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Benthic Invertebrate Communities of Barnegat Bay New Jersey : Effects of Hard-Clam (Mercenaria Mercenaria L.) Aquaculture Grow-Outs on Benthic Communities

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BENTHIC INVERTEBRATE COMMUNITIES OF BARNEGAT BAY NEW JERSEY: EFFECTS OF HARD-CLAM (*Mercenaria mercenaria* L.) AQUACULTURE GROW-OUTS ON BENTHIC COMMUNITIES

A DISSERTATION

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of the requirements
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by

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Montclair State University
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DISSERTATION APPROVAL

We hereby approve the Dissertation

BENTHIC INVERTEBRATE COMMUNITIES OF BARNEGAT BAY NEW JERSEY:
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ON BENTHIC COMMUNITIES

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ABSTRACT

BENTHIC INVERTEBRATE COMMUNITIES OF BARNEGAT BAY NEW JERSEY: EFFECTS OF HARD-CLAM (*Mercenaria mercenaria* L.) AQUACULTURE GROW-OUTS ON BENTHIC COMMUNITIES

by Rebecca Shell

Plots of three treatment types (industry-standard screens with clams, screens without clams, and control) were installed at Sedge Island, Barnegat Bay, in 2012. 177 species from eight phyla were collected. Hard-clam plots had lower Shannon-Weiner Index values and higher sedimentary sorting coefficients as compared to both control treatments. ANOSIM identified benthic communities inside hard clam plots as statistically distinct from the two control treatments. There was no significant effect of treatment on functional groups assigned by burrowing depth. Seasonal peaks in May are clear for *Polydora cornuta* and *Tritia obsoleta*, as well as for suspension feeders and omnivores. All burrowing-depth guilds except deep-burrowing taxa also peak in May. Grazer density, and *Microdeutopus gryllotalpa* in particular, peak in October. Shannon-Weiner and species richness do not differ significantly by season, though evenness is higher in August than May, reflecting the peaks of certain species evening out during the summer. The trends seen suggest bottom-up controls of the benthic invertebrate community structure in the Sedge Island area, which therefore has the potential to be disrupted either by the overconsumption of available seston from increased aquaculture or increased phytoplankton from increased eutrophication. These data can serve as a baseline for environmental monitors given either of these scenarios. These results do not provide any immediate reason to limit hard clam aquaculture acreage in the region. However, the observed increase in maldanid polychaetes and decrease in mobile suspension feeders could prove problematic if leasing acreage is increased. Full-scale within-industry research is recommended before increasing hard-clam aquaculture acreage, either as part of an environmental management strategy for eutrophication mitigation or for economic purposes.

Keywords: Mercenaria mercenaria, aquaculture, benthos, biodiversity, ecological effects

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DEDICATION

This dissertation is dedicated to my mother, Lynn Pebole Shell,
who raised three strong-minded and gentle-hearted children,
and to my own three strong-minded and gentle-hearted children,
Charlie, Will and Elliott.
I hope you will grow up to pursue your own answers to your own questions.

Lastly, I dedicate this dissertation to the next generation of scientist activists.
May we all get that balance right, because the world is counting on us.

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Chapter 1

Introduction

MERCENARIA MERCENARIA AS A MANAGEABLE RESOURCE

Recreational and commercial harvesting of hard clams has been a Mid-Atlantic and New England tradition for centuries. However, in recent decades wild stocks of many hard clam species, including the commercially and recreationally important *Mercenaria mercenaria,* have shown marked declines. Atlantic Coast landings of *M. mercenaria* peaked in 1950 at approximately 20.8 million pounds, dropping to 9.1 million in 1992; New Jersey harvests peaked at over 5 million pounds in 1950, falling to 1.2 million pounds in 1992 (McHugh 2001). Between 1986 and 2001, *M. mercenaria* stocks in Barnegat Bay fell 68% due to deteriorating water quality and overharvesting (Gastrich and Celestino 2003).

Aquaculture can relieve pressure on wild stocks while reinvigorating local industry. *Mercenaria mercenaria* is particularly well suited for aquaculture as it has high value at small sizes, decreases in value with age, and has low start-up costs (mostly associated with procuring large amounts of seed for hatchery operations) and a biology appropriate to sustainable aquaculture with minimal environmental impact. Commercial hard clam aquaculture operations have been in business in the United States since the early 1970s. Production expanded during the 1980s and farms can now be found all along the Atlantic Coast of the United States, British Columbia, Taiwan and Italy (FAO 1999). Local municipalities and community organizations, such as the Barnegat Bay Shell Restoration Program (BBSRP), have established small-scale hard clam aquaculture operations to revive this traditional local industry and improve water quality. The clams can filter out phytoplankton, transfer suspended sediments to the benthos, and provide other ecosystem services (e.g. mitigation of harmful algal blooms (Hargraves & Sieburth, 1988, Hégaret et al. 2007) and eutrophication (Grizzle et al. 2001, Cerrato et al. 2004, Wall et al. 2008), increasing oxygen penetration depth via bioturbation (Aller 1982, Diaz and Rosenberg 1995). The small scale and low densities (relative to the aquaculture of other species) of these operations, and the biology of *M. mercenaria*, has been assumed to minimize any negative effect of waste nutrient inputs to the system, an impact that has been shown to negatively affect biomass and biodiversity in areas of intense aquaculture of other species (Bartoli et al. 2001). Excessive nutrient input is of particular concern to operations in New York and New Jersey, both densely populated states with coastal waters widely used for recreation purposes and that contribute greatly to local economies (Houston 2008).

Much is known about the biology of *M. mercenaria*, however the literature pertaining to the high hard-clam densities such as would be seen in an aquacultural setting has been largely overshadowed by that on the blue mussel *Mytilus edulis* (L.) (and other *Mytilus* spp.) and, to a lesser extent, the oyster *Crassostrea virginica* (Gmelin 1791). Overall, any potential impacts of artificially large hard-clam populations on the environment remain speculative, and few overall impacts are consistently measured.

INTRODUCTION TO *MERCENARIA MERCENARIA*

Mercenaria mercenaria (Linnaeus, 1758), commonly known as the Northern quahog, hard clam, cherrystone, littleneck, and chowder clam, is a verenid clam native to the intertidal and subtidal sandy and sandy/muddy bottoms between the Gulf of St. Lawrence south to the Florida Keys and is patchy into the Gulf of Mexico (Figure 1-1). Wild introductions have been confirmed in Europe and the Northwestern United States and aquaculture production has been established in Italy, Taiwan and British Columbia.

The life cycle of *Mercenaria mercenaria* is typical of other venerid clams. Sexes are separate and fertilization is external. Fecundity is high, with females typically releasing between 1-5 million eggs per spawn (Kraeuter 2004) though they are capable of releasing up to 24 million eggs per spawn (Davis and Chanley 1956). Larvae spend between 7-21 days in the plankton before settling to the benthos, generating byssal threads and calcified shells. Sexual maturity is reached between 1-2 yrs (Eversole 1987, MacKenzie et al. 2002).

The species is tolerant of wide temperature and salinity ranges, with optimal growth occurring at 20°C. Adults can thrive in salinities as low as 24 ppt, and survive periods in salinities ranging from 4 to > 35 ppt (depending on the ambient temperature) with closed valves, though growth and reproduction greatly diminish (Eversole 1987). Egg and larval survival is more restricted (20 – 32.5 ppt, Eversole 1987). *M. mercenaria* is tolerant of low dissolved oxygen levels, surviving as long as three weeks at levels as low as 1 mg/L (Stanley and Dewitt 1983), though growth is greatly reduced below 4.2 mg/L (Morrison 1971). Feeding rates have been shown to vary according to temperature, current velocity and algal density (Walne 1972). The clams can bury in a variety of soft sediment habitats (sand, mud, eelgrass beds) to depths up to 12 m (Kraeuter and Castagna 2001) though are typically found between 2-20 cm (Eversole 1987). *M. mercenaria* are consumed by a variety of different predators at different sizes; newly recruited clams are particularly at risk. Blue swimmer crabs (*Callinectes sapidus* (Rathbun, 1896)) are the major predator in New Jersey, though moon snails (family Naticidae), rays, whelks (family Muricidae, especially *Busycon carica* (Gmelin, 1791)) and mud crabs have all been recorded as major predators.

The object of this dissertation is to investigate effects of artificially high hard clam density on benthic invertebrate communities. It is therefore necessary to first highlight the role *M. mercenaria* plays at natural, ambient densities. This includes impacts on oxygen penetration depth via bioturbation and bioirrigation; the reduction of suspended sediment and the effects of eutrophication; changes in nutrient deposition and remineralization rates; and impacts to benthic invertebrate biodiversity and eel grass (*Zostera marina*, Linné 1753) cover.

Bioturbation, the mixing of sediments by the burrowing of infaunal animals and rooting by infaunal plants, affects sediment size distributions, porosity and vertical profiles (e.g. of sediments oxygen, nutrients, etc). This can greatly affect the biota that can inhabit a given patch of benthic sediments, driving local benthic biodiversity and overall ecosystem functioning, furthering the overall potential for the gas and waste exchange/flushing known as bioirrigation, and increasing the potential for aerobic microbial activity (Norkko and Shumway 2011). This also serves to increase the overall oxygen penetration depth, or redox potential discontinuity layer (RPD), which is frequently used as a proxy for overall environmental health. Bioirrigation is the actual transport of solutes (oxygen, waste, etc.) between the water column and sediments, transport facilitated by the bioturbation process. These two functions are integral to healthy and functioning soft-sediment systems, and bivalves, due to their potentially large biomass and ability to filter large volumes of water, are especially valuable as both bioturbators and bioirrigators (Wall et al. 2008).

Digestible material, transported to the mouth and expelled as feces, and non-digestible material (non-organic, sediments, overly large particles, etc.), which is expelled via the inhalant siphon, are sorted internally, allowing the clam to regulate both food composition, often favoring higher nutrient foods, and the total amount of food consumed. Selection efficiency (the ratio of chlorophyll *a* to dry weight of pseudofeces and seston) is moderately high in *M. mercenaria* as compared to other suspension feeding bivalves (Grizzle et al. 2001). Feces and pseudofeces both typically settle nearby, thus filter feeders can have a direct impact on the sediment composition (pseudofeces) and nutrient load (feces) of the immediate sediment, directly linking the water column and benthos. Much of the research on this effect has focused on aggregating bivalves such as oysters and mussels rather than hard clams. Indeed, studies specifically of carbon transfer found that *M. mercenaria* had lower biodeposition rates than both *M. edulis* and *Crassostrea virginica* (Tenore et al. 1973). Even so, Doering et al. (1986) found gross sedimentation rates over 14g C/m^2 higher in mesocosms containing hard clams as compared to those without. This has been confirmed by many studies (e.g. Dame et al. 1980, Dame and Dankers 1988, Fréchette and Bourget 1985, Smaal 1991). Of course, the overall sedimentation rate from biodeposition is dependent on the concentration of both food and suspended sediments (Norkko et al. 2001), as well as on local currents (Coen et al. 2011). Aquacultural sites, located in shallow, calmer less exposed locations, could be expected to have higher potential for biodeposit build-up than areas in more exposed Barnegat Bay locations.

Biodeposits are high in organic content. Areas with low resuspension rates can thus be expected to retain higher levels of nutrient input from the infaunal bivalve community, benefitting local deposit feeding organisms (Norkko *et al.* 2001). These benefits, however, are seen over only a narrow range of inputs before increasing nutrient loads begin to instead cause anoxic conditions and disruption of the benthic community (Pearson and Rosenberg 1978). If biodeposited material accumulates sufficiently, decomposition of such organics can increase oxygen consumption, shifting the benthic microbial community from aerobic to anaerobic. Under such conditions, nutrient fluxes are altered: phosphorous is released and denitrification is inhibited (as nitrifying bacteria require well-oxygenated sediments), which in turn causes the release of ammonium from sediments (Newell et al. 2002). Bioturbation by bivalves can mitigate these effects. Doering et al. (1987) found *M. mercenaria* increased benthic flux of oxygen (increased the RPD) via bioturbation, helping to preserve aerobic conditions, thus preserving nitrification-denitrification coupling and minimizing phosphorous release. Thus we see that infaunal bivalves both release nutrients via feces and pseudofeces production, and stabilize them by facilitating remineralization, though typical clam densities do not produce sufficient biodeposits to incur the aforementioned effects (Norkko and Shumway 2011). Nizzoli et al. (2006) found that mussel farms impact oxygen and nutrients more strongly than clam farms due to the clams' ameliorating bioturbating ability. This hints at the possibility that an increased effect of bioturbation could mitigate potential negative oxygen and nutrient-related impacts of bivalve aquaculture in hard clams.

Though most (80%) of published studies find natural *M. mercenaria* densities to be between 1/m^2 and 15/m^2 (Fegley 2001), hard clam densities are variable. Rice (1989) measured non-fished natural densities in Narragansett Bay at 190/m^2, and numbers as high as 500/m^2 (over small scales) have been reported (e.g. Crane et al. 1975). Aquacultural hard clam densities can be several orders of magnitude higher, upwards of 3,000/m^2 (Castagna and Kraeuter 1981), an increase that would certainly alter the total effect. One study of a hard clam farm in a well-flushed Chesapeake Bay tributary (Luckenbach and Wang 2004) found that the clams (at densities between 550-1650/m^2) filtered as much as 81.9% of the water per day. Such a huge volume of water being filtered every day is certain to remove a much larger fraction of the available seston from the water column than the aforementioned studies have shown. Few studies exist for *M. mercenaria*, or indeed any non-mussel bivalve species, at farmed densities.

It is well established that biodiversity is positively correlated with niche heterogeneity, which is in turn largely determined by habitat heterogeneity. Though the infaunal *M. mercenaria* does not compare to reefing bivalves in this regard (e.g. mussels and oysters), live clams as well as deceased but attenuated hard-clam shells, create shelter on a soft-sediment plain and hard substrata for epifaunal organisms. Additional habitat, including the interstitial habitat located between shells, is also created by both dead and living animals (Gutierrez et al. 2003). Under the bivalve-induced habitat classifications (ASMFC 2007, Coen et al. 2011), *Mercenaria mercenaria* has been classified as a 'shell accumulation' contributor due to the tendencies of empty hard clam valves to persist in the benthos long after the organism has died (Dumbauld et al. 1993, 2000; Steimle and Zetlin 2000; NRC 2010). A fourth category has been suggested, 'shellfish aquaculture,' to which farmed hard clams would certainly contribute. Shells provides such valuable habitat that dead valve aggregations are often harvested for use in restoration projects, which in turn decreases the amount of available habitat in those harvested areas.[1] The changes in microflow within the benthic boundary layer as created by siphonal currents as well as created by the clams' physical structure will drive further microhabitat creation (Green et al. 1998). Naturally, these effects are directly related to both sediment type as well as the size and density of the benthic bivalves in question. There is evidence that in particularly dense aggregations, competition for space is sufficient to limit increases in biodiversity (Whitlatch et al. 1997).

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[1] Reviews have inferred that existing shellfish populations are no longer generating sufficient empty shell-based habitat (e.g. Powell et al. 2006, NRC 2010). Bivalve aquaculture is currently being discussed as a solution to the shell shortage, though this will not be investigated in this dissertation.

Submerged aquatic vegetation (SAV) is yet another source of habitat heterogenetity, and one that has been positively correlated with increasing *M. mercenaria* density (e.g. Wall et al. 2008). The physical removal of algae and suspended sediments from the water column clarifies the local water column, allowing for increased light penetration. The additional light and fertilized substratum can result in beneficial conditions for submerged and intertidal aquatic vegetation through fecal deposition. As early as 1984, Bertness found a positive relationship between the intertidal cordgrass *Spartina alterniflora* (Loisel) and the semi-infaunal intertidal mussel *Geukensia demissa* (Dilwin, 1817). More recently, several studies have shown higher SAV cover and primary production associated with high densities of hard clams and other suspension feeding bivalves (e.g. Reusch et al. 1994, Reusch and Williams 1998, Shumway and Kraeuter 2004, Wall et al. 2008). Peterson and Heck's work (2001) suggests that biodeposits from infaunal bivalves are responsible for at least some of these effects. Increased SAV necessarily increases habitat heterogeneity and biodiversity as many species of finfish and invertebrates are found in association with SAV beds, and juveniles of many more have been shown to use such areas as nurseries (e.g. Nagelkerken et al. 2001, Heck et al. 2003, Bostrom et al. 2011).

AQUACULTURE OF *MERCENARIA MERCENARIA:* METHODOLOGIES AND IMPACTS

Hard clam aquaculture operations follow a common general plan: seed is grown to 2-5mm in commercial hatcheries, after which the juvenile clams are kept at high densities in nursery tanks known as 'upwellers,' or in seawater tables or raceways (Castagna 2011). Ambient seawater is pumped through the tanks, providing food and removing waste (Figure 1-4). Between 8-15mm the clams are spread evenly across a sand/mud substratum at 550-1650 clams/m^2

(Castagna 2011) (densities can range up to 3000-4000 clams per m^2, Castagna and Kraeuter 1981, Figure 1-4). A lightweight, UV-resistant, polyethylene screening (sold as “barrier” or “predator” screen, e.g. Tenax®) is affixed to a PVC frame with zipties or lead line. The frame is spread over the bed and secured along the edges, with either rebar or barrier-cloth tubes filled with shell, sand or gravel, in order to prevent predation during this ‘grow-out’ phase. Some managers dig trenches around the beds and cave the screens in around the beds for additional protection. Screens are routinely cleaned during the yearlong grow-out phase, as biofouling of the screens is guaranteed. During this period the clams grow to legal, harvestable size (>38 mm), before being manually retrieved for sale after approximately one-two years via handraking (mechanical harvesters are not permitted in New Jersey).

Minimal environmental impact is expected during the first two stages of this process provided appropriate filtering precautions. The grow-out phase and subsequent harvest, however, do require direct interaction with the benthic community, though the impacts are as of yet largely unstudied. Though there is an extensive body of research on bivalve aquaculture, most of the studies have focused on mussel (esp. *Mytilus* spp.) and oyster culture. This is not surprising, as until recently 70% of global bivalve aquaculture was mussel culture (FAO 1999). There has been little research available on the potential effects specifically regarding culture of clams, and even less on hard clams including *M. mercenaria*. However, with clam and oyster aquaculture now dominating the global market (33% and 31.3% respectively in 2014, with mussels 12% and scallops at 11% (FAO 2014)), this is now starting to shift.

The literature deals primarily with the physical extraction of full-size clams from the benthos: It has been shown (e.g. Brown and Wilson 1997, Badino et al. 2004) that harvest by hand clam-rake alters infaunal communities both in terms of reduced abundance and species richness, due mainly to the mixing of sediment layers, though Brown and Wilson (1997) found that the frequency of hand-clam raking did not affect the severity of the raking impact. Studies have found the impacts from mechanical harvesting[2] (dredging, mechanical raking) to be even more severe (e.g. Kaiser et al. 1996, Hall and Harding 1997, Spencer et al. 1997, Boese 2002). Little research has focused on possible environmental repercussions of the grow-out stage itself rather than the mechanical harvest, and what studies have been done show contradictory results.

Several studies have shown negative impacts beneath, and associated with, bivalve cultures from the over contribution of nutrients (e.g. Hartstein and Rowden 2004, Callier et al. 2006, Metzger et al. 2007) while other studies have seen no such effects (e.g. Mojica and Nelson 1993). Hargrave et al. (2008) suggest that this variability is at least in part due to site-specific hydrologic variation, but this may be less relevant for infaunal hard clam aquaculture where water currents have less immediate access to waste nutrients as compared to long-line mussel culture (or bagged oyster culture). The negative effects nutrient effects documented in other shellfish aquaculture could be ameliorated in large *M. mercenaria* populations: Doering et al. (1987) showed in a mesocosm study that large *M. mercenaria* populations increased benthic oxygen flux, helping to preserve aerobic conditions, thus preserving nitrification-denitrification coupling and minimizing phosphorous release. Fewer *in situ* studies are available on nutrient profile shifts associated with clams, and those that are available (e.g. Bartoli et al. 2001 and Nizzoli et al. 2006 on *Ruditapes philippinarum* (Adams & Reeves 1850)) have generally found a slight net positive nutrient contribution being sequestered by the clams themselves, indicating that these effects are density dependent.

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[2] Mechanical harvesting is illegal in New Jersey.

Changes to sediment profiles in these studies resulting from the additional deposition of suspended sediments are also contradictory (e.g. Coen et al. 2000, Chamberlain et al. 2001, Crawford et al. 2003) as are changes in biological response variables. Whiteley and Bendell-Young (2007) found decreases in total non-target bivalve biomass on farmed sites as compared to unfarmed plots, but this was offset on the farmed sites by an increase in the target bivalve biomass (*R. philippinarum*). This contrasts with findings that screening on commercial farms increased total bivalve biomass (Spencer et al. 1997, Smith and Langdon 1998), increasing target bivalve survival (*R. philippinarum*) but without decreasing non-target bivalve abundance, and still others (e.g. Mojica and Nelson 1993) that found no such effect. Little, however, is known about these factors in small-scale operations. The variety of responses is particularly interesting when considering the issue of space and overcrowding. Presumably, as the seed clams grow and increase in size, the amount of space available to other benthic organisms is decreased, yet only a few of these studies found decreases in benthic diversity or abundances of non-target benthic invertebrates. All of these studies are all on the Manila clam (*Ruditapes philipaniarium*), however the Manila clam is of similar harvestable size to *M. mercenaria* (FIGIS 2004) and the issue of size and overcrowding would therefore be expeted to impact *M. mercenaria* aquaculture plots similarly.

The effects of *in situ* bivalve aquaculture on biodiversity and benthic infaunal assemblage in the literature are varied, and seemingly site-specific (Hargrave 2008). Some studies report positive impacts associated with mussel culture (e.g. predator abundance and diversity, Inglis and Gust 2003; epifaunal and total macroinvertebrate abundance, D’Amours et al. 2008), but there are also numerous studies that report minimal effect (e.g. Baudinet et al. 1990, Grant et al. 1995, Kaiser et al. 1996, Chamberlain et al. 2001, Crawford et al. 2003) and studies that report negative impacts to biodiversity (Hargrave et al. 2008, Cranford et al. 2009). Several studies have also found severely shifted benthic community structures beneath *Mytilus* spp. cultures (e.g. Beadman et al. 2004, Commito et al. 2005, Norling and Kautsky 2007 and Ysebaert et al. 2009) but again the presence and magnitude of any impacts are seemingly site-specific. In Sweden, Mattsson and Linden (1983) found that a community previously dominated by *Nucula nitidosa* (Winckworth, 1930), *Ophiura* spp. and *Echinocardium cordatum* (Pennant, 1777)) was dominated by three species of polychaetes (*Capitella capitata* (Fabricius 1780), *Scolelepis fuliginosa* (Claparede, 1870), and *Microphthalmus sczelkowii* (Metschnikow, 1865)) beneath and up to 20m away from the mussel lines after less than 18 months of mussel culture. Stenton-Dozey et al. (1999) found initial evidence of recovery (in terms of benthic invertebrate biodiversity metrics) beginning four years after *Mytilus galloprovincialis* (Lamarck, 1819) culture had ceased. Whether the same variability and strength of effect also applies to hard clam aquaculture remains to be seen as there is no literature investigating the effects of the grow-out phase of aquaculture operations for the locally abundant hard clam *Mercenaria mercenaria*, or on any hard clam in the mid-Atlantic region.

EFFECTS OF SCREENS ON BENTHIC COMMUNITIES

In New Jersey hard clam farmers lay screening (6.3-13 mm Tenax ®) over *in situ* clams for protection from predatory blue crabs (*Callinectes sapidus*). Such structures can greatly affect the hydrodynamics and physical environment of the caged area and immediate surrounds (Virnstein 1978), causing an overall slowing of currents and potentially generating eddies around structure depending on object size. Depending on structure and orientation, and on physical parameters such as grain size, current strength and sediment load, cages can cause scouring or locally increased sedimentation (Virnstein 1978). Coen et al. (2000) found that shear velocity of benthic boundary water was slowed by as much as 50% in areas between *M. mercenaria* pens and by as much as 90% within the pens. This slowing has the potential to cause ‘fall-out’ of suspended particles from the water column to the sediment, including both sediment particles and food particles. As clams feed from moving water currents above the bottom surface, this can severely reduce total food availability to feeding hard clams (Coen et al. 2000). Coen et al. (2000) also found that sediments adjacent to cages were lower in silt and clay than sediments located away from cages, implying that the caged areas trapped a larger proportion of smaller (and lighter) particulate, likely a result of slower moving waters. These changes were not, however, accompanied by a change in total (non-target) infaunal biomass, and were seen only within the pens themselves.

The screens also provide additional and novel habitat on what was a flat, sand/mud bottom, with potentially little habitat heterogeneity. Combined with the screening effects described earlier, which can create conditions inducing larval entrapment including a decrease in current velocity and changes in sediment composition within the cage as compared to nearby areas (Virnstein 1978), this can result in shifts to benthic community structure. The specific suggestion is that fouling of the netting apparatus itself can lead to increases in larval settlement and subsequent shifts in local community structure, as well as increases in overall biodiversity and biomass (Kaiser et al. 1996, Spencer et al. 1997, Whiteley and Bendell-Young 2007).

The build-up of fouling organisms can increase the total shaded percentage of benthic surfaces and therefore benthic primary productivity within the caged area, which can have a direct impact on food availability, particularly to deposit feeding organisms. These organisms can themselves provide habitat to other sessile organisms, as well as to mobile species that prefer habitats associated with particular sessile communities, such as amphipods, isopods and echinoderms. This creates, in effect, an artificial reef (Virnstein 1978), especially if screens are not maintained throughout the growing season.

