven 1969).

Temperature

Changes in temperature have several effects on *Chrysaora quinquecirrha* medusae and polyps (Mangum et al. 1972, Purcell et al. 1999, Sexton et al. 2010). Strobilation is known to be triggered by the warming of the waters in the spring to 15-20°C (Mangum et al. 1972). Polyps have been observed to encyst when water temperatures are below 4°C or above 34°C (Cargo and Schultz 1966).

Researchers subjected cold (12°C) and warm (22°C) maintained *Chrysaora quinquecirrha* polyps to several different temperatures and recorded oxygen consumption. The experimental temperatures were 12, 17, 22, 27 and 32°C. Polyps exposed to temperatures below 12°C degraded, this temperature change was sudden and it did not allow the polyp time to encyst (Mangum et al. 1972). Therefore, drastic changes in temperature may kill polyps. It was also shown that cold maintained *Chrysaora quinquecirrha* polyps have an overall higher oxygen consumption rate which stays higher than warm acclimated polyps as experimental temperatures increase, except at 22°C (Mangum et al. 1972). Cold acclimated polyps would require higher oxygen concentrations and be less able to tolerate hypoxic conditions.

Another study demonstrated that temperatures normally seen in the York River (1-29°C) were not lethal to polyps, but the extremely hot temperature of 35.5°C always caused polyps to form cysts (Cones and Haven 1969). A gradual change in temperature was easily tolerated by polyps (Cones and Haven 1969), but polyps always formed cysts at 34-36°C even if temperature was raised slowly (Cargo and Schultz 1967). These cysts formed at high temperatures were not observed to bud a polyp, therefore cysts do not always survive adverse conditions (Cargo and Schultz 1967). In the lab, cysts kept at 13.5°C will open up and become polyps at 18°C and strobilate at 27°C (Cargo and Schultz 1967). Polyps in the field will generally start strobilation at 18-19°C (Cargo and Schultz 1967).

Polyps acclimated to 25°C water were placed in 4°C water. They immediately shrank into the basal part of the polyp and encysted within 72 hours (Cargo and Schultz 1967). Polyps obtained from 13.8°C waters were placed in three treatment groups. The treatments reduced the water temperature by 1°C, 2°C, and 4°C per day. All of the polyps clumped at 8-10°C and proceeded to form cysts when polyps had been held at 2-3°C for 12 to 14 days (Cargo and Schultz 1967).

Medusae disappear in the fall when the waters cool. Visual counts on the Choptank River indicated medusa initially withdraw from the visible surface layers when water temperatures reach 15°C (Sexton et al. 2010). Medusae could still be caught in vertical net trawls until water temperatures reached 10°C (Sexton et al. 2010). In order to test the effect of cold on medusae, researchers kept them in 13°C water (control at 16°C), with no food and no light. Researchers determined that in the cold tank medusae swam slower and were located deeper than in the control tank (Sexton et al. 2010). It was concluded that *Chrysaora quinquecirrha* would likely be deposited on the bottom sediment as waters cooled below 10°C (Sexton et al. 2010).

Light

Chrysaora quinquecirrha medusae swim close to the top of waters more frequently than at the bottom, which may be caused by a positive response to light (Matanoski et al. 2001). A study of how light affects polyps and strobilation was done by Loeb (1973). Polyps were chilled in one of three treatment groups. They were exposed to 24 hours light, 10 hours of light, and complete darkness. After chilling polyps were placed in 19°C water but light conditions were changed. Overall, those kept in constant light strobilated first, polyps kept in a normal day/night cycle of 10 hours light strobilated second, and polyps kept in the dark took the longest to strobilate (Loeb 1973). If polyps were chilled in light conditions then put in the dark to warm it took them considerably longer to strobilate (Loeb 1973). If polyps were chilled in the dark and warmed in the dark, they did not strobilate at all during the 30 day trial (Loeb 1973). The polyps changed colors dependent on the light cycle; 24 hours of light produced brick red polyps, 10 hours

produced bright pink polyps, no light created pale pink polyps (Loeb 1973). An increase in photoperiod along with an increase in temperature stimulates the strobilation of *Chrysaora quinquecirrha* polyps (Loeb 1973). One study subjected polyps that were temporarily dark adapted to a microscopic spotlight, no response was noted until the polyps were darkly stained with neutral red. Stained polyps recoiled from the light and showed avoidance reactions after 10 seconds (Cargo and Schultz 1967).

Trophic interactions

Chrysaora quinquecirrha medusae are cruising, entangling predators (Suchman and Sullivan 1998). They are also important competitors in Atlantic estuarine and coastal trophic systems. They are however limited by temperature and salinity, only being found in large numbers between temperatures of 26-30°C and salinities of 10 -16ppt (Decker et al. 2007). Researchers determined that large populations of jellyfish can cause major changes in zooplankton and ichthyoplankton populations (Purcell et al. 1999). When blooms of this jellyfish occur, trophic interactions are altered. Studies done in the Chesapeake Bay indicate planktonic herbivore (mostly copepods) levels are high in early May (Feigenbaum and Kelly 1984). By mid to late May, herbivore levels had declined and populations of *Mnemiopsis leidyi* became abundant (Feigenbaum and Kelly 1984). In June the population of *Mnemiopsis leidyi* began to decrease as *Chrysaora quinquecirrha* medusae appeared and began to consume them (Feigenbaum and Kelly 1984). The herbivore level rapidly increased with the reduction of the *Mnemiopsis* population (Feigenbaum and Kelly 1984). By eating the ctenophore *Mnemiopsis leidyi*, *Chrysaora quinquecirrha* increases the amount of secondary productivity in a system (Matanoski et al. 2001). It has been estimated that *Chrysaora quinquecirrha* medusae can clear approximately 36% of the population of ctenophores daily (Feigenbaum and Kelly 1984). In other systems it has been estimated that a large bloom of jellyfish could consume most if not all of the available copepods in nearby waters (Uye 2011). In Feigenbaum and Kelly's study (1984), they found that after the initial rebound in numbers of herbivores, the population steadily declined through August. This was probably due to *Chrysaora* medusae also consuming copepods (Feigenbaum and Kelly 1984). An invasion of the ctenophore, *Mnemiopsis leidyi*, in the Black Sea coincided with a decrease in the amount of zooplankton and fish. It was assumed there was competition between the ctenophores and fish for the available zooplankton (Purcell and Arai 2001). Without the predation of *Chrysaora quinquecirrha*, the ctenophore altered the dynamics of the newly invaded system.

Experiments done in the Gulf of Mexico studied the effect of *Chrysaora* medusae on populations of red drum fish larvae. It was found that high populations of medusae can cause substantial mortality of the affected species (Duffy et al. 1996). Young larvae were more at risk because older more developed larvae could avoid contact with the medusa

(Duffy et al. 1996). This study was done in relatively high salinity waters of 28-34 ppt, therefore the *Chrysaora* species studied is one tolerant of high salinity.

It is evident that blooms of jellyfish can cause a negative impact on fish populations. Medusae consume fish eggs and larvae and compete with larger fish for zooplankton (Purcell and Arai 2001). When smaller they compete with fish larvae for prey (Purcell and Arai 2001). Medusae have also been shown to be a vector in parasite transmission to fish (Purcell and Arai 2001). Some medusa including *Chrysaora quinquecirrha* have been show to closely associate with three fish species, Atlantic bumpers (*Chloroscombus chrysurus*) (Purcell and Aria 2001), Butterfish (*Peprilus tricanthus*), and Harvestfish (*Peprilus alepidotus*) (Calder 1972b). These fish use the medusa as cover and may also feed on the medusa and steal its food (Purcell and Arai 2001). The medusa may benefit from this relationship if the fish remove parasites or if the medusa manages to catch one its accompanying fish (Purcell and Arai 2001). More than 50 fish species are documented to consume various pelagic coelenterates, but none of these fish feed solely on them (Purcell and Arai 2001). Overfishing may increase the numbers of jellyfish because of the lack of predation pressure and less competition for zooplankton prey (Purcell and Arai 2001).

Oysters and *Chrysaora quinquecirrha* have been found to have a somewhat symbiotic relationship (Breitburg and Fulford 2006). Polyps like to settle on a hard substrate and oyster shells are preferred settlement areas (Cargo and Schultz 1966). Medusae capture but do not digest oyster veliger larvae (Purcell et al. 1991). A study by Purcell et al. (1991) demonstrated: medusae that caught veligers released them alive, veligers placed on oral arms were rejected, and any veligers found in the gastric pouches of field collected medusae were closed and full of tissue. The shell probably offers some protection from the medusa (Purcell et al. 1991). *Chrysaora* medusae also protect oyster veligers by controlling the population of *Mnemiopsis leidyi* (Purcell et al. 1991). The predation rate of ctenophores on veligers is estimated to be 0.2 to 1.7% per day (Purcell et al. 1991). By controlling the populations of ctenophores, *Chrysaora quinquecirrha* medusa dramatically reduce the amount of veligers eaten by them. Ephyra and scyphistomae did ingest clam and oyster veligers but digested more clam than oyster veligers (Purcell et al. 1991).

A study by Brietburg and Fulford (2006) examined the relationship between oysters and medusae in the Chesapeake Bay. They determined that a decline in the population of oysters that began in 1985 due to disease, over harvesting, and loss of habitat negatively impacted the population of *Chrysaora quinquecirrha* (Brietburg and Fulford 2006). A decline in oysters will reduce the amount of hard substrate that is available for polyps (Cargo and Schultz 1966). Less medusae will mean more ctenophores, consequently the biovolume of ctenophores increased during the period from 1985 to 2002 (Breitburg and Fulford 2006). As noted before, increased ctenophore numbers will prey upon oyster

veligers and reduce the number of oysters produced (McNamara et al. 2010). The balance between ctenophores and *Chrysaora quinquecirrha* is facilitated by a healthy oyster population (Breitburg and Fulford 2006). Without a healthy oyster population, the numbers of medusae fall, ctenophore population increases, and predation on oyster larvae, fish larvae and other zooplankton increase (Breitburg and Fulford 2006). It is important to control ctenophore populations because they have a higher feeding rate per unit biomass than *Chrysaora quinquecirrha*, therefore they can rapidly increase in number (Breitburg and Fulford 2006). At peak density, *Mnemopsis leidyi* consumes 20-89% of zooplankton (including veligers) daily (McNamara et al. 2010). This could cause a permanent change in the ability of the system to support oysters in the future, declining to a low oyster state (Breitburg and Fulford 2006). Interestingly, oyster restoration efforts would probably also return high numbers of sea nettles to the Chesapeake Bay (Breitburg and Fulford 2006). Appendix I outlines previously studied trophic interactions of *Chrysaora quinquecirrha*.

