Stony Brook University

Macrobenthic species abundance and diversity associated with dense assemblages of the tube-building polychaete *Clymenella torquata.*

A Thesis Presented

by

Emily Hildebrandt

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Master of Science

in

Marine and Atmospheric Science

Stony Brook University

May 2017

Stony Brook University

The Graduate School

Emily Hildebrandt

We, the thesis committee for the above candidate for the

Master of Science degree, hereby recommend

acceptance of this thesis.

Glenn R. Lopez – Thesis Advisor
Professor, School of Marine and Atmospheric Sciences

Robert M. Cerrato – Second Reader
Associate Professor, School of Marine and Atmospheric Sciences

Nils Volkenborn– Second Reader
Assistant Professor, School of Marine and Atmospheric Sciences

This thesis is accepted by the Graduate School

Charles Taber
Dean of the Graduate School

Abstract of the Thesis

Macrobenthic species abundance and diversity associated with dense assemblages of the tube-building polychaete *Clymenella torquata.*

by

Emily Hildebrandt

Master of Science

in

Marine and Atmospheric Science

Stony Brook University

2017

Despite the evidence that *C. torquata* modifies the sedimentary habitat with respect to sediment permeability, porosity, oxygenation and organic matter content, few studies have examined their impact on the benthic community. The objective of this study was to determine if the marine polychaete *Clymenella torquata* affected certain biological parameters of the benthos surrounding their tubes, and how those parameters might change with *C. torquata* abundance. 100 total core samples were taken at two different study sites on the southern shore of Shinnecock Bay on either side of the tidal inlet. The benthic faunal contents of these cores were identified and counted, and reported as abundances per core. Chlorophyll-*a* samples were taken from the sediment several centimeters adjacent to the location of the sediment cores. Chlorophyll values were calculated as the amount in µg Chl-*a* cm^{-3} of surficial sediment. In total, 89 different species were identified across the two sites, with a sum of 49,697 individuals. Benthic species abundance data was used to calculate the community measures: species density, richness,

diversity and community similarity. Species density increased with increasing *C. torquata* abundance, while species richness decreased. Diversity and community similarity demonstrated no decisive trend in relation to *C. torquata* abundance. Multiple regression analysis demonstrated that *C. torquata* was a significant predictor for all four community measures, as well as Chl-*a* density ($p < 0.05$). When considering the specifics of the effects of *C. torquata* abundance on species assemblages, ANOSIM analysis demonstrated that there was a significant difference in community composition dependent on the presence or absence of *C. torquata* ($p < 0.001$). There was a significant difference in community composition dependent on the level of *C. torquata* abundance ($p < 0.001$). There was a significant difference in community composition dependent on the level of Chl-*a* density ($p < 0.001$). Results suggest that standing stocks of surficial MPB are positively related to *C. torquata*; density increased with *C. torquata* abundance. Patterns of distribution of *C. torquata*, along with the size and longevity of *C. torquata* beds, indicate that there is a mechanism of intraspecific facilitation that occurs within the bed, by which community facilitation may be a by-product. Moderate to high densities of *C. torquata* are strongly associated with an increase in density of infaunal species, facilitated by the availability of the resources *C. torquata* modifies, certainly in regards to oxygen, but also potentially in the availability of organic matter. Based on the results of this study, it can be concluded that *C. torquata* does have a significant effect on the benthic infaunal community, most likely forming "hotspots" of density where certain species proliferate against a smaller consistent background assemblage.

Table of Contents

List of Figures

List of Tables

Acknowledgments

I would like to thank the School of Marine and Atmospheric Sciences for the opportunity and the financial support to pursue this endeavor, and for the unfailing assistance of the administration throughout the process.

Thank you to Dr. Glenn Lopez for helping to guide me through this project, and my time at Stony Brook in general, and for the seemingly unending patience with which you answered all my questions. My education would not have been half of what it was without you.

Thank you to my committee members, Dr. Robert Cerrato and Dr. Nils Volkenborn, who so generously donated their time and advice to the detriment of their own convenience. Their experience and feedback was invaluable.

Thank you to Dr. Robert Cerrato and Dr. Darcy Lonsdale, who graciously allowed me unlimited access to their labs and equipment and who were always available to answer questions and deliver suggestions about methodology. I am so deeply grateful.

Thank you to Dr. Chet Rakocinski, who took the time from working on his own projects to help me get started with the data analysis of mine. Without his assistance, I would most likely still be sitting at my kitchen table, surrounded by excel sheets.

To Nick, for listening to me stress about this project for the last several years. I cannot imagine what the years would have been like without you and your ever-present dedication and encouragement, but I know they would have been infinitely worse. I love you.

Macrobenthic species abundance and diversity associated with dense assemblages of the tube-building polychaete *Clymenella torquata*

The organisms that dwell in benthic environments are not static beneath the surface; infaunal species modify the sedimentary and chemical characteristics of their environment in a process known as bioturbation. For the purpose of this study, the effects of bioturbation can be largely broken down into the two categories of particle transport and bioirrigation. In the process of feeding, burrowing, and creating and maintaining structures within the sediment, benthic organisms contribute to biomixing of sedimentary particles (Kristensen et al. 2012). Feeding and egestion of fecal matter can result in the movement of sediment either towards the surface or towards depth, respectively, redistributing particulates throughout the surface layer (Wendelboe et al. 2013). Faunal structures such as tubes or mounds may induce erosion when they exist singly by increasing local turbulence, or contribute to sediment stability at higher densities (Luckenbach 1986). Sediment may also be destabilized by more active infauna or the creation of feeding voids loosening sediment and increasing the amount of suspended particulates in the overlying water (Reise 2002). Organisms can contribute to the movement of water by increasing the permeability of the sediment and by ventilating burrows and tubes (i.e. bioirrigation), particularly in sandy sediment. Advective flow is one of the dominant processes in sand contributing to solute flux between the sediment and the overlying water. Advection is governed by the permeability of the sediment, and is driven by porewater pressure gradients that can be induced physically through the interaction of hydrodynamics and surface topography (Precht and Huettel 2003), or biologically by infaunal hydraulic activities (Woodin et al. 2010), resulting in

an increase in the transport of sediment particles (Rusch and Huettel 2000) and porewater solutes (Woodin et al. 2010). The transport of water and solutes increases flux rates of dissolved nutrients, metabolites, and oxygen across the sediment water interface (SWI), and can regulate the oxic/anoxic chemocline (Reise 2002). The effects of bioturbators on the sedimentary environment are so expansive and well-documented that many species have been described as ecosystem engineers (Kristensen et al. 2012).

One of the family groups responsible for bioturbation in near-shore sandy sediments are the maldanid polychaetes. Maldanids are commonly found from continental slopes and shelves to the intertidal zone, where they often form high density populations; they often reach hundreds of individuals per square meter, and have been documented as reaching over 10,000 individuals per m^2 (Dufour et al. 2008). Maldanids contribute to bioturbation primarily through the process of head down deposit feeding and building tubes. Deposit feeders significantly alter the sedimentary environment and are frequently the most common bioturbator in inter- and subtidal communities (Craig 1998). Like other head-down deposit feeding species, most maldanids contribute to particle movement in their environments through the consumption of sediment at depth, processing it through their intestines, and defecating at the surface (Mangum 1964). They also play a role in sediment subduction by using their posterior segments to pull sediment at the surface into their tubes (Dobbs and Whitlatch 1982); tracer particles have been shown to be subducted in maldanid beds and then consumed, the tracer then incorporated into other deposit-feeding infauna (Levin et al. 1997). Sediment subduction may contribute to the increased presence of organic material associated with maldanid tubes (Dufour et al. 2008), or it may be a result of the accumulation of organic particles from currents induced by the projection of tubes from the surface (Reise 2002), and advection through permeable sand (Rusch and Huettel 2000).

Most of the members of the maldanid family form tubes of varying size and shape (Dufour et al. 2008), comprised of particles of mud, sand, or shells (Mangum 1964). Tubes in aggregation can contribute to the stability of sediment (Luckenbach 1986), preventing the resuspension of surface particulates, but more importantly, tubes function as an extension of the SWI into the sediment. This extension contributes to a much higher flux of particles and solutes between the sediment and overlying water through the disruption of lateral flow by tube projections from the surface inducing fluid exchange, and the process of passive and active ventilation by the increased permeability of the sediment and worms moving within the tubes (Reise 2002). The presence of tube-building infauna has been shown to increase sediment pore water pH (Waldbusser et. al. 2004) as well as the transport of particles and dissolved metabolites through the sediment (Reise 2002). Tubes also contribute significantly to the oxygenation of the surrounding sediment (Rhoads and Stanley 1965; Forster and Graf 1995; Waldbusser et. al. 2004; Dufour et al. 2008; Du Close et al. 2013), facilitating oxygen availability and aerobic respiration at a depth that would otherwise not occur. This availability of oxygen supports microniches in the sediment directly adjacent to tubes, supporting bacterial and meiofaunal growth (Callaway 2006; Du Close et al. 2013). Tubes can also persist for relatively lengthy periods, which supports the notion that these structures play an important role in biogeochemical cycling (Dufour et al. 2008).

The physical and chemical changes made to the environment by maldanids in the process of feeding and building tubes can be accompanied by resulting changes in community structure. While papers that discuss the effects of maldanids on community composition are lacking, studies which looked at the effects of tube worms in general may provide some insight into the potential for maldanids to shape community structure. Genera of tube-building worms have been

shown to alter benthic communities, generating hot spots of structuring forces (Woodin et al. 2010), while other genera influence species diversity and abundance (Luckenbach 1986; Dubois et al. 2002; Bolam and Fernandes 2003). Tube-builders can negatively impact other infauna, (e.g. the survival rate of newly recruited bivalves and polychaetes), but studies have also demonstrated a positive effect on community structure, with species of tube-building polychaetes associated with higher species richness and abundance, compared to sediment without tubes (Callaway 2006). Effects of tube-builders are not limited to widespread variation either. While groups of 2-5 tubes had a greater effect on the community, single tubes have measurable effects on individual species as well (Callaway 2006). The results of these studies indicate the potential exists for maldanid tube-builders to shape small-scale environmental variation and differences in community composition.

The bamboo worm, *Clymenella torquata*, is a tube-building maldanid polychaete that deposit-feeds head down in sand to muddy sands in inter- and subtidal environments. Its common name is derived from its long, cylindrical segments and truncate ends that give it, like many of the maldanids, the appearance of a stalk of bamboo. The genus *Clymenella* can be identified within the family by the membranous collar on the anterior margin of the fourth setiger that extends up to cover part of the third setiger (Mach et al. 2012). Populations exist in one of two color morphs, either green or orange. Green *C. torquata* obtain their color by consuming cyanobacteria, while orange color morphs, such as those within this study's populations, are a result of consuming photooxidizable yellow-orange pigments, possibly carotenoids (Mangum 1964). Populations of *C. torquata* can be found along the eastern coast of North America, a habitat range extending from the Gulf of St. Lawrence to the Gulf of Mexico (Sanders et al. 1962). Larvae typically settle in stable, well-sorted sediments (Mangum 1964) in the inter- and

subtidal zones, in areas where the median particle size of the substrate is between 0.2 and 0.32 mm and where the salinity remains above 25°/oo (Kenny 1969). Larvae are primarily bottom dwelling, moving along the substratum until settling permanently around 14 days of development (Sanders et al. 1962). Adult *C. torquata* are sessile, often burrowing where they settle, forming tubes with a lining of woven strands of mucus (Zorn et al. 2006) and do not move unless the sediment is displaced (Du Clos et al. 2013).

While *C. torquata* occasionally occurs in low densities, particularly in muds, it is most commonly present in large, discrete populations in intertidal sandflats (Du Clos et al. 2013). Patches often have defined borders, making it possible for an area to transition from outside the bed to inside of it within the distance of a meter (Fig. 1), and can have densities of individuals up to 615 m^{-2} (Rhoads 1967); some populations have been reported as containing up to 1500 individuals m^{-2} (Craig 1998). The number of individuals in these populations is a visual usually compared to a "mat of spaghetti" in the sediment (Sanders et al. 1962), due to the color and close proximity of the tubes (Fig. 2). Populations of *C. torquata* can persist for many decades (Don Rhoads, *pers. comm*). One of the sites sampled by this study has a population that has existed continuously since at least 1975, and shows no signs of deteriorating (Glenn Lopez, *pers. comm*). These observations of population longevity and bed discreteness indicate that once some threshold has occurred, patches of *C. torquata* can be remarkably self-perpetuating.