RESEARCH QUESTIONS AND DISSERTATION STRUCTURE

The overall goal of this dissertation work was to understand the impact of small-scale hard clam aquacultural grow-out operations in New Jersey on benthic invertebrate communities, with aims to answer the following questions:

1) How do the infaunal and benthic invertebrate communities beneath and adjacent to netting enclosures change over the course of the 12-month grow-out cycle (diversity, richness, dominance, evenness), and how do they compare to communities in associated non-grow-out areas?

2) What portion, if any, of this change is caused by the increased density of clams in netted areas, and what by the screens, process and equipment themselves?

3) Over what physical distances are these changes seen?

4) What changes to biodiversity and/or total biomass are due to increased recruitment to the protective screen netting?

The results of this work will be made available to the Barnegat Bay Shellfish Restoration Program and the collaborating private and public organizations, in the hopes of informing New Jersey and regional policies around bottom acreage leasing for shellfish aquaculture. This dissertation is written as a series of individual manuscripts and therefore includes some necessary repetition within the introductory and methods sections. The second chapter contains results and analysis pertaining to the effects of the aquaculture itself on local benthic communities. The third chapter contains a discussion of data collected during the course of the experiment that describe the seasonal dynamics at play during the three-year time frame (2013-2015).

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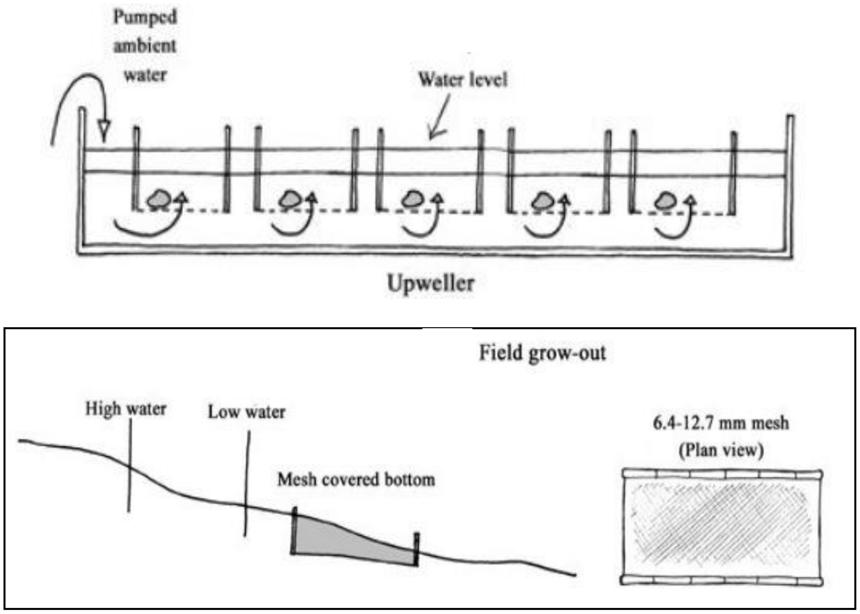
FIGURES

Figure 1-1. Typical *M. mercenaria* upweller and grow-out schematic (Kraeuter 2004).



Chapter 2

Effects of hard-clam (*Mercenaria mercenaria* L.) aquaculture grow-outs on benthic invertebrate communities in Barnegat Bay, NJ

ABSTRACT

Hard-clam (*Mercenaria mercenaria*) aquaculture operations maintain densities many magnitudes higher than those found naturally during the 2-3 year "grow-out" phase. Though high densities of other farmed species have been shown to detrimentally impact local communities due to locally-increased nutrient input, we hypothesize that hard-clam aquaculture will provide a net benefit to local communities (increased benthic invertebrate biodiversity and species richness) due to the increase in total filtering capacity. Plots of three treatment types (industry-standard screens with clams, screens without clams, and control) were installed at Sedge Island, Barnegat Bay, in 2012. 177 species from eight phyla were collected. Hard-clam plots had lower Shannon-Weiner Index values as compared to both control treatments, a result opposing the initial hypothesis, and higher sedimentary sorting coefficients. ANOSIM showed significant change to invertebrate community inside hard clam plots (Global R=0.147, p=0.1%). There was no significant effect of treatment on functional groups assigned by burrowing depth, and no evidence of change was apparent one meter away. Results do not indicate any immediate reason to limit hard clam aquaculture acreage in the region, but the observed increase in maldanid polychaetes and decrease in mobile suspension feeders could prove problematic if leasing acreage is increased as part of a future environmental management strategy.

INTRODUCTION

The hard clam *Mercenaria mercenaria* (L.) is a common inhabitant of soft-bottom coastal habitats throughout the western Atlantic with a commercial fishery that has experienced severe and well-documented declines (McHugh 2001). As a filter-feeding benthic bivalve often found in high density populations, the species is important in benthic-pelagic carbon transfer, consumption of excessive primary production, transfer of suspended sediments to the benthos, and nutrient recycling (see Kraeuter and Castagna 2001, Grizzle et al. 2001, Nizzoli et al. 2006, Wall et al. 2008). These characteristics have made *M. mercenaria,* and filter-feeding bivalves in general, species of interest in both coastal remediation and mariculture, especially in scenarios of high nutrient and suspended sediment loads.

Much is known about the biology of *M. mercenaria* (Bricelj and Malouf 1984, Bricelj et al. 1984, Kraeuter and Castagna 2001). However, work on the ecological effects of high-density hard-clam mariculture has been largely overshadowed by studies of the blue mussel *Mytilus edulis* (L.) and a handful of other commercially farmed species including *Crassostrea virginica* (Gmelin 1791)*, Mya arenaria* (L.) and *Ruditapes philippinarum* (Adams & Reeve 1850). Overall, the impacts of aquacultural densities of *M. mercenaria* on the environment remain largely speculative, and most study results are inconsistent, particularly during the ‘grow-out’ phase. Hatcheries typically maintain broodstock and sell clam juveniles as “seed” to nurseries that then keep them in self-contained “upwellers” or “raceways,” systems designed to provide the juvenile hard clams with phytoplankton from ambient water sources until the clams reach plantable size (10-12mm). This third phase, known as the “grow out”, is the only part of the aquacultural process that involves *in situ* placement and ambient sediments, and as such interacts with local ecosystems directly. Harvesting by hand has been repeatedly shown to alter benthic invertebrate abundance and community structure (Kaiser et al. 2001, Badino et al. 2004, Logan 2005), reduce benthic macrofaunal biomass and diversity and affect sediment nutrient profiles (Pranovi et al. 2004), and to alter seagrass densities (Peterson et al. 1987). Mechanical harvesting has produced more severe, longer lasting impacts (Kaiser et al. 1996, Hall and Harding 1997, Spencer et al. 1997, Boese 2002).

Regarding the effects of the grow-out phase itself, the literature is divided. Many studies have shown negative impacts beneath, and associated with, bivalve cultures from the overcontribution of nutrients (Hartstein and Rowden 2004, Callier et al. 2006, Metzger et al. 2007) while other studies have reported no such effects (Mojica and Nelson 1993). Doering et al. (1987) showed in a mesocosm study that large *M. mercenaria* populations increased benthic oxygen flux, helping to preserve aerobic conditions in the sediments, thus preserving nitrification-denitrification coupling and minimizing phosphorous release. Hargrave et al. (2008) suggested that this variability was at least in part due to site-specific hydrologic variation, but this may be less relevant for infaunal hard clam aquaculture where water currents have less immediate access to waste nutrients as compared to long-line mussel culture (or bagged oyster culture). Fewer *in situ* studies are available on nutrient profile shifts associated with clams, and those that are available (e.g. Bartoli et al. 2001 and Nizzoli et al. 2006 on *Ruditapes philippinarum* (Adams & Reeves 1850)) have generally found a slight net positive nutrient contribution being sequestered by the clams themselves, indicating that these effects are density dependent. Other studies have also shown inconsistent results about sediment profile changes resulting from the additional deposition of suspended sediments (Coen et al. 2000, Chamberlain et al. 2001, Crawford et al. 2003).

Whiteley and Bendell-Young (2007) found decreases in total non-target bivalve biomass on farmed sites as compared to unfarmed plots, but this was offset on the farmed sites by an increase in target bivalve (*Ruditapes philippinarum*) biomass. This observation contrasts with findings that screening on commercial farms increased total bivalve biomass (Spencer et al. 1997, Smith and Langdon 1998), increasing target bivalve survival (*R. philippinarum*) but without decreasing non-target bivalve abundance, and still others that found no such effect (Mojica and Nelson 1993). Little, however, is known about these factors in small-scale operations, or about any impacts of overcrowded and limitation of physical space. There is also speculation that fouling of the netting apparatus itself may increase larval settlement, subsequently shifting local community structure as well as increasing overall biodiversity and biomass (Kaiser et al. 1996, Spencer et al. 1997, Whiteley and Bendell-Young 2007).

The effects of *in situ* bivalve aquaculture on biodiversity and benthic infaunal assemblage are reported to be varied and probably site-specific (Hargrave 2008). Some studies reported positive impacts associated with mussel culture (e.g. predator abundance and diversity, Inglis and Gust 2003; epifaunal and total macroinvertebrate abundance, D'Amours et al. 2008), but there are also numerous studies that report minimal effects (e.g. Baudinet et al. 1990, Grant et al. 1995, Kaiser et al. 1996, Chamberlain et al. 2001, Crawford et al. 2003) and other studies that report significant negative impacts on biodiversity (Hargrave et al. 2008, Cranford et al. 2009). Several studies have also reported severely shifted benthic community structures beneath *Mytilus* spp. cultures (e.g. Beadman et al. 2004, Commito et al. 2005, Norling and Kautsky 2007 and Ysebaert et al. 2009) but again the presence and magnitude of any impacts are seemingly site-specific. Stenton-Dozey et al. (1999) found initial evidence of recovery (in terms of benthic community biodiversity metrics) beginning four years after *Mytilus galloprovincialis* (Lamarck,

1819) culture had ceased. Whether the same variability and strength of effect also applies to hard clam aquaculture remains to be seen, as there are no studies investigating the effects of the grow-out phase of aquaculture operations for the locally abundant hard clam *Mercenaria mercenaria*, or on any hard clam in the mid-Atlantic region. To better understand these issues, the present study examines the impacts of these grow-outs on local benthic communities.

Hard clam harvests experienced severe declines in the mid 20th century in New Jersey, peaking in New Jersey at just over 5 million pounds in 1950 and falling to 1.2 million pounds in 1992 (McHugh 2001). With declining harvests, industrial scale hard-clam aquaculture became profitable and was well established 1950s in New Jersey and the greater mid-Atlantic region (Castagna 2001, Calvo et al. 2013). More recently, municipalities and local community organizations have begun smaller-scale hard clam aquaculture operations. These efforts support this traditional local industry and utilize the biological capabilities of bivalves for both bioremediation and community outreach purposes. (ReClam the Bay, for example, a private environmental educational non-profit in Ocean County NJ, uses the hard clam as a tool to educate local residents about the ecology of Barnegat Bay and the impacts of residential and municipal fertilizer usage on eutrophication and general water quality, as well as other sustainability-related topics.) The small scale of these operations and the functional biology of *M. mercenaria* have been assumed to minimize any risk of excess nutrient contribution to the system, but the data for ecological impacts of hard clam aquaculture are too limited to support this conclusion. The present study therefore addresses the following questions: do hard clam grow-outs negatively impact local benthic invertebrate biodiversity or alter infaunal community structure? If so, do these impacts extend beyond the area of the grow-out plots?

METHODS

Barnegat Bay is a back-barrier lagoon located in central New Jersey, averaging < 2m in depth (Taghon et al. 2017). Three inlets connect the bay to the Atlantic Ocean to the east, one of which, Barnegat Inlet, is located within 3 km of the study site at Sedge Island. Sedge Island itself is located within the Sedge Islands Wildlife Management Area (WMA), which prohibits commercial fishing and clamming. The study site, off the southwestern edge of Sedge Island (Figure 2-1; 39º 47’ 48”N, 74 º 07’ 07”W) is a shallow cove (maximum depth 2m) enclosed on three sides, sparsely vegetated with *Zostera marina* (Linné 1753) and edged primarily with *Spartina alterniflora* (Loisel-Deslongchamps, 1807) salt marshes.

Through 2015, the Sedge Island cove (Figure 2-2) was the site of an on-bottom shellfish lease managed by the Barnegat Bay Shellfish Restoration Program operated by the Rutgers Cooperative Extension of Ocean County. Recreational clamming is permitted within the WMA, but is prohibited directly on the lease itself. ReClam the Bay purchases larvae from hatcheries and produces their own clam seed, maintaining the juvenile clams in nearby upwellers until they reach plantable size (10-15mm, Castagna 2001). At that size the clams are moved to benthic plots and kept under screening of ¼ - ½” mesh made of light polyethylene for the ‘grow-out’ phase until they reach marketable weight (Flimlin 2000). In New Jersey, these screens are typically 4.6m x 6.1m (Flimlin 2000). Tubular bags of shell and gravel are also used to line the screens to prevent blue crabs from entering under gaps in the rebar. Screens are raked periodically to prevent algae settling onto the screens.

Three experimental blocks of 15 x 7m were marked out in early October 2012 adjacent to screens being maintained concomitantly by ReClam the Bay and the BBP within the Sedge Island Cove. All blocks were fully subtidal and located more than 15 m from the edge of the marsh. Three plots measuring 3 m by 4.6 m were marked out within each block and randomly assigned to one of three treatments: Control (untouched), Screen Control (Tenax® and PVC screen frame affixed to the sediment with rebar and shell bags), or Screened Clam (Tenax® and PVC screen frame installed over clam seed and affixed to the sediment with rebar and shell bags) (see Figure 2-3).

Clams (~10mm) were hand-distributed ("planted") in the randomly selected plots at 1160/m^2 (15000/plot). A three-meter buffer was left between adjacent plots. Screens were built with Tenax®, a black UV inhibiting lightweight polyethylene, and attached to PVC pipes on all four sides using zipties. The PVC was secured to the bottom with curved rebar. Plots were sampled three times per year (May, August and October) between October 2012 and October 2015. Protocol for this study was designed to mimic the standard New Jersey hard clam aquaculture grow-out operation at 1:4 scale. Screens were therefore 'raked' biweekly during the season (May – October) just as is regularly done by farmers to prevent algal fouling. ("Rakes" do not have tines, but instead are like large windshield-wipers, designed to glide over the tops of the screening, removing what lies atop without grabbing onto the screening itself). While many hard clam farmers in New Jersey do remove their screens over the winter to prevent damage from ice scouring, the screens in this study were left in place so as to minimize disturbance from foot traffic. Given that the entire study area remained subtidal in even the shallowest tides, ice scouring was not a concern.

Three sediment cores (PVC corer, 3.8cm dia., 10 cm depth) were taken from within each of the nine plots on each sampling date. For all screened plots, screens were manually rolled back to provide access and then reaffixed to the bottom after sampling. Sediment samples were bagged and kept at 0˚C until processed, at which time they were dried at 80 °C and separated with stacked sieves into >2mm, 1–2mm, 0.5–1mm, 0.25–0.5mm, 0.125– 0.25mm, and 0.063–0.125mm fractions for 7 min on a shaker table before weighing. (These fractions are defined as "granule", "very coarse sand", "coarse sand", "medium sand", "fine sand", "very fine sand" and "silt/clay" according to Wentworth (1922)).

Benthic invertebrate communities were sampled with an Ekman grab (3.5L). In each plot, two benthic samples were randomly located within the plot itself (but at least 1 meter from the edge to minimize edge effects) and one sample was located 1 meter from the plot in each cardinal direction (Figure 2-3). The perimeter samples were taken before any within-plot samples so as to prevent any disturbance to sampling area. Benthic samples were sieved on site at 1mm, and fauna were preserved in 70% Ethanol for later identification.

Statistical Methodology

Sediment samples were analyzed individually using GRADISTAT v4.0 Blott and Pye (2001) that calculates mean grain size and sorting coefficient, and classifies them according to Folk and Ward (1957): very well sorted ($\sigma < 1.27$); well sorted ($\sigma = 1.27$-1.41); moderately well sorted ($\sigma = 1.41$-1.62); moderately sorted ($\sigma = 1.62$-2.00); poorly sorted ($\sigma = 2.00$-4.00); very poorly sorted ($\sigma = 4.00$-16.00); and extremely poorly sorted ($\sigma > 16.00$). Sediment fractions remaining in the pan after sieving (<0.063mm) were not included in the analysis but were accounted for in percent data (as prescribed by Blott and Pye (2001)). Mean grain size and sorting coefficient, as well as biodiversity measures (Shannon-Wiener Index (H'), Pielou's Evenness (J') and species richness (Smith and Wilson 1996)) were then analyzed with factorial MANOVA using treatment and season as the independent variables with blocks ungrouped.

To determine differences in benthic invertebrate community structure between treatments, an analysis of similarities (ANOSIM) and a subsequent SIMPER analysis were performed on benthic grab density data using PRIMER v. 5.2 (Clarke and Gorley 2001). Untransformed density data for all taxa of sample size ≥100 over the course of the experiment (combined across blocks) were also grouped by feeding type and by maximum burrowing depth[3] (infaunal position). The densities of these functional groups were converted with Principal Component Analysis (PCA). The resulting scores were analyzed with factorial ANOVA (independent variables: treatment and season) and with Tukey HSD *post hoc* analysis. Density data from the ten most dominant taxa were also analyzed individually using this same PCA plus factorial ANOVA technique using the same independent variables. All PCA and ANOVA/MANOVA analyses were performed in JMP Pro v. 13.2 (SAS Institute, Cary, North Carolina).

RESULTS

Sediment

Sediment sorting coefficient (min σ = 1.902 – max σ = 3.062) and mean sediment size (min 162.6 µm – max 246 µm) was consistent through the duration of the study (Table 2-1). The mean particle size remained fine sand (125-250 µm, Wentworth 1922) throughout, averaging 204.3 µm in 2013, 185 µm in 2014 and 212 µm in 2015. There was a significant main effect of treatment on sorting coefficient (ANOVA, F(2, 252) = 2.9071, p = 0.0565) but not on mean particle size (F(2, 252) = 2.0902, p = 0.1258). *Post hoc* Tukey HSD analysis indicated a significant difference

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[3] Burrowing depth maxima were obtained from an extensive literature survey, including Dauer et al. 1979, Schaffner 1990, Schaffner et al. 2001.

in sorting coefficients between control plots and plots with screened clams suggesting a more even distribution across particulate size classes in screened clam plots.

Biodiversity

177 species from eight phyla were collected during the three-year study (Table 2-2). Shannon-Weiner index values (H'), Pielou's Evenness values (J') and species richness values were calculated for each sampling site. Factorial MANOVA (independent variables: treatment and season) was significant for Shannon-Weiner index (F(17,466)=3.0786, $p < 0.0001$), and Pielou's evenness (F(17,466)=8.4610, $p < 0.0001$). The standard for significance was not met for species richness (F(17,466)=1.6061, p= 0.0587), and the main effect of treatment was not significant (F(5)=0.3541, p=0.8796). (Table 2-3) (The main effect of season was significantly different, and will be discussed in Chapter 3.)

Results for Shannon-Weiner Index (H') were significant only for the main effect of treatment (F(5)=8.1069, $p < 0.0001$), not season, with no significant interaction effect. Tukey HSD *post hoc* analysis indicated that samples inside screened clam plots had statistically lower H' values than the rest of the treatments (Figure 2-4). Results for Pielou's evenness (J') were significant for the main effect of treatment (F(5)=15.9352, $p < 0.0001$) and season (F(2)=11.2703, $p < 0.0001$), with a significant interaction (F(10)=2.6554, p = 0.0037) (Table 2-3). *Post hoc* analysis identified samples taken inside screened clam plots as having statistically lower J' values than the other treatments (Figure 2-4, additional seasonality differences to be discussed in Chapter 3). Further analysis of the interaction effect indicated that control samples were statistically different from inside clam plots samples in August and October, but not in

May. Screened clam perimeter samples and all screen control samples (inside and perimeter) were not statistically different from control plots (Figure 2-5).

Inside screen control samples were statistically different from inside screened clam plot samples in May but not in August or October, suggesting that the screen is having some effect on evenness distinct from the effect of the clam plots in May that was not statistically significant during August and October. All of the perimeter samples were placed in overlapping groups by the Tukey HSD pairwise comparisons, allowing for the assumption treatment does not effect evenness in perimeter samples differently according to season, or indeed at all (Figure 2-5).

Community Structure

Results from the ANOSIM showed a significant difference in invertebrate community between treatments (Global *R*=0.147, p=0.1%). The MDS plot (stress = 0.28) clearly shows samples from inside screened clam plots clustering strongly, with samples from other treatments grouping less tightly together (Figure 2-6). (The stress value is not low, however it is below the validity threshold posited by Sturrock and Rocha (2000).) The average similarities for each treatment are: Control Inside 19.63%; Control Perimeter 22.24%; Screen Control Inside 27.42%%; Screen Control Perimeter 22.43%; Screened Clam Inside 27.32%; Screened Clam Perimeter 21.05%. These low similarity values indicate great variability within the dataset. Pairwise comparisons were significant for all treatments when compared with inside screened clam plot samples (Table 2-4), and those differences were larger than for any other treatment pair. All perimeter and control comparisons were non-significant.

Dissimilarity results from the SIMPER analysis indicate moderate levels of dissimilarity among all treatments (Table 2-5). Among pairwise comparisons involving inside screen control samples, the comparisons with inside clam plot treatment samples are least dissimilar. For all other comparisons the inside clam plots have the highest dissimilarity scores, indicating that aquacultural communities have the least overlap in community makeup with communities in other treatments. SIMPER also identified the species most critical to each treatment overall. All taxa with contributions over 5% are listed in Table 2-6. All but three of the most critical (non-target) species were among the top ten most dominant taxa by overall abundance (*Scoloplos* sp. (Blainville, 1828), *Lysianopsis alba* (Holmes, 1905) and *Solemya velum* (Say, 1822)). These taxa were all among the taxa included in the functional group analysis to be discussed below. *Ameritella agilis* is one of two critical taxa significant to all six treatments (individual contribution >5% in all treatments), and the only one of the pair whose density differed significant between the treatments (ANOVA, F(17,466)=2.2594, p = 0.0029, main treatment effect F(5)=2.3230, p = 0.0449, Table 2-7). *Post hoc* analysis identified samples from inside screened clam plots as having statistically higher densities of *A. agilis* than perimeter screen control samples (Figure 2-7). The density of *A. agilis* also differed significantly by season (F(2)=14.0495, p < 0.0001) with no significant interaction effect (results to be discussed in Chapter 3). *M. mercenaria* was critical to the inside screened clam treatment as would be expected, but was also a statistically important member of the screened clam perimeter community and the screen control perimeter community. This is not surprising as *M. mercenaria* is also a naturally abundant species in the Sedge Island area.

Dominant Taxa

Densities of the ten most abundant taxa (Table 2-8) were grouped across blocks and converted with Principal Components Analysis (PCA) into linearly uncorrelated variables. The choice to include only the ten most abundant taxa was arbitrary and pre-hoc, to permit sufficient statistical power to examine patterns among the most common animals in the study plots. (The SIMPER analysis confirms the validity of this *pre-hoc* selection as mentioned above).

Three principal components were created with eigenvalues greater than 1.0. Again, treatment and season were the independent variables analyzed. The first (PC1, Eigenvalue 2.6632) explained 26.6% of the variance. The second (PC2, Eigenvalue 1.7302) explained 17.3% of the variance, and the third (PC3, Eigenvalue 1.5304) explained an additional 15.3% of the variance. The remaining components (PC4-PC10) had eigenvalues below 1.0 and were not used in analysis (Table 2-9).

Factorial ANOVA were then run on the scores of principal components 1 through 3 to isolate the effects of season and treatment. Results from the PC1 scores were not statistically significant (F(17,36)=.4929, p=0.9397), and neither were results from PC3 (F(17,36)=1.5446, p=0.1340). A Factorial ANOVA on PC2 scores (positive scores driven by densities of *Tritia obsoleta* (Say, 1822), *Polydora cornuta* (Bosc, 1802) and *Clymenella torquata* (Leidy, 1855) (see Figure 2-8) yielded an interesting but non-statistically significant trend F(17,36)=1.8117, p=0.0661) with a significant effect of treatment (F(5)=31982, p=0.0075) (Table 2-10) and a relevant but non-significant main effect of season (F(2)=3.1982, p=0.0527), to be discussed in Chapter 3. *Post hoc* analysis distinguishes samples taken from inside screened clam plots as having a PC2 score that is statistically different from samples taken at the perimeter of the screened clam plots and the screened control plots. Screened clam plots, with a mean PC2 score of -1.3215, can be linked to high densities of *Clymenella torquata* (Figure 2-9). No significant interaction effects were seen.

Functional Groups

All taxa meeting a minimum abundance of N>100 were classified by feeding functional group and by maximum burrowing depth (infaunal position) (Table 2-8). Feeding groups were not equal in number of taxa (Suspension N=10, Deposit N=12, Grazers N=5, Omnivores N=4, Predators N=4; commensal N=1, not included in this analysis.) When a species was known to use multiple feeding methods, it was placed in the category with which it is principally aligned to avoid pseudoreplication. A principal component analysis on feeding group densities produced three components with eigenvalues greater than 1.0. The first (PC1, Eigenvalue 1.8458) explained 36.9% of the variance, with positive scores driven primarily by deposit feeder and predator densities. The second (PC2, Eigenvalue 1.3) explained 26% of the variance in the dataset. Positive scores were driven by omnivore and suspension feeder densities. The third (PC3, Eigenvalue 1.222) explained 24.4% of the variance, with positive scores driven primarily by grazer density and negative scores driven by suspension feeder density. (Figure 2-10) The remaining two components had eigenvalues well below 0.5 and were not used in analysis.