Chapter 2. Settlement Survey of *Chrysaora quinquecirrha* polyps in Barnegat Bay, NJ.

INTRODUCTION

Chrysaora quinquecirrha has a complex metagenic life cycle, as a result, sea nettles reproduce both sexually and asexually. The familiar medusa is part of the sexual cycle while the cryptic polyp is the asexually reproducing part in this alternation of generations. Polyps are the enigmatic, unheralded harbingers of jellyfish blooms. This tiny unseen and often overlooked stage in the life cycle of *Chrysaora quinquecirrha* enables this jellyfish to persist in areas where the physical characteristics fluctuate and exceed the boundaries of the adult medusa's tolerance. Overwintering polyps can begin strobilating new generations of medusae as soon as the waters warm in the spring. Large populations of polyps indicate the possibility of large blooms of medusae and all the complications associated with those blooms.

Large populations of jellyfish are detrimental to fisheries because they are voracious feeders on zooplankton and ichthyoplankton and are therefore competitors and predators of fish (Brodeur et al. 2008). The trophic interaction between large jellyfish and commercially exploited fish could be enhancing jellyfish blooms. An analysis was done of jellyfish blooms in the East China Sea and researchers found a possible trophic feedback loop leading to jellyfish blooms (Hong et al. 2008). A Mixed Trophic Impact (MTI) analysis showed strong interactions between large jellyfish, Stromateoidea (butterfish), and small pelagic fish with zooplankton playing a role in mediating the interaction. Without control on this feedback loop, a jellyfish bloom will occur. Many commercial species of fish are known to use the estuary of Barnegat Bay as breeding grounds and nurseries for juveniles. Jellyfish blooms will have detrimental impacts on the fishery resources and ecosystem functioning, therefore it is desirable to understand why and when these blooms are happening (Hong et al. 2008).

Researchers have also defined a "jelly food chain" as a trophic dead end because of the low nutritional content of gelatinous zooplankton (Sommer et al. 2002). When tunicates (Ctenophora) take the position of primary herbivore and jellyfish become the main carnivore there is less energy in the system because of their high water content and low protein content (Sommer et al. 2002). The "jelly food chain" may become an alternate stable state by reducing fish recruitment through competition and predation on larval and juvenile fish (Sommer et al. 2002). Consequently, it is important to research effective methods to control jellyfish populations in Barnegat Bay before it evolves into a stable state composed of a gelatinous food chain.

Observations in the Chesapeake Bay indicate polyps begin to settle in July, with a peak in settlement in August or September (Cones and Haven 1969). Environmental conditions such as change in temperature, salinity, or food availability will cue the polyp to become a strobila. The scyphistomae then undergo a metamorphosis, absorbing feeding tentacles and dividing horizontally by transverse segmentation (strobilation), in order to bud off ephyra. These ephyra quickly develop into juvenile medusa (Cargo and Rabenold 1980). Once strobilation is complete the strobila reverts to its former polyp stage. Strobilation can occur many times in a season and can begin in overwintering polyps (cysts) as soon as waters warm to 20°C (Cargo and Rabenold 1980). In other species of jellyfish it was found that polyps will divide to form more polyps if adequate food is present or go through strobilation forming ephyra if food is limited (Hoover and Purcell 2009). Polyps also create colonies of clones by dividing themselves in various ways. This ability of polyps to persevere and asexually reproduce in many ways indicates the ecological and evolutionary implications of this type of reproduction in cnidarians have probably been underestimated (Fautin 2002) and may be more important than the obvious sexual cycle seen in the medusa for this species.

A potential management response for overpopulation of jellyfish is to destroy benthic polyp populations and prevent settlement (Richardson et al. 2009). A polyp settlement survey can determine the spatial and temporal patterns of settlement. Polyp population numbers will directly affect numbers of medusae in the bay; therefore these numbers should accurately predict population blooms.

Factors enhancing jellyfish blooms in Barnegat Bay

Global climate change

Global warming is causing changes in climates worldwide. Jellyfish populations are opportunistic and they respond quickly to physical and biological changes in the environment. Changes in temperature and salinity have been linked to variations in jellyfish abundance in several studies (Brodeur et al. 2008; Purcell et al. 1999; Richardson et al. 2009). A majority of moderate-temperature species have been shown to increase in number in warm temperatures. *Chrysaora quinquecirrha* reaction to warming waters in the Chesapeake Bay was found to be a larger overall population with adults found earlier in the year (Purcell et al. 2007). Warm water temperatures may increase asexual budding of polyps. If the waters remain warm enough polyps can overwinter without forming a cyst. These polyps will be ready to strobilate as soon as the water is warm enough (15-20° C) (Calder 1974; Cargo and Rabenold 1980) which will allow medusae to appear earlier than usual. This will produce a larger ratio of jellyfish to polyps (Purcell et al. 2007). It has also been shown that jellyfish populations often vary with climate frequently at decadal scales, but even though some studies suggest continuing upward trends (Graham 2001; Mills 2001); hard evidence for sustained

increases is lacking (Purcell et al. 2007). It is important to establish a baseline population count in Barnegat Bay to determine whether the population is continuing to increase or simply going through a decadal fluctuation.

Eutrophication

Eutrophication is a major global pollution problem and Barnegat Bay is known to be a highly eutrophic system (Kennish 2007). Excess nutrients, altered nutrient ratios and increased turbidity are all associated with eutrophication. An overabundance of nutrients can create a phytoplankton bloom which translates into more food for zooplankton. Well fed polyps then increase in number via asexual reproduction ultimately creating more medusa which leads to more sexual reproduction (Purcell et al. 2007, Richardson et al. 2009). Jellyfish blooms in the Chinese seas have been linked to high N:P ratios in severely polluted areas (Dong et al. 2010). In Mar Menor, Spain annual blooms of scyphomedusae were noted after a 10 fold increase in nitrate was found in waters even when phosphate was decreased (Perez-Ruzafa et al. 2002). These examples suggest high nitrogen ratios may favor jellyfish blooms (Purcell et al. 2007). Eutrophication is often associated with hypoxia (low dissolved oxygen levels). *Chrysaora quinquecirrha* jellyfish and polyps are reportedly tolerant of extremely low levels of oxygen (Breitburg et al. 1997; Condon et al. 2001; Graham 2001). Eutrophication reduces water clarity and light penetration, this may favor the non visual jellyfish over the visual feeding epipelagic fish (Purcell et al. 2007).

The presence of jellyfish blooms and subsequent death and decomposition of large numbers of medusae has been shown to alter the availability of nutrients cycling through a system (West et al. 2009). In a controlled mesocosm experiment, researchers added dead jellyfish to mesocosm sediments and found dissolved organic phosphorus and dissolved organic nitrogen effluxed at rates 8 to 25 times higher than in control mesocosms (West et al. 2009). Ammonium concentration also increased as the jellyfish decomposed. Bacterial decomposition decreased sediment oxygen content (West et al. 2009). Areas with large blooms of jellyfish and subsequent die off could contribute to rapid nutrient recycling. Reportedly, areas located in the northern part of Barnegat Bay have suffered blooms of *Chrysaora quinquecirrha* medusae for at least the last 5 years (personal observation, local media). Primary production could be positively altered by the increased nutrients available in the water column. Decomposing medusae have been shown to cause hypoxia in waters with a low degree of mixing (West et al. 2009). Coincidentally, most reported jellyfish blooms have occurred in heavily populated areas with semi-enclosed water bodies (Purcell et al. 2007), very similar to Barnegat Bay.

Artificial substrates

Structures that have altered the characteristics of coastal waters like docks, bulkheads, breakwaters, and marinas all provide solid surfaces for polyps to attach (Hoover and Purcell 2009; Holst and Jarms 2006; Purcell et al. 2007). These structures reduce the abundance and diversity of organisms by changing the structure of the ecosystem from shallow marsh or beach into a deep, turbulent, artificial environment (Jivoff 2006). The modification of Barnegat Bay from a sandy shored barrier island estuary into a largely bulk headed (36% by 2006) (BBNEP 2009) vacation destination may have given the jellyfish an unintended advantage.

In the past, conventional practice in Barnegat Bay was to construct bulkheads with chemically treated wood. Weis and Weis (1992) illustrated that this toxic material discouraged settlement of numerous species. Currently, individuals replacing bulkheads must comply with new regulations requiring the use of non-toxic (plastic) materials. Hoover and Purcell (2009) determined *Aurelia labiata* polyps prefer to settle on plastics. Holst and Jarms (2006) also found that five Scyphozoan species preferred plastic and glass to other substrates. The installation of new plastic bulkheads provides a clean non-toxic surface for *Chrysaora quinquecirrha* polyps to attach and grow.

Floating docks contribute to the problem of jellyfish blooms. A study done at Cornet Bay marina determined that *Aurelia labiata* polyps covered an area of 685m² with a estimated population of over one hundred million polyps (Hoover and Purcell 2009). Cargo and Schultz (1966) determined *Chrysaora quinquecirrha* polyps prefer to colonize the underside of oyster shells therefore they could readily exploit the surface provided by a floating dock. Previous observations concluded *Chrysaora quinquecirrha* polyps were only found in relatively shallow (<11 meters) waters (Cargo and Schultz 1966) which would make floating docks an attractive settlement area.

Invasive species

The alien invasion of jellyfish species has been documented in many locations around the world. Some of these jellyfish have caused major ecosystem disruptions. Blooms of invasive species are common and if favorable conditions prevail, jellyfish will continue to bloom (Dawson and Hamner 2009) and spread into new areas (Purcell et al. 2007). Since Barnegat Bay is part of the intercoastal waterway, boats from up and down the Atlantic coast travel through its channels possibly dumping new invasive species with their ballast water or shedding them from their hulls (Bayha and Graham 2009). If we can determine why Barnegat Bay is out of balance in relation to jellyfish blooms, then possibly we can avoid problems with other invasive species in the future.