The size and persistence of these beds is particularly interesting when the bioirrigation and potential sediment reworking of infaunal species is considered. Like other maldanids, *C. torquata* is a head-down deposit feeder, building tubes that extend from the surface to their feeding depth of 15 to 20 cm (Dobbs and Whitlatch 1983). In addition to incorporating sediment into tubes, they selectively ingest fine sediment particles (< 1 mm) (Featherstone and Risk 1977)

and egest unconsolidated fecal matter at the surface, resulting in a coarsening of the sediment at their feeding depth and the formation of a shell lag layer (Rhoads and Stanley 1965). In Barnstable Harbor, *C. torquata* has been documented as overturning sediment from the surface to an average depth of 20 cm at a rate of 274 ml yr^{-1}, per worm (Rhoads 1967). At a density of 615 m^{-2}, *C. torquata* is capable of reworking 168.5 liters m^{-2} $year^{-1}$ (Rhoads 1967). In warmer climates, this number may be even higher – up to twice this rate has been estimated from populations in Beaufort Harbor, NC (Rhoads 1967). In places of high densities, this can be a significant contribution to overall sediment cycling and the accompanying geochemical processes. Bioturbation by *C. torquata* has been shown to increase the flux of dissolved nutrients such as nitrate, iron and phosphate (Weinberg and Whitlatch 1983) and to modify the porewater hydrogen sulfide concentration at depth (Fuller 1994), as well as to reduce the quantity of particulate organic matter (POM) at the SWI (Weinberg and Whitlatch 1983). *C. torquata* has also been shown to significantly increase microbial presence and activity at depth (Dobbs and Whitlatch 1982). Indeed, due to the effect *C. torquata's* activities have on physical and chemical processes within the sediment, it has been described as a geochemical keystone species (Waldbusser et al. 2004).

Craig (1998) investigated the specific biogeochemical impact of *Clymenella torquata* at one of the two sites this study will be examining. The author found that the multiple empty tubes present within a bed, often as many as three times the number of worms, are not relic structures and are actively maintained by the worms. These empty tubes function as conduits, connecting the surface to a secondary oxidized layer at feeding depth, creating a confined biological micro-aquifer. While sediment permeability between tubes is lowered, *C. torquata* increases the overall permeability of the seabed due to their vertical tubes and a large zone of increased permeability

at feeding depth (Craig 1998). As a result, there is a much higher rate of oxygenation of the sediment in and around the feeding pockets. In addition, there is nearly four times the concentration of bioavailable organic matter within the bed compared to the adjacent sediment and absorption efficiency (which determines the bioavailability of organic matter to *C. torquata*) increases with depth within the bed, decreasing with depth outside of it (Craig 1998). This increase in the presence of bioavailable organic matter is a result of three main factors. 1) POM and dissolved organic matter (DOM) are trapped from water advected through the permeable sediment. Typically, local exchange occurs between the benthic environment and the overlying water, with particles moving back and forth across the SWI through advective or diffusive mixing. Because of the abundance of vertical tubes that act as conduits in *C. torquata* beds, non-local exchange can occur, resulting in the direct injection of organic matter from surface to depth. This dominates particle transport in *C. torquata* beds (Craig 1998). 2) Particles are trapped by open tubes – especially particles moved as bedload. 3) *C. torquata* perform a behavioral action termed "hoeing" (Dobbs and Whitlatch 1982), where the posterior end of the worm is extended out and scraped along the surface of the sediment towards the tubes. The particles collected from this action can be ingested or used for tube construction. This action may also explain the presence of diatoms in gut analysis of *C. torquata*, as they are typically contained in surface sediment (Dobbs and Whitlatch 1982).

Increased concentrations of organic matter in the sediment in combination with increased rates of porewater advection and oxygen supply may further impact the productivity of the sediment through the provision of nutrients to microphytobenthos (MPB) living at the sediment surface. Populations of diatoms and other microalgae constitute a major food source for deposit feeders in otherwise carbon-poor sandy sediments (Sanders et al. 1962; Craig 1998). While Craig

(1998) has shown that beds of *C. torquata* are enriched in organic matter, and organic matter at depth, as compared to adjacent sediment, surficial MPB still contribute to the diets of benthic infauna, as evidenced by their presence in the gut analysis of *C. torquata* (Featherstone and Risk 1977), likely drawn into the sediment to feeding depth by "hoeing" at the surface (Dobbs and Whitlatch 1982). It is known that both microalgal populations and *C. torquata* are often found in low-energy beds of sand (Sanders et al. 1962; Featherstone and Risk 1977), and that the tubes of polychaetes like *C. torquata* are a contributing factor to sediment stability (Woodin et al. 2010). It is also known that abundance of diatoms increases in the presence of polychaete tubes (Luckenbach 1986) and studies acknowledge that a diatom mat will often form in beds of *C. torquata* (Campbell 2012), but few have examined the relationships between the two.

Despite the evidence that *C. torquata* modifies the sedimentary habitat with respect to sediment permeability, porosity, oxygenation and organic matter content, few studies have examined their impact on the benthic community. Studies that have looked at relationships between *C. torquata* and other organisms have typically focused on single species commensalism. The bivalve *Gemma gemma* has been shown to co-exist with *C. torquata* beds at high densities (Weinberg 1984), and to grow at a faster rate in the presence of *C. torquata* (Weinberg and Whitlatch 1983). These two papers theorized that populations of *G. gemma* may be facilitated by increased microfloral populations due to an increase of nutrients pumped from pore water into the overlaying water, stimulated by worm activity (Weinberg and Whitlatch 1983; Weinberg 1984). *C. torquata* has also been positively correlated with numbers of the bivalve *Kelliopsis elevata* (originally *Montacuta elevata*) (Gage 1966), and the amphipod *Listriella clymenellae* (Sanders et al. 1962), both of which live commensally within *C. torquata* tubes. In fact, both *A. elevata* and *L. clymenellae* are rarely found outside *C. torquata* tubes and

when displaced, will actively burrow or search along the surface (for *K. elevata* and *L. clymenellae*, respectively) for a tube to inhabit (Sanders et al. 1962). In the light of the well-supported notion that tube building polychaetes can enhance local diversity and abundance, and that *C. torquata*, like many maldanids, is an ecosystem engineer (*sensu* Jones et al. 1994), it is clear that work is needed to examine the relationships between *Clymenella torquata* and benthic communities in intertidal sandflats.

Objectives:

There are two main objectives of this study. The first is to determine the patterns of macrobenthic community composition, abundance and diversity in relation to *Clymenella torquata* abundance along an intertidal transect. The second is to determine the concentration of surficial MPB, and how microalgal biomass changes in response to *Clymenella torquata* abundance. I hypothesize that 1) Due to higher concentrations of organic matter and increased oxygen supply within *Clymenella torquata* beds as a result of their sediment bioengineering, there will be a higher abundance and diversity of benthic organisms within the *Clymenella torquata* patch; benthic species abundance and species diversity will be positively correlated to *C. torquata* abundance, although variation in response amongst species is expected. And that 2) Due to the increase in sediment nutrients as a result of the breakdown of the organic matter found in higher concentrations in *Clymenella torquata* beds, fertilization of surficial MPB will be stronger than grazing effects, leading to an increase in surficial MPB standing stocks with abundance of *Clymenella torquata*. Ultimately, the intention of this study is to demonstrate whether *C. torquata* not only has an effect on the geochemical functioning of an area where it is prevalent, but that these changes accompany significant biological changes.

Methods and Materials

Study Site

Sampling was conducted over a two month period from mid-September to late-October, 2014. 50 core samples were taken at two different study sites of comparable sizes and physical condition for a total of 100 samples. Sampling at two separate sites served as a way to replicate trends. The sites are discreet and non-continuous, on either side of the Shinnecock inlet. Site one is an intertidal sand flat just east of Ponquogue Bridge. Site two is eastward down the beach from Shinnecock East County Park (Fig. 3). Both sites are large intertidal sand flats located on the south shore of Shinnecock Bay, Long Island, NY. Temperature ranges from 0 to 30 °C annually. Salinity varies between 23°/oo and 34°/oo. The sediment is a medium to fine grained sand (220 ± 15 µm) (mean ± SD) with the exception of sediment from *C. torquata's* feeding depth where coarse material tends to accumulates (350 ± 160 µm) (Craig 1998). Tidal amplitude near the study sites averages 2.4 m (measurements taken over a month period from tide charts near Ponquogue Bridge, Shinnecock Bay, October 2016) (tides.mobilegeographics.com) and the tidal velocity at the inlet averages 4.6 meters/second (nctc.fws.gov). All cores were taken in the intertidal region of the flat which was aerially exposed for up to 4 hours of each tidal cycle, depending on the direction and magnitude of the winds and tides.

Field Sampling

Samples were taken along two transects parallel to the water line, with a distance of 5 meters between transects and from core to core, resulting in a grid pattern. Transects were

positioned in relation to the bed so that samples were taken both within and outside the *C. torquata* bed, to ensure at least some of the samples would contain no *C. torquata*. Clear polycarbonate cores with a 7.0 cm inner diameter were inserted to a depth reaching the lag layer, roughly 34 cm. Sediment-filled cores were pulled out and their contents sieved *in situ* with a 500 micron sieve, and contents were preserved in a 5% buffered formaldehyde-seawater mixture containing rose bengal.

The biomass of surficial MBP was measured through the proxy of surface chlorophyll-*a*. Samples were collected with a core 1.4 cm internal diameter from the top 1 cm of sediment. Chlorophyll-*a* samples were taken from the sediment several centimeters adjacent to the location of the sediment cores, prior to core insertion. Chlorophyll-*a* samples were placed immediately on ice in the dark, by way of a cooler in the field, then were transferred to a freezer once processed back at the laboratory at Stony Brook.

Lab analysis

Sieved sediment samples were transferred to a 70% ethanol solution before sorting and counting benthic fauna. For each core, all macrofaunal organisms were identified and counts were taken of the number of species and individuals present. All organisms were identified to the family level. Some organisms could not be identified past family, and some could only be specified to genus. In those cases where a more specific designation could not be made, a system was created to label species so as to be able to identify them as compared to other organisms in the samples, usually by assigning a set of letters to be included post-genus or family designation. Sizes of *C. torquata* were recorded in mm diameter across the fourth setiger (directly behind the membranous collar) and reported as a maximum size per core and an average size per core.

For surficial chlorophyll-*a* analysis, wet sediment samples were extracted with 10ml of 100% acetone, shaken, then placed in the freezer. Once the chlorophyll-*a* was extracted, samples were stored in the freezer until analysis. Samples were analyzed using spectrofluorometry (Lorenzen 1967), using a dilution of 1ml extracted chlorophyll in 9 ml of acetone. Chlorophyll values were calculated as the amount in µg Chl-*a* cm^{-3} of surficial sediment.

Data Analysis

Species count data were used to calculate density, species richness, and diversity. Each core was considered a sampling unit. Species density was calculated as the number of individuals per cm^2. Species richness was measured with Menhinick's index (D). D was calculated using the formula:

$$D = \frac{Number\ of species}{\sqrt{Number\ of\ individuals}}$$

Diversity was calculated using the Shannon-Wiener index for diversity (H'):

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

where S is equal to the total number of species in a sample (richness) and Pi is the proportion of individuals belonging to the *i*th species in the data set.

Community similarity, which measures the number of species that are the same in two chosen samples, was calculated to quantify how composition changes from one core to another. Community similarity was calculated using Sørensen's coefficient (Sørensen 1948):

$$CC = (2C)/(S1 + S2)$$

where CC is community similarity (or coefficient of community), S1 is the total number of species in the first sample, S2 is the total number of species in the second sample, and C is the number of species that the two samples have in common.

Density, richness (D), diversity (H') and community similarity were analyzed using multiple regression with Microsoft Office Excel 2012 software. Density, richness, and diversity were calculated both with and without *C. torquata* in order to ensure that changes in those measures were not being significantly determined by *C. torquata* alone. Density and richness were log (x+1) transformed for use in multiple regression, as were the measures of Chl-*a* and abundance of *C. torquata*. For all tests, a p value of < 0.05 was required for significance.

Species abundance and composition data were analyzed using statistical software PRIMER7 (Clarke and Gorley 2015). Before analysis with PRIMER7, the data matrix of all benthic species was square-root transformed in order to down-weight abundant species. The Bray-Curtis index was calculated between each possible pair of samples. Differences in the community composition were described using ANOSIM, CLUSTER, and SIMPER analysis (Clarke 1993). ANOSIM analysis tests for statistically significant differences in species abundance data for chosen factors – in this case *C. torquata* abundance. CLUSTER analysis, using the SIMPROF test, can be used to sort abundance data into statistically significant groupings when no *a priori* group structure is defined. SIMPER analysis breaks down the contribution of each species to the observed similarity between samples. Community composition results were visualized using non-parametric multi-dimensional scaling (nMDS) (Clarke 1993).

Results

Clymenella torquata numbers throughout the patch was not characterized by any specific pattern; abundance varied along the four transects between 0 to 30 individuals per core. In sampling, as effort was made to collect samples both within and outside the patch. The western edge of Site 1 and the eastern and western edges of Site 2 as well portions of the higher tidal transect all included cores that would be considered outside the patch. However, because density of *C. torquata* was shown to vary in cores from within the patch, and even some cores from outside the patch had *C. torquata* present, for ease of consideration, designations of "inside" and "outside" were dropped, in favor of considering abundance of *C. torquata* alone. *C. torquata* abundance per core was significantly higher within Site 1 (M=8.28, SD=7.12) as compared to Site 2 (M=2.02, SD=2.45, $t(98) = 5.88$, $p < 0.001$), and towards the lower tidal line (M=3.8, SD= 6.14) than the higher (MD=6.5, SD=5.94, $t(98) = 2.24$, $p < 0.05$), but large individual clusters of the species are present throughout both study sites (Figs. 4 and 5).