Factorial ANOVA were then run on the scores of the principal components to investigate the effects of season and treatment. There were no significant effects of treatment or season on PC1 (F(17,36)=1.4170, p=0.1855) but a factorial ANOVA on PC2 scores (treatment and season as independent variables) was significant (F(17,36)=2.4818, p=0.0108) with significant effects of both treatment (F(5)=2.8143, p=0.0303) and season (F(2)=3.6903, p=0.0348) (Table 2-11; seasonality results to be discussed in Chapter 3). No significant interaction effects were found. *Post hoc* analysis indicates that samples taken from inside control plots had higher PC2 scores than inside screened clam plots (Figures 2-11 and 2-12), implying higher densities of omnivorous and suspension feeding taxa inside control plots. Factorial ANOVA on PC3 scores was interesting but non-significant (F(17,36)=1.8124, p=.0660).

Similar analyses were also run on the same taxa grouped by infaunal position. Taxa were divided into epifaunal (N=16), shallow-burrowers (max depth <5cm, N=10) medium-burrowers (max depth 5-15cm, N=5) and deep-burrowers (max depth >15cm, N=4). The principal components analysis produced two components with Eigenvalues greater than or approaching 1.0. The first (PC1, Eigenvalue 2.6523) explained 66.3% of the variance. The second (PC2, Eigenvalue 0.9491) explained 23.7% of the variance in the dataset. The remaining two components had Eigenvalues well below 0.5 and were not used in analysis. ANOVA performed on the scores for components 1 and 2 both produced results that were not statistically significant. PC1: F(17,36)=1.0674, p=0.4185) PC2: F(17,36)=1.6648, p=0.0978.

DISCUSSION

The ten most dominant taxa (as determined from overall abundance data across the entire experimental time frame) were *Ameritella agilis, Capitella* sp., *Clymenella torqutata, Microdeutopus anomalus, M. gryllotalpa, Polydora cornuta, Prionospio heterobranchia, Scoletoma fragilis, Streblospio benedicti* and *Tritia obsoleta* (Table 2-8). Six of the ten are polychaetes, a proportion supported both by recent studies of benthic macroinvertebrate communities associated with shellfish aquaculture (64% of critical taxa associated with mussel culture in Tasmania, Crawford et al. 2003) and by studies of benthic macroinverte communities in Barnegat Bay post-Hurricane Sandy (Taghon et al. 2017). These critical taxa as determined by the SIMPER analysis were highly redundant across treatments. *Ameritella agilis* and *Scoloplos sp*. were critical to all six treatments while *Clymenella torquata*, an abundant, deposit-feeding, tube-dwelling, deep-burrowing species (maximum burrowing depth >20cm), was important to communities in five of the six treatments. This study found higher densities inside hard clam plots of the bamboo worm *C. torquata* (Figure 2-13) and smaller densities of omnivorous and suspension-feeding taxa as compared to control plots. These changes were not seen in the screened control plots, and can therefore be linked, directly or indirectly, to the presence of high densities of the planted hard clams. It appears that at the aquacultural densities used in this study (1160/m^2), the rate at which fecal material and pseudofeces were being deposited was sufficient to increase the food supply for this deep-dwelling maldanid polychaete, especially given the increased sedimentary mixing indicated by the increased sorting coefficient inside these plots.

Deeply-burrowing deposit feeders are connected to the surface by virtue of their burrowing and the irrigation action of their feeding. Though most maldanid polychaetes feed from below, effectively transporting subsurface sediments to the surface, *C. torquata* and other members of the subfamily Euclyminae are head-down conveyor-belt feeders, pulling surface material down into their tubes on which to feed (Dobbs and Whitlatch 1982), though they will also feed at the surface after the deposition of fresh detritus (Weinberg 1988). A study by Levin et al. (1997) supports this, having found that maldanid polychaetes can transport deposited carbon to depths of more than 10cm in only 1.5 days. This has been shown to subsidize microbial communities at the surface (Bianchi et al. 1998) and exert negative pressures on surface invertebrates such as burrowing amphipods (Flach 1992). Weinberg (1988) that found that detritus added to surface sediments enhanced *C. torquata* growth after as little as one month. The additional feces and pseudofeces contributed to surface sediments by the stocked *Mercenaria mercenaria* would be expected to have the same effect found by Weinberg. This would likely also benefit *Ameritella agilis*, an infaunal deposit-feeding bivalve of small size that would be able to easily access deposited feces and pseudofeces, and could potentially explain the increased density seen inside clam plots in this study (Figure 2-7). This is contrary to findings of population and growth-rate decreases in *A. agilis* under aquaculture scenarios (Callier et al. 2009). The relative rates of fecal production by the stocked *M. mercenaria* and the removal of said feces in the aquacultural plots at Sedge Island, either by benthic detritivores or by resuspension, appear to result in a net-improvement to habitat quality for *A. agilis,* in spite of their intolerance to organic enrichment. Certainly the decreasing available physical space left by the growing *M. mercenaria* over time hasn’t proved an obstacle to these small infaunal bivalves.

The four omnivores in the group include three mobile taxa (*Alitta succinea* (Leuckart, 1847), *Elasmopus levis* (S.I Smith, 1873) and *Rhithropanopeus harrisi* (Gould, 1841) and the suspension-feeder functional group includes many motile fauna such as *Ampelisca verrilli* (Mills, 1967), *Crepidula convexa* (Say, 1822), *Microdeutopus anomalus* (Rathke, 1843) and *Polydora cornuta*, the latter two in such abundance that they were among the top ten most dominant taxa throughout the experimental timeframe. Decreases in plankton-feeding taxa in hard clam plots hint at potential food resource competition. This study maintained grow-outs in place for three years, one year beyond which most aquacultural grow-outs remain since the clams are harvestable at littleneck size (15-22 clams/kg, 47.6 – 54mm) inside a two-year timeframe. The growth rate of the stocked clams anecdotally seemed to be slowing during year 3, and a *post hoc* growth curve seems to generally support this observation (Figure 2-14). When compared with published *M. mercenaria* growth curves it is clear that the growth rate seen inside the hard clam plots in this study tails off well before the natural growth rate, which continues unchanged in all three studies cited here to at least four years (Figure 2-15 a-c). The growth chart from Carmichael et al. (2004) highlighting the extremely high growth rates seen in eutrophic coastal estuaries is particularly relevant given the well documented eutrophic conditions in the northern sections of Barnegat Bay (Kennish et al. 2001). While admittedly circumstantial, if the decrease in clam growth is in fact a response to an increasingly limited seston resource within the clam screens, it is unsurprising that this overcrowding would also increase local competition with other suspension-feeding taxa.

This would not necessarily have environmental management implications for hard clam farming since grow-outs do not usually remain in place for three years, and especially not for New Jersey where screens are removed each winter. However, if decreases in suspension feeders are causally linked with increased clam densities as they appear to be from this study, an increase in clam leasing acreage could contribute to an overall decrease in potential mitigation of suspended algae, leading to an increase in eutrophication in an estuary that already suffers from high nutrient loads and suspended seston. This is unlikely, however, as the increase in overall algae and seston removal by the clams themselves would more than compensate.

As wild stocks become more heavily depleted (Ricard et al. 2012), aquaculture's recent ascendancy over the global seafood market will continue to increase. As with terrestrial farming, the monoculture is the most efficient use of farming resources, but these economic and logistical gains can come at an ecological cost (e.g. Guo and Gifford 2002, Cardinale et al. 2006, Worm et al. 2006, Piotto 2008, McDaniel et al. 2014). Recent meta-analysis by Gamfeldt et al. (2014) suggests a connection between species richness and ecosystem functioning relevant to proponents of on-bottom shellfish aquaculture. Though more species-rich communities were found to have generally higher levels of functioning (higher productivity, higher consumption and similar levels of biogeochemical flux) than species-poor communities, the same species-rich assemblages had lower rates of productivity and consumption, and similar biogeochemical flux levels as compared to monocultures of the most ecologically beneficial member species (Gamfeldt et al. 2014). Though the work performed at Sedge in this study did not manipulate community structure directly, the block/control design did in effect create an aquatic effective monoculture in triplicate. Surprisingly, and defying the study's initial hypothesis, species richness did not differ between treatments. (This was also the case in a study by Beadman et al. of on-bottom *Mytilus edulis* aquaculture from 2004.) Regardless, given that the ecological functioning of *Mercenaria mercenaria* is well documented as essential to soft-bottom estuarine communities, the results from this study, in concert with the conclusions by Beadman et al. and Gamfeldt et al., effectively advocate for the effective monoculture that is infaunal hard-clam aquaculture.

Overall, non-target infaunal biodiversity within the screened clam treatment plots is lower than in either of the two control treatments, or in any of the perimeter samples. Mean Shannon-Weiner (H') inside screened clam treatment plots is 2.239 and the highest mean value across all treatments is 2.90 (screen control perimeter). H' values between 0.5-2.5 are common in estuarine and benthic invertebrate communities, so potential shifts of this magnitude are not minor. Evenness (J') and species richness are both components of the Shannon-Weiner index calculation, and though species richness did not change significant at all throughout the experimental period, shifts in Pielou's evenness are clearly visible in both screened treatments (Figure 2-4, 2-5). This shift in the screen controls is particularly interesting as no functional group or taxon differed significantly between screen control treatments. May sees a significant difference in evenness between the screen control and screened clam treatments that disappears for August and October, though it is not until October that the screen control is indistinguishable from the unscreened control. The volatility in this statistic, without the corresponding shifts in abundance data or species richness, is likely a result of background instability, small sample size, or the inherent patchiness in soft-sediment marine systems (Barry and Dayton 1991).

A study by Orth (1973) found that *Zostera marina* coverage was positively correlated with differences in sorting coefficient of as little as 0.5: areas with sorting coefficients of σ = 1.12 and 1.31 had higher *Z. marina* coverage, while areas with coefficients of σ = 0.63 and 0.74 had less *Z. marina*. Eelgrass shoot density and ambient *M. mercenaria* density and growth rate are positively correlated (Peterson 1982, Peterson et al. 1984) and have both been shown to slow wave action at the benthic boundary in a similar way (Wall et al. 2008), as have the protective screens (Virstein 1978) so it is unsurprising that higher abundances of *M. mercenaria* inside screened clam treatment plots would have a similar effect on sorting coefficient as was seen by Orth. However, this is still a difference in sorting coefficient of only 0.5, larger than the effect seen in this study. On a scale of 0-16, an increase of 0.156 over three years is small in proportion to the scale on which it is measured, and though statistically significant is not likely to have practical consequences.

Hurricane Sandy caused record flooding in the study area from 28-30 October 2012, three weeks after the plots in this study were installed. The hurricane, though downgraded to a tropical storm before reaching New Jersey, approached the coast at an angle that was “closer to perpendicular than any previous hurricane in the historic record” (Hall and Sobel 2013). This, combined with the full moon, contributed to the abnormally high water levels during the storm, as high as 3.5 meters above normal spring high tide in some locations (Blake et al. 2013). More than 305 mm of rain fell in New Jersey, with wind gusts to 60 knots, and reports of hurricane force winds in New Jersey in the latter half of the storm as verified by the National Hurricane Center (Blake et al. 2013). The storm resulted in two breaches of the barrier island at

Mantoloking, New Jersey, 28 km north of the Sedge Island site. During the five months immediately following the hurricane, winter storms caused anomalously high water levels several times (Aretxabaleta et al. 2014) but this was unrelated to the geomorphological changes caused by Hurricane Sandy (Aretxabaleta et al. 2014) as the breach was closed by November 4, 2012.

The destruction left by the storm prevented the ReClam the Bay team from accessing the site until May 2013 before the originally scheduled 2013 sampling dates. Sediments in shallow sandy and muddy habitats are frequently scoured and resuspended during strong storm events like Hurricane Sandy. Fortunately, all of the screens and plot markers were still in place after the storm, though a few of the tubular bags had become detached from the screened clam plot in Block 1, and one corner of that screen was drifting a few inches above the bottom. There was no substantial decrease in *M. mercenaria* abundance in subsequent benthic samples from that plot (effect=date, F(8)= 0.3885, p=0.9252) or as compared to other blocks (effect=block, F(2)=0.8819, p=0.4165) (Figure 2-16). We can therefore infer that there was no significant increase in predation in that plot as compared to the two other screened clam plots resulting from this breach in the predator screening.

Strong storm-related winds and wave-action can stochastically suspend and transport benthic sediments across large distances (Miles et al. 2015) as well as individual *Mercenaria mercenaria* (Prezant et al. 2010). Screening installed over hard-clam beds should in theory decrease the water velocity at the water-sediment boundary, mitigating the resuspension effect of both sediment and clams (e.g. McCall 1977, Virnstein 1978). In South Carolina, Coen et al. (2000) found that shear velocity of benthic boundary water was slowed by as much as 50% in areas between *M. mercenaria* cages and by as much as 90% within them. Sediments under cages were higher in silt and clay than sediments located even short distances away from cages (Coen et al. 2000), indicating that the caged areas trap a larger proportion of smaller (and lighter) particulate. Results from the current study on Sedge Island do not replicate any effect of this screening apparatus on mean particle size, and sediment samples from within the screened clam plots were only slightly greater in sorting coefficient from 2.13 to 2.29, a slight shift towards a more evenly sorted regime, with no differences in mean particle size between treatments. Non-impacted estuary sediments tended to remain within the σ = 0.5-2.5 range, so even in this altered state remains within the natural range. Given the lack of changes to mean sediment size predicted, the increased hard-clam densities inside the treatment plots appear to have sufficiently increased the overall mixing of the sediments without altering the grain size itself via increased bioturbation. Surprisingly, there were no treatment specific effects for any of the infaunal burrowing depth classes indicating any protective effect of the screening in either screened treatment. This may be due to the aforementioned high water levels associated with Hurricane Sandy. *M. mercenaria* abundance also did not spike in perimeter samples in this study's initial post-storm samples, so if the impact of the hurricane is indeed responsible for the lack of screen effect on particle size, the predator screening did at least prevent storm-caused relocation of *M. mercenaria* as described by Prezant et al. (2010).

The objective of this study was to evaluate any negative impacts that intensive hard clam aquacultural grow-outs might be having on local benthic communities, both from the cultivation-appropriate densities and the predation screening itself. And yet what is perhaps most conspicuous about the results revealed here is the lack of serious impact overall, and the lack of any significant impacts at even 1 meter's distance from the treatment plots. This is consistent with the one similar study on *M. mercenaria* culture (Luckenbach et al. 2016). Of the 39 response variables tested in that study on benthic invertebrates, finfish and other mobile taxa on hard clam aquaculture sites in NJ and VA, values for 26 variables did not differ between cultivated and uncultivated reference sites during any of the sampling seasons (Luckenbach et al. 2016). The suggestion in the literature (e.g. Whiteley and Bendell-Young 2007) that the predator screening would contribute to overall increases in biodiversity and species richness through increased diversity in larval settlement and subsequent changes to community structure is also not borne out by this study.

This study found limited negative impacts to benthic infaunal biodiversity associated with small-scale grow-out plots in New Jersey over a three-year period. Statistically significant decreases in biodiversity directly beneath hard clam aquacultural plots, as well as shifts in community structure and a slight shift towards a more evenly sorted sediment profile all disappeared within one meter of the plots. Still missing is information on longer-term redundant use of grow-out plots and possible changes that might occur in the much larger commercial plots. Also missing is information on larger-scale operations, particularly in the more extensive areas in which these commercial farms generally operate in New Jersey and in the mid-Atlantic region. An increase in maldanid polychaete density and decrease in mobile suspension feeders would require monitoring should leasing acreage vastly increase with future changes to New Jersey State aquacultural policies.

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TABLES

Table 2-1 Sediment granulometric data pooled for all sampling dates and all treatments. Mean particle size (min 162.6 µm – max 246 µm) remained within the fine sand category for the duration of the experiment in all treatments (125-250 µm, Wentworth 1922). Sorting coefficient was significantly higher inside screened clam treatment plots.

						Sand % (avg)							
Year		**Sample**	**Mean particle size µm**	**Sorting Coef.**	**Sorting Regime**	**Granule**	**Very Coarse**	**Coarse**	**Medium**	**Fine**	**Very Fine**	**Silt/Clay % (avg)**	**Total wgt. (g)**
2012	**Oct**	Control	167.8	1.977	Moderately Sorted	0.32	3.63	7.87	22.6	45.45	16.8	3.33	1008.35
		Screen Control	170.6	2.101	Poorly Sorted	0.32	4.96	7.72	23.05	45.06	15.87	3.00	1059.49
		Screened Clams	194.3	1.962	Moderately Sorted	0.77	5.44	8.98	23.62	42.79	15.27	3.13	1193.19
2013	**May**	Control	232.6	2.160	Poorly Sorted	1.18	4.62	13.57	26.97	38.93	11.88	2.86	1204.04
		Screen Control	188.4	1.935	Moderately sorted	0.93	5.46	4.96	21.44	48.26	15.04	3.90	1261.08
		Screened Clams	191.5	1.927	Moderately sorted	1.17	5.38	5.30	23.65	48.93	12.51	3.04	993.03
	Aug	Control	191.9	1.943	Moderately sorted	`3	4.99	5.36	21.14	51.40	11.58	3.19	958.06
		Screen Control	184.1	1.930	Moderately sorted	2.37	4.45	3.82	15.46	55.12	14.69	4.09	1072.66
		Screened Clams	192.9	1.945	Moderately sorted	1.08	6.84	5.82	19.98	51.63	11.55	3.10	881.89
	Oct	Control	226.9	2.254	Poorly sorted	2.45	8.79	6.71	16.44	48.64	13.70	3.26	774.30
		Screen Control	196.7	1.953	Moderately sorted	1.21	7.59	6.22	22.29	49.09	10.10	3.51	1325.75
		Screened Clams	233.3	2.280	Poorly sorted	2.17	10.94	5.21	17.74	48.54	12.28	3.12	934.97
2014	**May**	Control	164.7	2.110	Poorly sorted	1.20	5.22	4.84	13.62	51.48	16.36	4.58	879.48
		Screen Control	167.2	2.157	Poorly sorted	2.48	5.41	4.40	19.58	47.44	16.67	4.02	972.55
		Screened Clams	162.6	2.162	Poorly sorted	3.00	4.41	4.51	14.23	51.34	18.02	4.49	634.50
	Aug	Control	166.1	2.165	Poorly sorted	3.98	3.86	4.55	15.62	52.31	16.18	3.51	865.46
		Screen Control	190.7	1.927	Moderately sorted	1.61	4.45	5.72	23.06	48.53	13.28	3.36	1100.55
		Screened Clams	189.0	1.966	Moderately sorted	2.74	4.35	5.73	18.97	49.89	15.08	3.23	1637.66
	Oct	Control	189.3	1.948	Moderately sorted	2.15	4.83	5.87	17.53	52.79	13.55	3.27	730.27
		Screen Control	194.0	2.422	Poorly sorted	4.18	5.50	5.59	16.86	45.99	15.29	6.59	803.14
		Screened Clams	241.0	2.373	Poorly sorted	4.38	9.57	8.38	15.62	44.66	13.81	3.57	674.25
2015	**May**	Control	193.5	1.902	Moderately sorted	1.40	6.53	5.08	18.84	57.80	7.15	3.19	1087.34
		Screen Control	198.9	1.928	Moderately sorted	1.03	8.35	4.83	25.35	47.51	7.57	5.35	1247.58
		Screened Clams	224.8	2.131	Poorly sorted	3.15	7.54	5.43	20.51	54.58	6.50	2.30	1051.33
2015	**Aug**	Control	193.7	1.988	Moderately sorted	1.96	6.99	6.07	18.02	48.36	13.16	5.44	1038.44
		Screen Control	194.3	2.403	Poorly sorted	4.12	5.22	5.98	21.14	43.75	15.51	4.28	1344.62
		Screened Clams	199.6	2.524	Poorly sorted	4.53	4.93	8.65	17.60	40.66	17.22	6.41	699.58
	Oct	Control	226.6	2.239	Poorly sorted	2.45	8.23	7.07	18.16	47.51	13.35	3.23	1247.10
		Screen Control	231.4	2.314	Poorly sorted	2.97	8.75	6.86	14.99	43.76	14.53	8.14	1290.06
		Screened Clams	246.0	3.062	Poorly sorted	5.28	10.23	8.56	15.53	40.41	15.99	4.01	1063.20

Table 2-2 177 taxa were recorded in benthic samples between October 2012 and October 2015 across eight phyla.

PHYLUM	CLASS	FAMILY	TAXA
Bryozoa	Gymnolaemata	Electridae	2
		Membraniporidae	1
Nemertea	Anopla	Lineidae	1
Cnidaria	Anthozoa	Campanulariidae	2
		Diadumeidae	1
Arthropoda	Malacostraca (Amphipoda)	Caprellidae	5
		Gammariidae	32
	Malacostraca (Anomura)	Paguroidea	2
	Malacostraca (Brachyura)	Cancridae	2
		Carcinidae	1
		Panopeidae	4
		Pinnotheridae	2
		Portunidae	1
	Malacostraca (Caridea)	Crangonidae	1
		Hippolytidae	1
		Palaemonidae	3
	Malacostraca (Cumacea)	Diastylidae	2
	Malacostraca (Isopoda)	Anthuridae	1
		Idoteidae	3
	Malacostraca (Mysida)	Mysidae	1
	Ostracoda	Halocyprididae	1
		Other (unidentified)	1
	Pycnogonida	Phoxichilidiidae	1
Annelida	Polychaeta	Amnicolidae	1
		Capitellidae	4
		Cirratulidae	2
		Flabelligeridae	1
		Glyceridae	1
		Goniadidae	2
		Lumbrineridae	2
		Magelonidae	1
		Maldanidae	5
		Nephtidae	1
		Nereididae	4*
		Onuphidae	1
		Orbiniidae	2
		Oweniidae	1
		Pectinariidae	1

PHYLUM	CLASS	FAMILY	TAXA
Annelida	Polychaeta	Phyllodocidae	6
		Polynoidae	3
		Sabellidae	2*
		Serpulidae	3
		Spionidae	12
		Syllidae	6*
		Terebellidae	3
		Unknown	4
	Clitellata (Oligochaeta)		1
Mollusca	Bivalvia	Arcidae	1
		Astartidae	1
		Hiatellidae	1
		Lasaeidae	1
		Lyonsiidae	1
		Mactridae	2
		Myidae	1
		Mytilidae	2
		Nuculanidae	1
		Nuculidae	1
		Pharidae	1
		Pholadidae	1
		Semelidae	1
		Solecuritdae	1
		Solemyidae	1
		Tellinidae	1
		Veneridae	2
	Gastropoda	Acteonidae	1
		Calyptraeidae	3
		Cerithiidae	2
		Cerithiopsidae	1
		Columbellidae	1
		Hydrobiidae	1
		Nassariidae	2
		Pyramidellidae	2
		Tornatinidae	1
Echinodermata	Holothuroidea	Sclerodactylidae	1
		Synaptidae	1
Chordata	Ascidiacea	Styelidae	1

* One species unconfirmed, but identified confirmed to family level.

Table 2-3 Factorial MANOVA table for biodiversity measures. Significant results in bold, interesting but non-significant results underlined.

ANOVA Shannon-Weiner Index (H')					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	17	14.69906	0.864650	3.0786	< **0.0001**
Error	466	130.88191	0.280862		
C. Total	483	145.58096			
Effect Tests					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Treatment	5	5	11.384569	8.1069	**<0.0001**
Season	2	2	0.258436	0.4601	0.6315
Treatment * Season	10	10	2.942981	1.0478	0.5019
ANOVA Pielou's J' (Evenness)					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	17	3.551051	0.208885	8.4610	**<0.0001**
Error	466	11.504585	0.024688		
C. Total	483	15.055625			
Effect Tests					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Treatment	5	5	1.9670415	15.9352	**<0.0001**
Season	2	2	0.5564808	11.2703	**<0.0001**
Treatment * Season	10	10	0.65556000	2.6554	**0.0037**
ANOVA Species Richness					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	17	2274.331	133.784	1.6061	0.0587
Error	466	38816.669	83.298		
C. Total	483	41091.000			
Effect Tests					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Treatment	5	5	274.24507	0.6585	0.6552
Season	2	2	928.13593	5.5712	**0.0041**
Treatment * Season	10	10	625.31842	0.7507	0.6765

Table 2-4 ANOSIM *R* statistic pairwise comparisons for all treatments. All *R*-values for comparisons involving samples from inside clam plots are larger than any other treatment pairs.

	Clams Inside	Clams Perimeter	Screen Inside	Screen Perimeter	Control Inside
Clams Perimeter	**0.432**				
Screen Control Inside	**0.312**	**0.269**			
Screen Control Perimeter	**0.424**	NS	**0.173**		
Control Inside	**0.441**	NS	**0.183**	NS	
Control Perimeter	**0.386**	NS	**0.198**	NS	NS

Table 2-5 SIMPER dissimilarity pairwise comparisons for all treatments. Comparisons involving samples from inside screened clam treatment plots in bold.

		Dissimilarity
Control Inside	Control Outside	78.98
	Screen Control Inside	78.67
	Screen Control Perimeter	78.86
	Screened Clams Inside	**82.51**
	Screened Clams Perimeter	79.63
Control Perimeter	Screen Control Inside	77.69
	Screen Control Perimeter	77.53
	Screened Clams Inside	**81.84**
	Screened Clams Perimeter	78.32
Screen Control Inside	Screen Control Perimeter	78.27
	Screened Clams Inside	**77.33**
	Screened Clams Perimeter	78.84
Screen Control Perimeter	**Screened Clams Inside**	**82.26**
	Screened Clams Perimeter	78.37
Screened Clams Inside	**Screened Clams Perimeter**	**82.53**

Table 2-6 Percentage contributions (SIMPER analysis) for critical species for all treatments. Contributions from twenty or more taxa were required to meet the 90% threshold for cumulative SIMPER contribution in all treatments except inside screened clams, which only required 16 taxa to meet the threshold.