Most calculations of jellyfish biomass, population, and distribution have been done on large oceanic scales (Graham 2001; Brodeur et al. 2008; Purcell et al. 2007). An

initial population study of the polyps of *Chrysaora quinquecirrha* in Barnegat Bay could serve as a basis for future population counts of medusae in the bay. Surveying the population in this way may prove to be the most time and cost effective way to estimate jellyfish biomass in the future. Determinations about the physical characteristics within the bay that enhance polyp population numbers can also help scientists predict jellyfish blooms in the future. The definition of temporal and spatial settlement patterns of *Chrysaora quinquecirrha* polyps in Barnegat Bay is an important starting point for the study of this organism in New Jersey. Additional information on species found with these polyps may help researchers better understand trophic relationships affecting polyp growth and longevity.

MATERIALS AND METHODS

Study sites in Barnegat Bay

Barnegat Bay includes open waters and wetlands from Point Pleasant to Tuckerton, NJ. The Metedeconk River and Toms River are the major rivers associated with Barnegat Bay. There are also several smaller streams that run into the bay: Cedar Creek, Forked River, Oyster Creek, Mill Creek, Cedar Run, Westecunk Creek, Tuckerton Creek and Mill Branch. Barnegat Bay is approximately 68 km long with a width of 2-6.5km. It is a shallow estuary with depths averaging 1.5m. There are three inlets that connect Barnegat Bay to the Atlantic: Manasquan Inlet via the Bay Head- Manasquan Canal at the north end, Barnegat Inlet in the middle of the bay, and Little Egg Harbor Inlet at the south end. Generally, the bay is shallower on the eastern side and deeper on the western side. (Dowhan 1997). Settlement plates were placed in eight locations throughout the bay (Table 1). Sites were not intended to blanket the bay, but rather showed a distribution to assess settlement potential throughout the bay (Fig.4). A greater focus was placed in the northern bay which has see the greatest number of adult medusae.

Table 1. Site abbreviation, location, latitude and longitude for all sites

Site	Location	Latitude	Longitude
MB	Mantoloking Bridge	40.04043	74.05665
CB	Chadwick Beach Island	40.00047	74.07181
CI	Cattus Island Park	39.98955	74.1348
TR	Toms River	39.95008	74.1911
BI	Berkley Island, Bayville	39.87312	74.13368
LC	Lighthouse Center, Waretown	39.77767	74.18758
PS	Parson's Seafood, Tuckerton	39.57778	74.32766
RU	RUMFS, Tuckerton	39.50894	74.32234

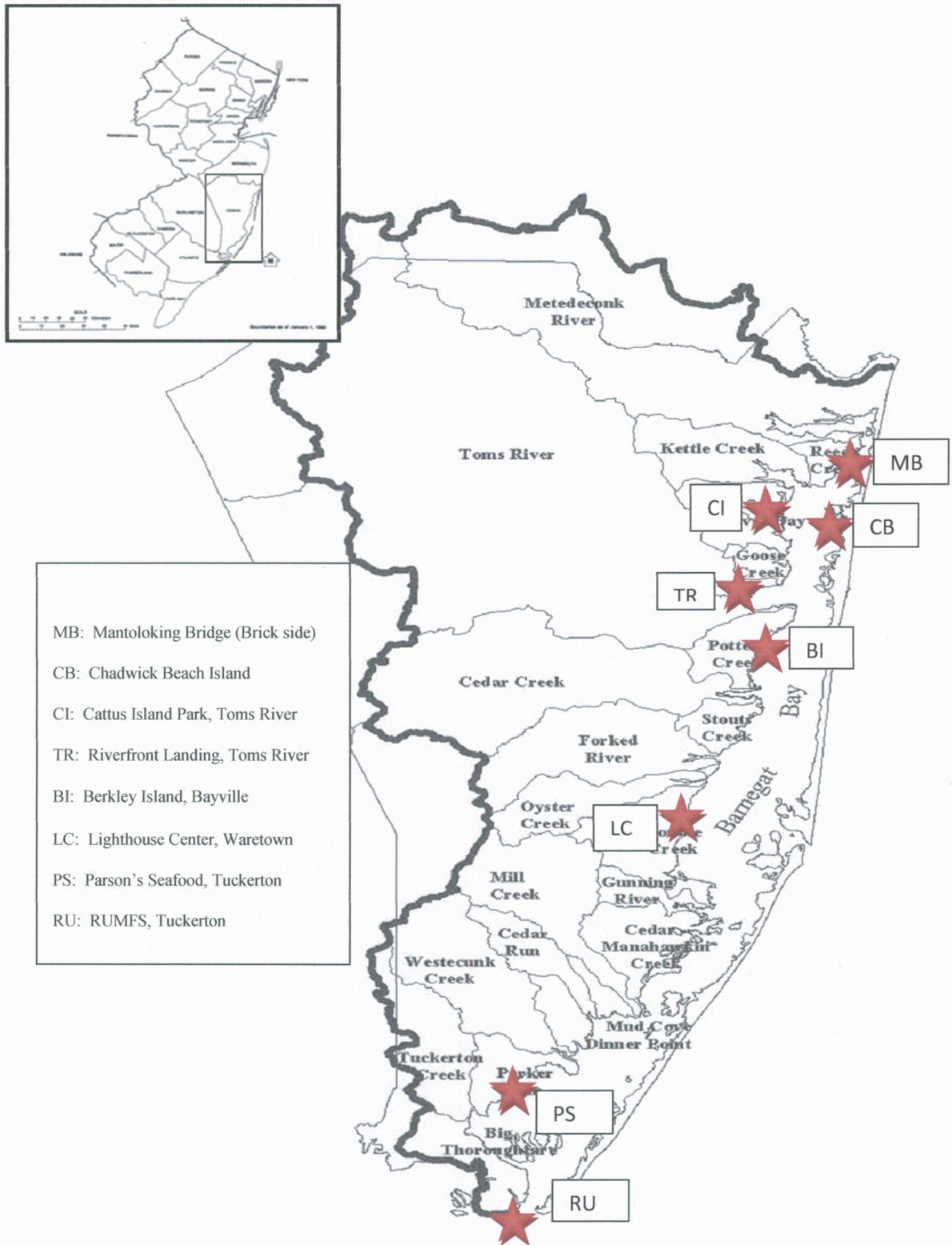


Figure 4: Barnegat Bay -Settlement Plate locations 

Settlement assessment of *Chrysaora quinquecirrha* in Barnegat Bay, NJ

Previous researchers in Barnegat Bay have suggested that a population assessment is necessary to document the distribution and abundance of *Chrysaora quinquecirrha* (Kennish 2007). Additional research may indicate biomass numbers for jellyfish could be estimated in the future based on polyp surveys.

In order to assess several variables, the plates were designed to include slides for settlement on three levels and have upward and downward mounted removable slides. The plates (see diagram in Appendix II) were made from PVC plastic tubing and PVC sheets and arranged in 3 layers 30cm apart. The plates were moored to piers and placed directly on the bottom and anchored by a poured concrete block with a stainless steel screwhook which was tied to rope that went through the center of PVC tubing and was used to tie the plate to a dock. Each settlement plate had two arms at each depth. Each arm held a 15cm x 15cm x 0.5cm PVC sheet (plate) which was attached to the end of the arm to enable placement of PVC slides on the top and bottom of each sheet. There were a total of 6 arms with 4 slides on each side (upper and lower) of each plate. The slides and plates were drilled to allow the secure attachment of slides to the plates. Slides were 2.5cm x 10cm x 0.1cm (surface area of 0.0025m²) and made of clear flexible PVC. Plastic screws and wing nuts were used to enable quick exchange of slides.

A field study was done in eight sites throughout the bay (Fig. 4). Plates were placed in May 2010, in areas with year round access and a water depth that would allow top of plate and slides to be covered (optimum of 1.5 m minimum depth). Docks were used as secure attachment placements. Some plates were located in areas of large tidal fluctuation. These plates at Mantoloking, Cattus Island, and RUMFS were cut down to keep the top level below the lowest tide.

Two slides from each side (upper and lower) of each arm were gathered monthly for analysis. New slides were placed on the settlement plate monthly from June 2010 through November 2010. Twenty four slides per settlement apparatus were analyzed monthly. In November, 12 long term (6 month) slides were collected (one set from each arm). The remaining slides (12) on the plate were left on for the duration of the experiment (until April 2011) to determine the population of overwintering polyps (cysts/podocysts) after one year. Polyps often form podocysts when dividing or encyst when conditions become unfavorable, therefore cysts were also counted.

Slides were removed from settlement plates and immediately placed in a labeled plastic bag containing bay water from the site. Slides were transported to Montclair State University in a cooler and reviewed live in the lab as soon as possible. Because the slides were viewed wet, the polyps could be easily recognized. Other sessile attached

organisms and related fauna were also identified. Slides were photographed and preserved in ethanol.

Temperature, salinity, and oxygen levels were recorded with a YSI® meter (model 85/25 FT) during each collection. All samples included three separate measurements for each depth of the settlement plate. This created a record of conditions at the top, middle and bottom of each site. Differences from top to bottom were often noted in temperature, salinity, and oxygen concentration (see Appendix III and IV for complete data). Weather conditions were also noted, as windy conditions often lead to choppy well mixed waters.

Measurements of pH, turbidity, and nitrate levels were recorded for all sites during the July collection. Measurements of pH were obtained using an IQ150 pH meter with stainless steel ISFET pH electrode (IQ Scientific Instruments, Carlsbad, CA). For turbidity an Orbeco Model TB200 turbidity meter was utilized (Orbeco-Hellige Inc., Sarasota, Florida). Nitrate ion was measured using the Zinc reduction technique and read on a Varian Cary UV/Vis spectrophotometer in a cm pathlength cell at a wavelength of 504 nm. These water analyses were performed under the direction of Kevin Olsen at the Montclair State University Chemistry Laboratory.

Polyps obtained from slides in Cattus Island were analyzed by Dr. John Gaynor at Montclair State University. He was able to determine that the polyps collected were definitively *Chrysaora quinquecirrha* based on DNA sequence analysis of the 16S rRNA locus of mtDNA (unpublished data).