In total, 89 different species were identified across the two sites, with a sum of 49,697 individuals. Most abundant species included five members of the family *Syllidae* (average abundances per core ranged from 241 to 8, depending on the species), ostrocods ($\overline{x} = 30$ per core), one species of *Capitellid* ($\overline{x} = 7$), and two species of marine oligochaetes ($\overline{x} = 21$ and $\overline{x} = 15$). Other common species included *Streblopsio benedicti* ($\overline{x} = 14$), *Lumbrineris spp.*, ($\overline{x} = 10$), *Nereis grayi* ($\overline{x} = 8$), and *Gemma gemma* ($\overline{x} = 6$). Species distributions, and how they relate to *C. torquata*, are discussed further in the results, in relation to SIMPER analysis. The data sets for calculated species density ($t(198) = 0.12$, $p > 0.05$), richness ($t(198) = 0.838$, $p > 0.05$) and diversity (H') ($t(198) = 0.578$, $p > 0.05$) were not significantly different when calculations

included *C. torquata* in the data set and when they did not – calculations that included *C. torquata* were used in all subsequent statistical tests.

Scatterplots revealed weak linear relationships between the calculated values of density, richness (D), diversity (H'), community similarity (CC) and *C. torquata* abundance. Log-transformed density increased with *C. torquata* abundance (2.73 min/43.21 max, for untransformed values), with an R^2 of 0.287 (Fig. 6). Log-transformed species richness decreased with *C. torquata* abundance (1.76 max/0.44 min for untransformed values), with an R^2 of 0.145 (Fig. 7). Diversity (H') over all 100 samples had no definitive pattern (with an R^2 less than 0.001) (Fig. 8), as did diversity for Site 1 (n=50, $R^2 < 0.001$) (Fig. 9). However, diversity for Site 2 (n=50) displayed a general decrease in diversity as *C. torquata* abundance increased, with an R^2 of 0.372 (Fig. 10). Community similarity increases only slightly in relation to *C. torquata* with an R^2 of 0.048.

Multiple Regression Tests on Macrobenthic Species Measures

Multiple regression was used to predict species density, richness (D), diversity, and community similarity based on independent variables of *C. torquata* abundance, average and maximum size of *C. torquata*, site location (Site 1 or Site 2), tidal elevation (low or high), position along the transect (1 to 25), and Chl-*a* density (μg cm^{-3}). The variables of maximum size ($r(98) = 0.465$ $p < 0.01$), average size ($r(98) = 0.283$, $p < 0.01$), and Chl-*a* ($r(98) = 0.319$, $p < 0.01$) were all significantly correlated with *C. torquata* abundance; maximum size and Chl-*a* were positively correlated, and average size was negatively correlated with *C. torquata* abundance. Multiple regression tests were run with a single dependent variable – either density, richness, diversity, or community similarity – with the entire set of independent variables. Non-

significant predictors were discarded until the model reflected the best R^2 with the most significant predictors.

For macrofaunal density, the best regression model was found with the variables of *C. torquata* maximum size and *C. torquata* abundance ($F(2,97) = 45.109$, $p < 0.001$), with an R^2 of 0.482. Predicted species density is equal to 0.851 + 0.277 (*C. torquata* abundance) + 0.056 (*C. torquata* max size). Both *C. torquata* abundance and maximum size were significant predictors of density ($p < .05$).

For species richness (D), the best regression was found with the variables of *C. torquata* maximum size, *C. torquata* abundance and site location ($F(3,96) = 9.194$, $p < 0.001$), with an R^2 of 0.223. Predicted species richness was equal to 0.333 + 0.017 (site location) – 0.05 (*C. torquata* abundance) – 0.009 (*C. torquata* max size). Only *C. torquata* abundance was a significant predictor of species richness ($p < 0.001$). Maximum size ($p = 0.222$) and site ($p = 0.139$) were not significant. When regressed as the only predictor, *C. torquata* maximum size was significant ($p < 0.001$) with an R^2 of 0.192 ($F(1,98) = 16.526$, $p < 0.001$). When *C. torquata* abundance and maximum size were regressed together ($F(2,97) = 12.523$, $p < 0.001$), only *C. torquata* abundance was significant ($p < 0.05$) with an R^2 of 0.205. Site was not a significant predictor when regressed alone ($p = 0.291$) ($F(1,98) = 1.129$, $p > 0.05$).

For diversity (H’), the best regression was found with the variables of *C. torquata* abundance, *C. torquata* maximum size, site location, and tidal elevation ($F(4,95) = 8.649$, $p < 0.001$), with an R^2 of 0.267. Predicted diversity was equal to 1.718 – 0.082 (*C. torquata* max size) + 0.131 (tidal elevation) + 0.285 (site location) – 0.180 (*C. torquata* abundance), where tidal elevation is coded as high or low, and site location is coded as 1 or 2. Both site location ($p < 0.001$) and tidal elevation ($p < 0.05$) were significant predictors of diversity, with *C. torquata*

abundance and maximum size near significance ($p = 0.087$ and $p < 0.065$, respectively). When regressions were run with site location, tidal elevation, and either *C. torquata* abundance or maximum size, all predictors were significant for both models ($p < 0.5$). When a regression was run with site, elevation and *C. torquata* abundance ($F(3,96) = 10.11$, $p < 0.001$) R^2 is 0.24. When a regression was run with site, elevation and *C. torquata* maximum size ($F(3,96) = 10.317$, $p < 0.001$) R^2 is 0.244.

Community similarity (CC) was not well represented by multiple linear regression, with the best model found with the variables of average size, position along the transect, Chl-*a* and *C. torquata* abundance ($F(4,95) = 2.666$, $p < 0.05$), with an R^2 of 0.101. Predicted community similarity was equal to 0.706 - 0.002 (position) - 0.016 (average size) + 0.048 (Chl-*a*) + 0.05 (*C. torquata* abundance). All four predictors were significant ($p < 0.05$).

Chlorophyll-a Analysis

Density of Chl-*a* (µg cm^{-3}) throughout each study site was not characterized by any definitive pattern. There was a slight west to east increase in density, parallel along the waterline, but there was variation present throughout both study sites (Figs. 12 and 13). Chl-*a* was significantly higher within Site 1 (M=11.86, SD=5.105) as compared to Site 2 (M=9.054, SD=5.056, $t(98) = 2.76$, $p < 0.05$). There was no significant difference between higher tidal elevations and lower elevations ($t(98) = 1.39$, $p = 0.08$). As reported above, there was a significant positive correlation of Chl-*a* with *C. torquata* abundance ($r(98) = 0.319$, $p < 0.01$). A scatterplot revealed a positive linear relationship between abundance of *C. torquata* and Chl-*a* (Fig. 14); Chl-*a* increased as *C. torquata* abundance increases (5.41 µg cm^{-3} min/ 37.36 µg cm^{-3} max, for untransformed values), with an R^2 of 0.134. Multiple linear regression was calculated to

predict Chl-*a* density (µg cm^{-3}), dependent on *C. torquata* abundance, the average and maximum size of *C. torquata*, site location (Site 1 or Site 2), tidal elevation (low or high), and position along the transect (1 to 25). The best regression was found with the variables of *C. torquata* abundance and position ($F(2,97) = 14.884$, $p < 0.001$), with an R^2 of 0.235. Predicted Chl-*a* was equal to 0.795 + 0.166 (*C. torquata* abundance) + 0.007 (position), where position was coded as an integer from 1 to 25. Both *C. torquata* abundance and position were significant predictors of Chl-*a* ($p < 0.001$ and $p < 0.05$, respectively).

Community Species Composition

There was a significant difference in community composition dependent on the presence or absence of *C. torquata* (ANOSIM, $R = 0.473$, $p < 0.001$) (Fig. 15), as well as between Site 1 and Site 2 (ANOSIM, $R = 0.597$, $p < 0.001$) (Fig 16). A two-way nested ANOSIM of site number and whether *C. torquata* was present was also significant ($R = 0.647$, $p < 0.001$). CLUSTER analysis was run on the resemblance matrix of all 100 samples, using SIMPROF analysis to determine statistically significant groupings within the data set, which also showed significant relationships within sites, and between the presence or absence of *C. torquata* (Fig. 17).

Changes in the individual species that account for these differences were analyzed using SIMPER analysis. SIMPER examines the percentage contribution each species makes to the similarity within and the dissimilarity between communities. The grouping with *C. torquata* present had an average similarity of 60.5. *C. torquata* was highly associated with species of *Syllidae* (both *sp. B* and *SG*.) and ostracods, as well as *Nereis grayi* and *Streblospio benedicti* (Table 1). The grouping where *C. torquata* was absent had a similarity of 61.8. *Gemma gemma*

was much more prevalent in the absence of *C. torquata*, as was *Brania sp*. These differences in species contributions were also seen between sites (Table 2). Site 1, with an average similarity of 59.8 had a larger presence of *S. benedicti, N. grayi* and ostracods, as well as *Lumbrineris spp*. Site 2, with an average similarity of 65.5 has a more *Brania spp*. and *G. gemma*.

Non-log (x+1) transformed *C. torquata* abundance ranged from 0 to 30 per core. These abundances were split into levels: absent (0 *C. torquata* per core, n=28), low (1 to 3 *C. torquata* per core, n=23), moderate (4 to 8 *C. torquata* per core, n=27), high (9 to 14 *C. torquata* per core, n=11) and very high (15 to 30 *C. torquata* per core, n=10). There was a significant difference in community composition dependent on the level of *C. torquata* (ANOSIM, $R = 0.361$, $p < 0.001$). A two-way nested ANOSIM of site number and the level of *C. torquata* present was also significant ($R = 0.488$, $p < 0.05$). SIMPER analysis for levels of abundance yielded similar results to the SIMPER analysis between the presence and absence of *C. torquata* (Table 3). Groupings absent any *C. torquata* had an average similarity of 60.8. Both *Brania spp*. and *G. gemma* contributed to those differences. The low grouping had an average similarity of 60.6. Here again, *Brania spp*. was an important contributor, although indicators of the presence of *C. torquata* such as *Syllidae sp. B* and *N. grayi* were also present. Ostracods, *Syllidae sp. B* and *N. grayi* were also contributors to the moderate grouping, which had an average similarity of 63.3, along with *Lumbrineris spp.* These latter three species continued to contribute to both to the high level and very high level grouping, which had an average similarity of 71.8 and 65.4 respectively. Ostracods were not a major contributor to the very high level grouping. *Syllidae sp. SG* was a major contributor to the high and very high groups, as was *S. benedicti* and *Exogone spp. C. torquata* began to contribute to community differences at the moderate level and for all

higher levels as well. The separation in species composition between levels was visualized with a nMDS plot (Fig. 18).

ANOSIM and SIMPER analysis were also used to determine community differences as a result of Chl-*a* density. The non-log (x+1) transformed data set of Chl-*a* values ranged from 3 to 37 µg cm^{-3}. The data set was divided into four levels of Chl-*a* density; low (3 to 7 µg cm^{-3}, n=40), moderate (8 to 12 µg cm^{-3}, n=37), high (13 to 17 µg cm^{-3}, n=16) and very high (18 to 37 µg cm^{-3}, n=10). There was a significant difference in community composition dependent on the level of Chl-*a* present (ANOSIM, $R = 0.094$, $p < 0.001$) (Fig. 19). A two-way nested ANOSIM of site number and the level of Chl-*a* present was also significant ($R = 0.885$, $p < 0.05$). SIMPER analysis identified an average similarity of 58.8 for low levels of Chl-*a* and an average similarity of 56.7 for moderate levels of Chl-*a*, with species such as *Brania sp*., *Gemma gemma* and *Nereis grayi* associated with these lower groupings of Chl-*a* (Table 4). High levels of Chl-*a* had an average similarity of 59.5, while very high levels of Chl-*a* had an average similarity of 62.3. Species common at these higher levels of Chl-*a* include *Exogone sp*., *Lumbrineris sp*., and *Syllidae sp. SG*. *Clymenella torquata* was a contributor to group similarity for only the very high level of Chl-*a*.

Discussion

The objective of this study was to determine if *Clymenella torquata* affected certain biological parameters of the benthos surrounding their tubes, and how those parameters might change with *C. torquata* abundance. Previous studies suggest that *C. torquata* is a geochemical keystone species (Waldbusser et al. 2004), capable of modifying the composition of the sediment surrounding tubes in respect to nutrient availability (Weinberg and Whitlatch 1983), organic material, and oxygen concentration (Craig 1998). There is also evidence to support the potential for *C. torquata* to influence the infaunal populations for the sand beds they reside within; tube builders have been shown to increase species density (Callaway 2006), several species are highly associated with *C. torquata* (Sanders et al. 1962; Gage 1966), and growth of *G. gemma* is facilitated in the presence of *C. torquata* (Weinberg and Whitlatch 1983). Craig (1998), while focusing on chemical processes in the *C. torquata* patch, included a passage in her discussion wherein the author states that she observed a higher diversity and abundance of benthic macrofauna associated with the *C. torquata* bed. Based on the results of this study, it can be concluded that *C. torquata* does have a significant effect on the infaunal community, most likely forming "hotspots" of density where certain species proliferate against a smaller consistent background assemblage.