Control Inside (25 critical taxa)	**% ind. contribution**	**% cum. contribution**	**Control Perimeter (24 critical taxa)**	**% ind. contribution**	**% cum. contribution**
Tritia obsoleta	16.05	16.05	*Tritia obsoleta*	18.99	18.99
Ameritella agilis	11.86	27.9	*Ameritella agilis*	16.34	35.33
Clymenella torquata	8.35	36.26	*Scoloplos sp.*	9.9	45.23
Scoloplos sp.	8.28	44.54	*Capitella sp.*	6.15	51.38
Scoletoma fragilis	5.47	50.01	*Clymenella torquata*	5.19	56.57
Polydora cornuta	5.13	55.14			
Screen Control Inside (20 critical taxa)	**% ind. contribution**	**% cum. contribution**	**Screen Control Perimeter (23 critical taxa)**	**% ind. contribution**	**% cum. contribution**
Clymenella torquata	15.4	15.4	*Tritia obsoleta*	23.61	23.61
Ameritella agilis	13.7	29.09	*Ameritella agilis*	13.6	37.22
Scoloplos sp.	9.58	38.68	*Scoloplos sp.*	9.23	46.44
Lysianopsis alba	7.96	46.64	*Clymenella torquata*	7.1	53.55
Capitella sp.	7.19	53.82			
Solemya velum	7.13	60.96			
Prionospio heterobranchia	6.11	67.07			
Scoletoma fragilis	5.71	72.78			
Screened Clams Inside (16 critical taxa)	**% ind. contribution**	**% cum. contribution**	**Screened Clams Perimeter (24 critical taxa)**	**% ind. contribution**	**% cum. contribution**
Mercenaria mercenaria	34.84	34.84	*Tritia obsoleta*	17.89	17.89
Clymenella torquata	16.73	51.57	*Ameritella agilis*	17.09	34.98
Ameritella agilis	6.25	57.82	*Capitella sp.*	8.07	43.04
Scoletoma fragilis	6.06	63.88	*Scoloplos sp.*	6.13	49.17
Scoloplos sp.	5.24	69.12	*Scoletoma fragilis*	5.94	55.11
			Polydora cornuta	5.85	60.96

Table 2-7 Factorial ANOVA table for density of *Ameritella agilis*. Significant results in bold, interesting but non-significant results underlined.

ANOVA					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	17	1854240	109073	2.2594	**0.0029**
Error	466	22496276	48275		
C. Total	483	24350516			
Effect Tests					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Treatment	5	5	552648.7	2.2896	**0.0449**
Season	2	2	1356482.7	14.0495	**<0.0001**
Treatment * Season	10	10	472733.2	0.9792	0.4606

Table 2-8 All taxa with abundance of N≥100 between 2012-2015 were used in feeding and infaunal functional group analysis. When a species was known to use multiple feeding methods, it was placed in the category with which it is principally aligned to avoid pseudoreplication. Taxa in bold are the ten most dominant taxa.

Group	Taxa	N	1° feeding	Position
Gastropoda	*Acteocina canaliculata*	188	predator	Epifaunal
Polychaeta	*Alitta succinea*	222	omnivore	Medium (>5-20cm)
Amphipoda	*Ampelisca abdita*	184	deposit	Epifaunal
Amphipoda	*Ampelisca verrilli*	291	suspension	Epifaunal
Amphipoda	*Ampithoe longimana*	110	herbivore	Epifaunal
Amphipoda	*Ampithoe valida*	276	suspension	Epifaunal
Polychaeta	***Capitella* sp.**	**1636**	**deposit**	**Shallow (<5cm)**
Polychaeta	***Clymenella torquata***	**2230**	**deposit**	**Deep (>20cm)**
Gastropoda	*Crepidula convexa*	226	suspension	Epifaunal
Amphipoda	*Cymedusa compta*	225	herbivore	Epifaunal
Amphipoda	*Elasmopus levis*	382	omnivore	Epifaunal
Amphipoda	*Erichsonella filiformis*	217	suspension	Epifaunal
Amphipoda	*Ericthonius sp.*	109	omnivore	Epifaunal
Polychaeta	*Exogone naidina*	273	deposit	Medium (>5-20cm)
Amphipoda	*Gammarus mucronatus*	150	grazer	Epifaunal
Bivalvia	*Gemma gemma*	120	suspension	Shallow (<5cm)
Polychaeta	*Glycera dibranchiata*	207	predator	Medium (>5-20cm)
Polychaeta	*Glycinde solitaria*	143	predator	Deep (>20cm)
Polychaeta	*Heteromastus filiformis*	138	deposit	Deep (>20cm)
Amphipoda	*Lysianopsis alba*	404	herbivore	Epifaunal
Amphipoda	***Microdeutopus anomalus***	**626**	**suspension**	**Epifaunal**
Amphipoda	***Microdeutopus gryllotalpa***	**777**	**herbivore**	**Epifaunal**
Bivalvia	*Nucula proxima*	159	deposit	Deep (>20cm)
Polychaeta	***Polydora cornuta***	**862**	**suspension**	**Shallow (<5cm)**
Polychaeta	***Prionospio heterobranchia***	**629**	**deposit**	**Shallow (<5cm)**

Group	Taxa	N	1° feeding	Position
Polychaeta	*Prionospio pygmaeus*	283	deposit	Shallow (<5cm)
Decapoda	*Rhithropanopeus harrisii*	157	omnivore	Epifaunal
Polychaeta	***Scoletoma fragilis*	**595**	**predator**	**Shallow (<5cm)**
Polychaeta	*Scoloplos sp.*	505	deposit	Medium (>5-20cm)
Bivalvia	*Solemya velum*	252	commensal	Shallow (<5cm)
Polychaeta	*Spio setosa*	128	suspension	Shallow (<5cm)
Polychaeta	*Spiochaetopterus costarum*	151	suspension	Shallow (<5cm)
Polychaeta	***Streblospio benedicti*	**1521**	**deposit**	**Medium (>5-20cm)**
Bivalvia	***Ameritella agilis*	**1512**	**deposit**	**Shallow (<5cm)**
Gastropoda	***Tritia obsoleta*	**2191**	**deposit**	**Epifaunal**

Table 2-9 Eigenvector scores and loading values for dominant taxa principal component analysis. ANOVA analyses were NS, though PC2 showed an interesting trend at p=00.0661.

	Eigenvectors			**Loading Matrix**		
	PC1	**PC2**	**PC3**	**PC1**	**PC2**	**PC3**
Ameritella agilis	0.46863	-0.24781	-0.13789	0.77183	-0.34694	-0.16653
Tritia obsoleta	0.09322	0.61117	0.0264	0.15353	0.85563	0.03188
Streblospio benedicti	0.47887	-0.15114	-0.34013	0.7887	-0.21159	-0.41079
Capitella sp.	0.45357	0.30999	-0.12997	0.74703	0.43398	-0.15696
Microdeutopus anomalus	-0.11214	0.31614	-0.03195	-0.18469	0.44259	-0.03859
Microdeutopus gryllotalpa	-0.11243	0.05448	-0.47091	-0.18518	0.07627	-0.56873
Clymenella torquata	-0.10591	-0.3331	0.51144	-0.17443	-0.46634	0.61769
Scoletoma fragilis	0.42416	-0.16607	0.33574	0.69859	-0.2325	0.40549
Polydora cornuta	0.19624	0.44696	0.47382	0.32321	0.62573	0.57224
Prionospio heterobranchia	0.28598	-0.07005	0.16166	0.47101	-0.09807	0.19524

Table 2-10 ANOVA table for dominant taxa principal component 2 across treatments and months. Significant results in bold, interesting but non-significant results underlined.

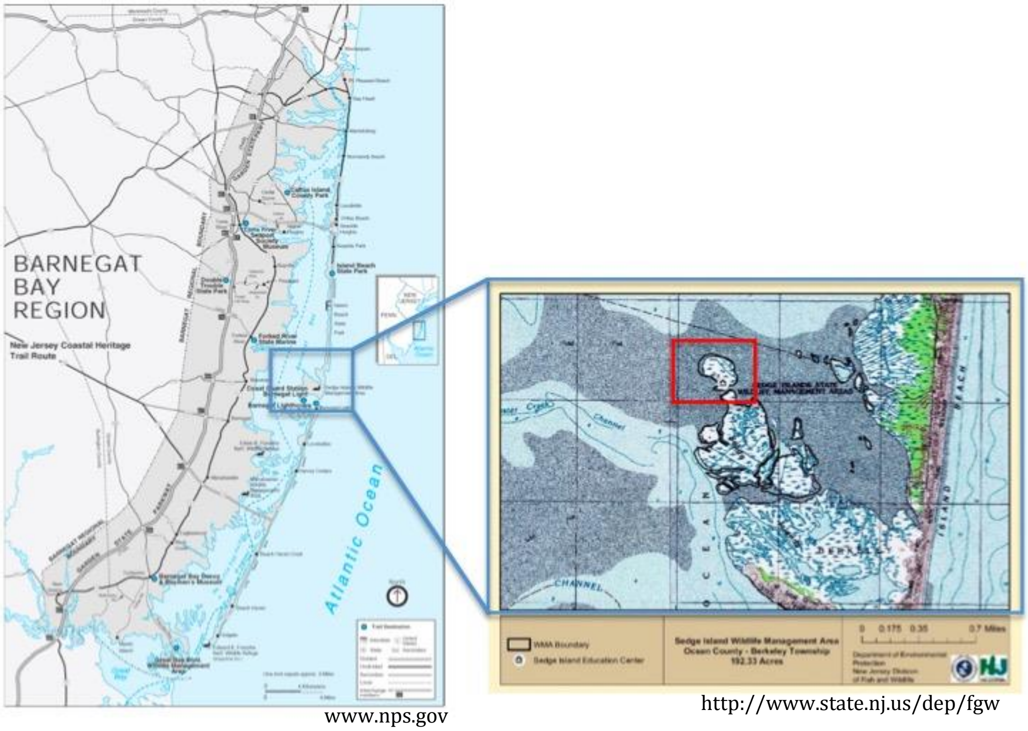
ANOVA					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	17	46.70953	2.7462	1.8117	0.0661
Error	36	54.59625	1.51656		
C. Total	53	101.30578			
Effect Tests					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Treatment	5	5	28.604399	3.7723	**0.0075**
Month	2	2	9.700464	3.1982	0.0527
Treatment * Month	10	10	8.404663	0.5542	0.8393

Table 2-11 ANOVA table for feeding functional group principal component 2 across treatments and months. Significant results in bold, interesting but non-significant results underlined.

ANOVA					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	17	39.192009	2.30541	2.4818	**0.0108**
Error	36	33.441506	0.92893		
C. Total	53	72.633515			
Effect Tests					
Source	**Nparm**	**DF**	**Sum of Squares**	**F Ratio**	**Prob > F**
Treatment	5	5	13.071496	2.8143	**0.0303**
Month	2	2	6.856069	3.6903	**0.0348**
Treatment * Month	10	10	19.264445	2.0738	0.0536

FIGURES

Figure 2-1 The Sedge Island Wildlife Management Area is located within the central portion of Barnegat Bay, just north of the Barnegat Inlet. Sedge Island is boxed in red. (39º 47’ 48”N, 74 º 07’ 07”W)



www.nps.gov

http://www.state.nj.us/dep/fgw

Figure 2-2 Photographs of the Sedge Island Cove. The photo on the left shows the full array of plots across the cove. The photo on the right shows the margins of one screen clearly marked with PVC poles. The poles behind show the outlines of an additional incomplete experimental block.

Figure 2-3 Diagram of individual treatment plots arranged within the larger experimental block. Individual sampling locations are marked in black. Block placement shown in image at bottom. Within plot samples were randomly placed, but were kept 1 meter from plot edges. Buffer zones shown in red dotted lines.

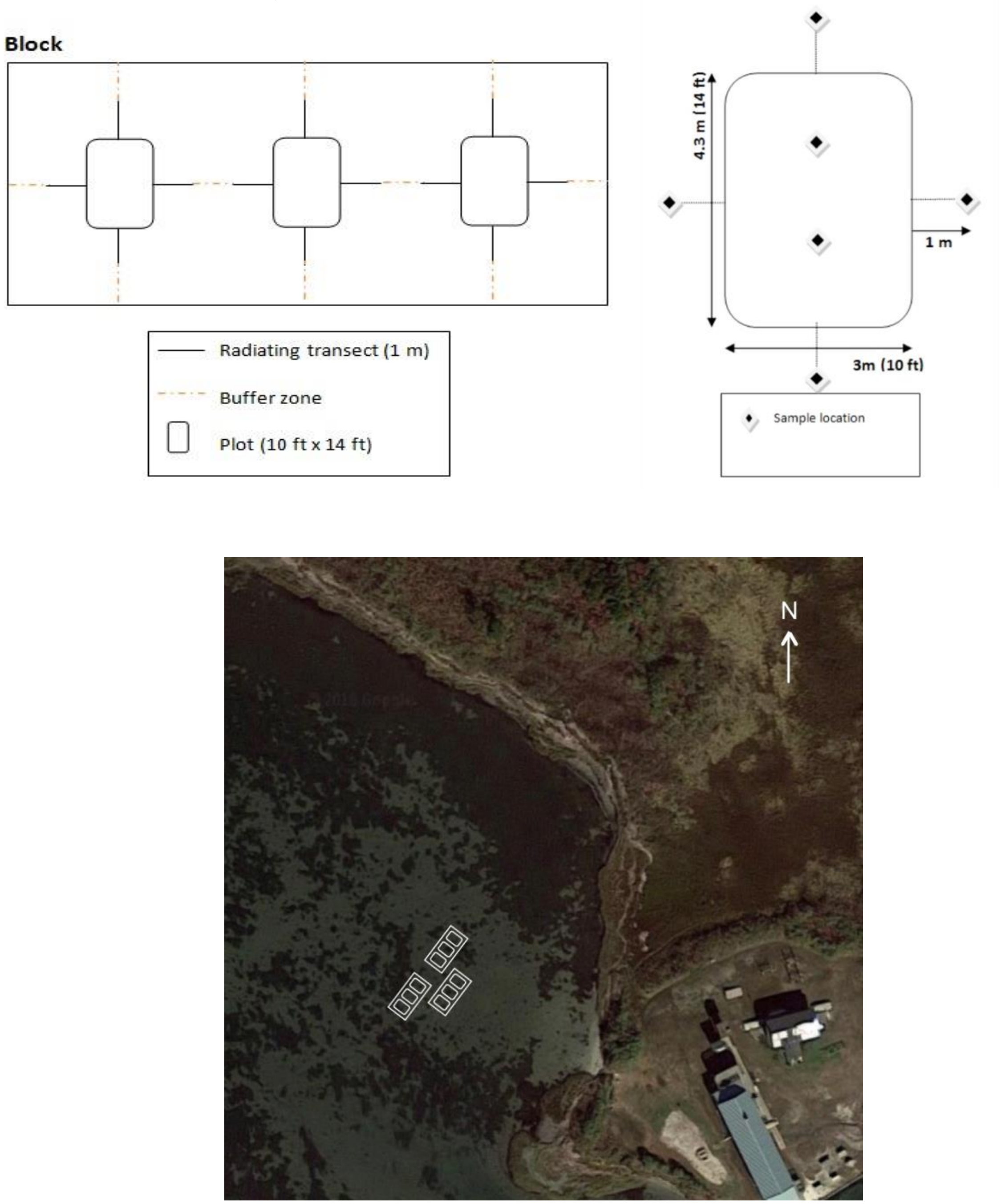


Figure 2-4 Mean Shannon-Weiner Index value (H') and Pielou's evenness (J') for all treatments. Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.) Samples from inside screened clam plots are statistically lower in both measures.

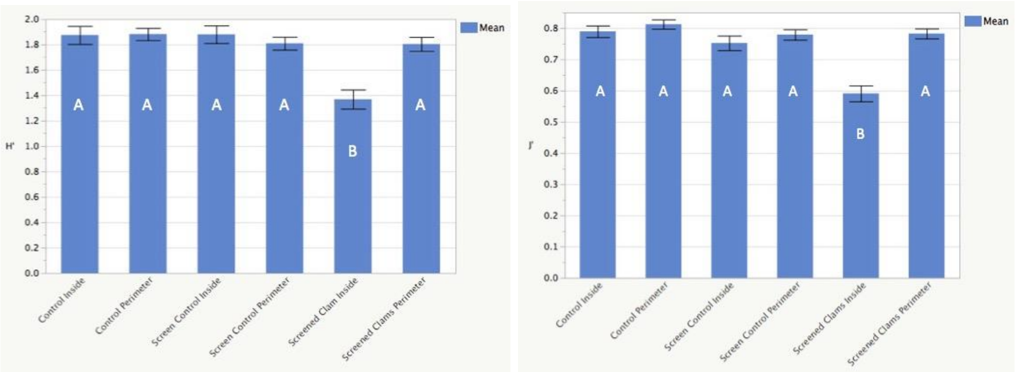


Figure 2-5 Treatment-specific Pielou's evenness (J') values interact significantly with season . Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.) The inside screen control samples straddle the difference between the clam plots and the controls/perimeter samples, while the inside clam plot samples are consistently grouped together. Controls from August and October are statistically different from clam plot samples, while inside screen control samples differ significantly only in May.

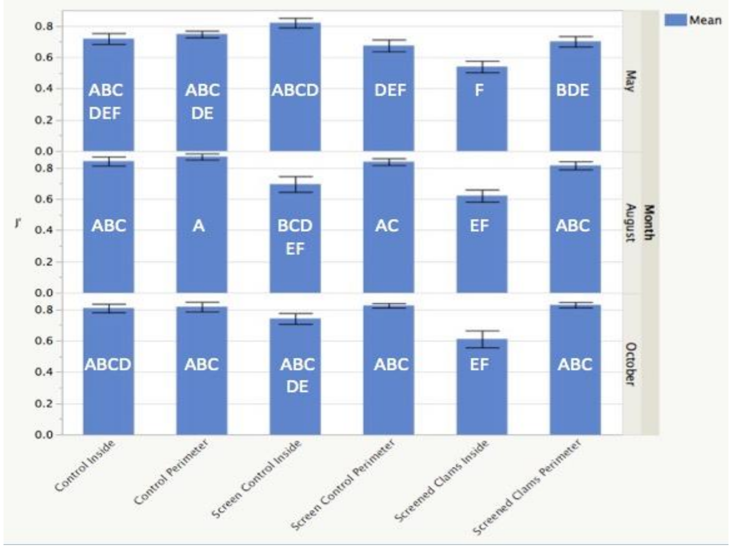


Figure 2-6 Non-parametric Multidimensional Scaling Plot of the six treatments based on benthic macroinvertebrate density data.

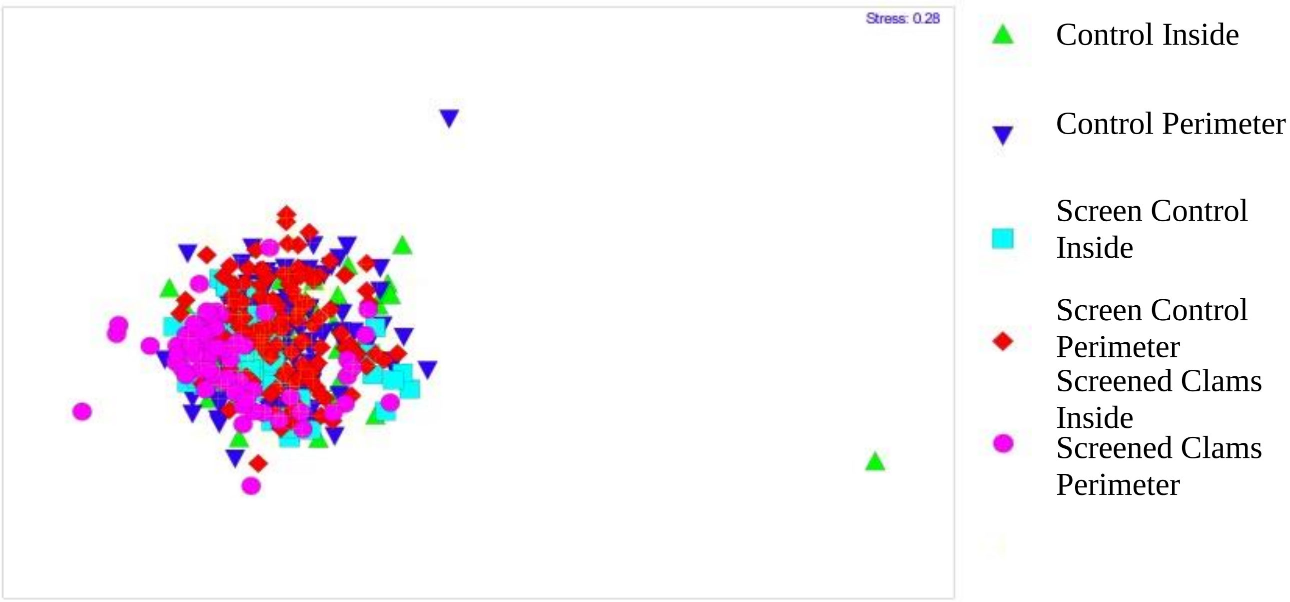


Figure 2-7 *Ameritella agilis* density across treatments. Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

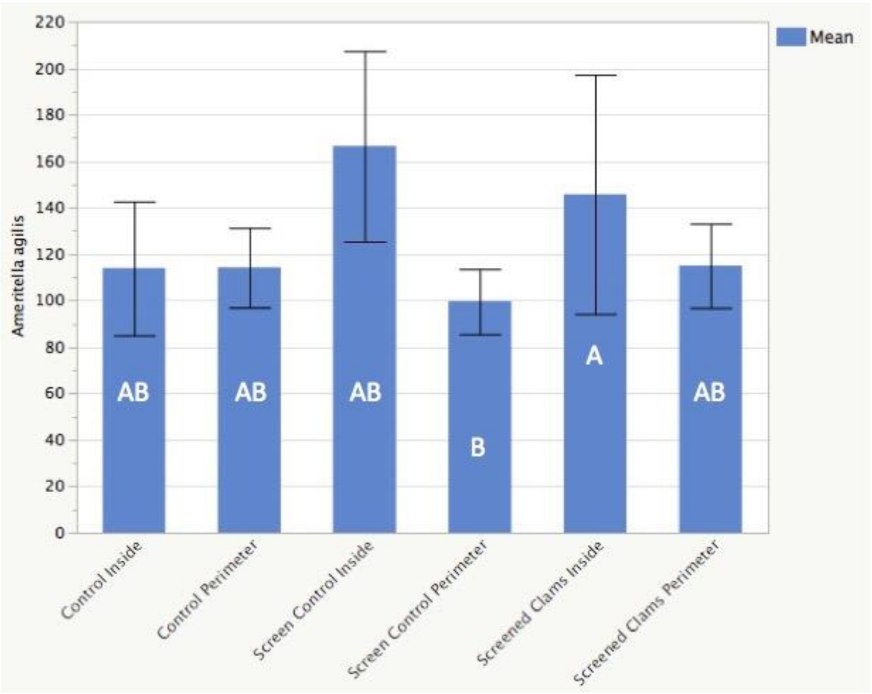


Figure 2-8 Plot showing the contribution of the ten dominant taxa variables into the three principal components.

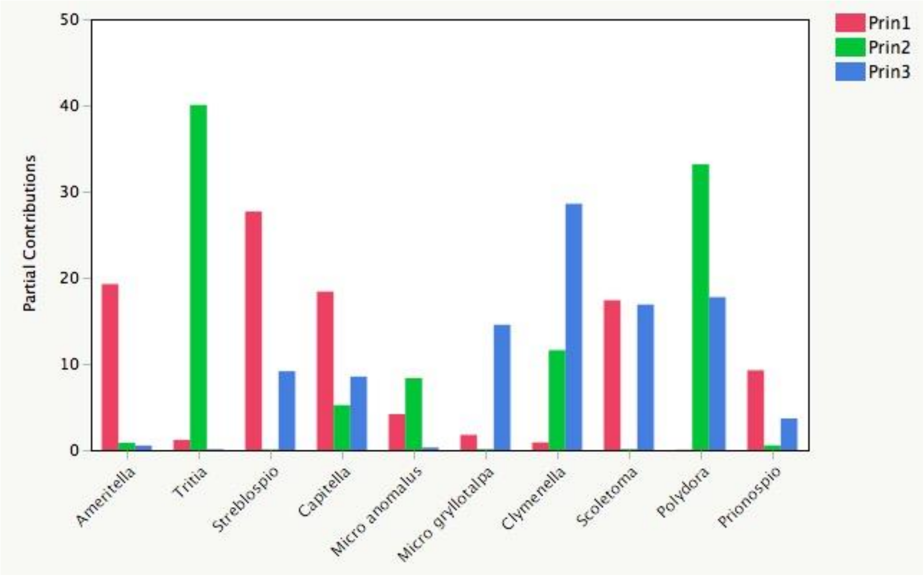


Figure 2-9 Tukey HSD *post hoc* comparisons of dominant taxa Principal Component 2 scores (least squared mean) between treatment sites. Levels not connected by the same letter are significantly different. PCs 1 and 2 together explain 43.9% of the data variability. (Error bars equal ±1 SE of the mean.)