Statistics were compiled utilizing SAS® (2002-2003) to create two 4-way ANOVAs using the PROC GLM procedure for the polyp and cysts counted. Variables in this analysis included: site of plate, depth of slide on plate, orientation of slide (up or down) and the date (month) slide was retrieved.

RESULTS

Physical Characteristics of sites: Salinity

Salinity readings taken at each site (Fig. 5) indicate that two sites in the northern part of the bay, Chadwick Island and Cattus Island, were the only sites with salinities compatible with polyp settlement and growth (i.e. 5-20ppt). The Toms River site was within the range of salinity late in the year, but otherwise salinity was too low. A steep halocline was evident in all Toms River samples making settlement possible only on the lowest level of settlement plate which was always thickly covered in sediment. All of the other sites south of Toms River were heavily influenced by the saltwater from Barnegat Inlet and Little Egg Harbor Inlet (>20ppt). The Mantoloking Bridge site was affected by the saltwater flow from the Manasquan canal at the most northern end of Barnegat Bay (>20ppt from June on).

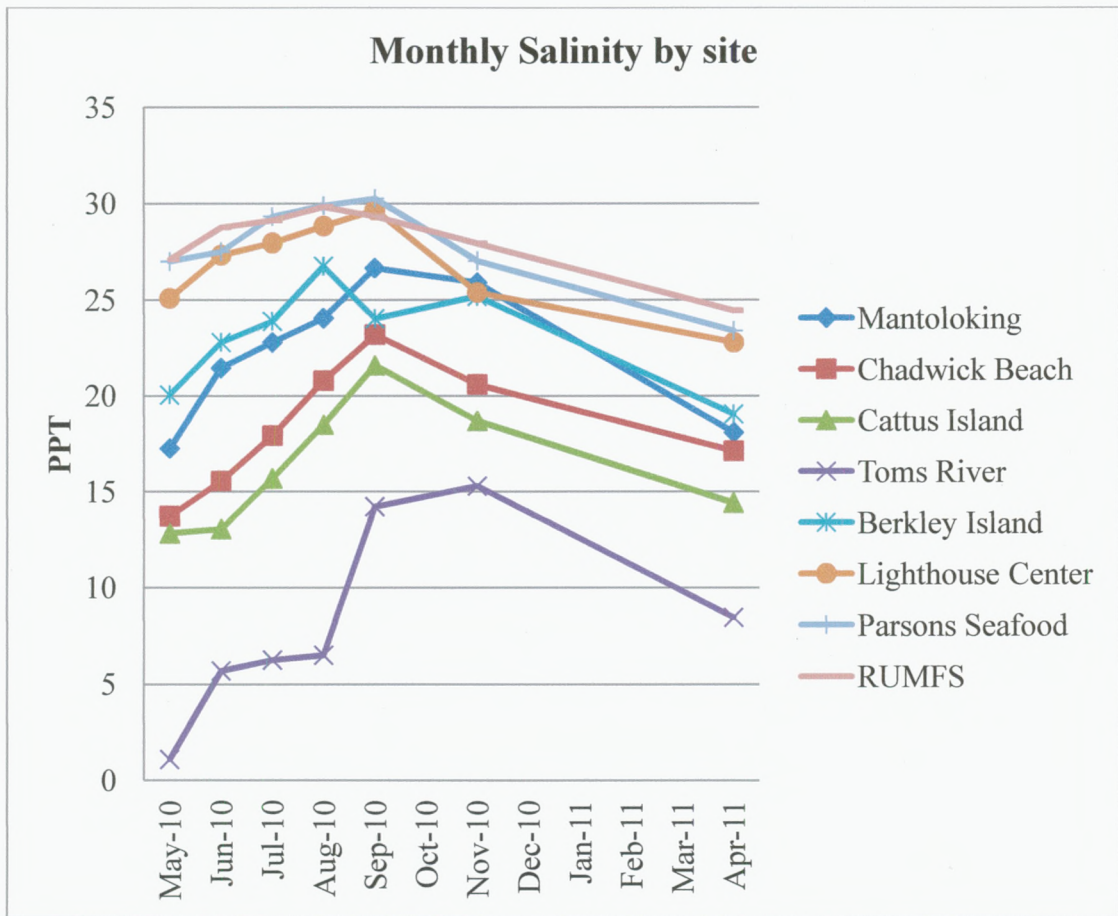


Figure 5. Monthly average salinities at all sites were based on three separate readings per site (top, middle, and bottom). (See Appendix III for full data set)

Physical Characteristics of sites: Oxygen

Oxygen concentration numbers were the lowest overall at Cattus Island with an averaged low of 4.44 mg/l in August when polyp counts were the highest. Sites were noticeably more oxygenated in the colder months. As temperatures warmed, oxygen concentrations dropped at all sites. All readings were taken in daylight hours when oxygen levels should be highest. Low oxygen concentration levels were found at Cattus Island in June, July, August and September.

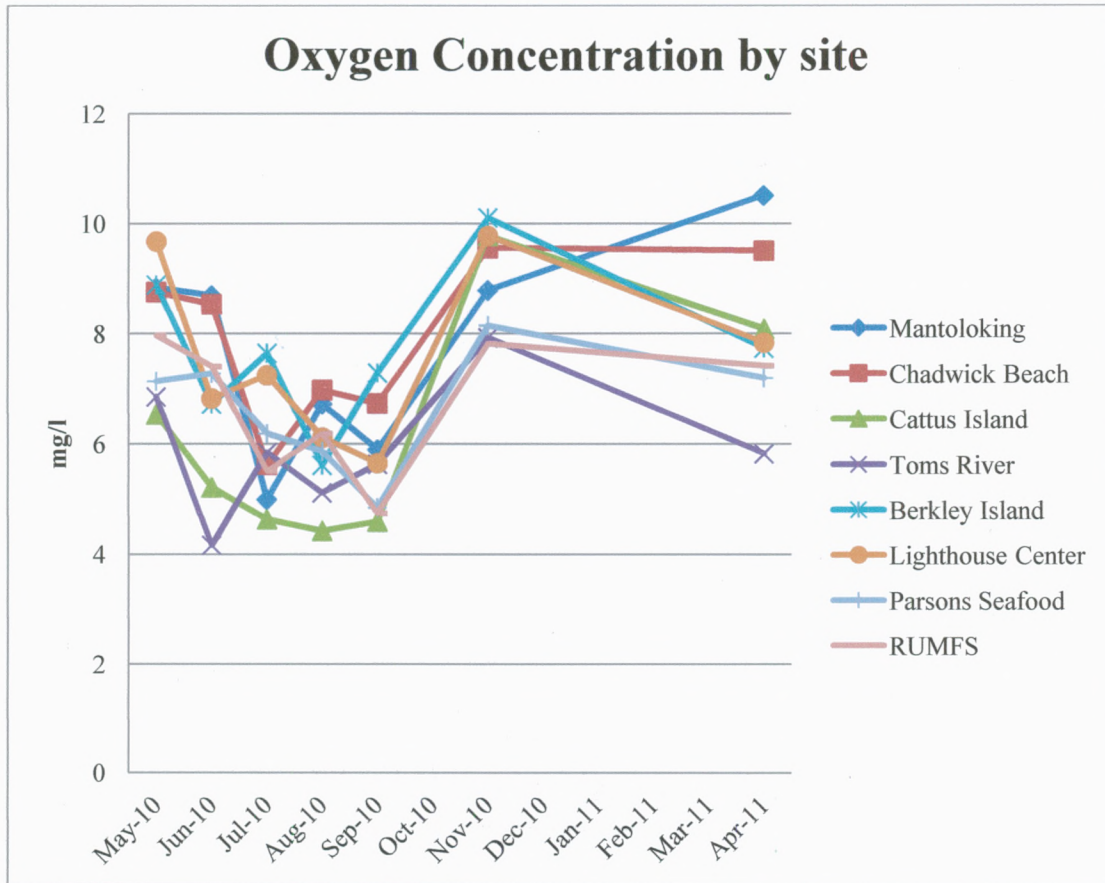


Figure 6. Oxygen Concentration

Oxygen concentration numbers were averaged based on three separate readings per site (top, middle, and bottom).

Physical Characteristics of sites: Temperature

All of the sites followed a similar pattern of seasonal temperature fluctuation. Variations in readings at RUMFS were lessened by its proximity to the Little Egg Harbor Inlet. Readings at Cattus Island indicate swift changes in temperatures with warmer water temperatures in the spring (May, April) and the coldest reading in the late fall (Nov).

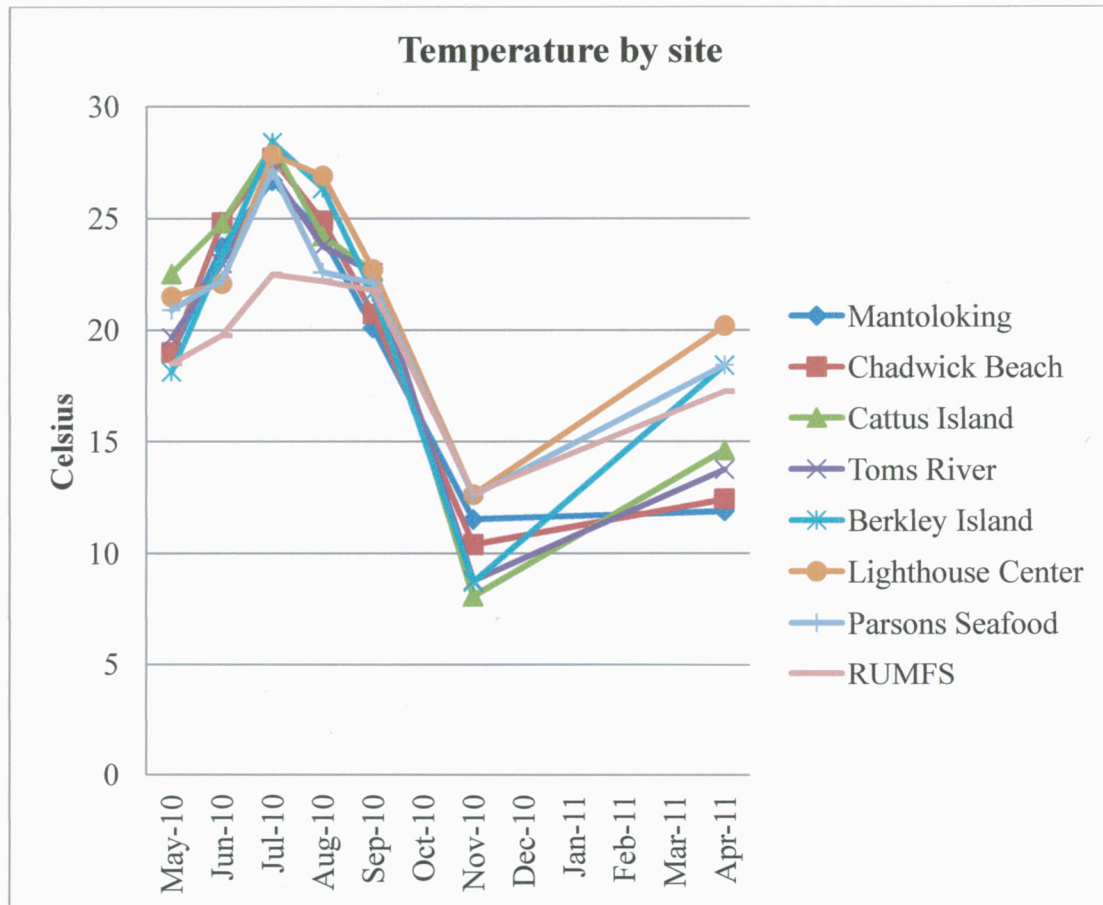


Figure 7. Water Temperature by site

Temperatures were averaged based on three separate readings per site (top, middle, and bottom).