In order to reach this conclusion, it must first be noted that the distribution of *C. torquata* across the bed was not consistent at the scale sampled. *C. torquata* density varied from core to core, with very high and very low abundances found throughout the bed. While it is known that *C. torquata* tubes are spatially clustered (Craig 1998), the exact distribution of individuals of *C. torquata* within their beds has not been studied, to our knowledge, with densities generally only

reported as individuals per square meter. It was thought going into this study that *C. torquata* density would be uniform throughout the bed, or perhaps would increase towards the center. However, as can be seen in Figs. 4 and 5, there was no discernable pattern in distribution from west to east, although there was a general increase in abundance at the lower tidal elevation for both sites. Because *C. torquata* extends into the subtidal zone, there is the potential that this increase towards the lower tidal elevations would extend under water, and that the true "center" of the bed is located in the subtidal zone, towards which density would increase, but as sampling stopped in the intertidal zone, it is difficult to say. It is also important to note that sampling was conducted with 7 cm diameter cores every 5 meters along the bed. It is possible that a sampling method using larger cores would capture a more even spatial distribution of *C. torquata*. Regardless, despite heterogenous distribution of *C. torquata* there were still discernable patterns associated with *C. torquata* abundance.

Of the four parameters used to characterize the benthic community - density, richness, diversity, and community similarity - density was the measure most strongly affected by *C. torquata*. It had the highest R^2 for both a linear relationship and when accounting for multiple regression. However, *C. torquata* was a significant predictor of all community measures, as determined by multiple regression. Maximum *C. torquata* size was also a significant predictor for all measures except for community similarity, where average size was instead significant. However, both maximum and average size were correlated with *C. torquata* abundance. When considering the effects of multi-collinearity between independent variables, it is worth considering that when regressed separately, *C. torquata* was always a significant predictor, as was maximum size. *C. torquata* abundance had a positive relationship with species density; density increased with *C. torquata* abundance. This can be seen both in the sign of the predictor

and on the scatterplot (Fig. 6). Richness was negatively affected by *C. torquata* abundance; the predictor sign is negative and the trend line is decreasing (Fig. 7). Because density increases and richness decreases as *C. torquata* increases, the species composition near higher levels of *C. torquata* appears to be dominated by a smaller number of species that persist in high density.

Based on the scatter plots of diversity and community similarity versus *C. torquata*, *C. torquata* did not account for a very large portion of the variation present in the data sets (Figs. 8, 11). However, as evidenced by the regression analysis, *C. torquata* was a significant predictor of diversity, along with maximum size, site location and tidal transect. *C. torquata* was also a significant predictor for community similarity, along with Chl-*a* density (which is also positively correlated to *C. torquata*). Like richness, diversity decreases as *C. torquata* increases in abundance (negative sign change in the regression equation). The discrepancy between the multiple regression results and the scatter plot data (where diversity stays fairly constant regardless of *C. torquata* abundance) could be a result of an overall consistent diversity created by a background assemblage of species that is nevertheless decreased in the presence of increasing *C. torquata* abundance. This idea is supported by the community similarity results, for which *C. torquata* abundance was a positive predictor. *C. torquata* positively predicts the level of similarity between samples by cultivating a contingent of species commonly located nearby, while diversity decreases in the presence of *C. torquata* because of the dominance of a smaller number of a select few species. This trend holds when considering the overall diversity data set. However, when considering each site separately, *C. torquata* negatively impacted diversity at Site 2 (Fig. 10), while having no apparent relationship in Site 1 (Fig. 9). This could be because the total abundance of *C. torquata* only reached 9 individuals per core at Site 2 as compared to a high of 30 at Site 1, or that the bed at Site 2 is not as well-established as Site 1, so it has not had

the opportunity to develop the background assemblage of species across the patch, meaning diversity decreases with *C. torquata* along with richness as density of certain species increases in *C. torquata* presence.

What is interesting is when we consider the plots of density, richness, diversity, and community similarity versus *C. torquata* abundance (Figs. 6, 7, 8, 11) if they are fitted with a polynomial trend line versus a linear one. In all cases, the R^2 values for these relationships increase. Density would now increase with *C. torquata* with an R^2 of 0.405, and richness still decreases with *C. torquata*, but with an R^2 of 0.186. While the R^2 values for both diversity and community similarity would also increase when fitted with a polynomial trendline, the R^2 is still low enough for the effect of *C. torquata* on these measures to seem negligible (0.084 and 0.056, respectively). This increase in R^2 values with a polynomial trendline indicates that the relationship between density and richness might be quadratic, with the peak in density associated with moderate to high densities of *C. torquata*, and peak richness negatively associated with moderate to high densities of *C. torquata*. This could be explained by very high densities of *C. torquata* outcompeting even species that are facilitated by their presence, or by causing too much disturbance in active tube maintenance, so that they are the predominant organisms in those places where they reach upwards of thirty individuals in a core.

When considering the specifics of the effects of *C. torquata* on species assemblage, ANOSIM analysis demonstrated that there was a significant difference between samples that contained *C. torquata*, and to a lesser degree, even differences between levels of *C. torquata* abundance. When looking at nMDS plots (Figs. 15, 16 and 18), clear separations can be seen between groups. The clearest delineation is between communities at Site 1 and Site 2, which may be a combination of there being significantly fewer *C. torquata* at Site 2, or simply a difference

in condition due to the separation between sites across the inlet. For *C. torquata* presence (Fig. 15), samples that contain *C. torquata* are clustered together to the right side of the graph, while samples without are clustered to the left, without much overlap between the two groups. This indicates that while site is a determining factor in community assemblages, there is still a difference in community composition when *C. torquata* is present and when it is absent that is different from the differences that can be seen between sites. The pattern evident in the *C. torquata* presence/absence nMDS plot was also present when considering differences between levels of *C. torquata*, with the highest and lowest abundances of *C. torquata* grouped on the right and left sides of the graph (respectively), although there is more overlap between groups, particularly in samples that have high and very high densities of *C. torquata* present. The significance of the separation in community assemblages between Site 1 and Site 2 as well as between the presence and absence of *C. torquata* seen in the ANOSIM and nMDS plots was also present in CLUSTER analysis. Using the SIMPROF test when analyzing data with the CLUSTER routine allows the dendrogram to be interpretable for which groups are statistically distinguishable when no *a priori* group structure has been imposed. Site location and *C. torquata* abundance show clear grouping on the graph (Fig. 17), separated by the black lines that indicate statistically significant support. This diagram indicates that even when the data set is analyzed with a more exploratory test – without groups pre-designated – site and *C. torquata* abundance are still determining factors in the way that benthic species composition is aggregated. Both ANOSIM and CLUSTER analysis together indicate that *C. torquata* was a significant determining factor in community assemblages.

Based on the trends evident in the scatterplots, the multiple regressions, and ANOSIM analysis, as well as the patchy distribution of abundance of *C. torquata* throughout the bed, it

appears as though there was a consistent assemblage of background species that accounted for the majority of the diversity (possibly determined by site), while the presence of *C. torquata* increased the density of a select few species that increased in density as *C. torquata* abundance increased. This supposition is supported when considering SIMPER analysis results, where there was a particular set of species that contributed to every grouping, regardless of factor chosen to analyze (primarily from the families *Syllidae*, *Naididae* and *Capitellidae*) (Tables 1-4). Meanwhile, species associated with *C. torquata* such as *Nereis grayi*, *Syllidae sp SG*, *Lumbrineris spp.*, and *Exogone spp.* increased in their presence, contributing higher and higher percentages to the group assemblage, particularly in the case of *Syllidae sp SG*, where species counts increased into the thousands per core in the presence of *C. torquata*.

An interesting note to make about the community results, aside from how they relate to *C. torquata*, was the relationship between *C. torquata* and *G. gemma*. It is widely considered that these two species coexist (Sanders et al. 1962), and that the growth of *G. gemma* is facilitated in the presence of *C. torquata* (Weinberg and Whitlatch 1983). However, this study found that there was an inverse relationship between the two species; *G. gemma* was most prolific in areas where *C. torquata* was absent, or was present in very low numbers. It can be seen in the SIMPER analysis (Table 3) that *G. gemma* was only a significant contributor to the group with no *C. torquata* present. An unpublished masters thesis also posited this relationship between *C. torquata* and *G. gemma* (Dobbs 1981), where *G. gemma* was negatively correlated with *C. torquata*, indicating that these two species may not be as commensally linked as previously considered. It is possible that *G. gemma* is found in the same areas as *C. torquata*, attracted to the same conditions of low-energy sand beds, and the increased presence of MPB from the nutrient-rich pore water ventilated into the SWI by worm activity, but are precluded from actually

presiding in the patch by some unknown mechanism – either pushed out by other established species, or moved away from small scale high-density aggregations of *C. torquata* due to the long-cited preference of suspension feeders to avoid co-existing with strong bioturbators (Rhoads and Young 1970).

In addition to benthic macrofaunal dynamics, the other objective of this study was to determine how standing stocks of surficial MPB, as measured by Chl-*a*, varied in response to *C. torquata* abundance. It has been previously shown that microalgal mats will form in the presence of *C. torquata* (Campbell 2012), and this study can confirm that they are in fact positively related. Chl-*a* concentrations were shown to increase with increasing abundance of *C. torquata* (Fig. 14), and *C. torquata* was a significant predictor in the distribution of Chl-*a* according to multiple regression analysis. ANOSIM analysis indicates that there was a significant difference between communities when analyzed by the factor of Chl-*a* level, and the nMDS plot for the Chl-*a* levels (Fig. 19) shows sample groupings that are similar to the plot for *C. torquata* levels (Fig. 18). While there are moderate levels of Chl-*a* throughout the site, low levels of Chl-*a* are clustered at the same end of the graph as the groups without *C. torquata*, and the high and very high levels of Chl-*a* are clustered near the right, the same as groups with high densities of *C. torquata*. SIMPER analysis also shows similar species assemblages for the levels of Chl-*a* as levels of *C. torquata* (Tables 3 – 4). For example, *G. gemma* is a significant contributor to communities only where *C. torquata* is absent and where Chl-*a* levels are low. Conversely, *Lumbrineris spp.* is found both with high levels of Chl-*a* as well as high levels of *C. torquata* abundance. Factors that govern MPB standing stock levels are varied and population densities can change for a number of reasons, however these results suggest that standing stocks of surficial MPB are positively related to *C. torquata*, increasing in concentration with *C. torquata*

abundance. Because standing stock of MPB is increasing, fertilization must be occurring at a higher rate than grazing. It is not particularly surprising that fertilization of surficial MPB is positively related to *C. torquata* abundance, based on the high availability of organic matter for decomposition measured in the patch and that increased nitrification suggests enhanced microbial activity in the bed (Craig 1998).

When considering the patterns of species assemblages, one of the main questions asked by the results is the reason behind the proliferation of certain species associated with *C. torquata* abundance. As seen in the results of this study, *C. torquata* distribution is highly aggregated, clustering in abundances varying from 1 to 30 worms per core at different points throughout the patch. Size structure of the population – maximum size per core increases while average size decreases with increasing *C. torquata* abundance – indicates that there is often large individual *C. torquata* per core associated with a contingent of smaller *C. torquata*, which increase in abundance the larger the individual *C. torquata* is. These patterns, along with the size and longevity of *C. torquata* beds, indicate that there is a mechanism of intraspecific facilitation that occurs within the bed, by which community facilitation may be a by-product.

One possibility is the decrease of hydrogen sulfide. It has been shown that *C. torquata* can reduce concentrations of pore water hydrogen sulfide (Fuller 1999). In addition, Fuller (1999) cites both *Streblospio benedicti* and two different species of the genus *Nereis* as being limited by the presence of hydrogen sulfide in feeding activities at much lower threshold concentrations than *C. torquata*. Interestingly, *Streblospio benedicti* and *Nereis grayi* were two of the most common species found where *C. torquata* was abundant, compared to where *C. torquata* was absent (Table 1), indicating that these species may be taking advantage of *C. torquata's* ability to mediate hydrogen sulfide. However, because empty tubes function as

conduits to a secondary oxidized layer within the bed, tidal pumping in addition to bioirrigation provides consistent oxygenation throughout the patch, so hydrogen sulfide may be consistently lowered throughout the patch, which would not explain the increase in macrobenthic density in correlation to *C. torquata* abundance specifically, which is not continuous throughout the patch.