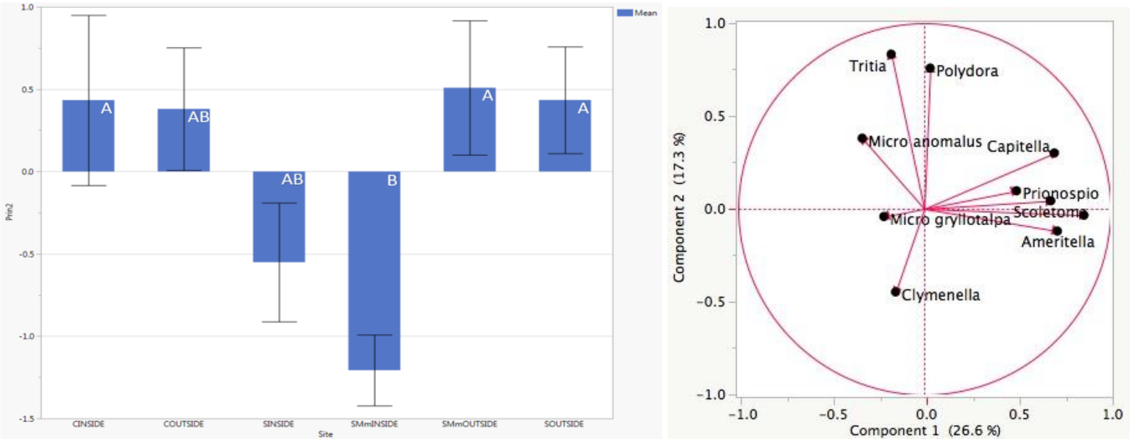


Figure 2-10 Plot showing the contribution of the five feeding group variables into the principal components.

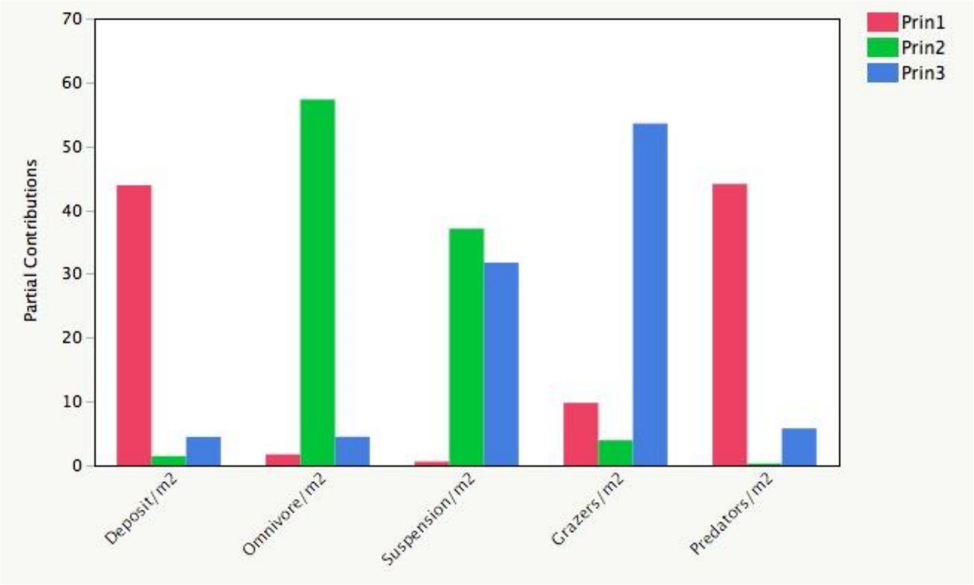


Figure 2-11 Tukey HSD *post hoc* comparisons of feeding group Principal Component 2 scores (least squared mean) between treatment sites. Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

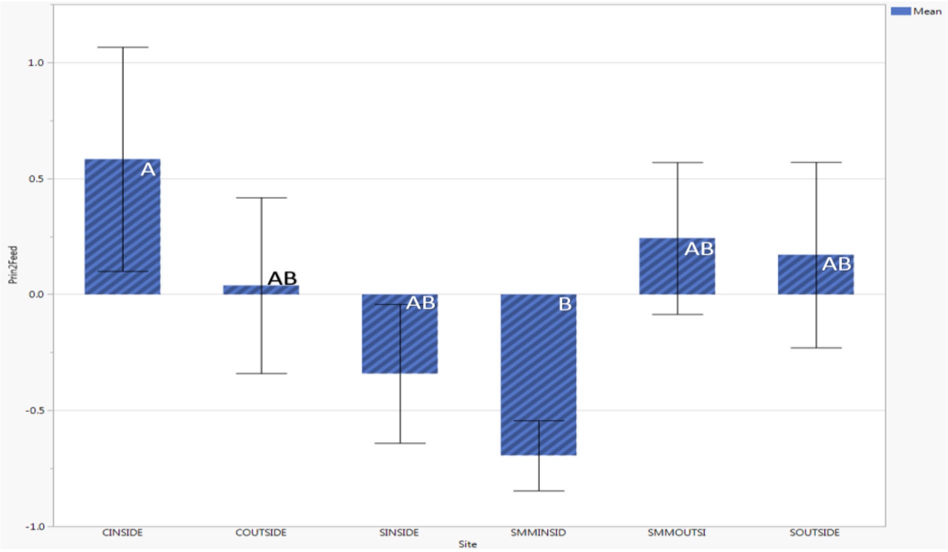


Figure 2-12 a&b Principal Components Vector plot for feeding group data. PCs 1-3 together explain 88.1% of the data variability. Figure 2-9a shows PC 1&2; Figure 2-9b shows PC 1 & 3.

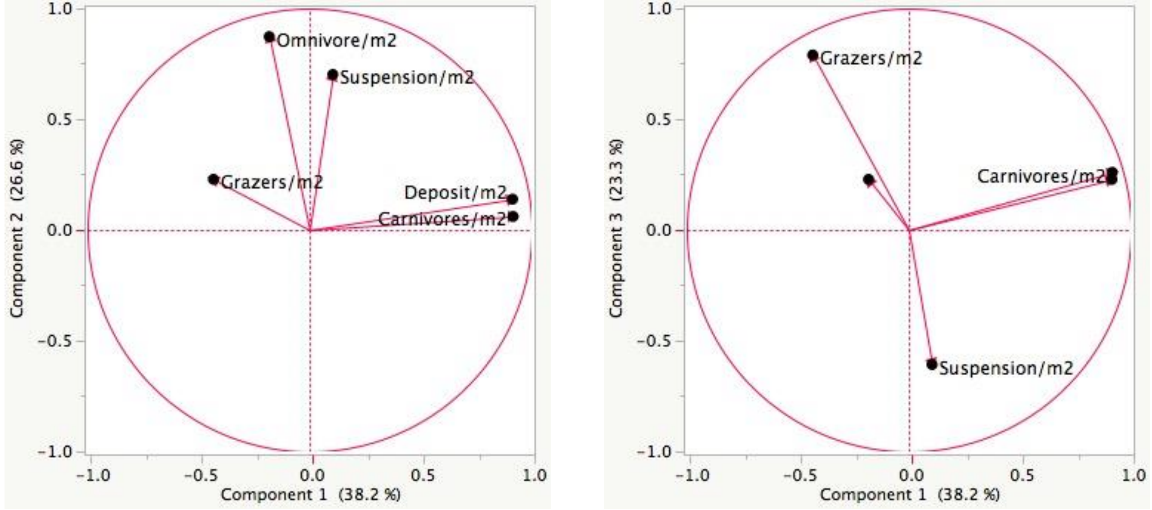


Figure 2-12a **Figure 2-12b**

Figure 2-13 Changes in density of *Clymenella torquata* with different treatments. Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

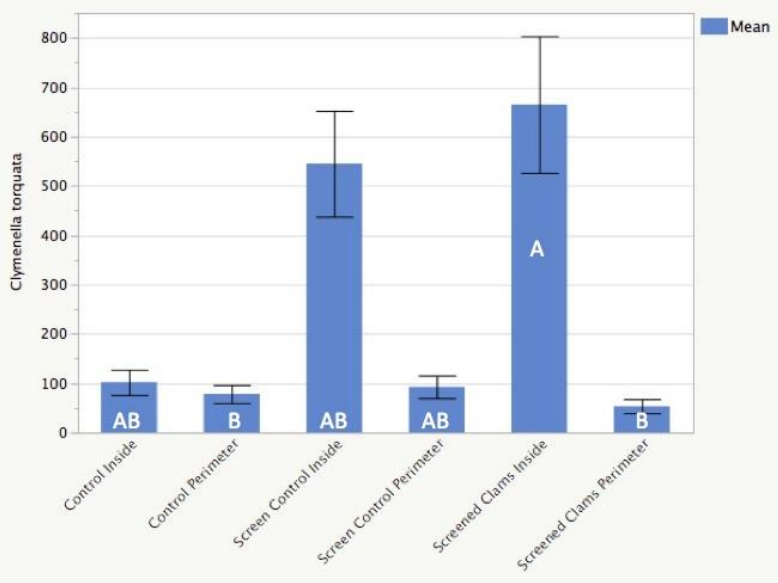


Figure 2-14 Planted *M. mercenaria* growth appears to tail off as of October 2014. Average length taken post-hoc from benthic samples. All clams in the sample were roughly divided into five size classes and sub-samples of 20 individuals (when available) were taken equally from the five groups. (August 2014 data was not available for this analysis.)

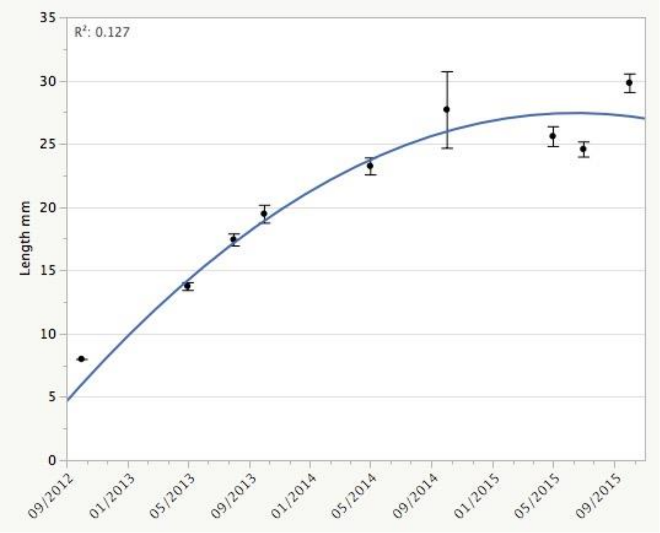


Figure 2-15a-c Growth curves of *M. mercenaria* published as cited. All three figures show growth rates continuing unchanged for at least four years.

Figure 2-15a
Ridgway et al. 2011

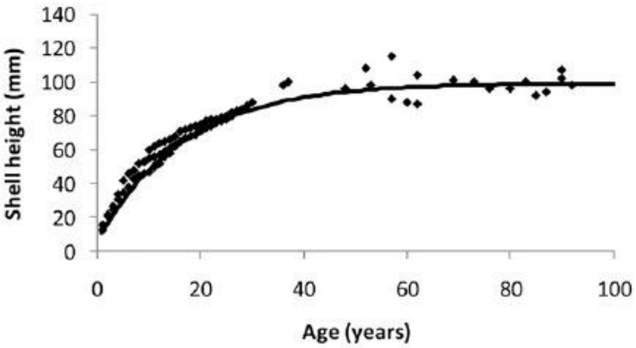


Figure 2-15b
Henry and Nixon 2008

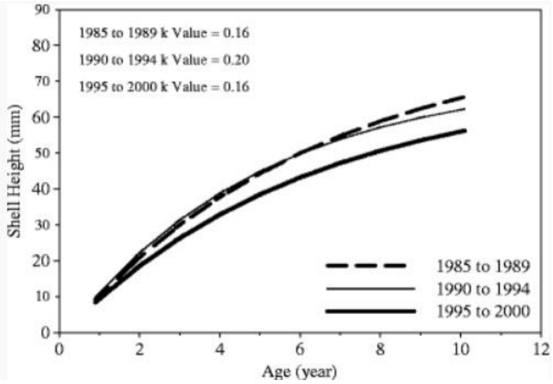


Figure 2-15c
Carmichael et al. 2004

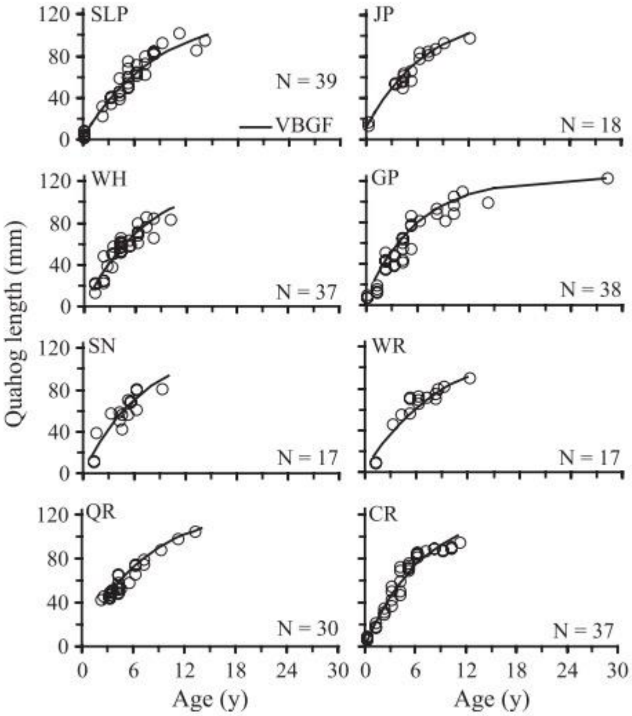
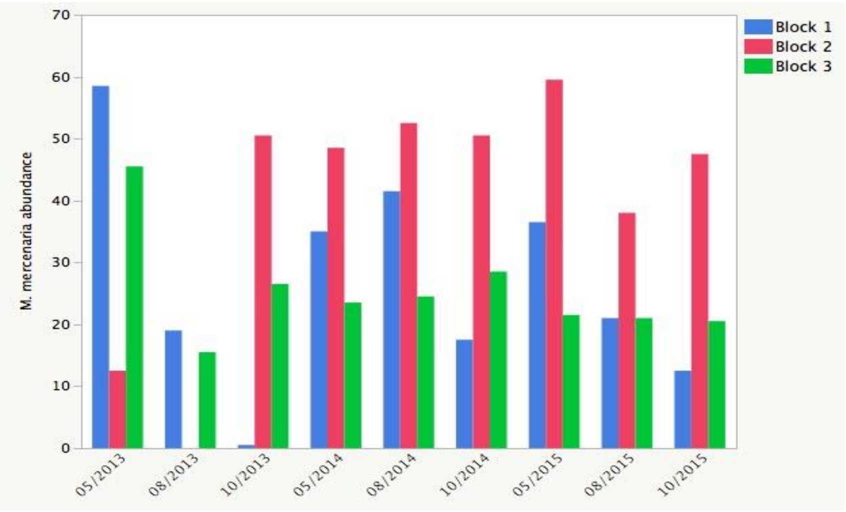


Figure 2-16 *M. mercenaria* abundance for all blocks across all sampling dates. The screened clam plot in block 1 was slightly lifted off the bottom on one corner by Hurricane Sandy, but predation doesn't seem to have increased compared to other blocks. *M. mercenaria* abundance was not significantly different between blocks or between sampling dates, and there was no interaction between date and block .



Chapter 3

Benthic Invertebrate Community Structure in Northern Barnegat Bay: Seasonal Variability in a Highly Impacted Coastal Lagoon

ABSTRACT

Barnegat Bay is a highly eutrophic lagoon with naturally poor connectivity with the Atlantic Ocean to the east. As part of a larger study of the effects of hard-clam aquaculture on benthic invertebrate communities, benthic invertebrate and sediment data were collected from control plots between 2012 and 2015. Seasonal peaks in May are clear for *Polydora cornuta* and *Tritia obsoleta*, as well as for suspension feeders and omnivores. All burrowing-depth guilds except deep-burrowing taxa also peak in May. Grazer density, and *Microdeutopus gryllotalpa* in particular, peak in October. Shannon-Weiner and species richness do not differ significantly by season, though evenness is higher in August than May, reflecting the peaks of certain species evening out during the summer. These trends suggest bottom-up controls of benthic invertebrate community structure in the Sedge Island area. Given the ongoing eutrophication trend in Barnegat Bay and the potential for increased aquaculture in the region, a community controlled by phytoplankton and seasonally available suspended food sources has the potential to be disrupted either by the overconsumption of available seston from increased aquaculture or increased phytoplankton from increased eutrophication. These data can serve as a baseline for environmental monitors given either of these scenarios.

INTRODUCTION

The Barnegat Bay-Little Egg Harbor Estuary (BB-LEH) is a shallow lagoon in central New Jersey (Figure 3-1) at naturally high risk of eutrophication from low freshwater inflow and poor connectivity with the Atlantic Ocean to the east. In concert with New Jersey's dense population and highly developed coastline, these natural limitations have inevitably led to water quality degradation. Kennish et al. (2001) summarized increased eutrophication signals through the 1990s and 2000s, including estimated inputs of total suspended solids to BB-LEH at 74 kg/yr, total nitrogen loads at 1.19 Gg/yr, and total phosphorous loads at 0.17 Gg/yr. The highest nitrogen levels and turbidity consistently occurred in the same region at issue in this dissertation. The same study recorded summertime phytoplankton production levels of 500g C/m^2/yr, exceeding levels in the Gulf of Mexico at Barataria Bay, LA and Apalachicola Bay, FL (Styles et al. 1999, from Kennish et al. 2001).

Harmful algal blooms, a long recognized product of eutrophication (Heisler et al. 2008), have also been well documented in BB-LEH. Blooms of *Aureococcus anophagefferens* (Hargraves and Sieburth) in the bay were reported in 1995, 1997, 1999, 2000, 2001 and 2002 (Barnegat Bay Partnership ((BBP). These events have likely continued, however the program monitoring for *A. anophagefferens* bloom events was ended in 2004 (BBP, 2018). Eutrophication is also clearly linked to decreased submerged aquatic vegetation (SAV) cover (Larkum et al. 2006, Ralph et al. 2007), which in turn is correlated with decreased ambient densities of *Mercenaria mercenaria* (L.) (Peterson 1982, Peterson et al. 1984, Kennish et al. 2011). Indeed, natural densities of *M. mercenaria* have been steadily declining in New Jersey since the early 20th century (McHugh 2001).

In October 2012, a series of experimental treatments were installed in the Sedge Island Wildlife Management Area to investigate the effects of hard clam aquaculture on local benthic invertebrate biodiversity and community structure. While results pertaining to the treatments have been discussed previously, the data can also provide specific insights into background seasonal distribution patterns, continuing in the tradition of early 20th century observational studies but on an ecosystem heavily influenced by 21st century anthropogenic impacts including eutrophication and aquaculture.

Recent reviews of the seasonal population dynamics of temperate suspension-feeders find patterns of increased activity and abundance during spring and summer and decreasing abundance in autumn and winter (Coma et al. 2000). Seasonal patterns in deposit-feeders are generally similar, with spring increases in growth and reproduction due to a late-winter/early-spring surge in detritus deposition (Marsh and Tenore 1990, Cheng et al. 1993, Levinton and Kelaher 2004) and increased availability of phytodetritus (Thompson and Nichols 1988, Marsh et al. 1989, Marsh and Tenore 1990). Higher temperatures, as would be seen in the shallower waters in Barnegat Bay, have been shown to interact with food supply and cause population crashes resulting from increased metabolic costs (Levinton and Stewart 1988, Cheng et al. 1993). This chapter will summarize the specific seasonal patterns contained within the dataset collected at Sedge Island between 2012-2015, as well as changes to benthic community structure during the full experimental timeline.

METHODS

The study site, off the southwestern edge of Sedge Island (Figure 2-1; 39º 47’ 48”N, 74 º 07’ 07”W) is a shallow cove enclosed on three sides, sparsely vegetated with *Zostera marina*

(Linné 1753) and edged primarily with *Spartina alterniflora* (Loisel-Deslongchamps, 1807). The cove is shallow, with a maximum depth of 2 m.

Three experimental blocks of 15 x 7m were marked out in early October 2012 within the Sedge Island Cove. All blocks were fully subtidal and located more than 15 m from the edge of the nearest marsh. Three plots measuring 3 m by 4.6 m were marked out within each block (Figure 2-2) and randomly assigned to one of three treatments: Control (untouched); Screen Control (Tenax® and PVC screen frame affixed to the sediment with rebar and shell bags); or Screened Clam (Tenax® and PVC screen frame installed over clam seed and affixed to the sediment with rebar and shell bags) (see Figure 2-2). A three-meter buffer was left between each plot.

Benthic invertebrate communities were sampled with an Ekman grab (3.5L) three times per year, in May, August and October. In each plot, two benthic samples were randomly located within the plot itself (but at least 1 meter from the edge to minimize edge effects) and one sample was located 1 meter from the plot in each cardinal direction (Figure 2-2). The perimeter samples were taken before any within-plot samples so as to prevent any disturbance to sampling area. Benthic samples were sieved on site at 1mm, and preserved in 70% ethanol for later identification.

Three sediment cores (PVC corer, 3.8cm dia., 10 cm depth) were taken from inside each of the nine plots on each sampling date. Sediment samples were bagged and kept at 0˚C until processed, at which time they were dried at 80 °C and separated with stacked sieves into >2mm, 1-2mm, 0.5–1mm, 0.25–0.5mm, 0.125– 0.25mm, and 0.063–0.125mm fractions for 7 min on a shaker table before weighing. (These fractions are defined as “granule”, “very coarse sand”, “coarse sand”, “medium sand”, “fine sand”, “very fine sand” and “silt/clay” according to Wentworth (1922)).

This study design was intended to isolate and quantify the effects of aquacultural hard clam densities and the predator screening apparatus on macrobenthic community structure and biodiversity, results that were discussed in Chapter 2. Additional results from the study regarding seasonality and background trends will be discussed here concerning the data collected from the control plots only.

Statistical Methodology

Sediment data from control samples were analyzed using GRADISTAT v4.0, a statistical program designed for sedimentary analysis by Blott and Pye (2001) that calculates mean grain size and sorting coefficient, and classifies them according to Folk and Ward (1957): very well sorted ($\sigma < 1.27$); well sorted ($\sigma = 1.27$-1.41); moderately well sorted ($\sigma = 1.41$-1.62); moderately sorted ($\sigma = 1.62$-2.00); poorly sorted ($\sigma = 2.00$-4.00); very poorly sorted ($\sigma = 4.00$-16.00); and extremely poorly sorted ($\sigma > 16.00$). Sediment fractions remaining in the pan after sieving (<0.063mm) were not included in the analysis as prescribed by Blott and Pye (2000) but were accounted for in percent data. Sediment data and biodiversity measures (Shannon-Wiener Index (H’), Pielou’s Evenness (J’) and species richness (Smith and Wilson 1996)) were analyzed with MANOVA using season as the independent variable with blocks ungrouped.

Untransformed density data for all taxa of sample size ≥ 100 were also grouped by feeding type and by maximum burrowing depth (infaunal position). The control plot densities of these functional groups were converted with Principal Component Analysis (PCA). The resulting scores were analyzed with ANOVA and Tukey HSD *post hoc* procedures, again using season as the independent variable. Densities of the ten most dominant taxa from the three control plots were also analyzed individually using this same PCA plus ANOVA technique. Non-parametric correlation analyses (Spearman’s ρ) were also conducted on dominant taxa and functional group densities. All statistical analyses were performed in JMP Pro v. 13.2 (SAS Institute, Cary, North Carolina).

RESULTS

Sediment

In the control plots as in the greater experimental sediment data, mean sediment size distribution and sorting coefficient remained reasonably constant through the duration of the study (Table 2-1). There are eight outlier samples containing larger pieces of shell (Figure 3-1). Mean sediment size within the control plots ranged between 123.4 µm – 868.2 µm, while sorting coefficient ranged from σ = 1.54 – 3.993, with an average of σ = 2.138 ± SE 0.046 (summary statistics calculated in GRADISTAT, Blott and Pye (2000)). MANOVA did not indicate any significant effects of season on control plot sediment data.

Biodiversity

MANOVA was run on Shannon-Weiner (H’) index values, Pielou’s Evenness (J’) values, and species richness on control plot data with season as the independent variable. Results were interesting if non-significant for Shannon-Weiner Index (F(2,176)=2.7326, p=0.0678). Species richness was not significant (F(2,176)=2.1727, p=0.1169), but evenness (Pielou’s J’) was significantly different among seasons (F(2,176)=4.6921, p=o.0103, Table 3-1). Given that both evenness and richness are components of the biodiversity index, the lack of significance in the Shannon-Weiner results at α = 0.05 likely reflects this split in significance amongst the constituent factors. Tukey HSD analysis of mean H’ values did not have sufficient statistical power to significantly differentiate between seasons, however *post hoc* analysis of J’ indicated that May had significantly lower J’ value than August (Figure 3-2).

Dominant Taxa

PCA was conducted on the ten most dominant taxa (by relative abundance) (Table 2-5). The choice to include only the ten most abundant taxa was arbitrary and pre-hoc, to permit sufficient statistical power to examine patterns among the most common animals in the study plots. Density data for these taxa from all control samples were converted into three linearly uncorrelated components with eigenvalues greater than 1.0. (The remaining components (PC4-PC10) had eigenvalues below 1.0 and were not used in analysis.)