Physical Characteristics of sites: pH, Turbidity, Nitrate

Levels for pH were found from 6.9 at Berkley Island to 8.0 at RUMFS and Chadwick Beach. Turbidity readings varied from a low of 4.64 NTU at RUMFS to a high of 10.36 NTU at Toms River. Nitrate levels were between 1.18 ppm(Cattus Island) and 1.45 ppm

(Parson's Seafood) for all sites except Toms River which had the highest level recorded at 3.22 ppm. Additional sediment analysis (not published) revealed that sediment at Toms River site contained high amounts of sewage which probably caused the increase in NO₃ at that site (Kevin Olsen unpublished data, personal communication 2010). Generally the level of NO₃ increased as you move south through the bay.

Table 3. July readings of pH, Turbidity, and NO₃

	pH	Turbidity NTU	NO ₃ PPM
Mantoloking	7.80	5.84	1.24
Chadwick Beach	8.00	5.21	1.28
Cattus Island	7.70	6.45	1.18
Toms River	7.30	10.36	3.22
Berkley Island	6.90	6.10	1.45
Lighthouse Center	7.95	5.63	1.43
Parsons Seafood	7.80	9.20	1.45
RUMFS	8.00	4.64	1.42

Polyps and cysts

Chrysaora quinquecirrha polyps were found in varying numbers at Chadwick Beach and Cattus Island (Table 4). Salinity is a limiting factor for settlement and these two sites fall within the acceptable range for *Chrysaora quinquecirrha* polyps (Fig.5). Statistical analysis established that the site of polyp settlement was significantly different among sites (F-value 9.71, P value <0.0001 for polyps) with only Cattus Island and Chadwick Beach showing any settlement.

Table 4 illustrates podocysts were only found at Cattus Island. A large number (224) of podocysts were found on the two long term (6 month) slides collected in Oct/Nov. The Year slides, which overwintered, were collected from Cattus Island in April and contained 292 podocysts. Salinity had become unfavorably high in September (Fig.5) for polyps and water temperatures had dropped to 8.1°C by the last collection in Oct/Nov encouraging the conversion of polyps to cysts (Fig.7). Polyps will typically encyst at temperatures below 3°C (Purcell et al. 1999).

Table 4. Density of *Chrysaora quinquecirrha* polyps and podocysts/square meter

Cattus Island and Chadwick Beach were the only sites with polyps. Cattus Island was the only site with podocysts. *Due to loss of plates, Year readings were not available for Chadwick Beach, Berkley Island, and Parson's Seafood.

Average Density of polyps /m ²	6						Year
	June	July	Aug	Sept	Nov	Month	
Mantoloking	0	0	0	0	0	0	0
Chadwick Beach	0	33.3	100.0	0	16.6	0	*
Cattus Island	0	216.6	25466.6	3533.3	50.0	5733.0	0
Cattus Island podocysts	0	0	133.0	1266.6	0	7466.6	11680.0
Toms River	0	0	0	0	0	0	0
Berkley Island	0	0	0	0	0	0	0
Lighthouse Center	0	0	0	0	0	0	0
Parson's Seafood	0	0	0	0	0	0	0
RUMFUS	0	0	0	0	0	0	0

Polyps were found in densities ranging from 1 per slide at Chadwick Beach in November to 416 per slide in August at Cattus Island. This translates into possible densities from 400 /m² up to 166,400 /m². Cysts were found in densities ranging from 2 per slide (6 month) to 217 per slide (year-overwintering). The 217 overwintering cysts found on one slide demonstrate the possibility of cysts being found in densities up to 86,000 /m² in the spring.

No cysts were found at Chadwick Beach. Significant differences in polyp settlement were determined by site ($P < 0.001$), depth ($P = 0.0362$), orientation – polyps that settled on the upper versus lower slides ($P = 0.0166$) and date – month of settlement ($P = 0.0001$).

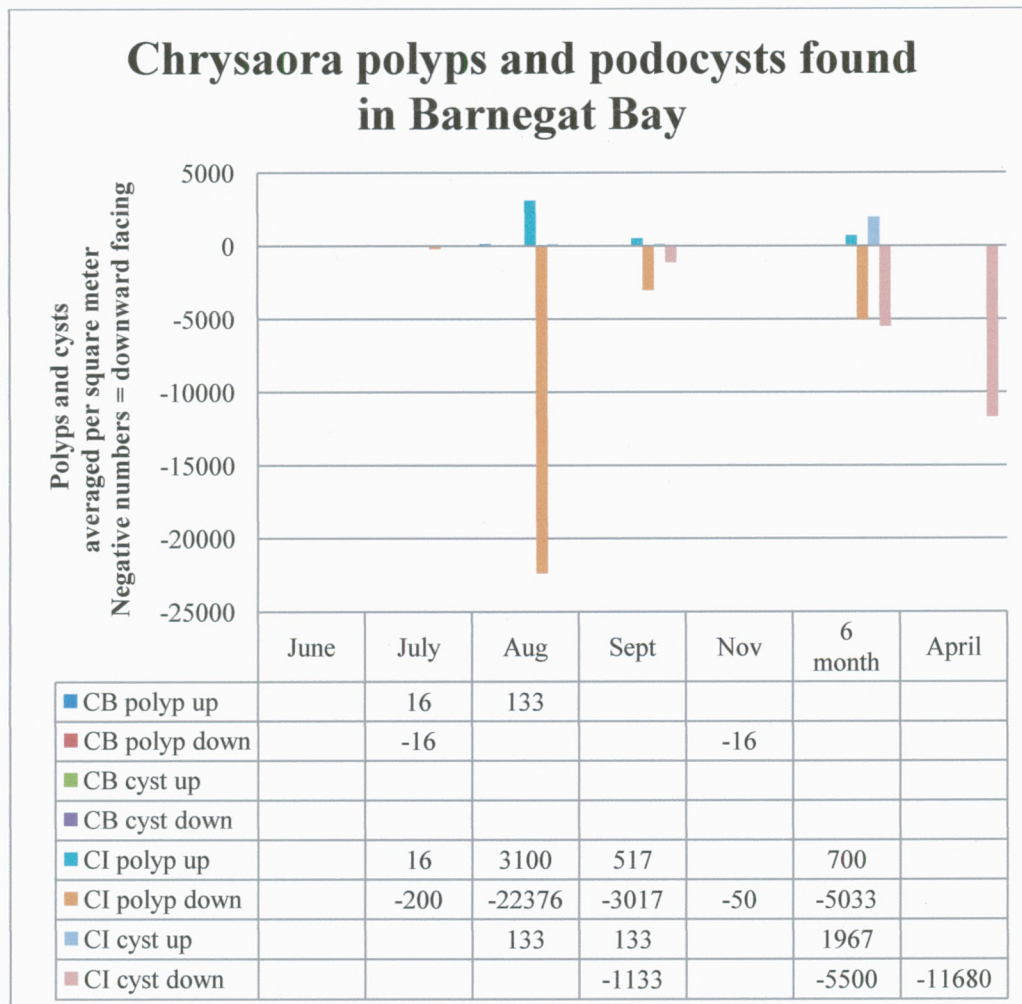


Figure 8. Polyps and podocysts position

CB- Chadwick Beach CI – Cattus Island

up- top of plate (facing up) down – underside of plate (facing down)

Blank spaces indicate no polyps or cysts were found.

June-Nov 24 slides/plate/month, 6 Month 12 slides/plate, April 10 slides/plate

Other Species found at Chadwick Beach and Cattus Island

In addition to *Chrysaora quinquecirrha*, slides were surveyed for all settling organisms. Since salinity was a limiting factor for polyp settlement and growth in other plate locations, species composition will be noted only for Chadwick Beach and Cattus Island. There were differences in species between Chadwick Beach and Cattus Island. Both sites contained *Hydroides diathus* (Carnation worm), *Balanus* (Acorn barnacle), *Membranipora membranacea* (lacy encrusting bryozoans), and nudibranchs. Barnacles were found in much greater abundance (624 counted throughout year) at Chadwick Beach, while Cattus Island only supported 129 barnacles. *Membranipora membranacea*

had a much higher percentage of cover (up to 58.75% mean cover/slide in September) at Chadwick Beach than at Cattus Island (22.7% mean cover/slide in September). A small number of tunicate colonies (*Botryllus schlosseri*) began settling at Chadwick Beach in July. Cattus Island did not support any tunicates. However, tunicates settled on over 60% of slides gathered during the July collection in waters with salinity above 20ppt. This finding may be significant when considering the possibility of a “jelly food chain” developing in Barnegat Bay. Nudibranchs were found on 12 out of 24 slides at Chadwick Beach in June with up to 50 found on one slide. Nudibranchs and flatworms were found in large numbers at Chadwick Beach. Only a few nudibranchs were noted on slides in June at Cattus Island. A table with overall numbers of nudibranchs and flatworms can be found in the Appendix (IV). Both of these species are known polyp predators (of jellyfish polyps and other species)(Cargo and Schultz 1967). Chadwick Beach supported a larger number and assortment of gastropod and polychaete species. The list of species found at Chadwick Beach and Cattus Island (Appendix V) demonstrates greater species richness at Chadwick Beach.