The most likely explanation can be found in the preceding biogeochemical study done by Craig (1998). In her dissertation, Craig (1998) found that there was four times the amount of organic material in the *C. torquata* patch as compared to sediment outside the patch. In addition, she demonstrated that organic matter absorption efficiency (which determines bioavailability of organic matter to *C. torquata*) from ingested sediment by *C. torquata* increased with depth, from 33% at the surface to 73% at feeding depth (as compared to 6% at feeding depths outside the patch). Craig (1998) postulated that sediment structuring by *C. torquata* increased bioavailable carbon throughout the bed as a whole. However, while she noted that *C. torquata* tubes were often aggregated within the bed, her work was more concerned with comparing conditions within the patch to conditions outside, with most of the focus in sampling on creating depth profiles. The results of this study confirm that *C. torquata* are aggregated within the bed. It is possible that the increase in organic material within the *C. torquata* bed is also heterogeneously distributed and is related to *C. torquata* abundance. This is potentially corroborated by the Chl-*a* results. Based on the results of this study, it does seem as though surficial MPB are positively related to *C. torquata* abundance, as measured through the proxy of Chl-*a*. Because higher concentrations of Chl-*a* are likely to be correlated to areas where there is an increased flux of nutrient-rich pore water brought into the SWI, the correlation of Chl-*a* concentration to the abundance of *C. torquata* suggests organic matter availability, and subsequent decomposition, varies with *C. torquata* abundance. The patterns of distribution present in community

macrofauna - species density is positively related to *C. torquata* abundance - are possibly tied to the increase in organic matter facilitated by the activities of *C. torquata* at depth. *C. torquata* may excrete an enzyme that dissolves the mucus coating on microalgae to make it more digestible, or the increase in bioavailable organic matter could be a result of *C. torquata* cultivating a microbial garden, such as other noted bioturbators like *Abarenicola spp*. (Hylleberg 1975). Because the R^2 values for the scatterplots and multiple regressions are relatively low, it is difficult to state with certainty that no other explanations are available for the distribution of community dynamics other than *C. torquata* abundance, however the data provided does indicate a strong likelihood for these patterns.

Bioturbation by infaunal species is now recognized as a type of ecosystem engineering, due to the modification of geochemical gradients and the redistribution of food resources (Kristensen et al. 2012). While studies on the effects of *C. torquata* on the structure of infaunal communities are relatively rare, there are other studies that demonstrate the effects of other tube worm species on community assemblage. Callaway (2006) demonstrated that the terebellid polychaete *Lanice conchilega* was associated with an altered community structure and an increase in overall abundance compared to samples without *L. conchilega* tubes. Levin et al. (1997) showed a similar pattern with community data from the North Carolina slope and the maldanid *Praxiella sp*; data indicated a positive correlation between the abundance of maldanids and the abundance of other infauna. Levin et al. (1997) proposed the term keystone resource modifiers for species like maldanids, due to their ability to rapidly redistribute labile organic matter within the benthos. There is no question that this term could be applied to *C. torquata*, as Craig (1998) showed that there is a large increase in the amount of bioavailable carbon in *C. torquata* patches. *C. torquata* has also been accurately described as a geochemical keystone

species (Waldbusser et al. 2004). As demonstrated in these three and many other studies, *C. torquata* significantly alters the geochemistry of the sediment surrounding their tubes, creating local hotspots of oxygen and organic matter within the sediment, cementing the species' role as an ecosystem engineer (*sensu* Jones et al. 1994). Based on the results of this study, it appears that *C. torquata's* ability to modify the surrounding sedimentary environment is also accompanied by significant biological changes. Moderate to high densities of *C. torquata* are strongly associated with an increase in density of infaunal species, facilitated by the availability of the resources *C. torquata* modifies, certainly in regards to oxygen, but also potentially in the availability of organic matter.

Future Work. To expand our understanding of this species beyond the results of this study, future work would benefit from more consideration of spatial distribution as well as a temporal component. As a comparison of the benthos between sections of the study sites with and without *C. torquata*, a singular time period was sufficient, however, for a more in depth understanding of community dynamics present in these areas, sampling over multiple time periods would be beneficial. It would also be interesting to examine both Site 1 and Site 2 in more detail and as separate from one another, instead of considering them as two parts of the same data pool. Complications arose when considering the significant differences between Site 1 and Site 2, as compared to the presence and absence of C. torquata. Concentrating on a single site would also allow for more focus on small scale spatial distribution of species, perhaps using multiple core sizes to detect the scale of minimal and maximal sample variance. In addition, field and lab studies that examine how conditions and resources – primarily bioavailable carbon - change with *C. torquata* abundance, and how associated species respond, could shed light on some of the mechanisms controlling species density distributions.

Figures

Figure 1. *Clymenella torquata* bed during low tide at site 2. The bed outline is marked by the higher retention of water within the bed than in the adjacent sediment, making the boundary between inside the bed and outside clearly visible.

Figure 2. *Clymenella torquata* tubes in the sediment.

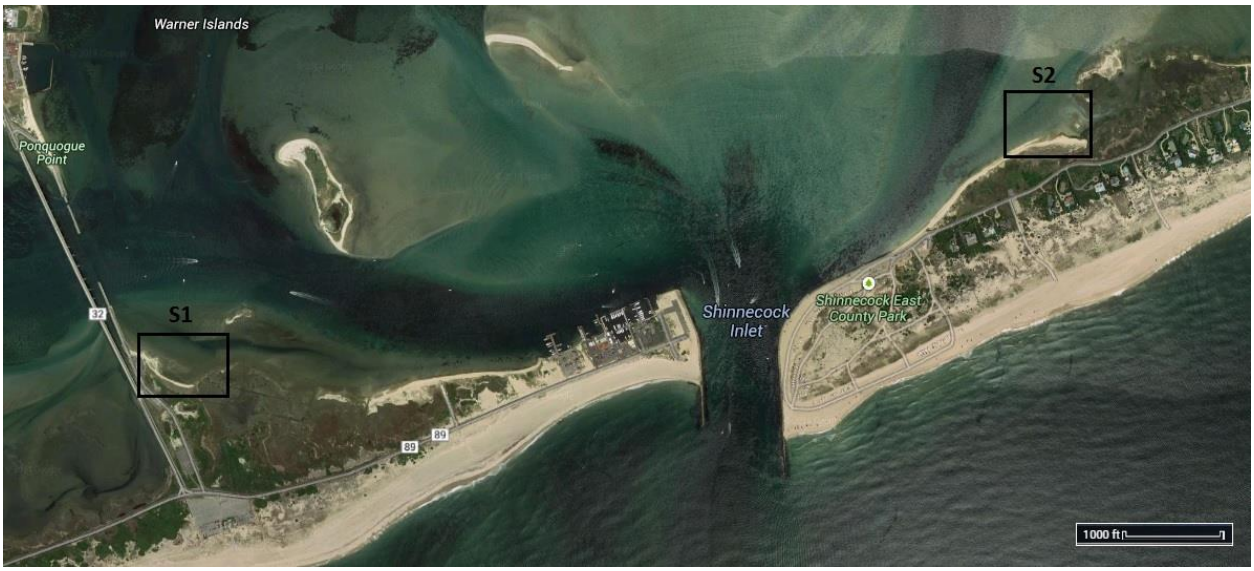

Figure 3. Study sites 1 and 2, located on either side of Shinnecock Inlet.

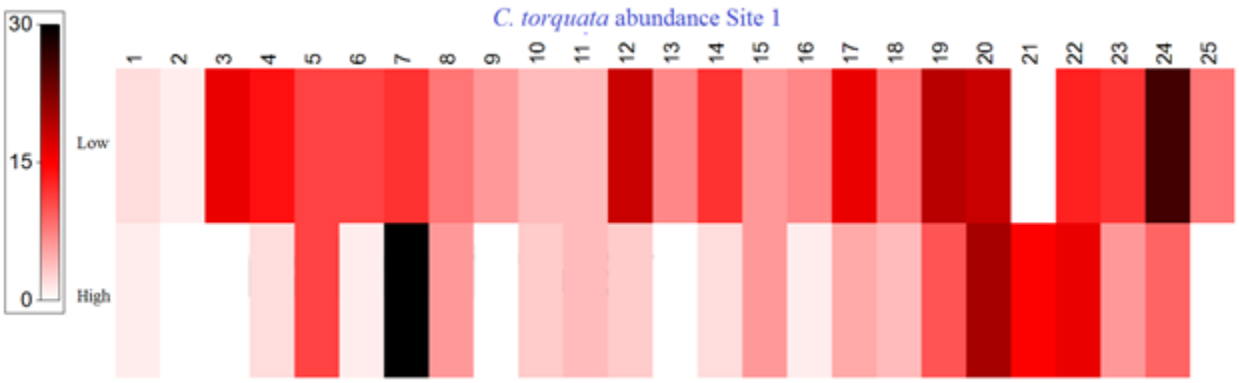

Figure 4. *C. torquata* abundance (individuals/core) for Site 1, Ponquogue Bridge study site (n=50). Low and High refer to tidal elevation. Numbers 1 through 25 are sample numbers; positions along the transect moving west (No. 1) to east (No. 25), facing the waterline.

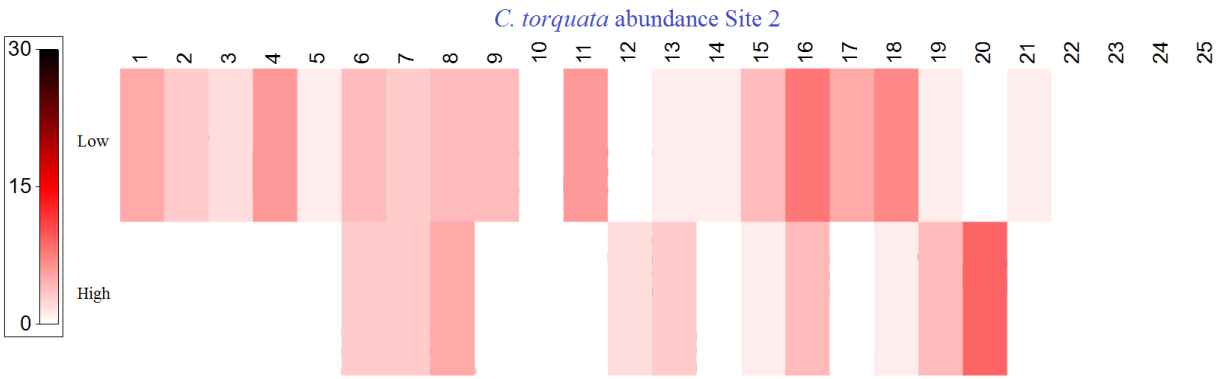

Figure 5. *C. torquata* abundance (individuals/core) for Site 2, Shinnecock East County Park study site (n=50). Low and High refer to tidal elevation. Numbers 1 through 25 are sample numbers; positions along the transect moving west (No. 1) to east (No. 25), facing the waterline.

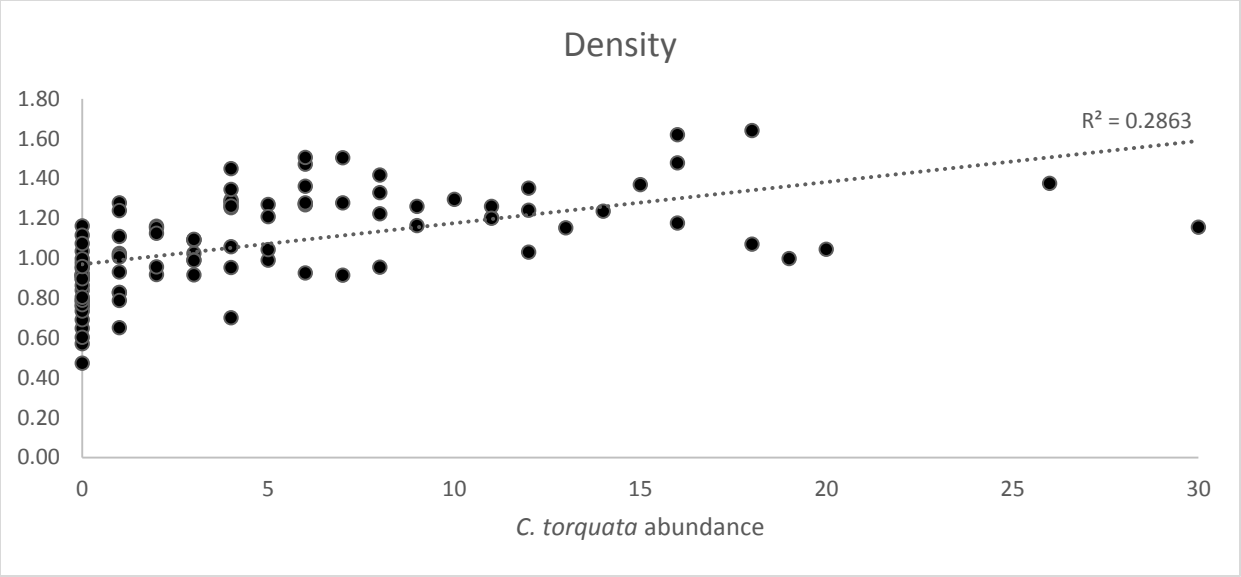

Figure 6. Log (x+1) transformed species density (individuals per cm^2) for both study sites (n=100).