Principal component 1 (Eigenvalue 3.0817, with positive scores driven primarily by the abundances of *Streblospio benedicti* (Webster, 1879) and *Prionospio heterobranchia* (Reish, 1959)) explained 30.82% of the variance. The second (PC2, Eigenvalue 1.5367) explained 15.37% of the variance, with positive scores primarily driven by abundances of *Polydora cornuta* (Bosc, 1802) and *Tritia obsoleta* (Say, 1822). The third component (PC3, Eigenvalue 1.3487, negative scores driven by *Microdeutopus gryllotalpa* abundance) explained an additional 13.5% of the variance (Figure 3-3).

ANOVA did not indicate any significant effects of season on PC1, but there were significant effects of season on PC2 (F(2,55)=6.8004, p=0.0023) and PC3 scores (F(2,55)=5.2745, p=0.0080) (Table 3-2). Tukey HSD *post hoc* analysis indicates that May had significantly higher PC2 scores than August or October, likely related to high *Polydora cornuta* and *Tritia obsoleta* densities (Figure 3-4). *Post hoc* analysis also indicates that PC3 scores in

October are significantly lower than May or August. This is likely associated with high sample densities of *Microdeutopus gryllotalpa* (Costa, 1853) (Figure 3-5), but may also be linked with a spike in *M. gryllotalpa* in October 2014 (Figure 3-6).

Several taxa were significantly correlated and are bolded in the correlation table (Table 3-3). *Streblospio benedicti* and *Ameritella agilis* (Stimpson, 1857) are significantly positively correlated (ρ = 0.3605, p = 0.0054), as are *S. benedicti* and *Capitella* spp. (Blainville, 1828) (ρ = 0.4363, p = 0.0006), *S. benedicti* and *Scoletoma fragilis* (O.F. Müller, 1776) (ρ = 0.3380, p = 0.0095) and *S. benedicti* and *Prionospio heterobranchia* (ρ = 0.6417, p < 0.0001). *S. benedicti* is only significantly negatively correlated with one taxa, *Microdeutopus gryllotalpa* (ρ = -0.3126, p = 0.0169). *A. agilis* is also significantly correlated with *S. fragilis* (ρ = 0.2693, p = 0.0409) and *P. heterobranchia* (ρ = 0.4632, p = 0.0003) both positive correlations. The other significant correlations involving *Capitella* spp. are mixed: in addition to the aforementioned positive correlation with *S. benedicti*, *Capitella* spp. are positively correlated with *Polydora cornuta* (ρ = 0.2659, p = 0.0436) and *P. heterobranchia* (ρ = 0.3670, p = 0.0046) and negatively correlated with *Clymenella torquata* (ρ = -0.3681, p = 0.0045).

Tritia obsoleta is significantly positively correlated with two taxa, *Microdeutopus anomalus* (Rathke, 1843) (ρ = 0.2615, p = 0.0474) and *Polydora cornuta* (ρ = 0.2905, p = 0.0269). *M. anomalus*, in addition to *T. obsoleta*, is positively correlated with *P. cornuta* (ρ = 0.3278, p = 0.0120) and negatively correlated with *Prionospio heterobranchia* (ρ = -0.3036, p = 0.0205). *Microdeutopus gryllotalpa* is significantly negatively correlated with several species, including *S. benedicti* as mentioned above, *Ameritella agilis* (ρ = -0.4984, p < 0.0001), *Clymenella torquata* (ρ = -0.4203, p = 0.0010), *Scoletoma fragilis* (ρ = -0.3169, p = 0.0154) and

P. heterobranchia (ρ = -0.3005, p = 0.0219). *P. heterobranchia* is also significantly positively correlated with *S. fragilis* (ρ = 0.2744, p = 0.0371).

Functional Groups

All taxa meeting a minimum abundance of N>100 in the larger study were classified by feeding functional group and by maximum burrowing depth (infaunal position). (As mentioned previously, only density data from control plots were analyzed for this chapter though the taxa were chosen based on abundances from the larger experiment.) The number of taxa in each functional group was uneven (Suspension N=10, Deposit N=12, Grazers N=5, Omnivores N=4, Predators N=4; commensal N=1, not included in the analysis.) (Table 2-8) When a species was known to use multiple feeding methods, it was placed in the category with which it is principally aligned in order to avoid pseudoreplication.

A principal component analysis of feeding group densities produced three components that collectively explained over 80% of the variance in the dataset. The first (PC1, Eigenvalue 1.6624) explained 33.25% of the variance. Positive PC1 scores were driven primarily by omnivore density and suspension feeder density, and, to a lesser extent, deposit feeder density. The second (PC2, Eigenvalue 1.4803) explained 29.6% of the variance. Positive PC2 scores were influenced by omnivore, suspension feeder and grazer density, but not dominated by the influence of any one group. The third (PC3, Eigenvalue 0.8855) explained 17.7% of the variance. Positive PC3 scores were also influenced by grazer density, with a secondary influence of predator density (Figure 3-7).

There was a significant main effect of season on PC1 score (F(2,57)=11.4044, p<0.0001) and on PC3 score (F(2,57)=7.7637, p=0.0010) (Table 3-4). Tukey HSD *post hoc* analysis indicates that samples from May have significantly higher PC1 scores than either August or October (Figure 3-8) likely associated with higher densities of suspension feeders or omnivorous taxa. It also indicates that October samples have significantly higher PC3 scores than August samples (Figure 3-9), associated with higher grazer densities. Results of ANOVA on PC2 scores were not significant (F(2,57)=.1432, p=.8669).

Significant feeding group correlations are bolded in the correlation table (Table 3-5). Suspension feeder density and omnivore density are strongly and significantly positively correlated ($\rho = 0.6599$, $p < 0.0001$) as are predator and deposit feeder density ($\rho = 0.2648$, $p = 0.0409$). Predator and grazer density are significantly negatively correlated ($\rho = -0.2589$, $p = 0.0458$), as are deposit feeder and grazer density ($\rho = -0.3932$, $p = 0.0019$).

Similar analyses were also conducted on the same taxa (minimum overall abundance N>100) grouped by burrowing depth (infaunal position). Groups were again unevenly distributed amongst epifaunal taxa (N=16), shallow-burrowers (max depth <5cm, N=10), medium-burrowers (max depth 5-15cm, N=5), and deep-burrowers (max depth >15cm, N=4) (Table 2-8). Principal components analysis produced two components with eigenvalues greater than or approaching 1.0. The first (PC1, Eigenvalue 2.0059) explained 50.15% of the variance. Positive scores were driven by shallow- and medium-burrowing taxa densities. The second (PC2, Eigenvalue 0.9040) explained an additional 22.599%, for a cumulative total of 72.746% of variance explained. Positive scores were driven primarily by epifaunal density (Figure 3-10).

There were significant main effects of season on PC1 scores (F(2,57)=4.9594, p<0.0103) and on PC2 scores (F(2,57)=4.5557, p=0.0146) (Table 3-6). *Post hoc* analysis indicates that May samples have significantly higher PC1 scores than August, likely driven by higher densities of shallow and medium burrowing taxa (Figure 3-11) and also higher PC2 scores than either August or October, likely associated with increased epifaunal densities (Figure 3-12**)**.

Aquacultural Plot Comparison

As a comparison point to the background control dataset, MANOVA was run on Shannon-Weiner (H') index values, Pielou's Evenness (J') values, and species richness on clam plot data, again with season as the independent variable. As in the dataset from the control plots, Shannon-Weiner Index value (H') was not significant (F(2,176)=1.4874, p=0.2288) while Pielou's evenness (J') was significant (F(2,176)=7.1010, p=0.0011) with the same specific seasonal pattern (lowest in May, Figure 3-13a) seen in J'. Species richness, however, was significantly different between months (F(2,176)=6.7856, p=0.0014), a different result from that of the control dataset. Tukey HSD *post hoc* analysis identifies species richness in clam plots as higher in May than August (Figure 3-13b).

PCA was conducted on the ten most dominant taxa (by relative abundance) for the clam plot data (Table 2-5). Density data for these taxa from all clam plot samples were converted into four linearly uncorrelated components with eigenvalues greater than 1.0. (The remaining components (PC5-PC10) had eigenvalues below 1.0 and were not used in analysis.) Principal component 1 (Eigenvalue 2.0773) explained 20.77% of the variance. Positive scores were driven primarily by the abundances of *Streblospio benedicti*, *Prionospio heterobranchia,* just as in the control dataset, with the addition of *Capitella* sp. The second (PC2, Eigenvalue 1.4700) explained 14.70% of the variance. As with the control data, positive scores were driven by abundances of *Polydora cornuta* and *Tritia obsoleta.* The third component (PC3, Eigenvalue 1.1748) explained an additional 11.75% of the variance, with negative scores driven by

Microdeutopus gryllotalpa abundance just as with the control plot data, and the fourth (PC4, Eigenvalue 1.0344, positive scores driven by *Ameritella agilis and Microdeutopus anomalus* density) explained an additional 10.34% of the variance (Figure 3-14).

Factorial MANOVA indicated significant effects of season on all four principal components (Table 3-7). The results from PC2 and PC3 indicate patterns identical to those detailed in the control plots, specifically increased *P. cornuta* and *T. obsoleta* density in May as compared to August (as inferred from significantly higher PC2 scores in May) and higher *M. gryllotalpa* density in October (as inferred from significantly lower PC3 scores during May). Seasonal patterns specific to the aquacultural plots are indicated by statistically significant ANOVA results from PC1 (F(2,176)=6.1373, p=0.0027) and PC4 (F(2,176)=10.2885, p<0.0001). Tukey HSD *post hoc* analysis indicates that May and October had significantly higher PC1 scores than August, indicating higher densities of *Polydora cornuta, Tritia obsoleta* and *Capitella* sp. While the first two species were also higher in control plots, *Capitella* sp. is not statistically higher in control plots. *Post hoc* analysis also identifies PC4 scores in May as significantly higher than scores in August or October, which suggests higher densities of both *Ameritella agilis* and *M. anomalus* (Figure 3-15) during the spring. This supports results previously discussed in Chapter 2, in which *A. agilis* was found to have significantly higher densities inside aquacultural plots with a statistically significant main effect of season, but no interaction effect.

DISCUSSION

In marine systems, near-surface phytoplankton is the primary food for suspension-feeding organisms (Cloern et al. 2002), however in estuarine systems this link is more complex. Additional food sources, including riverine particulate organic matter (RPOM), microphytobenthos (benthic phytoplankton, diatoms), macroalgal detritus, and bacteria contribute to this first consumptive linkage (Langdon and Newell 1990, Kang et al. 1999, Herman et al. 2000, Riera 2007, Lefebvre et al. 2009). Though these foods are primarily consumed by deposit-feeders, omnivores, and detritivores, many suspension-feeders have also adapted to the seasonal availability of these additional food sources by modifying their feeding modes to include these foods when available. The overlapping consumption of these food resources helps to explain the positive correlation between omnivore and suspension-feeding taxa (Table 3-5). Numerous studies have, however, shown repeatedly that phytoplankton constitutes the bulk of the diets of coastal benthic invertebrates even with these additional seasonally available food sources (Kaehler et al. 2000, Yokoyama et al. 2005).

While always available to deposit-feeders, macroalgal detritus, microphytobenthos and benthic bacteria are likely to be more available to suspension-feeders during months of higher turbidity and resuspension activity. In estuaries this generally translates to spring (or other periods of seasonally heavy rainfall). As growth, reproduction and development are all highly dependent on food supply (Kang et al. 2006), and as food supply in estuaries is strongly tied to inputs that are themselves seasonally variable, it is unsurprising that this seasonal volatility would be reflected in community structure. Though overall biodiversity indices may not have shown seasonal patterns in this particular study, changes in species richness and densities of the highly abundant *Polydora cornuta* (shallow-burrowing suspension-feeder) and *Tritia obsoleta* (epifaunal detritivore and deposit-feeder) hint at a natural background volatility. This is also true for densities of epifaunal taxa and classes burrowing to less than 20 cm in depth (i.e. those taxa with better access to these additional food sources). It is likely that the seasonal availability of RPOM and other food sources helps to explain the positive correlations between omnivores and suspension feeders and between predators and deposit feeders. The increased turbidity during spring would create an influx of additional food resources previously unavailable to both groups, while predators and deposit feeders would be equally unaffected.

Macroalgal detritus makes up a particularly small part of bivalve diets in estuarine systems, (Wiedemeyer and Schwamborn 1996). Lefebvre et al. (2009) contend this is largely due to the bivalve's ability to selectively sort food before ingestion, adding that suspension- and deposit-feeding polychaetes source more carbon from macroalgae and microphytobenthos than suspension feeders in general. If food availability is primarily responsible for these seasonal patterns, a stronger seasonal signal would be expected for deposit-feeding and suspension-feeding polychaetes than with bivalves or other suspension-feeders. In the control data there is a strong seasonal signal of an effect on a suspension-feeding polychaete (*Polydora cornuta*), however there is a shift in suspension-feeders in general as well, providing initial support for bottom-up control. Unsurprisingly, given that the aquacultural plots are covered with screening designed to limit predation, the trends seen in the aquacultural dataset also suggest bottom-up controls. The aforementioned effect on *P. cornuta* is also seen in the aquacultural plots, as is a seasonal effect of *Microdeutopus anomalus* density, a suspension-feeding benthic amphipod. (Clam plots were also statistically higher in suspension-feeders than control treatments overall, for more see Chapter 2.)

Trophic control, long under investigation, has proved difficult to directly quantify (Boyce et al. 2015.) One indirect method that has emerged depends on correlations between trophic groups. Strong negative correlations imply top-down control, while strong positive correlations imply bottom-up control, as both groups are likely responding to the same productivity-related stimuli (Boyce et al. 2015). The functional group correlations from Sedge Island are split, not particular strong, and are likely based on too little data to draw conclusions from. Drilling down to individually dominant taxa, the only documented predator involved in statistically significant correlations is *Scoletoma fragilis*, which has been shown to consume small polychaetes and benthic amphipods, (as well as detritus, copepods and nematodes (Valderhaug 1985)). *S. benedicti*, maximum length 20 mm but often only growing to 6mm, (Gosner 1978, Bridges and Heppel 1996)) and *P. heterobranchia* (also small at 16.5mm for a 70 setiger specimen (Maciolek 1985)), would fit this description, but the correlations between these species are positive, further supporting bottom-up control. (The weak positive correlation between *S. fragilis* and *A. agilis* is further support, though the deposit feeding infaunal clam is likely too large for the predator to consume anyway.) The spionid predator is however negatively correlated with the benthic grazing amphipod *M. gryllotalpa*, also potential prey, and not particularly strongly (though significantly).

With one exception, the statistically significant correlations between *Prionospio heterobranchia* and *S. benedicti* density (both non-epifaunal deposit feeders) and all non-deposit-feeding taxa are negative, while both taxa are positively correlated with at least three deposit feeding taxa. These relationships in sum further support the earlier assertion that bottom-up controls, specifically food availability and in particular macroalgal and microphytobenthic food sources, are driving much of the seasonal pattern seen in this data set. Even so, this is just circumstantial without nutrient data.

The density of *Clymenella torquata*, a deep-burrowing deposit feeder highlighted in Chapter 2, is negatively correlated with the densities of two taxa (the deposit feeding *Capitella* spp. and the grazer *Microdeutopus gryllotalpa*) and positively correlated with the suspension feeding *Microdeutopus anomalus*, the opposite relationship found between *C. torquata* and suspension-feeding taxa in hard clam plots in Chapter 2. The negative correlation between *C. torquata* and *Capitella* spp. is particularly interesting as the two are the only polychaete taxa represented here with non-planktonic larval stages. (*C. torquata* has a heavy, bottom-dwelling larva (Newell 1951) while New York populations of *Capitella* spp. have been shown to be largely direct-developing, with some larvae settling in as little as 30 minutes (Dubilier 1988, Méndez et al. 2000.) Though it is possible that this is a function of competition for food, *C. torquata* is a deep-dwelling polychaete while *Capitella* spp. remains within the top 5 cm, so it is more likely that there is another dynamic driving this relationship.

While much of the seasonal variation mimics the control dataset, deposit feeders are one of the primary differences between the two datasets: spring peaks of two deposit feeders *Ameritella agilis* and *Capitella* sp. were seen only in aquacultural plots, perhaps due to an influx of feces from the stocked *M. mercenaria*. The spring influxes of primary productivity described earlier would necessarily result in a concurrent spring influx of fecal nutrients deposited to shallow sediments. *Capitella* sp. and *A. agilis,* as shallow-burrowing deposit feeders, would have immediate access to the wealth of newly deposited material, potentially driving population increases. For *Capitella sp.* this is supported by research showing positive responses of the infaunal polychaete to organic enrichment in aquacultural and other pollution scenarios, in both mesocosm and *in situ* studies (Webb 1996, Callier et al. 2007, Callier et al. 2009). But for *A. agilis* these results are at odds with studies finding that the bivalve has a poor tolerance for organic enrichment (Callier et al. 2009). *A. agilis* is also statistically higher in clam plots overall, Figure 2-7. Generally speaking, the relative rates of fecal production and removal at Sedge Island appear to be sufficiently balanced to result in a net-increase in habitat quality for the deposit-feeding bivalve. Perhaps the concurrent spike in the organic-tolerant *Capitella* sp. is responsible for an overall increase in the rate of removal of organic material.

In the control dataset, deposit feeders as a group were positively correlated with predators and negatively correlated with grazers. The particles cast-off during the act of predation contributes to the very detritus that makes up a major portion of the deposit feeder's carbon budget (Levinton et al. 1984), making the immediate sediments more suitable for deposit feeding organisms and contributing to the positive correlation seen in this study. Deposit feeders, whose carbon needs are divided between microorganisms and detritus (Levinton 1985), and grazers each require very different food sources from different microhabitats (fine, muddy sediments vs. vegetated sediments or suitable structure). This separation is likely partly responsible for the negative correlations between the two groups. An additional signal is seen in the seasonality of *Tritia obsoleta*, classified in this study as a deposit feeder, and *Microdeutopus gryllotalpa*. PCA clearly indicates, in both control and aquacultural plots, that the *T. obsoleta* density signal is significantly higher in May than in summer or autumn while the *M. gryllotalpa* signal is significantly higher in October. Though the correlation between the two species is not statistically significant, this temporal separation supports results from DeWitt and Levinton (1985) indicating a causational negative relationship. *M. gryllotalpa* emigrates to snail-free sediments due to bioturbation-caused disturbance, not due to competition for food. There is no evidence that, as has also been shown with other burrowing amphipods (Coffin et al. 2012) that the amphipods are also consumed by the snail, or that they become trapped by the snail's mucus trail, however the possibility remains that the phenomenon has just not yet been documented. Further study is required to ascertain exactly what is driving this temporal resource division in the Sedge cove.

October samples have statistically higher densities of *Microdeutopus gryllotalpa*, an epifaunal grazer, but a closer look reveals that this is largely driven by a population spike in October 2014. October is also statistically higher in grazer density than August, but this pattern cannot be attributed merely to the October 2014 *M. gryllotalpa* spike. Removing October 2014 from the analysis proves the validity of this seasonal pattern: even though *M. gryllotalpa* is the most abundant herbivore in the functional group analysis, the main effect of season is still statistically significant, with October significantly higher than August. There is a dramatic increase in the amount of irradiance during the summer months due to an increased photoperiod and increased sun angle, as well as an overall increase in average temperature. As phytoplankton density increases, this can serve to decrease the total amount of light received by submerged plants and algae during the summer as compared to spring and fall. This generally translates to increased grazer populations at the end of summer/early fall (Nelson et al. 1997, Lee et al. 2007, Amundrud et al. 2015), and current results concur with these general findings.

Other environmental parameters besides riverine input and its effects on food availability can drive seasonal fluctuations in estuarine benthic community structure and biodiversity, including temperature, salinity and sediment hypoxia/anoxia (not generally an issue in Barnegat Bay due to its well-mixed water column (Kennish et al. 2007)). These gradients drive local-scale species distributions (Seitz 1998), selectively permitting only those species with intrinsic attributes to persist in specific locations. For example, salinity changes are often more drastic in upper-estuary locations, restricting organisms that cannot tolerate the higher energy demand of osmotic regulation at lower salinities (Seitz 1998), while filter-feeding organisms including *M. mercenaria* avoid areas with high proportions of small particulate where feeding efficiency is lowered (Anderson et al. 1978, Stanley and Dewitt 1983). These environmental parameters often vary seasonally and as such can control seasonal variation in benthic biodiversity both directly and indirectly. Direct influences can be seen in the case of seasonal temperature flux influencing water and sediment temperature gradients, while indirect influences can be seen in the case of seasonal temperature flux driving larval dispersal and settlement timing (not quantified in this study). With the exception of *Microdeutopus gryllotalpa* density, May samples are generally different from samples taken during the other two seasons. It is likely that consistency is due to the direct environmental changes in temperature, salinity and their effects on overall food availability.

The experiental block design necessarily placed the control plots within a few meters of experimental treatment plots, presenting the possibility of spill-over or other interaction effects. Over the three-year experimental time-frame, only nine control samples (5%) contained a specimen of *Mercenaria mercenaria notata*, the strain planted in the neighboring experimental aquaculture plots. The direct impact of these treatment plots is therefore likely minimal, if in fact these clams did even come from one of the experimental treatment plots used in this study.[4] This

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[4] *M. mercenaria notata* is also the strain used by ReClam the Bay in cultivation plots located approximately 20-30 meters away from the study blocks, selected mainly for ease of recognition. The clams found in control samples may have migrated from the plots maintained by ReClam the Bay, or could have been dropped by error during the more than five years the cove was used for cultivation.

is further supported by the overall lack of impact seen in experimental perimeter samples (see Chapter 2). Even so, the possibility that neighboring experimental treatment plots have affected the control plot sampling data cannot be fully eliminated.

The general season patterns predicted (spring peaks and summer crashes for deposit-feeding polychaetes, and spring maximums for suspension-feeding taxa) are not clear in the dataset from Sedge Island. Seasonal signals are strong for *Polydora cornuta* but also for suspension-feeders as a group, while grazer density increases over the summer months. In concert these results imply that food-resources are driving seasonal shifts in community structure, however nutrient and primary production data would be necessary to confirm the direct relationship.

Eutrophication is closely linked to decreased submerged aquatic vegetation (SAV) cover (Larkum et al. 2006, Ralph et al. 2007), which is correlated with decreased hard clam (*Mercenaria mercenaria*) density (Peterson and Heck 2001, Kennish et al. 2011) as discussed in Chapter 1. *Mercenaria mercenaria*, as an ecosystem engineer, both enhances habitat quality for deposit feeders via fecal and pseudofecal deposition and provides shell surface appropriate for certain grazers. In an ecosystem with increasing eutrophication and decreasing SAV density, the predictable subsequent decreases in ambient *M. mercenaria* density could result in net decreases in grazer and deposit feeder density.

If current eutrophication trends continue, further declines in SAV would likely lead to increased *Ulva spp.* cover and macroalgal-associated invertebrate communities, with increased grazer and omnivore densities. However, evidence that hard clam aquaculture enhances seagrass density (Grizzle et al. 2006, Coen et al. 2007) suggests that changes in policy leading to increased hard clam aquaculture could result in increased SAV cover. Data from this study can be seen as a baseline for use in evaluating future environmental policy.

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TABLES

Table 3-1 MANOVA table for biodiversity measures, control plot data only. Significant results in bold, interesting but non-significant results underlined.

Shannon-Weiner Index					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	1.347437	0.673719	2.7326	<u>0.0678</u>
Error	176	43.393146	0.246552		
C. Total	178	44.740583			
Species Richness					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	770.109	385.054	2.1727	0.1169
Error	176	31191.466	177.224		
C. Total	178	31961.575			
Pielou's Evenness					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	0.1680118	0.084006	4.6921	**0.0103**
Error	176	3.1510475	0.017904		
C. Total	178	3.3190592			

Table 3-2 ANOVA table for dominant taxa principal component scores, control plot data only. Significant results in bold, interesting but non-significant results underlined.

Principal Component 2 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	17.366417	8.68321	6.8004	**0.0023**
Error	55	70.228048	1.27687		
C. Total	57	87.594466			
Principal Component 3 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	12.371653	6.18583	5.2745	**0.0080**
Error	55	64.502820	1.17278		
C. Total	57	76.874474			

Table 3-3 Dominant taxa correlation table (control plot data only). Significant correlations (Spearman's ρ) in bold.

	A. agilis	*T. obsoleta*	*S. benedicti*	*Capitella spp.*	*M. anomalous*	*M. gryllotalpa*	*C. torquata*	*S. fragilis*	*P. cornuta*	*P. heterobranchia*
A. agilis	1	-0.0209	**0.3605**	0.2368	-0.1249	**-0.4984**	0.0946	**0.2693**	0.0422	**0.4632**
T. obsoleta	-0.0209	1	-0.0249	0.0721	**0.2615**	-0.0392	0.2235	-0.0457	**0.2905**	-0.0377
S. benedicti	**0.3605**	-0.0249	1	**0.4363**	-0.1001	**-0.3126**	-0.1614	**0.3380**	-0.0266	**0.6417**
Capitella spp.	0.2368	0.0721	**0.4363**	1	-0.0034	-0.0155	**-0.3681**	0.1389	**0.2659**	**0.3670**
M. anomalous	-0.1249	**0.2615**	-0.1001	0.0034	1	-0.0875	**0.2594**	-0.0263	**0.3278**	**-0.3036**
M. gryllotalpa	**-0.4984**	-0.0392	**-0.3126**	-0.0155	-0.0875	1	**-0.4203**	**-0.3169**	-0.1496	**-0.3005**
C. torquata	0.0946	0.2235	-0.1614	**-0.3681**	**0.2594**	**-0.4203**	1	-0.0090	0.0190	-0.2413
S. fragilis	**0.2693**	-0.0457	**0.3380**	0.1389	-0.0263	**-0.3169**	-0.0090	1	-.1724	**0.2744**
P. cornuta	0.0422	**0.2905**	-0.0266	**0.2659**	**0.3278**	-0.1496	0.0190	-0.1724	1	0.0653
P. heterobranchia	**0.4632**	-0.0377	**0.6417**	**0.3670**	**-0.3036**	**-0.3005**	-0.2413	**0.2744**	0.0653	1

Table 3-4 ANOVA table for feeding group principal component scores, control plot data only. Significant results in bold.