DISCUSSION

***Chrysaora quinquecirrha* polyps and cysts found in Barnegat Bay**

Medusa produce sperm or eggs once sexually mature about two months from strobilation (Calder 1972b). The timing of settlement (Table 4) indicates some medusae were sexually mature in June which would suggest overwintering polyps began to strobilate in April. A large peak in settlement (1528) in August at Cattus Island points to a larger strobilation event in May or the slower overall growth of medusae to sexual maturity. Numbers of new polyps declined markedly after August although they were still present in September and Oct/Nov slides. Long term (6 month) slides collected from the Cattus Island settlement plate in Oct/Nov registered 172 polyps and 224 cysts. The slides collected in April 2011 were on the settlement plate for almost a year. At Cattus Island 292 cysts were counted on two slides (the settlement plate at Chadwick Beach was lost during a winter storm). Although physical conditions favored settlement at Chadwick Beach and medusae were present in large numbers (personal observation), only a few polyps and no cysts were found on the slides from that site.

The dense covering of polyps on retrieved slides from Cattus Island may have initiated the movement of polyps away from competing polyps. The polyps created cysts as they relocated (Cargo and Rabenold 1980). The polyp can move across a substrate surface with the help of a stolon leaving a trail of podocysts (Arai 2009). Stolons bud from the side of the polyp stalks and once they reach the substrate, form a new polyp or a podocyst (Cargo and Schultz 1966). Each podocyst can develop into a polyp and produce ephyrae increasing the reproductive capacity of the original polyp. These new polyps can also make more podocysts increasing the numbers in a polyp colony. In many species of jellyfish encystment creates more individuals than strobilation (Arai 2009).

One slide retrieved from Cattus Island in April (Year-overwintering) contained 217 cysts, which translates into a density of 86,800cysts/ m². Previous research has shown that approximately 53% of cysts could survive to regenerate polyps (Arai 2009). If 115 cysts survived (53%) the approximate density would be 46,000 cysts/m². If you have a suitable surface for settlement that is approximately 10m² (ie. the floating dock at Cattus Island) the population of excysting polyps could begin at 460,000. Each of these surviving polyps could create approximately 5 ephyra per strobilation (2,300,000 ephyra). Each overwintering polyp strobilates approximately 3 times per season creating approximately 6,900,000 ephyra from the surface of one 10m² floating dock. In addition to strobilation, polyps will also produce more polyps. Experimental studies have found colonies of polyps with a population of more than one hundred polyps and cysts. One polyp kept in optimal conditions at 21-23°C formed 52 cysts and 6 polyps during the summer (Cargo and Schultz 1966). The ability of the polyp to overwinter as a cyst and reproduce itself in many ways increases the possibility of massive jellyfish blooms.

Physical factors

Variations in physical factors have been shown to limit *Chrysaora quinquecirrha* polyp growth and planula settlement. Readings of temperature from May through September at all sites indicate temperatures warm enough for polyps (18°C) to grow and strobilate. RUMFS had the least overall variation in temperature while Cattus Island warmed quickly. At the sites polyps were found, the water temperature (Fig. 7) is slightly higher at Cattus Island than at Chadwick Beach.

Changes in temperature have several effects on *Chrysaora quinquecirrha* medusae and polyps. Strobilation is known to be triggered by the warming of the waters in the spring to 15-20°C (Mangum et al. 1972). The water temperatures (Fig. 7) at Cattus Island and Chadwick Beach are above the minimum strobilation temperature of 16-18°C until the Oct/Nov sample. Polyps have been observed to encyst when water temperatures are below 4°C or above 34°C (Cargo and Schultz 1966). Previous experiments have determined that polyps clump at 8-10°C and proceeded to form cysts when they were held at 2-3°C for 12 to 14 days (Cargo and Schultz 1967). The slides collected in April (slides on plate for 1 year) indicated all surviving overwintering polyps had encysted. *Chrysaora quinquecirrha* medusae begin to disappear and be deposited on the bottom sediment as waters cool below 10°C (Sexton et al. 2010) effectively ending any new polyp settlement by the November collection in Barnegat Bay.

As noted in previous research (Cargo and Schultz 1966; Purcell et al. 1999; Wright and Purcell 1997) *Chrysaora quinquecirrha* polyps are found in lower salinity waters. Cargo and Schultz (1966) determined the preferred salinity range for polyps was 5 – 19 ppt. High salinity limits the dispersion and growth of polyps (Cargo and Schultz 1966). Research has also indicated polyps were most productive at salinities higher than 11 ppt

and lower than 25ppt (Purcell et al., 1999). Increased ionic stress at low salinities may cause lower productivity (Wright and Purcell 1997). Changes in salinity will also affect iodide concentrations which have been shown to influence strobilation (Black and Webb 1973).

Cargo and Schultz (1966) noted most polyps died or encysted at salinities of 5ppt and below and at salinities higher than 25ppt. Only two of the sites tested, Chadwick Beach and Cattus Island, were consistently within this acceptable range of salinity. The salinity range (Fig. 5) is slightly higher at Chadwick Beach, but it only goes above 20ppt (negative for settlement) in September which is one month past the peak settlement date at Cattus Island. Based on previous research in the Chesapeake Bay, it was postulated that polyps would not be found in the saltier southern end of the bay. Interestingly, *Chrysaora quinquecirrha* adult medusa can be found throughout mesohaline, polyhaline (18-30ppt) and euhaline (30-35ppt) waters in several areas of the world (Calder 1972b).

Low levels of oxygen will limit some species, but seemingly not the *Chrysaora quinquecirrha* polyp. Researchers have tested the ability of *Chrysaora quinquecirrha* polyps to tolerate hypoxic conditions (Condon et al. 2001). Polyps were placed in dissolved oxygen concentrations of 3.5 mg/l – 0.5 mg/l. High polyp survival was seen in all concentrations for the first five days, even after 24 days of extremely hypoxic conditions (0.5 mg/l) over 40% of the polyps still survived. None of the polyps in Condon's experiment formed cysts, but polyps in all oxygen concentrations formed strobila (Condon et al. 2001). The capacity of *Chrysaora quinquecirrha* to tolerate extremely hypoxic conditions may allow it to compete more effectively than other more sensitive benthic fauna. The average oxygen concentrations were consistently lower at Cattus Island than at any other site tested. Oxygen levels readings were taken during the day when concentrations should be highest. Researchers studying hypoxia in the York River, monitored oxygen levels throughout the day. They determined that even during normoxic conditions oxygen levels changed by 1-3mg/l during the day (Pihl et al. 1992). Therefore, the oxygen level at Cattus Island most likely was lower at night and possibly hypoxic. This lower oxygen level may limit the ability of more sensitive species to populate the area thereby reducing predation and or competition (Wu 2002). Chadwick Beach has a consistently higher oxygen concentration and Cattus Island has the lowest oxygen concentration (4.44 mg/l) of all sites during the August sampling when the highest number of polyps was found.

The lower levels of oxygen could also limit predation on polyps and podocysts by altering the actions of other organisms. Studies have shown that fish and mobile invertebrates will leave areas with less than 4mg/l of dissolved oxygen (Schaffner et al. 2007). A study on the effects of periodic hypoxia indicated the behavior of epifaunal organisms changes with lowered oxygen levels with nudibranchs, flatworms, snails and polychaetes going to the top of hypoxic experimental aquariums (Sagasti et al. 2001).

Low oxygen levels were also shown to decrease predation by flatworms and nudibranchs. (Sagasti et al. 2001). Turbellarians (including flatworms) have been documented consuming several species including ciliates, hydroids, amphipods, and annelids (Martens and Schockaert 1986) while nudibranchs are known predators of coral polyps, hydroids, and jellyfish polyps (Cargo and Schultz 1967).

Additional water quality readings, turbidity, pH, and NO₃ were taken for all areas. All turbidity readings were within the acceptable range (<50 NTU for one time sample) for aquatic life (Osmond et al. 1997). Nitrate levels were above drinking water standards (>1ppm) but well within a tolerable range for aquatic life. Levels of pH were slightly acidic at Berkley Island (6.9). The pH for Toms River was also slightly low for an estuary at 7.3. All other sites registered 7.7 – 8 for pH levels which is more typical for salt water readings.

Other Species

In addition to counting *Chrysaora quinquecirrha* polyps and podocysts, an assessment was done on the settlement of all identifiable species on each slide. All identified species associated with Chadwick Beach and Cattus Island have been outlined in Appendix V. Chadwick Beach and Cattus Island displayed several differences in species. Chadwick Beach had a larger percentage cover of encrusting bryozoans, more barnacles, and more nudibranchs than Cattus Island. In addition, tunicates were present on slides removed from Chadwick Beach beginning in July, while no tunicates were found at Cattus Island. Cattus Island had lower species richness when considering all species found on settlement plate slides. The mix of species could have affected the settlement and growth of polyps at both locations. Even though numerous medusae were spotted adjacent to the Chadwick Beach settlement plate (personal observation), only a few polyps were collected from the slides on this plate.

Nudibranchs and marine flatworms were numerous at Chadwick Beach in June and also appeared in counts for July, August and September. Nudibranchs are known to consume polyps of other cnidarians species. In Sweden, the nudibranch, *Coryphella verrucosa* is a predator of the scyphozoan polyps of *Cyanea lamreckii*. Polyps of this jellyfish encyst to avoid predation (Holst and Jarms, 2006). Total numbers of nudibranchs and flatworms found on settlement plates can be found in the Appendix (VI).

The small unidentified flatworms (turbellarian species) present in large numbers on slides from Chadwick Beach could have negatively affected the polyp population numbers. Marine flatworms are known to be predators or scavengers (Martens and Schockaert 1986). They are capable of swallowing large bits of food, sucking out prey larger than themselves, and feeding on hydroids (Martens and Schockaert 1986). It is therefore plausible that the flatworms were preying on polyps. The presence of seven

different gastropod species at Chadwick Beach, as opposed to only three species at Cattus Island, could have also had an effect on the low numbers of surviving polyps at Chadwick Beach. Gastropods are known to be voracious predators of other species polyps.