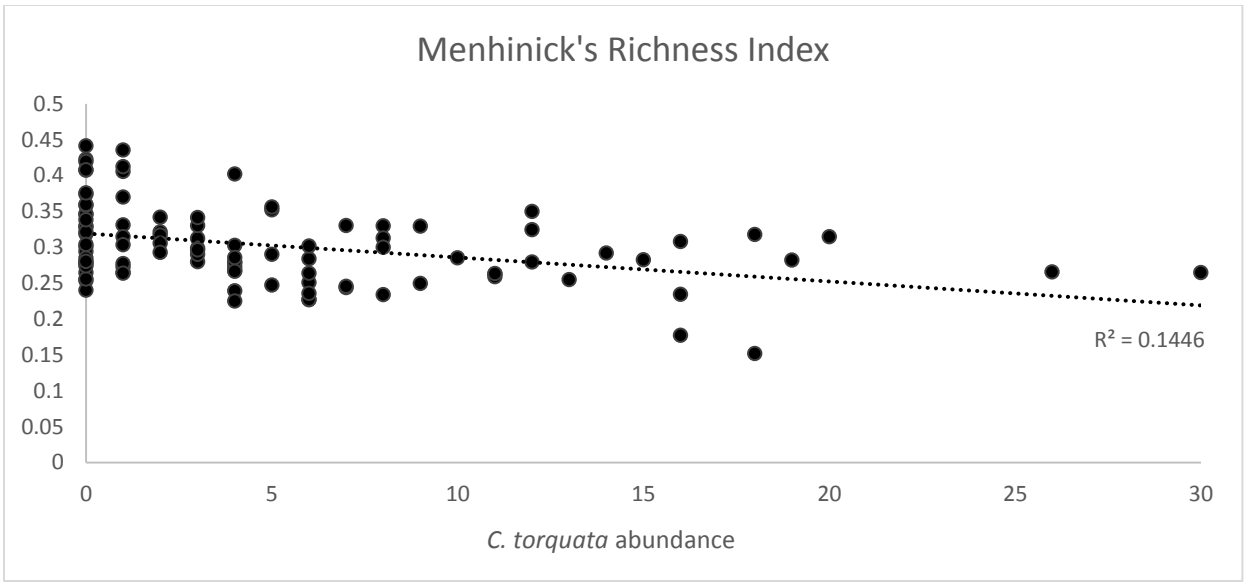

Figure 7. Log (x+1) transformed species richness for both study sites (n=100).

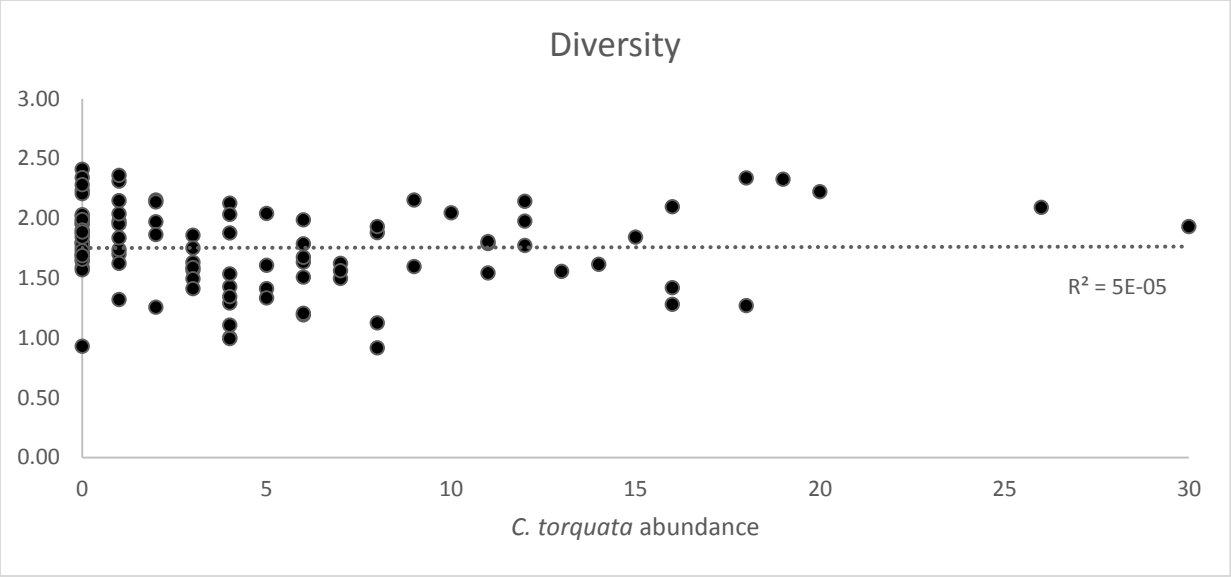

Figure 8. Species diversity (H') for both study sites (n=100).

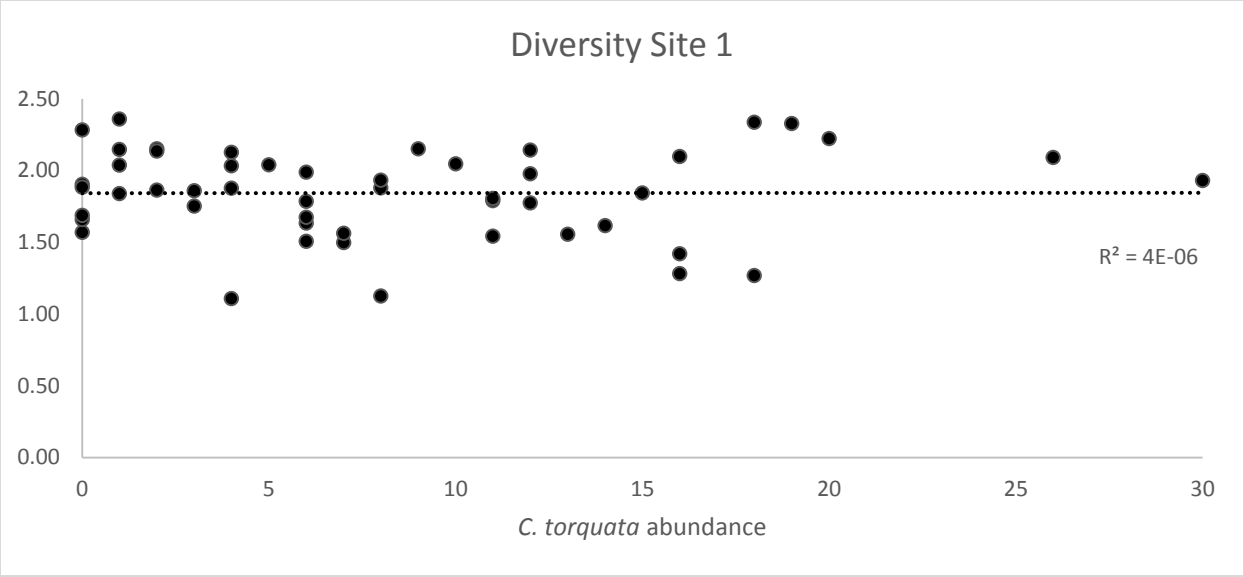

Figure 9. Species diversity for Site 1, the Ponquogue Bridge study site (n=50).

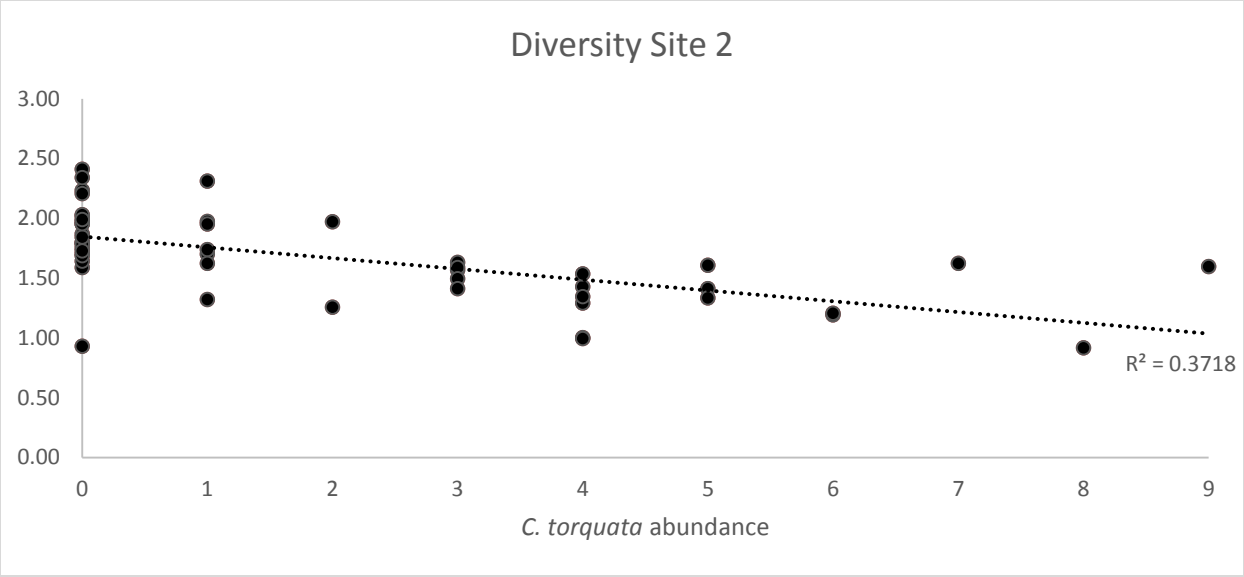

Figure 10. Species diversity for Site 2, the Shinnecock East County Park study site (n=50).

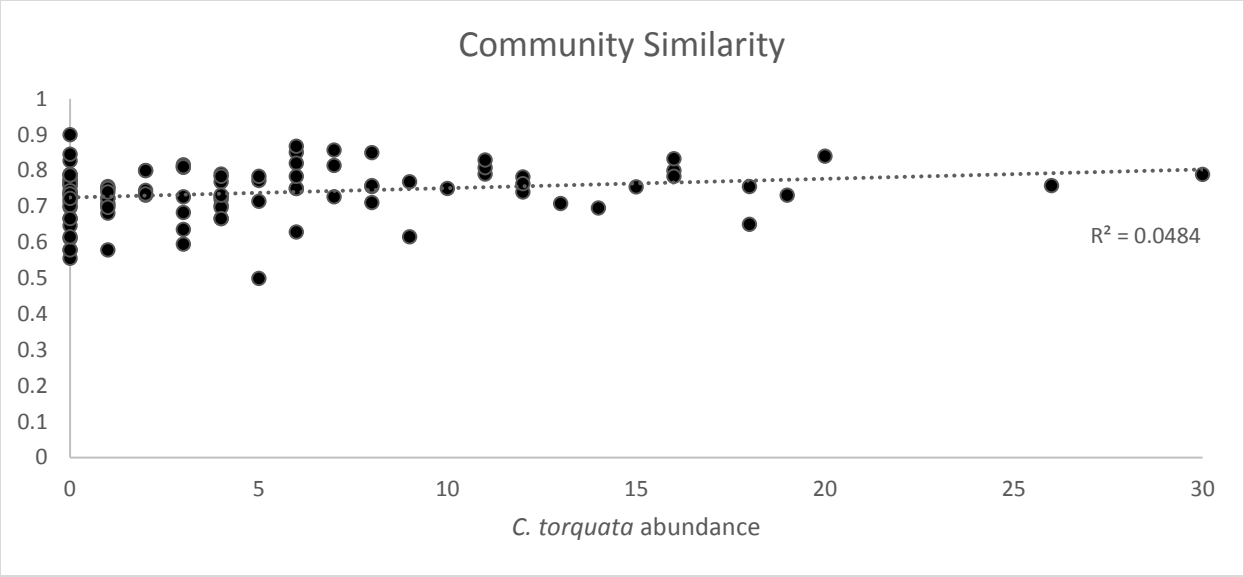

Figure 11. Community similarity, as determined by Sørensen's coefficient, for both study sites (n=100).