Principal Component 1 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	28.030791	14.0154	11.4044	**<0.0001**
Error	57	70.049711	1.2289		
C. Total	59	98.080502			
Principal Component 3 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	11.184703	5.59235	7.7637	**0.0010**
Error	57	41.058510	0.72032		
C. Total	59	52.243213			

Table 3-5 Feeding group correlation table (control plot data only). Significant correlations (Spearman's ρ) in bold.

	Omnivores/m^2	**Grazers/m^2**	**Suspension/m^2**	**Predators/m^2**	**Deposit/m^2**
Omnivores/m^2	--	0.1632	**0.6599**	0.0634	0.1006
Grazers/m^2	0.1632	--	-0.1560	**-0.2589**	**-0.3932**
Suspension/m^2	**0.6599**	-0.1560	--	0.1892	0.2157
Predators/m^2	0.0634	**-0.2589**	0.1892	--	**0.2648**
Deposit/m^2	0.1006	**-0.3932**	0.2157	**0.2648**	--

Table 3-6 ANOVA table for infaunal group principal component scores, control plot data only. Significant results in bold, interesting but non-significant results underlined.

Principal Component 1 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	17.54148	8.77074	4.9594	**0.0103**
Error	57	100.80457	1.76850		
C. Total	59	118.34604			
Principal Component 2 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	7.350348	3.67517	4.5557	**0.0146**
Error	57	45.983031	1.80672		
C. Total	59	53.333379			

Table 3-7 ANOVA table for dominant taxa principal component scores, clam plot data only. Significant results in bold, interesting but non-significant results underlined.

Principal Component 1 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	24.10658	12.0533	6.1373	**0.0027**
Error	176	345.65136	1.9639		
C. Total	178	369.75794			
Principal Component 2 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	9.07663	4.53831	3.1623	**0.0447**
Error	176	252.58190	1.43512		
C. Total	178	261.65853			
Principal Component 3 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	13.35362	6.67681	6.0028	**0.0030**
Error	176	195.76269	1.11229		
C. Total	178	209.11632			
Principal Component 4 Score					
Source	**DF**	**Sum of Squares**	**Mean Square**	**F Ratio**	**Prob > F**
Model	2	19.27361	9.63680	5.2745	**<0.0001**
Error	176	164.85152	0.93666		
C. Total	178	184.12513			

FIGURES

Figure 3-1 Mean sediment grain size data for control plots only (3-1a), for all sampling dates, Oct 2012-October 2015, clearly showing outlying samples. These are caused by larger pieces of shell, and are also reflected in the sorting coefficient data (3-1b).

Figure 3-1a

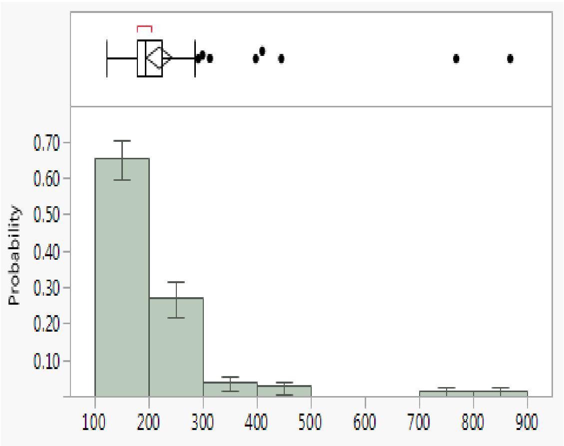


Figure 3-1b

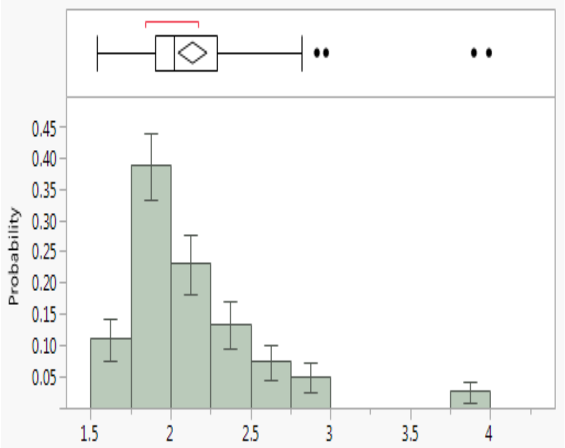


Figure 3-2 Tukey HSD *post hoc* comparisons of Pielou's Evenness (J') values (least squared mean) between seasons (control samples only). Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

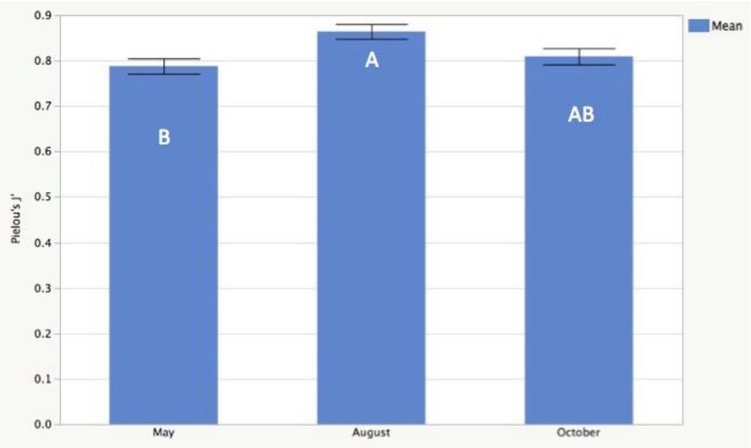


Figure 3-3 Plot showing the contribution of the independent dominant taxa variables into the three principal components.

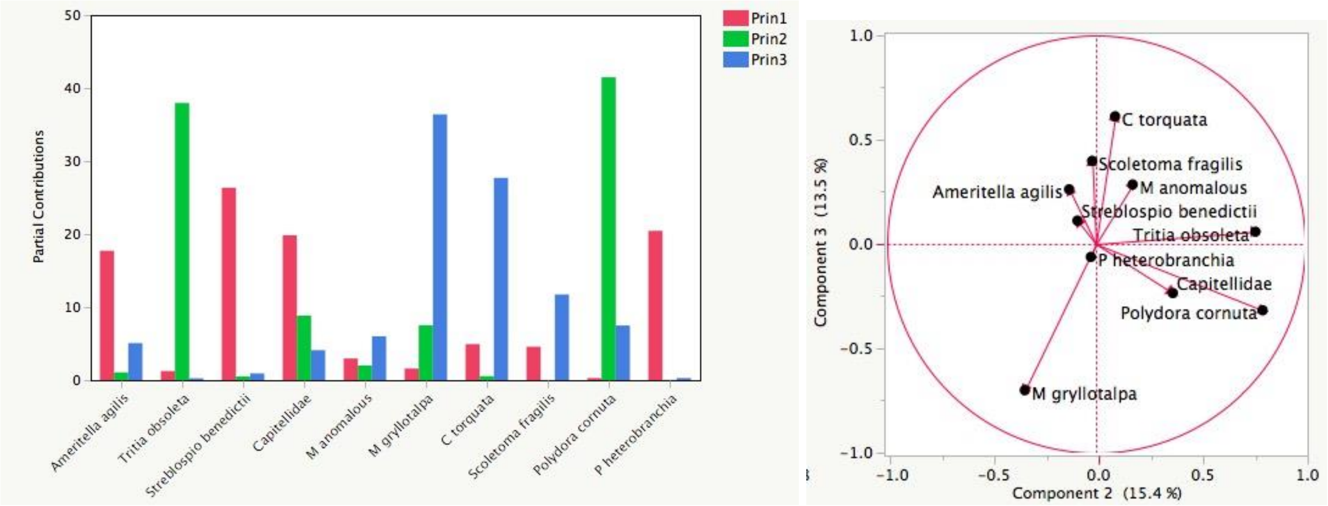


Figure 3-4 Tukey HSD *post hoc* comparisons of dominant taxa Principal Component 2 scores (least squared mean) between seasons (control samples only). Levels not connected by the same letter are significantly different. Error bars equal ±1 SE of the mean.

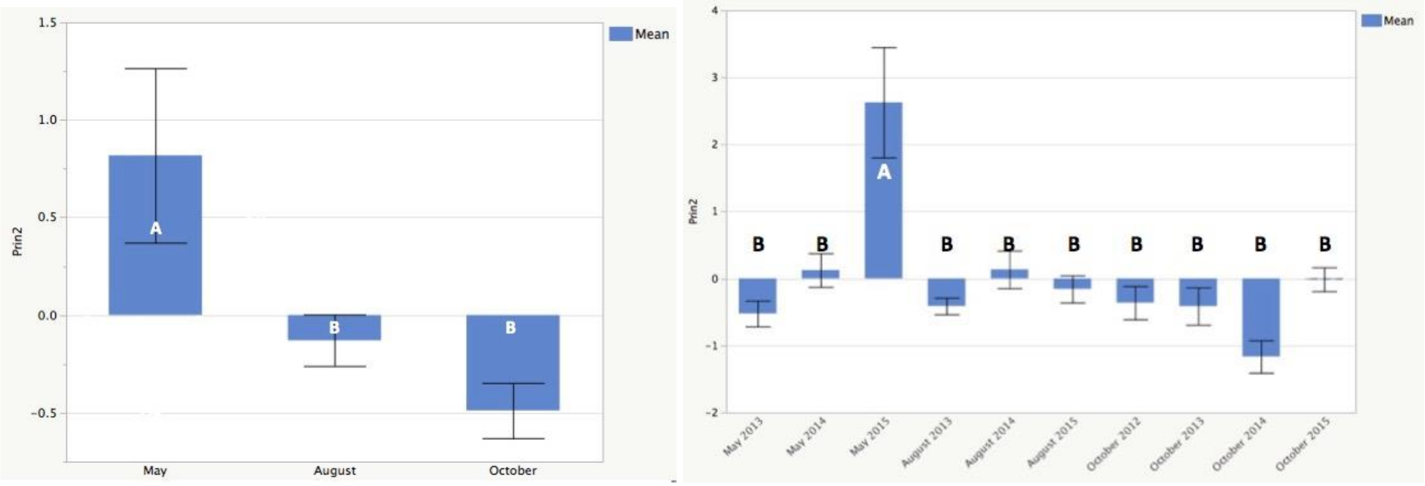


Figure 3-5 Tukey HSD *post hoc* comparisons of dominant taxa Principal Component 3 scores (least squared mean) between seasons (control samples only). Levels not connected by the same letter are significantly different. October 2014 is significantly different from all months except May 2015 and October 2015. Error bars equal ±1 SE of the mean.

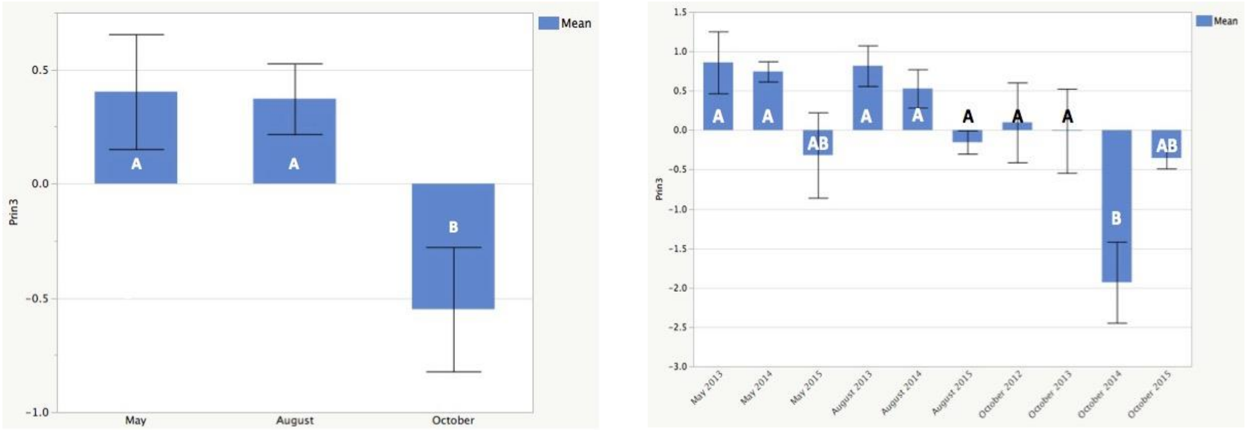


Figure 3-6 Density of *Microdeutopus gryllotalpa* during individual sampling dates, clearly showing the spike during October of 2014, possibly beginning in 2013.

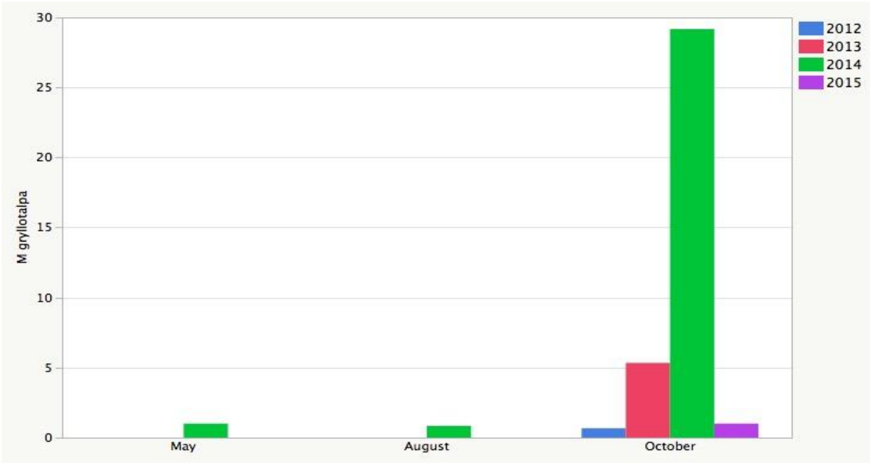


Figure 3-7 Plot showing the contribution of the five independent feeding group variables into the three principal components.

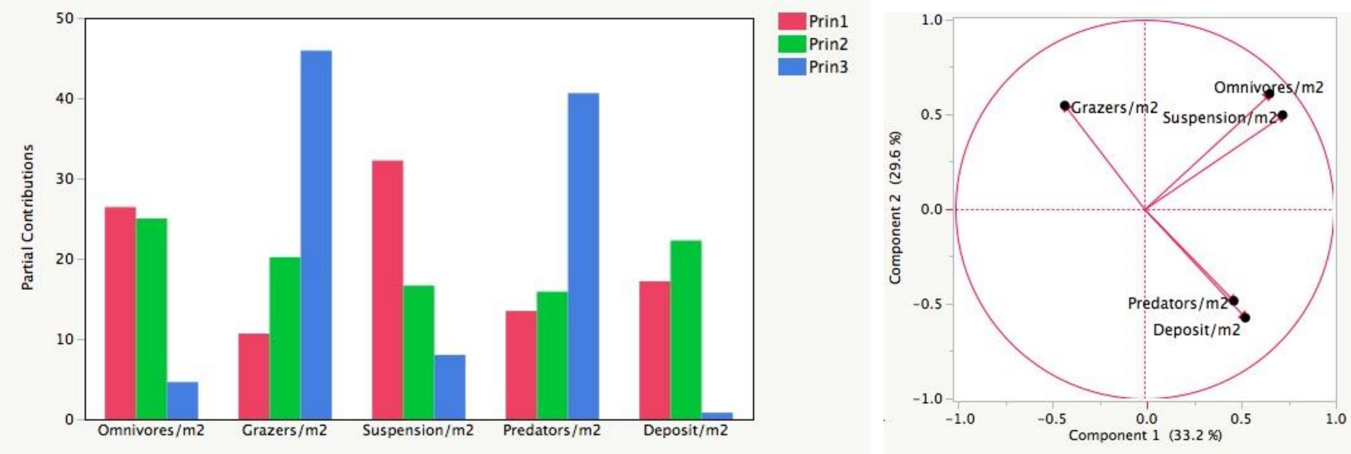


Figure 3-8 Tukey HSD *post hoc* comparisons of feeding group Principal Component 1 scores (least squared mean) between seasons (control samples only). Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

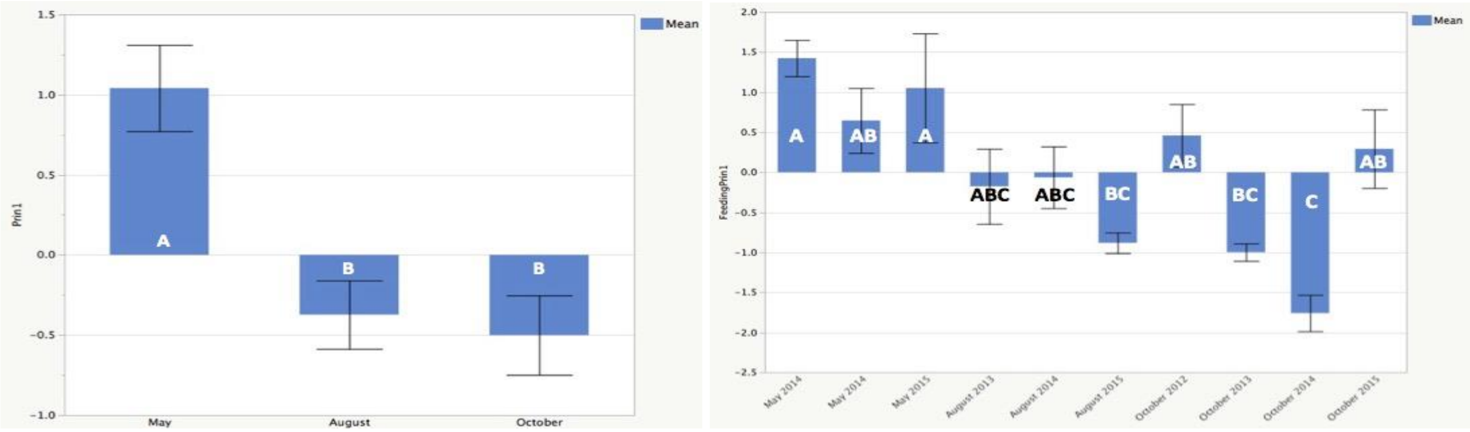


Figure 3-9 Tukey HSD *post hoc* comparisons of feeding group Principal Component 3 scores (least squared mean) between seasons (control samples only). Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

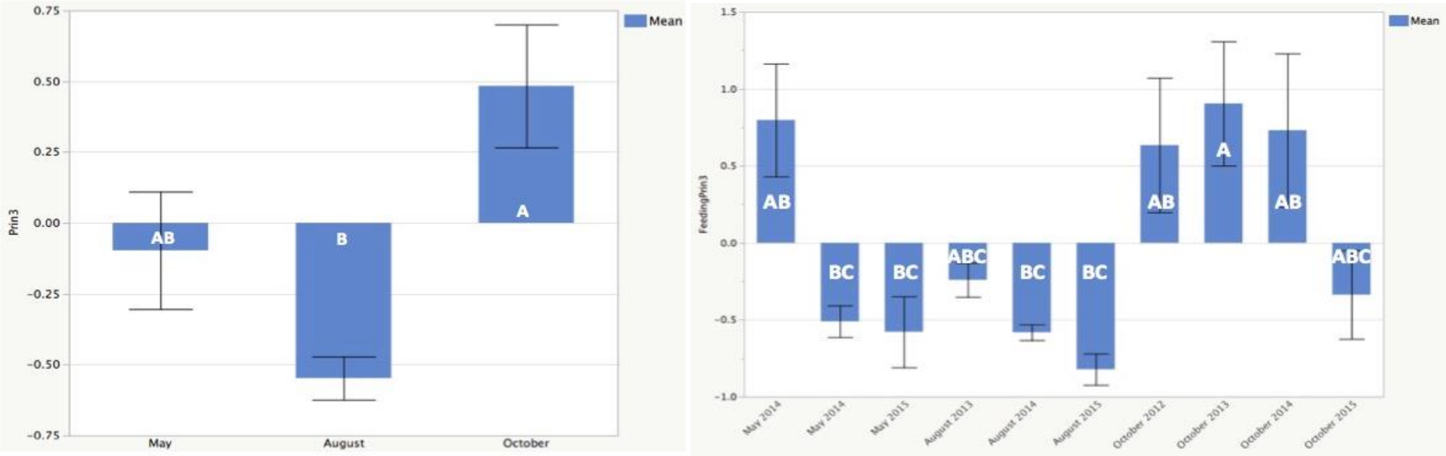


Figure 3-10 Plot showing the contribution of the four independent burrowing group variables into the principal components.

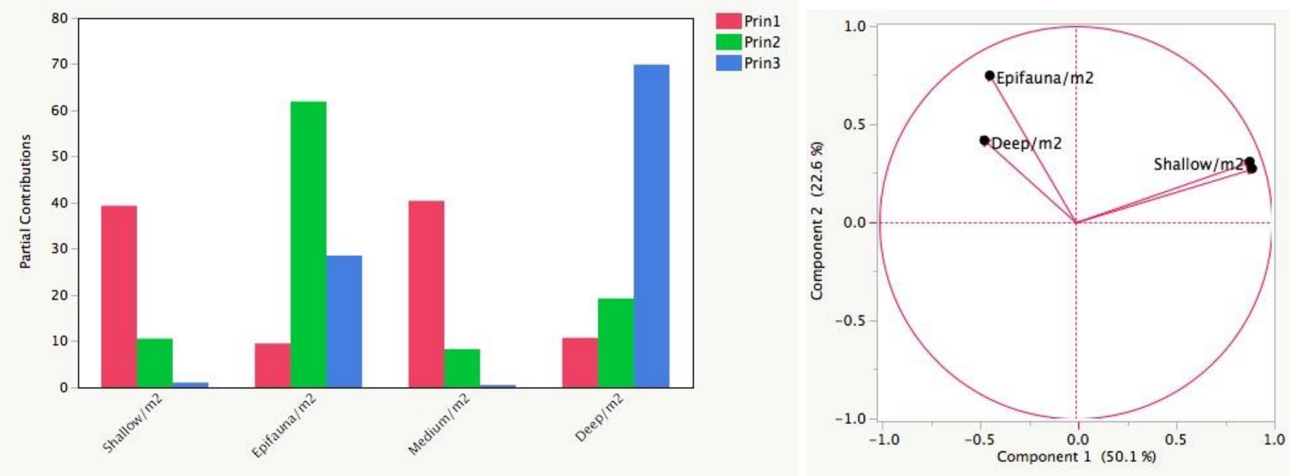


Figure 3-11 Tukey *post hoc* comparisons of infaunal group Principal Component 1 scores (least squared mean) between seasons (control samples only). Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

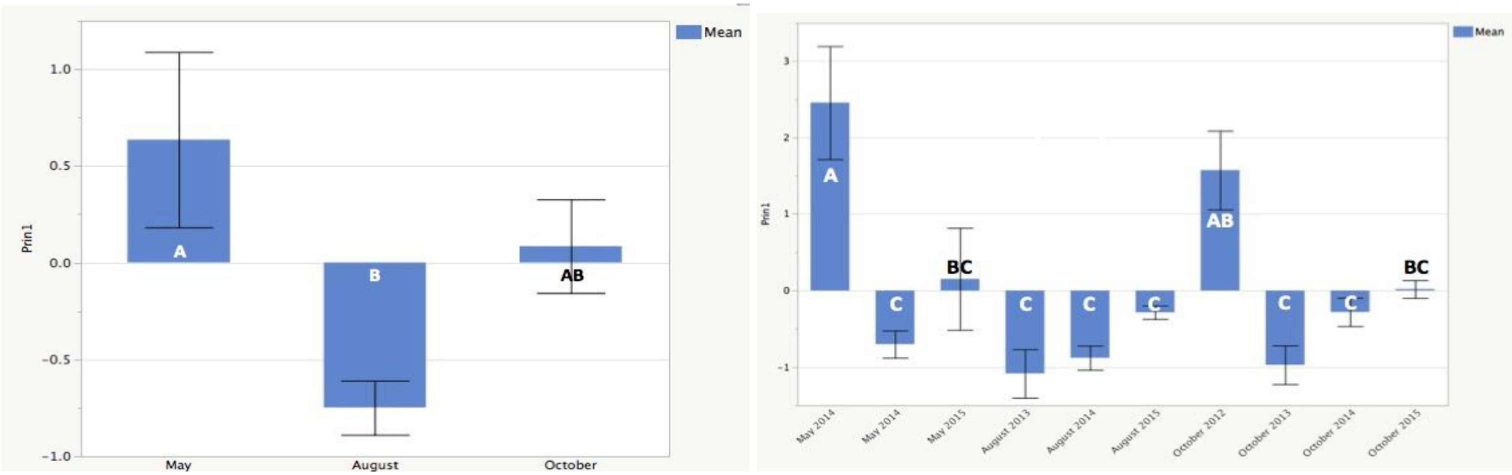


Figure 3-12 Tukey *post hoc* comparisons of infaunal group Principal Component 2 scores (least squared mean) between seasons (control samples only). Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