Barnacles have been linked to predation of ephyra (Cones and Haven 1969). A consistently higher number of barnacles were found on slides from Chadwick Beach as opposed to those from Cattus Island. Throughout the year, 129 barnacles were found on all slides from Cattus Island while 624 barnacles were counted from Chadwick Beach slides. The barnacles also competed for prime space with the polyps since they overwhelmingly (92 % Cattus Island, 87% Chadwick Beach) settle on downward facing slides. The larger number of barnacles at Chadwick Beach may also consume planktonic planulae before they were able to settle. Twenty four sea anemones (*Diadumene leuocolena*) were found at Chadwick Beach during the year while only one was found at Cattus Island. Sea anemones are known ephyra predators (Cargo and Schultz 1967).

Floating dock versus new bulkhead

Floating docks have been implicated in the facilitation of jellyfish blooms (Miyake et al. 2002). There is a floating dock located immediately adjacent to the Cattus Island Settlement Plate. This floating dock was placed in service in 2008. It has been shown that jellyfish polyps prefer to settle on plastic surfaces upside down (Holst and Jarms 2007); therefore the floating dock could be a reservoir for overwintering polyps and cysts. Based on this research, a small floating dock (10m²) could be the site of 460,000 polyps, with the possibility of creating almost seven million ephyra in one season.

Development and changes in land use have altered the shoreline in Barnegat Bay. Over 45% of the natural shoreline was bulkheaded by 1999 and only 29% of the shoreline was unaltered at that time (Lathrop et al. 1999). Bulkheads reduce species abundance and diversity, change sediment composition, and create water turbulence (Jivoff 2006). The area surrounding Chadwick Beach is nearly all bulkheaded, but in Cattus Island there are large areas of natural shoreline (park area). In Chadwick Beach the bulkhead was replaced in 2007 with a new vinyl bulkhead. This could be an area of increased polyp production due to the preference jellyfish species have shown for settlement on plastics (Hoover and Purcell 2009).

Other factors

Three new laws have recently been enacted in New Jersey to improve the water quality in Barnegat Bay. These laws include a statute which requires storm water basins to be repaired or replaced, an amendment to the Soil Erosion and Sediment Control Act and most importantly a new statute which controls the application of fertilizers (Duss 2011). Together these laws will help control excess nutrient flows into the bay thereby

reducing eutrophication. Ideally these laws will facilitate an ecosystem with fewer large jellyfish blooms in the future. Continued studies will help quantify this connection in Barnegat Bay.

CONCLUSION

In this study it was demonstrated that polyps can quickly establish large colonies in favorable habitats. The ability of *Chrysaora quinquecirrha* polyps to encyst and persevere even when environmental conditions are harsh enables this species to persist in Barnegat Bay. Consequently, the polyp stage is the most important stage to study in order to control blooms of the medusae. As the characteristics that regulate *Chrysaora quinquecirrha* polyp settlement in Barnegat Bay are established, the specific areas in the bay that support polyp growth can be targeted for additional study. As this study has noted, salinity is the major physical factor limiting polyp settlement in Barnegat Bay. Additional surveys should be done in areas of low salinity (5-20ppt). Zones of low oxygen concentration located within the low salinity areas should be targeted for further study because polyps can settle in these areas and be undisturbed by most competitors or predators. A survey of medusae should be recorded and correlated with numbers of polyps found in the previous year. Polyp counts could become the predictor of *Chrysaora quinquecirrha* blooms.

Once the areas for polyp recruitment are defined, practices should be established to limit the availability of settlement substrate. It has been substantiated that floating docks can become reservoirs of polyp colonies therefore in these areas floating docks should be restricted. Bulkheads in low salinity areas should be naturalized with rocks and sand to create more intertidal area (Douglass and Pickel 1999). Additional intertidal zones will facilitate more species to populate the area. Juvenile fish and other smaller organisms will reclaim shallow intertidal habitat. Competition and predation will naturally limit the jellyfish population.

Actions need to be taken quickly to insure Barnegat Bay does not spiral into a "jelly food chain". The "jelly food chain" places jellyfish as the top predator and tunicates as the main herbivore. Jellyfish numbers have not been documented, but the local press has reported unusually high numbers of medusa for several years. Tunicates were found on 60% of slides collected in July (where salinity was 20ppt or higher). Tunicates were identified on 40% of all slides (20ppt or higher) each month except September. The overwintering cysts found on slides could create millions of medusa if found in similar density under the adjacent floating dock. This is just one small sample which demonstrates the large numbers of medusae that are possible. With large numbers of jellyfish and large coverage of tunicates, Barnegat Bay could be moving toward a "jelly food chain".

ACKNOWLEDGEMENTS

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APPENDIX

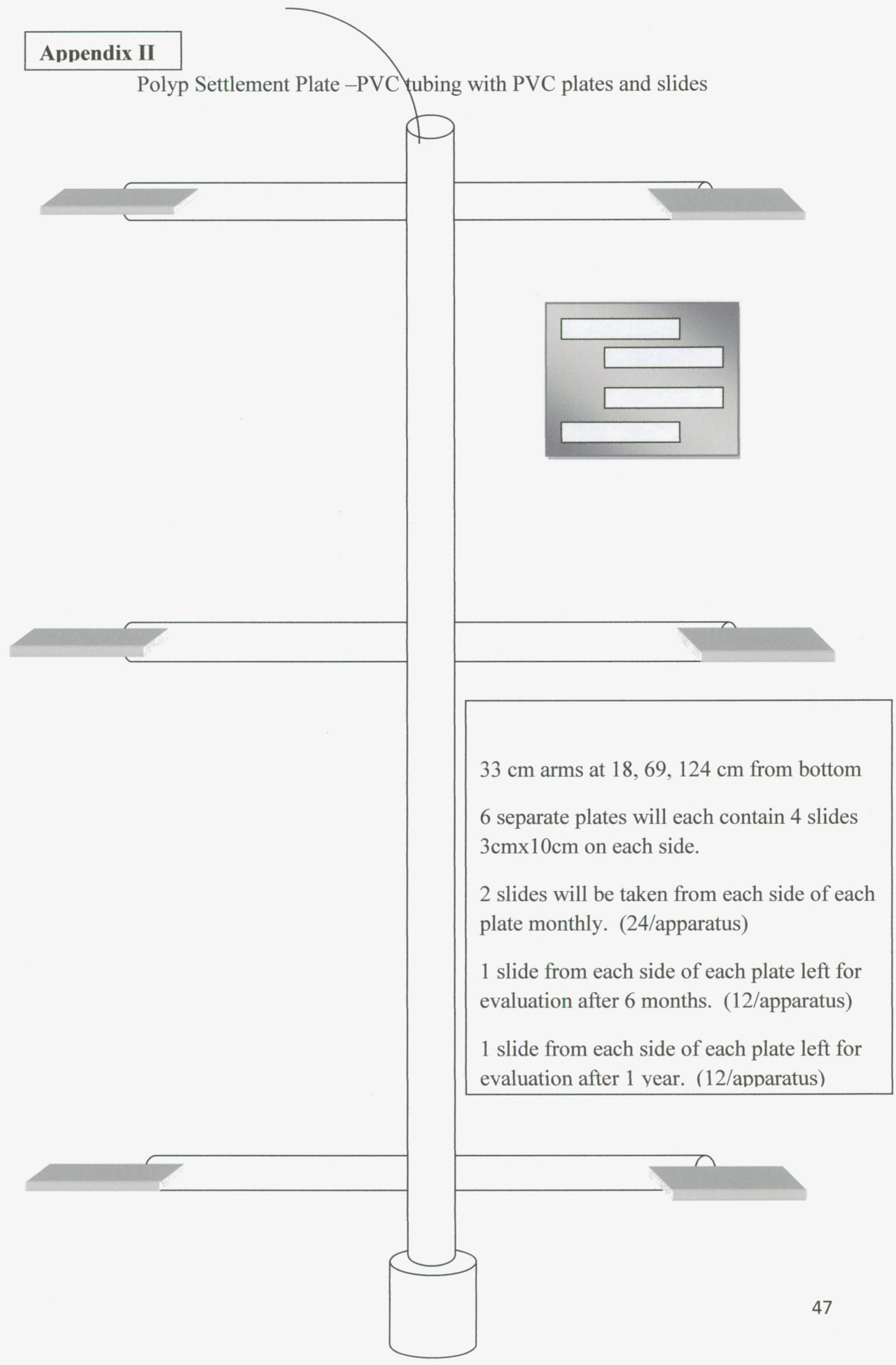
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Life Stage	Prey	Common name	Reference	What prey eats	Reference	Competitors for prey items			
Appendix I. Trophic Interactions									
<i>Chrysiora quinquecetra</i>	Prey								
Juvenile	zooplankton								
Adult medusa	zooplankton, ctenophores, ichthyoplankton								
	<i>Mnemiosopsis leidyi</i>	ctenophore	Feigenbaum and Kelly 1984		Briedburg and Fulford 2006	<i>Mnemiosopsis leidyi</i> Beroe	ctenophore		Calder 1972b
	<i>Acartia tonsa</i>	copepod	Suchman and Sullivan 1988	oyster larvae copepods	Decker et al. 2007				
	Copepods in general*	copepod	Purcell et al. 1991	phytoplankton		<i>Anchoa mitchilli</i> Menhaden	Bay anchovy		Purcell et al. 1991
	Oithona copepods		Decker et al. 2007						
	molluscs		Decker et al. 2007						
	Larvaeans		Decker et al. 2007						
	<i>Anchoa mitchilli</i> eggs and larvae	Bay anchovy	Decker et al. 2007			<i>Morone saxatilis</i>	Striped bass		Decker et al. 2007
	<i>Sciaenops ocellatus</i> larvae	Red Drum	Duffy et al. 1997			<i>Pomatomus saltatrix</i>	Bluefish		Decker et al. 2007
*medusae will not eat oyster larvae									
Life Stage	Predators	Common name	Reference						
polyp	<i>Coryphella</i>	nudibranch	Cones and Haven 1969						
ephyra	<i>Dialaneme Leucolina</i>	sea anemone	Cargo and Schultz 1967						
ephyra	<i>Balanus eburneus</i>	ivory barnacle	Cones and Haven 1969						
medusa	Fish								
	Sea Turtles	Leatherback and others							
	<i>Mola mola</i>	Sea Turtle							
	<i>Peprilus triacanthus</i>	Butterfish	Purcell and Arai 2001						
	<i>Peprilus alepidonus</i>	Harvestfish	Calder 1972b						
	<i>Libinia dibia</i>	Spider crab	Calder 1972b						
	<i>Aluera schoeffi</i>	Orange filefish	Cargo and Schultz 1966						
	<i>Chloroscombus chrysurus</i>	Atlantic humpers	Purcell and Arai 2001						
	Competitor								
	<i>Cliona**</i>	Boring Sponge	Cones and Haven 1969						
*up to 5% of population in C.B. per day									
**polyps not found on shells with this sponge									

Appendix II

Polyp Settlement Plate –PVC tubing with PVC plates and slides



33 cm arms at 18, 69, 124 cm from bottom

6 separate plates will each contain 4 slides 3cmx10cm on each side.