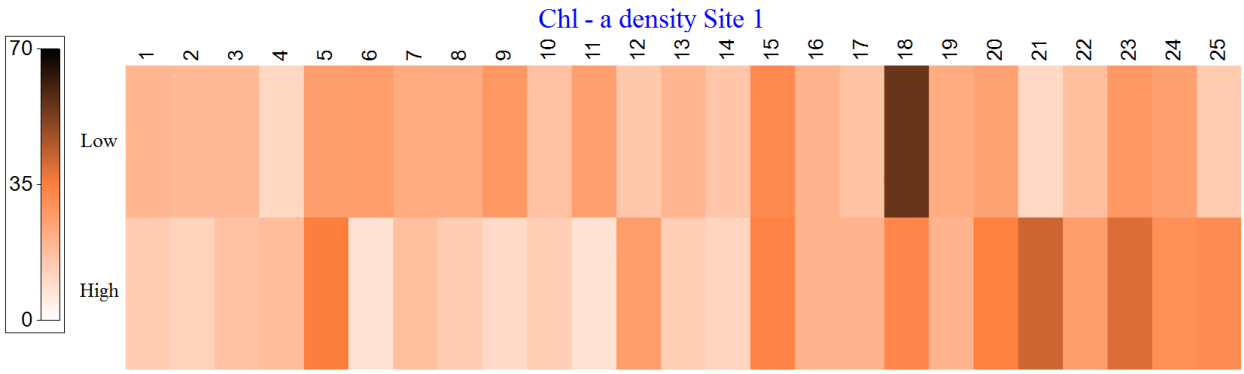

Figure 12. Chl-*a* in µg/cm^3 for Ponquogue Bridge study site (n=50). Low and High refer to tidal elevation. Numbers 1 through 25 are sample numbers; positions along the transect moving west (No. 1) to east (No. 25), facing the waterline.

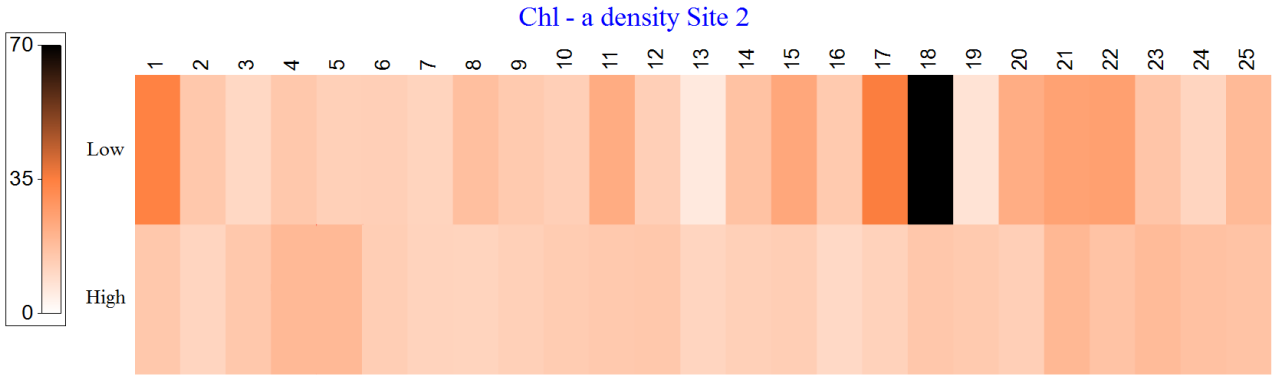

Figure 13. Chl-*a* in µg/cm^3 for Shinnecock East County Park study site (n=50). Low and High refer to tidal elevation. Numbers 1 through 25 are sample numbers; positions along the transect moving west (No. 1) to east (No. 25), facing the waterline.

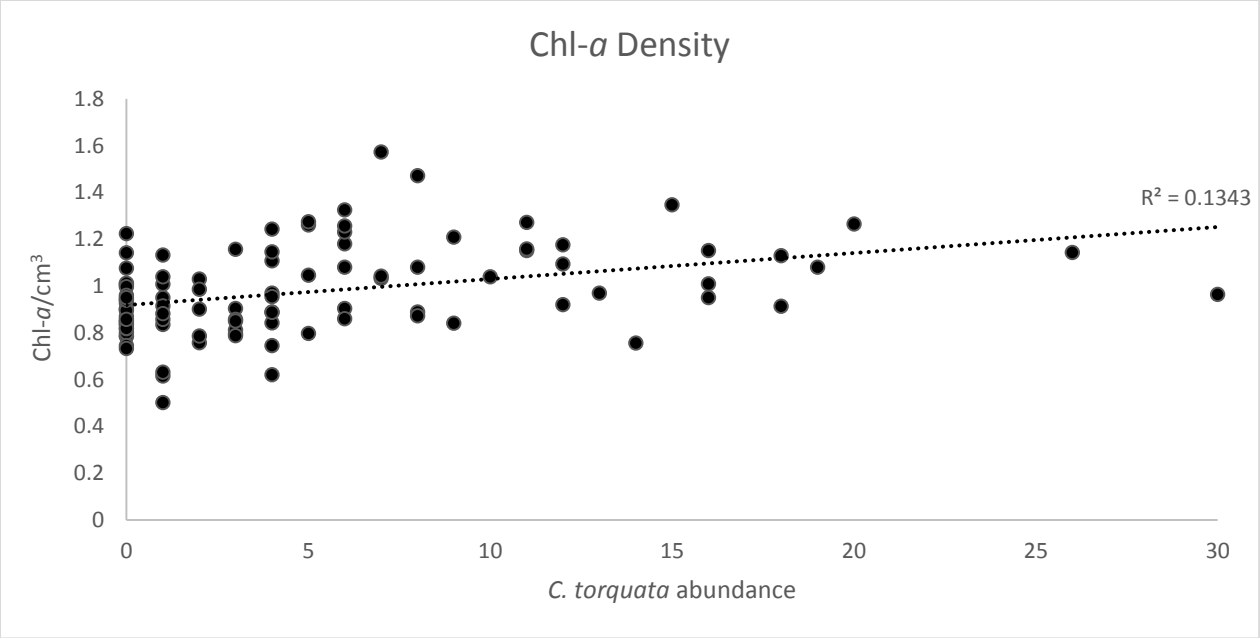

Figure 14. *C. torquata* abundance and log (x+1) transformed Chl-*a* density for both study sites (n=100).

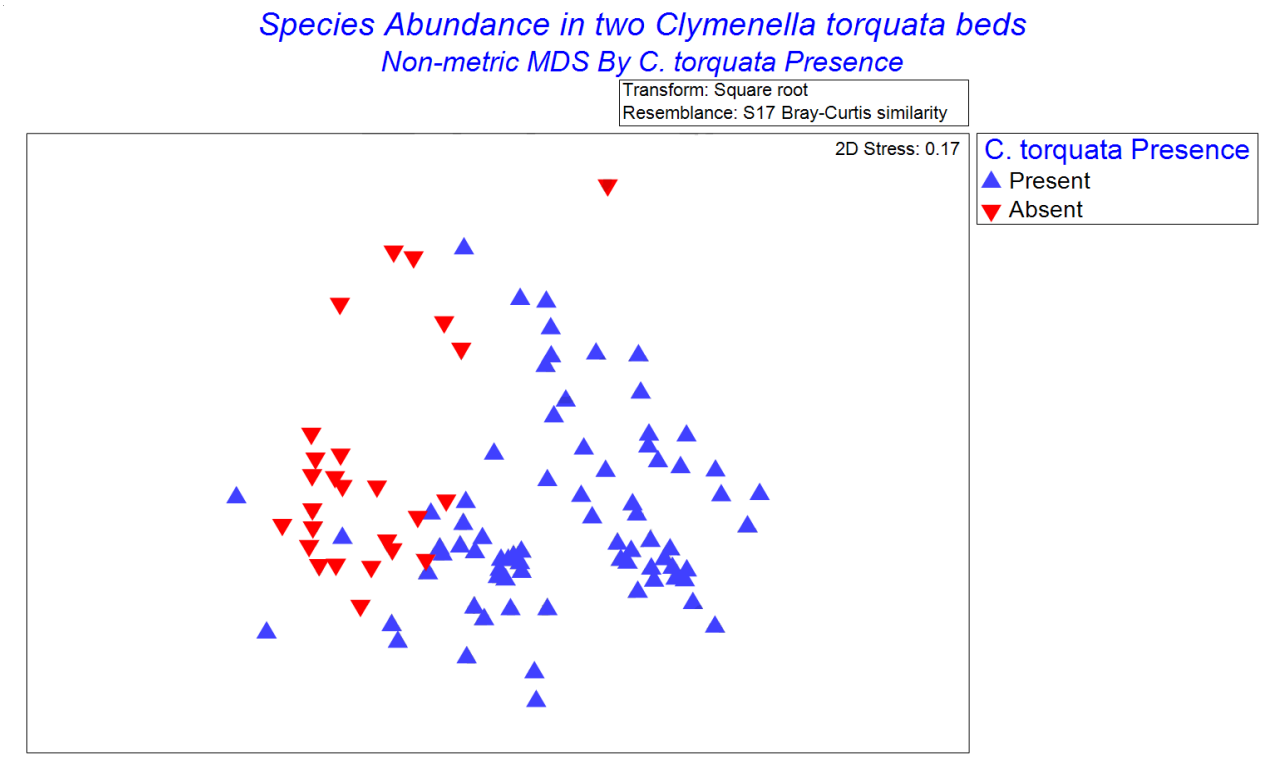

Figure 15. Species composition for both study sites (n=100) as determined by the factor of *Clymenella torquata*. Presence of *C. torquata* is indicated by blue triangles, samples without *C. torquata* are represented by red triangles.

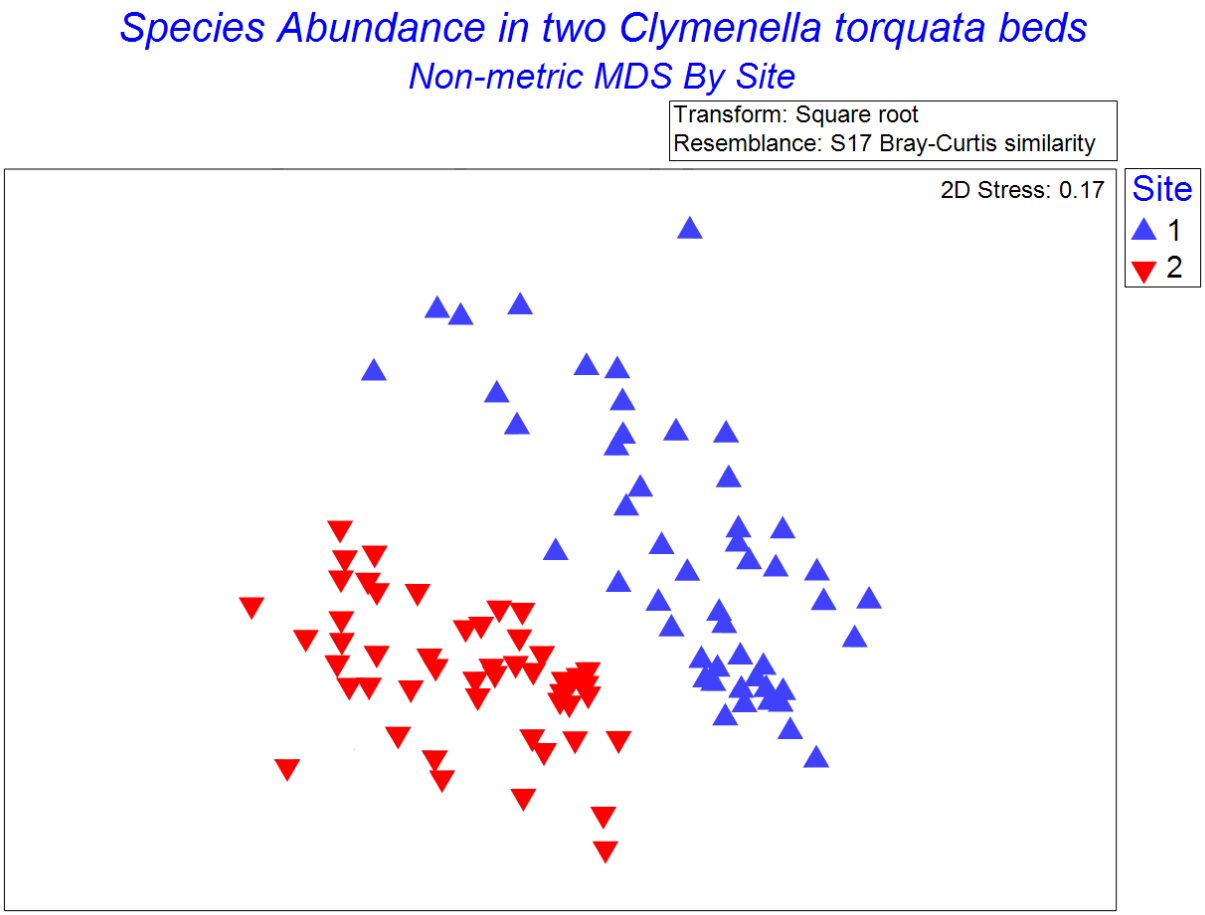

Figure 16. Species composition for both study sites (n=100) as determined by the factor of Site. Site 1 is indicated by blue triangles, Site 2 is represented by red triangles. Data points include cores without *C. torquata* present.