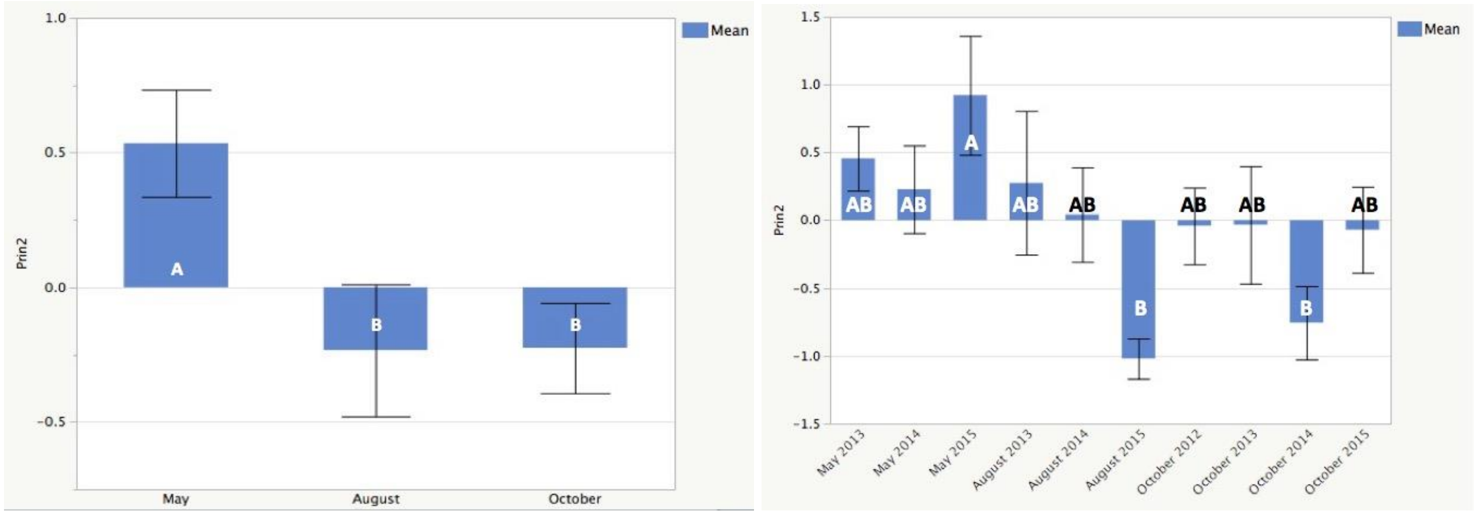


Figure 3-13a&b Tukey HSD *post hoc* comparisons of Pielou's Evenness (J') values (least squared mean) between season (control samples only). Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

Figure 3-13a

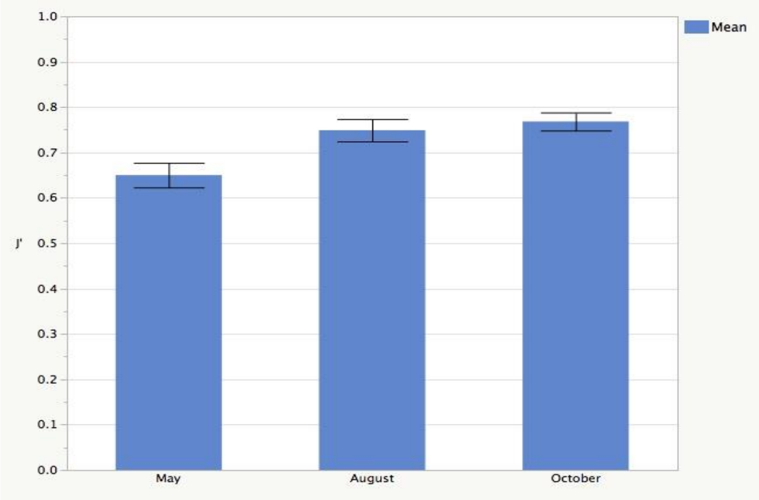


Figure 3-13b

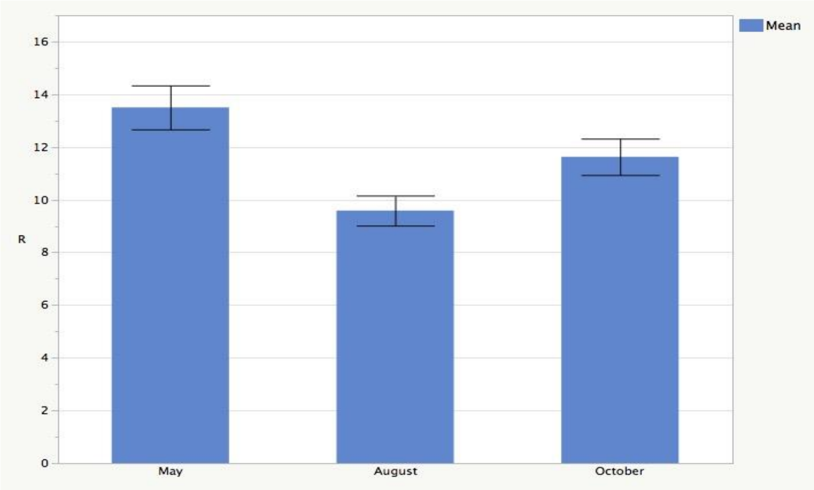


Figure 3-14 Plot showing the contribution of the independent dominant taxa variables (clam plot data only) into the principal components, as well as vector plots for all four components.

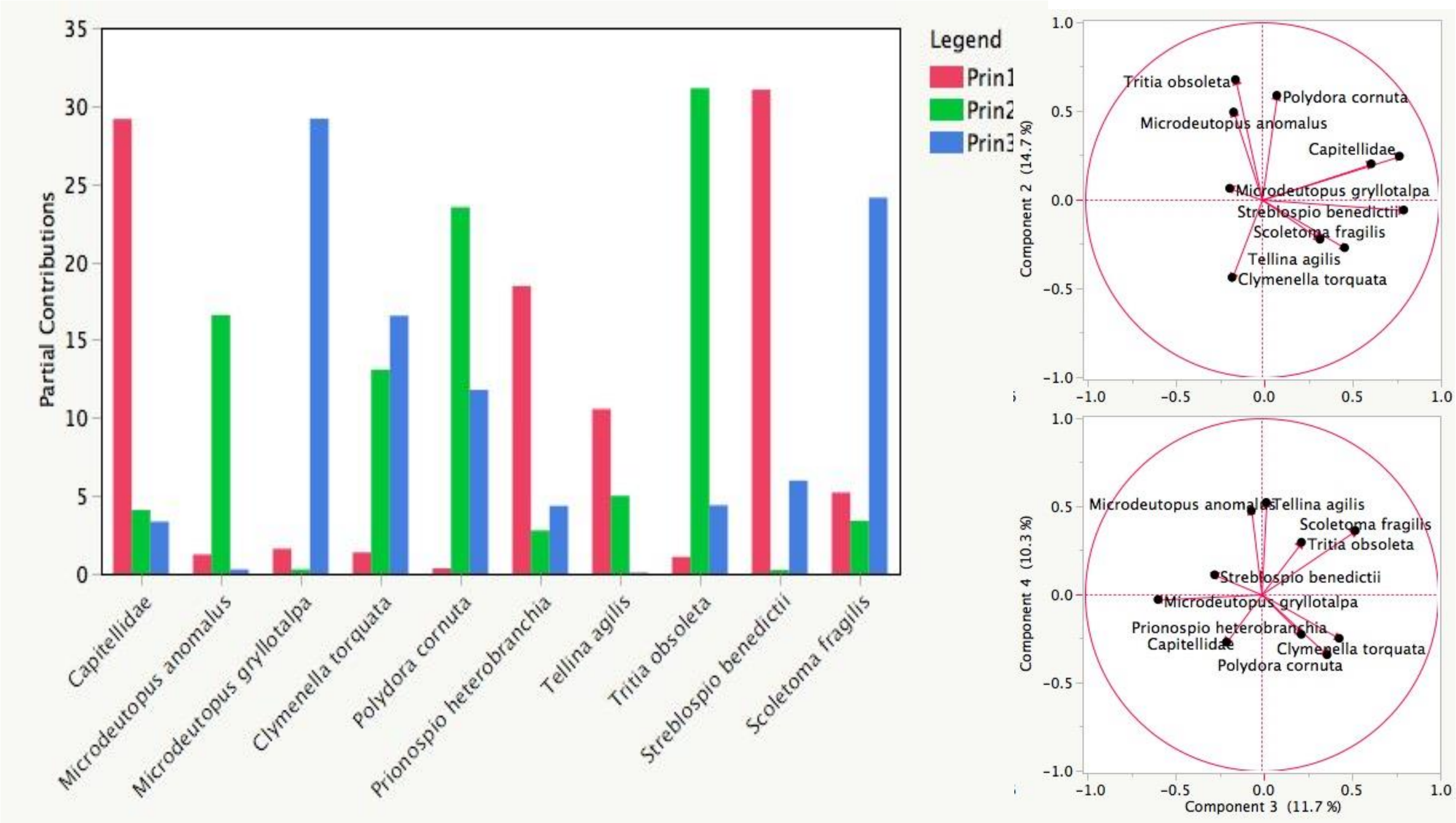


Figure 3-15a&b Tukey HSD *post hoc* comparisons of dominant taxa group Principal Component 1 (3-15a) and Principal Component 4 (3-15b) scores (least squared mean) between seasons (clam plot samples only). Levels not connected by the same letter are significantly different. (Error bars equal ±1 SE of the mean.)

Figure 3-15a

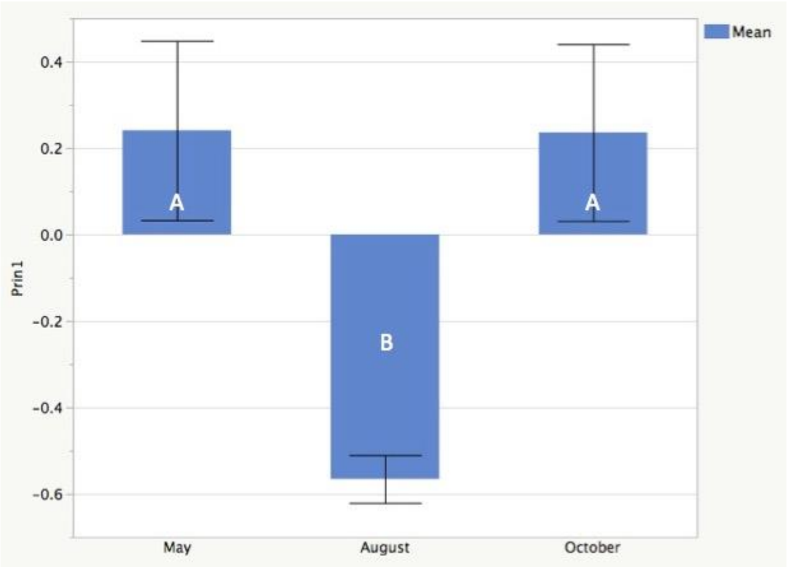
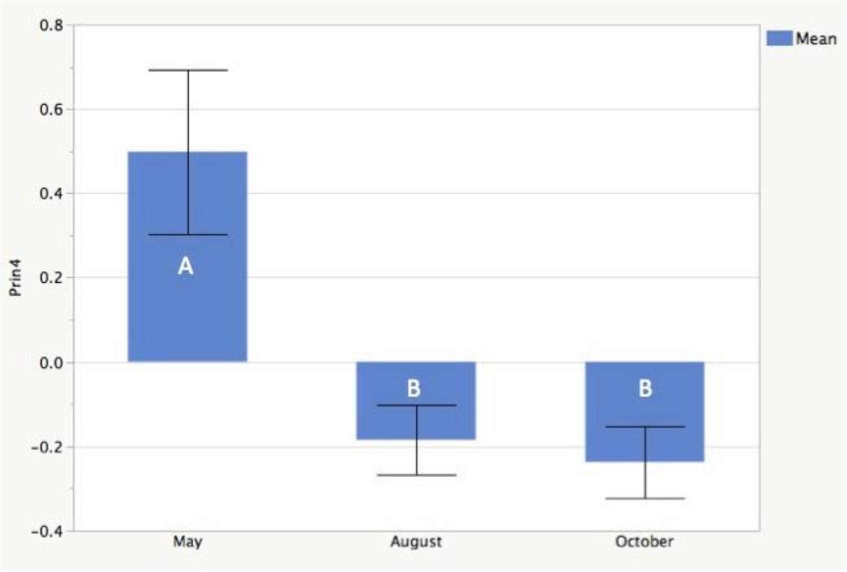


Figure 3-15b



Dissertation Summary

Hard clam (*Mercenaria mercenaria*) aquaculture operations during the 3 year “grow-out” phase maintain densities many magnitudes higher than those found naturally in surrounding sediments. Aquacultural densities of other bivalve species have inconsistently been shown to detrimentally impact benthic invertebrate communities. This study sought to quantify the impacts of hard clam grow-outs to benthic invertebrate biodiversity and community structure.

Three experimental blocks of 15 x 7m were marked out in early October 2012. Each block contained 3 plots measuring 3 m by 4.6 m, one each of the following three treatments: Control (untouched), Screen Control (Tenax® and PVC screen frame affixed to the sediment with rebar and shell bags), or Screened Clam (Tenax® and PVC screen frame affixed to the sediment with rebar and shell bags). Sediment cores (3.8cm dia., 10 cm depth) and benthic Ekman grab samples (3.5L) were taken from inside the plots (under screens) and 1 meter in each direction from the plot edge three times each year (May, August, October) for three years (2012-2015).

Mean sediment grain size did not statistically differ between treatments, however sorting coefficient was significantly higher inside screened clam plots, indicating a more evenly distributed sediment profile. There was no significant effect of season on sediment profile.

177 species were collected from across eight phyla. Shannon-Weiner Index values were statistically lower inside screened clam plots than in any other sampling location, with no effect of season. Pielou’s evenness was also significantly lower inside of screened clam plots, and also in May than in August or October. There was a significant effect of season on species richness in aquacultural plots only, not in control plots, peaking in May.

The ten most dominant taxa (as determined from overall abundance data) were six polychaetes (*Capitella* sp., *Clymenella torquata, Polydora cornuta, Prionospio heterobranchia,* *Scoletoma fragilis, Streblospio benedicti*), two gammarid amphipods (*Microdeutopus anomalus, M. gryllotalpa*) one bivalve (*Ameritella agilis*) and one gastropod (*Tritia obsoleta*). Density data from these taxa were converted with Principal Components Analysis into linearly uncorrelated variables. Factorial MANOVA was then run on the resulting variables to determine the effects of treatment and season. The results suggest that samples from inside clam plots have component scores indicating higher densities of *Clymenella torquata*, a deep-dwelling deposit-feeding polychaete. Results also show that samples from May have component scores indicating higher *Polydora cornuta* (a shallow-burrowing suspension-feeder) and *Tritia obsoleta* (an epifaunal detritivore and deposit-feeder) densities. Samples from October have scores indicating higher densities of *Microdeutopus gryllotalpa* (a grazing amphipod). Clam plots were also shown to have higher densities of *Capitella* sp. in May and October as compared to August, and higher densities of *A. agilis* and *M. anomalus* (a suspension-feeding amphipod) in May.

All taxa meeting a minimum abundance of N=100 were also classified into functional groups according to primary feeding type and maximum burrowing depth. The same PCA plus Factorial MANOVA analysis was run on the resulting data. Results show that control plot samples have component scores indicating higher densities of omnivorous and suspension-feeding taxa as compared to aquacultural plots, and that samples from May have component scores indicating significantly higher densities of the same groups than later months. Scores also indicate that October samples have higher densities of grazing taxa than August samples, likely linked to the aforementioned *M. gryllotalpa* peak. Analyses of burrowing depth groups show only a significant effect of season, with May component scores indicating higher densities of epifaunal, shallow-burrowing and medium-burrowing taxa in spring than in later months.

Results from an ANOSIM run on the full dataset showed a significant difference in invertebrate community between treatments. The average similarities ranged between 19.6% and 27.4%, the low values indicating both the great variability within the data set and likely also the low number of replicates. Pairwise comparisons involving inside-screened clam plot samples were all significant, and larger than any other pairwise comparisons. All comparisons involving only perimeter and control plots were non-significant. Dissimilarity results from the SIMPER analysis indicate moderate levels of dissimilarity among all treatments, with particularly low levels between inside screen control samples and inside clam plot treatment samples. For all other comparisons the inside clam plots have the highest dissimilarity scores, indicating that aquacultural communities have the least overlap in community makeup with communities in other treatments. All but three taxa designated as critical by SIMPER analysis were all amongst the dominant taxa considered in earlier analysis, verifying that *pre hoc* decision. *Ameritella agilis*, the diminutive deposit-feeding clam, was the only taxa significant to all treatments (individual contribution >5%) to have a significant effect of treatment. *Post hoc* analysis determined inside clam plot samples to be higher in *A. agilis* density than all other treatments. *A. agilis* density also differs significantly by season, peaking in May.

This study found limited negative impacts to benthic infaunal biodiversity associated with small-scale grow-out plots in New Jersey over a three-year period. The suggestion that screening would contribute to overall increases in biodiversity and species richness is not borne out here. Control and aquacultural plots are controlled by bottom-up processes, with suspension and omnivorous taxa peaking in the spring and grazers peaking in fall. Additional research is still required before any changes to leasing policy should be considered. The plots in this study were constructed at 1:4 the scale of industrial screens. And, at nine plots in size (only six of which were screened), the installation studied in this dissertation is much smaller and less dense than a typical industrial aquacultural grow-out facility. Edge effects could be minimizing the impacts of the aquacultural plots, especially as the plots are effectively situated within a wide field of unfarmed reference area themselves to further confound the data.

This study also provides no data on the use of redundant use plots across time. Aquacultural grow-outs necessarily re-use acreage on a yearly basis, while this study newly installed plots. There is a wealth of data showing quick recovery to baseline from the physical harvesting (Kaiser et al. 1996, Hall and Harding 1997, Spencer et al. 1997, Boese 2002), both by manual raking and mechanical dredging. Though this study does not directly address the issue, it is unlikely that the grow-out phase requires longer recovery time than such a directly destructive process.

The decrease in biodiversity seen inside the aquacultural plots is linked almost entirely to changes in evenness, not in overall species richness. This provides some reason to think that the overall shift in community make up might be minimal, but this requires confirmation before expanding the overall acreage made available to industry. Decreasing biodiversity and species richness in coastal systems is clearly causally linked with decreased productivity and filtering capacity, decreased effectiveness as a nursery habitat and decreased number of uncollapsed fisheries (Worm et al. 2006). Systems with lower biodiversity also are increasingly susceptible to ecological destabilization and catastrophic events including invasion by non-native species (Worm et al. 2006). Interestingly, increases to species richness as caused by these invasive species do not seem replace the aforementioned services (Worm et al. 2006). But these effects are linked to decreases in biodiversity and species richness. The decrease in biodiversity of 0.5 inside aquacultural plots seen in this work is caused by decreases in evenness, not in species richness. Other studies, though few in number, have seen similarly weak effects, including one study on hard clam aquaculture facilities in NJ and VA, in which 26 variables did not vary between aquacultural and reference sites during any single sampling date (Luckenbach et al. 2016). The New Jersey data from this study also showed no significant differences in benthic species richness between *M. mercenaria* grow-out plots and reference sites. (The Virginia data similarly showed no differences between grow-out plots and reference sites, though both were significantly higher in species richness than buffer zones between plots. This effect was not apparent in NJ (Luckenbach et al. 2016.) This study, conducted as it was on a full-scale industrial operation, suggests that there may be minimal decreases in species richness and biodiversity at industrial scales, though the total amount of sampling of benthic infauna in the Luckenbach et al. project was limited in scope.

Other results from this dissertation, including changes to *Clymenella torquata* density and signals suggesting decreases in suspension feeder densities, also indicate a need for close monitoring should changes to New Jersey State aquacultural policies increase overall leasing acreage in the future. This dissertation should be seen as sufficient to consider a full-size follow-up study in a New Jersey grow-out operation, and as an encouraging first step towards bolstering the New Jersey hard clam aquacultural industry.

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Appendix: Full Species List

PHYLUM	CLASS	SPECIES
Bryozoa	Gymnolaemata	*Electra sp.*
		Membranipora tenuis
Nemertea	Anopla	*Cerebratulus lacteus*
Cnidaria	Anthozoa	*Clytia hemisphaerica*
		Diadumene leucolena
		unknown hydroid sp.
Arthropoda	Malacostraca (Amphipoda)	*Acanthohaustorius millsi*
		Aeginina longicornis
		Americulodes edwardsi
		Ampelisca abdita
		Ampelisca vadorum
		Ampelisca verrilli
		Ampithoe longimana
		Ampithoe valida
		Apocorophium (Corophium) acutum
		Batea catharinensis
		Caprella carina
		Caprella penantis
		Cerapus tubularis
		Corophium volutator
		Crassicorophium (Corophium) bonelli
		Cymedusa compta
		Elasmopus levis
		Eobrolgus spinosus
		Ericthonius sp.
		Gammarus mucronatus
		Idunella (Listriella) barnardi
		Idunella (Listriella) clymenellae

		Lembos websteri
		Leptocheirus plumulosus
		Lysianopsis alba
		Microdeutopus anomalus
		Microdeutopus gryllotalpa
		Microprotopus raneyi
		Monocorophium ascherusicum
		Monocorophium insidiosum
		Monocorophium tuberculatum
		Orchomenella pinguis
		Paracaprella tenuis
		Pseudosymtes glaber
		Uhlorchestia uhleri
		Unciola irrorata
		unknown Caprellidae sp.
		unknown Gammariidae sp.
	Malacostraca (Anomura)	*Pagurus longicarpus*
		Pagurus pollicarpus
	Malacostraca (Brachyura)	*Callinectes sapidus*
		Cancer borealis
		Cancer irroratus
		Carcinus maenas
		Crangon septemspinosa
		Dyspanopeus sayi
		Eurypanopeus depressus
		Neopanope texana
		Pinnixa chaetopterana
		Pinnixa sayana
		Rhithropanopeus harrisii
	Malacostraca (Caridea)	*Hippolyte zostericola*
		Palaemon (Palaemonetes) intermedius
		Palaemon (Palaemonetes) pugio
		Palaemon (Palaemonetes) vulgaris

	Malacostraca (Cumacea)	*Diastylis sculpta*
		Oxyurostylis smithi
	Malacostraca (Isopoda)	*Cyathura polita*
		Edotia triloba
		Erichsonella filiformis
		Idotea balthica
	Malacostraca (Mysida)	*Americamysis bigelowi*
	Ostracoda	Halocyprididae spp.
	Ostracoda	non-Halocypridid ostracod spp.
	Pycnogonida	*Anoplodactylus lentus*
Annelida	Clitellata	unknown Oligochaete sp.
	Polychaeta	*Alitta succinea*
		Alitta virens
		Amastigos caperatus
		Amnicola brasiliensis
		Amphitrite sp.
		Aonidella (Prionospio) cirrobranchiata
		Bushiella (Spirorbis) granulata
		Capitella spp.
		Circeis spirillum
		Cirratulus grandis
		Clymenella torquata
		Clymenella zonalis
		Diopatra cuprea
		Eulalia sp.
		Eumida sanguinea
		Eusyllis lamelligera
		Exogone naidina
		Glycera dibranchiata
		Glycinde solitaria
		Goniada sp.
		Harmothoe sp.
		Heteromastus filiformis

		Hiatella sp.
		Hobsonia florida
		Hypereteone lactea
		Lepidonotus squamatus
		Lepidonotus sublevis
		Lumbrinerides acuta
		Magelona rosea
		Maldane sarsi
		Maldanidae sp.
		Neanthes arenaceodentata
		Nephtys sp.
		Notomastus latericeus
		Orbiniidae sp.
		Owenia fusiformis
		Paradexiospira violacea
		Paranaitis speciosa
		Parapionosyllis longicirrata
		Paraprionospio pinnata
		Parasabella (Sabella) microphthalma
		Pectinaria goulidii
		Pherusa plumosa
		Phyllodoce mucosa
		Polydora cornuta
		Prionospio heterobranchia
		Prionospio pygmaeus
		Prionospio steenstrupi
		Prionspio sp.
		Sabaco elongata
		Salvatoria clavata
		Scoletoma (Lumbrineris) fragilis
		Scoloplos sp.
		Spio setosa
		Spiochaetopterus costarum oculatus

		Spiophanes bombyx
		Spiophanes wigleyi
		Spirorbid spp.
		Streblospio benedictii
		Syllides longocirratus
		Terebellides stroemi (unconfirmed)
		Tharyx acutus
		Nereis sp.
		unknown Sabellid sp.
		unknown Syllidae sp.
		unknown species A
		unknown species B
		unknown species C
		unknown species D
Mollusca	Bivalvia	*Ameritella (Tellina) agilis*
		Anadara transversa
		Astarte undata
		Astyris lunata
		Ensis directus
		Gemma gemma
		Geukensia demissa
		Lyonsia hyalina
		Mercenaria mercenaria
		Mulinia lateralis
		Mya arenaria
		Mysella planulata
		Mytilus edulis
		Nucula proxima
		Nuculana tenuisulcata
		Pholas sp.
		Semele proficua
		Solemya velum
		Spisula solidissima

		Tagelus divisus
	Gastropoda	*Acteocina (Retusa) canaliculata*
		Bittiolum alternatum
		Boonea bisuturalis
		Cerithiopsis sp.
		Crepidula convexa
		Crepidula fornicata
		Crepidula plana
		Ecrobia truncata
		Ittibitium oryza
		Japonacteon punctostriatus
		Tritia (Ilyanassa) trivittata
		Tritia (Ilyanassa) obsoleta
		Turbonilla interrupta
Echinoderamata	Holothuroidea	*Leptosynapta tenuis*
		Sclerodactyla briareus
Chordata	Ascidiacea	*Botryllus schlosseri*

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