2 slides will be taken from each side of each plate monthly. (24/apparatus)

1 slide from each side of each plate left for evaluation after 6 months. (12/apparatus)

1 slide from each side of each plate left for evaluation after 1 year. (12/apparatus)

Appendix III

Salinity by Site/Month/Depth

Mantoloking

	Top	Middle	Bottom
May	16.9	17	17.9
June	20.7	21.8	21.9
July	22.8	22.8	22.8
Aug	24	24.1	24.1
Sept	26.3	26.3	27.4
Oct/Nov	25.6	25.9	26.2
April	17.7	18.3	18.3

Cattus Island

	Top	Middle	Bottom
May	12.8	12.8	12.9
June	13.2	13	13
July	15.7	15.7	15.7
Aug	18.5	18.5	18.5
Sept	21.5	21.5	21.8
Oct/Nov	18.7	18.7	18.7
April	14.3	14.4	14.6

Berkley Island

	Top	Middle	Bottom
May	19.8	20.1	20.3
June	22.7	22.8	22.9
July	23.9	23.9	23.9
Aug	26.5	26.6	27.2
Sept	23.8	24	24.3
Oct/Nov	24.6	25.5	25.5
April	18.6	18.9	19.7

Parson's Seafood

	Top	Middle	Bottom
May	25.5	26.5	29
June	26.7	27.9	27.9
July	29.3	29.3	29.4
Aug	29.9	29.9	29.9
Sept	30.2	30.3	30.3
Oct/Nov	27	27.1	27
April	23.4	23.4	23.4

Chadwick Beach

	Top	Middle	Bottom
May	13.7	13.7	13.8
June	15.3	15.7	15.7
July	17.8	18	18
Aug	20.8	20.8	20.8
Sept	23	23.2	23.4
Oct/Nov	20.5	20.6	20.7
April	17.1	17.2	17.1

Toms River

	Top	Middle	Bottom
May	1	1.1	1.2
June	1.2	6	9.9
July	2.6	3.8	12.4
Aug	3.4	3.34	12.8
Sept	8.8	13.5	20.4
Oct/Nov	11.2	17.2	17.5
April	5.3	5.4	14.7

Lighthouse Center

	Top	Middle	Bottom
May	25.1	25.1	25.1
June	27.1	27.3	27.6
July	27.8	27.9	28.2
Aug	29	29	28.5
Sept	29.5	29.7	29.8
Oct/Nov	25.4	25.4	25.4
April	22.8	22.8	22.8

RUMFS

	Top	Middle	Bottom
May	26.1	26.5	28.8
June	28	29	29.3
July	28.8	28.9	29.7
Aug	29.7	29.9	29.9
Sept	28.9	29.3	29.8
Oct/Nov	27.9	28	27.9
April	24.4	24.5	24.5

Appendix IV. Oxygen concentrations mg/l (by level) for sites that contained polyps.

Chadwick Beach				Cattus Island			
	Top	Middle	Bottom		Top	Middle	Bottom
May	8.86	8.63	8.8	May	7	6.65	5.98
June	8.88	8.82	8	June	5.65	5.02	5
July	5.9	5.7	5.3	July	5.45	4.45	4.03
Aug	7.3	6.82	6.83	Aug	5.09	4.13	4.09
Sept	7.24	6.78	6.22	Sept	4.85	4.63	4.32
Oct/Nov	9.96	9.34	9.39	Oct/Nov	9.99	9.65	9.71
April	9.7	9.5	9.32	April	8.28	8.32	7.68

Appendix V. Species found with *Chrysaora quinquecirrha* at Chadwick Beach and Cattus Island

	Chadwick Beach	Cattus Island
Annelida/Polychaeta		
<i>Hydroides dianthus</i>	X	X
<i>Nereis pelagica</i>	X	
<i>Nereis succinea</i>	X	X
<i>Polydora sp.</i>	X	X
<i>Sabella sp.</i>	X	
<i>Spirorbis spirillum</i>	X	
<i>Streblospio benedicti</i>		X
Arthropoda/Crustacea		
Amphipoda	X	X
<i>Balanus sp.</i>	X	X
<i>Caprella penantis</i>	X	
Isopoda sp.	X	
Bryozoans/Gymnolaemata		
<i>Bugula simplex</i>	X	
<i>Membranipora membranacea</i>	X	X
Chordata/Urochordata		
<i>Botryllus schlosseri</i>	X	
Cnidaria/Anthozoa		
<i>Diadumene leucolena</i>	X	X
Cnidaria/Hydrozoa		
Hydroids	X	X
Cnidaria/Scyphozoa		
<i>Chrysaora quinquecirrha</i>	X	X
Mollusca/Gastropoda		
<i>Cratena pilata</i>	X	
<i>Crepidula convex</i>	X	
<i>Crepidula fornicata</i>	X	
<i>Crepidula plana</i>	X	
<i>Doridella obscura</i>	X	
<i>Ercolania fuscata</i>		X
<i>Ilyanassa obsoleta</i> (egg)	X	
<i>Tenellia fuscata</i>		X
Eolidacea (other nudibranch)	X	X
Platyhelminthes/Turbellaria		
<i>Plagiostomum sp.</i>	X	X
<i>Stylochus zebra</i>	X	

Appendix VI. Nudibranch and flatworm numbers for all sites.

Plates missing (totally or partially-0*)

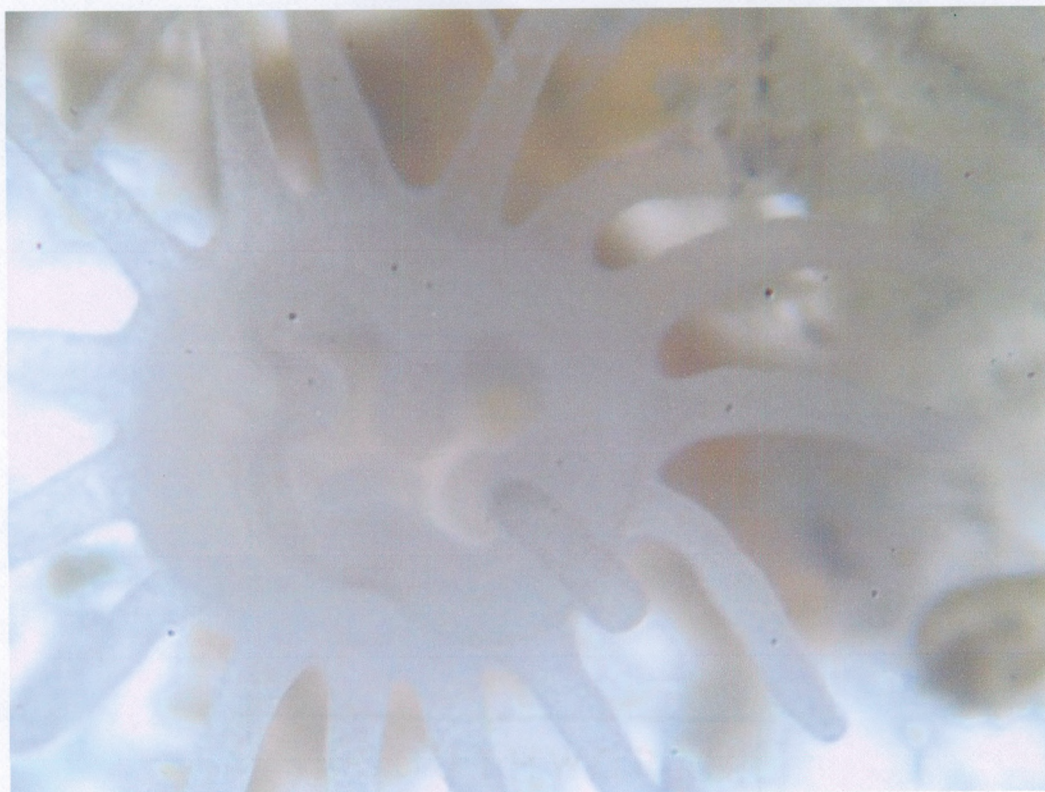
Eolidacea Nudibranch totals

	June	July	Aug	Sept	Nov	6 Month	Year
Mantoloking							
Bridge	1	0	0	0	0	0	0*
Chadwick Beach	173	9	8	4	0	0	*
Cattus Island	18	0	0	0	0	0	0
Toms River	0	0	0	0	0	0	0
Berkley Island	0	0	0	3	0	0	*
Lighthouse Center	0	0	0	0	0	0	0
Parson's Seafood	0	0	0	0	0	1	*
RUMFUS	0	0	0	1	0	0	0

Platyhelminthes Flatworm totals

	June	July	Aug	Sept	Nov	6 Month	Year
Mantoloking							
Bridge	0	1	1	4	1	3	1*
Chadwick Beach	128	6	0	43	1	4	*
Cattus Island	0	2	1	2	3	0	0
Toms River	0	0	0	0	4	0	0
Berkley Island	0	5	0	3	4	10	*
Lighthouse Center	0	0	53	1	1	0	0
Parson's Seafood	0	6	4	0	0	24	*
RUMFUS	0	0	1	0	0	1	0

Appendix VII. Pictures of *Chrysaora quinquecirrha* polyps collected on slides



25% Cotton fiber