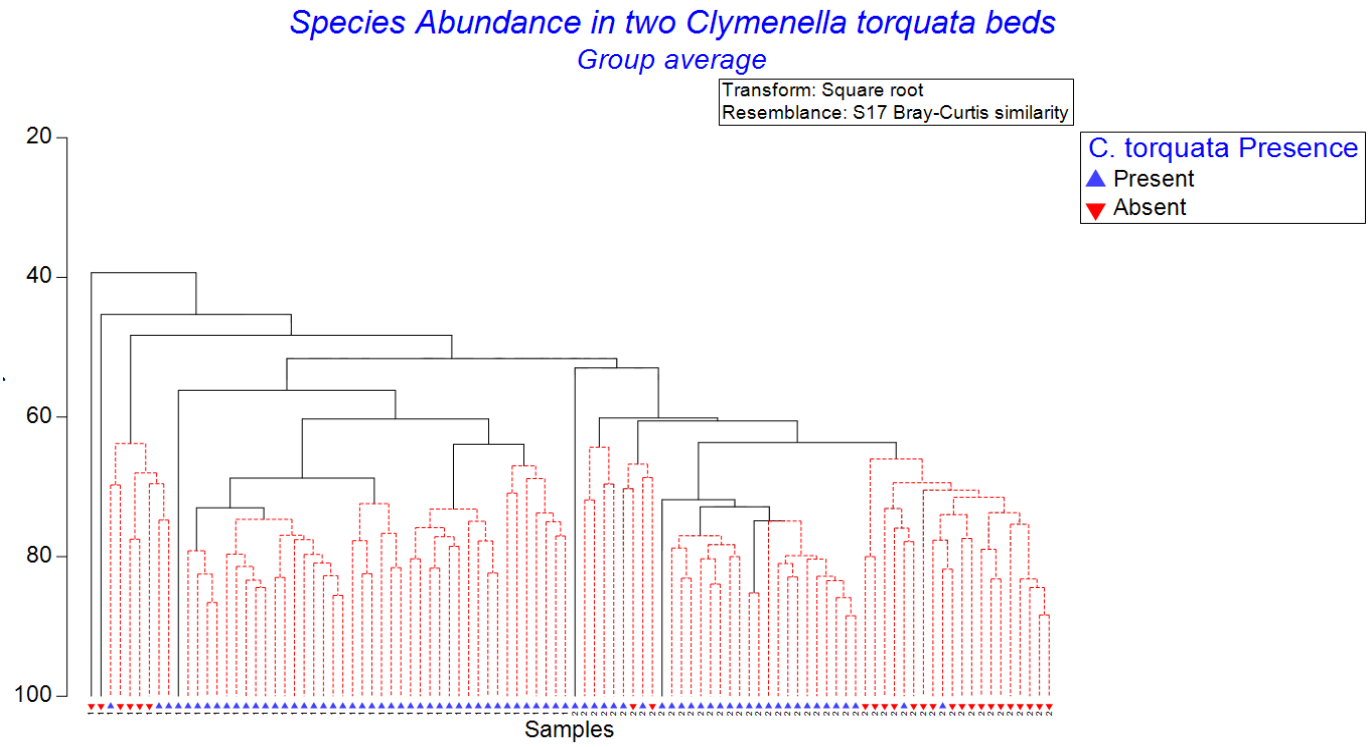

Figure 17. CLUSTER analysis of both sites (n=100). Numbers indicate Site 1 or 2. Black lines represent statistically significant relationships. Red dashed lines are statistically insignificant relationships.

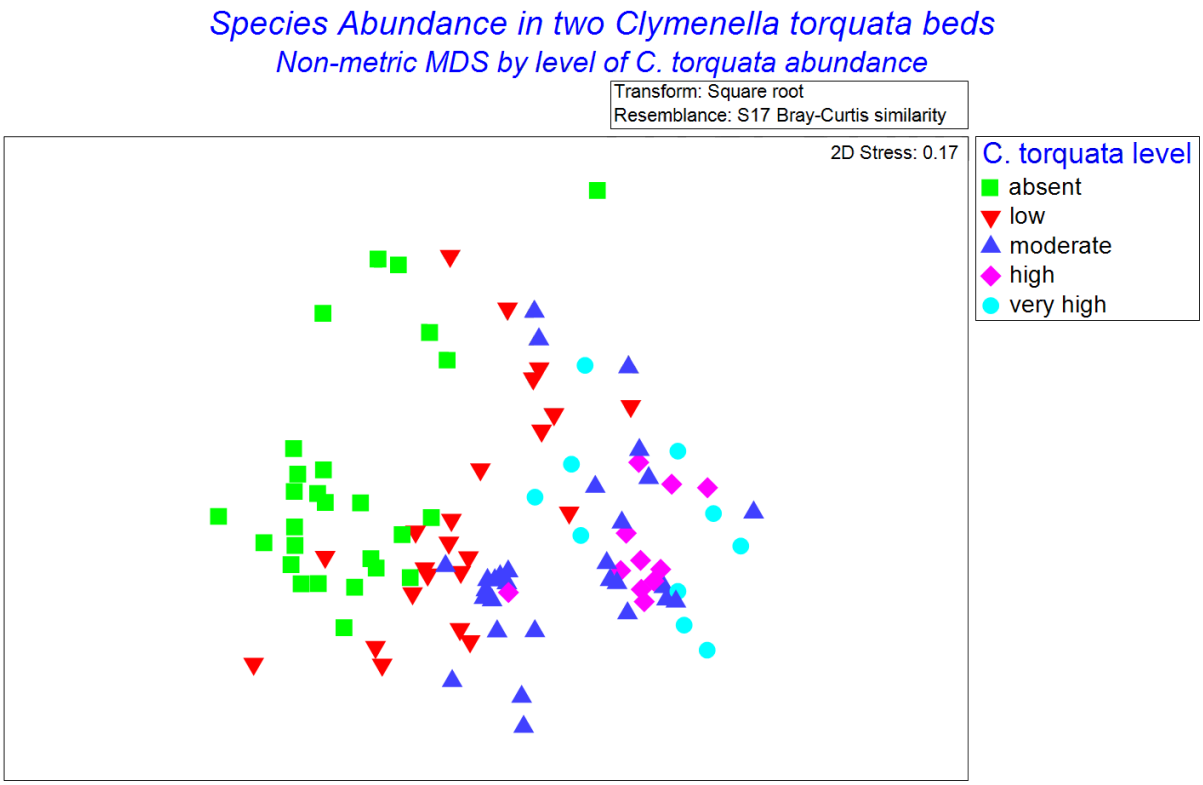

Figure 18. Species composition for both study sites (n=100) as determined by the factor of *C. torquata* level. Non log (x+1) transformed *C. torquata* abundance ranged from 0 to 30. These abundances were split into levels: absent (n=28), low (n=23), moderate (n=27), high (n=11) and very high (n=10).

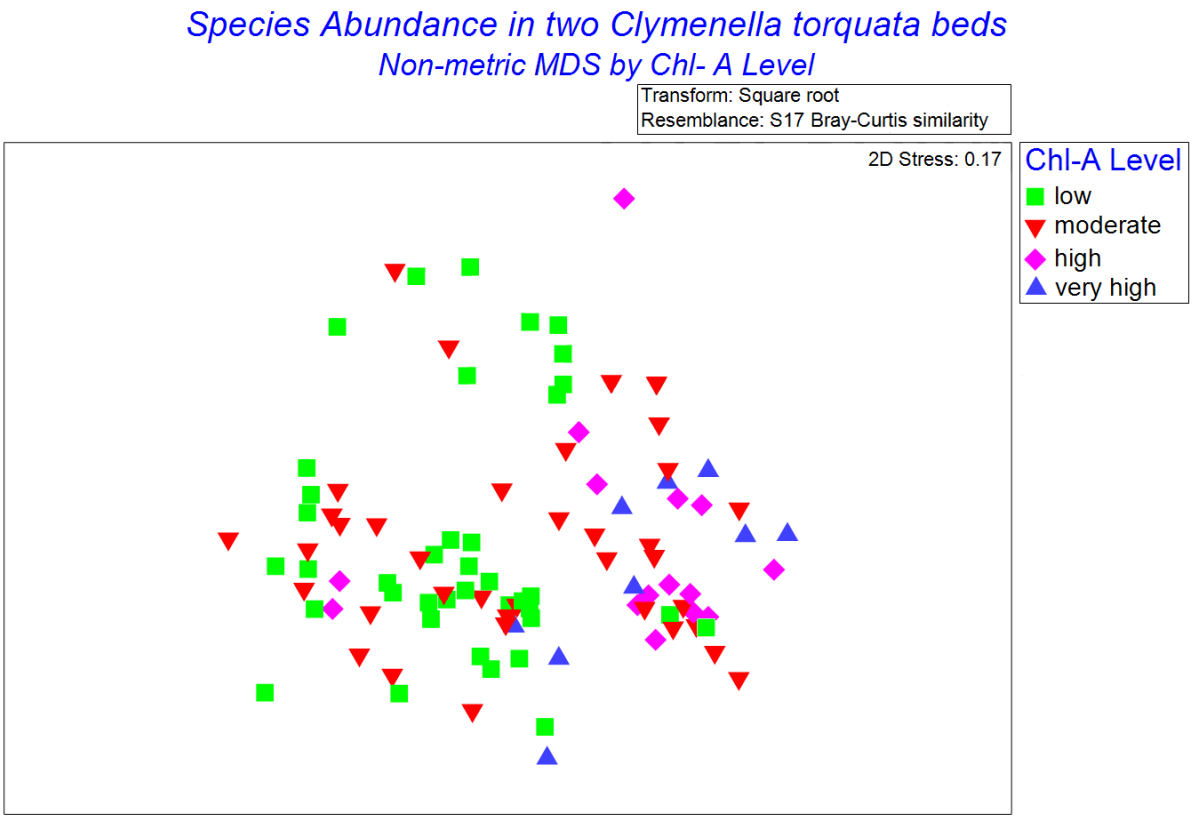

Figure 19. Species composition for both study sites (n=100) as determined by the factor of Chl-*a* level. The non-log (x+1) transformed data set of Chl-*a* values ranges from 3 to 37 µg/cm^3. The data set was divided into four levels of Chl-*a* density; low (n=40), moderate (n=37), high (n=16) and very high (n=10).

Present			Absent		
Species	Average Abundance	Contributing Percent	Species	Average Abundance	Contributing Percent
Syllidae sp. SG	16.22	26.28	*Brania spp.*	8.66	25.06
Brania spp.	6.14	10.04	*Syllidae sp. SG*	6.52	15.56
Nereis grayi	3.00	5.28	*Naididae sp. NE*	4.05	10.01
Naididae sp. MO	3.88	5.21	*Capitellid sp. C*	2.70	7.27
Naididae sp. NE	3.29	5.20	*Naididae sp. MO*	3.85	6.97
Syllides sp. B NE	3.70	4.98	*Gemma gemma*	2.40	5.85
Streblopsio benedicti	3.59	4.65	*Ostracods*	3.09	5.57
Ostracods	4.80	4.64			
Syllides sp. B	3.34	4.58			
Lumbrineris spp.	3.02	4.25			
Clymenella torquata	2.44	3.96			

Table 1. SIMPER analysis for groups in which *C. torquata* is present (n=73) and absent (n=27). Species are listed in descending order of contributing percent. The cutoff percentage for contributing variables was 80. Average abundance and contributing percent are calculated per the specified group. Average similarity for the group where *C. torquata* is present is 60.46. Average similarity for the group where *C. torquata* is absent is 60.46. Average dissimilarity is 49.33.

Site 1			Site 2		
Species	Average Abundance	Contributing Percent	Species	Average Abundance	Contributing Percent
Syllidae sp. SG	14.37	19.65	*Syllidae sp. SG*	12.84	22.15
Streblopsio benedicti	5.03	9.14	*Brania spp.*	8.29	19.09
Brania spp.	5.35	7.87	*Naididae sp. NE*	4.16	8.76
Syllides sp. B NE	4.60	7.02	*Gemma gemma*	2.94	6.20
Naididae sp. NE	3.76	5.85	*Ostracods*	3.43	6.20
Lumbrineris spp.	3.59	5.43	*Naididae sp. MO*	3.81	5.93
Syllides sp. B	3.16	5.32	*Capitellid sp. C*	2.28	4.71
Nereis grayi	3.93	4.98	*Paraonis fulgens*	2.27	4.63
Naididae sp. MO	5.25	4.22			
Ostracods	2.43	4.10			
Exogone spp.	2.94	3.95			

Table 2. SIMPER analysis for Site 1 (n=50) and Site 2 (n=50). Species are listed in descending order of contributing percent. The cutoff percentage for contributing variables was 80. Average abundance and contributing percent are calculated per the specified group. Average similarity for Site 1 is 59.75. Average similarity for Site 2 is 65.46. Average dissimilarity is 49.30.

Absent			Low			Moderate			High			Very High		
Species	Average Abund.	Contrib. Percent	Species	Average Abund.	Contrib. Percent	Species	Average Abund.	Contrib. Percent	Species	Average Abund.	Contrib. Percent	Species	Average Abund.	Contrib. Percent
Brania spp.	8.66	25.06	*Syllidae sp. SG*	11.17	21.51	*Syllidae sp. SG*	18.82	30.69	*Syllidae sp. SG*	17.87	27.37	*Syllidae sp. SG*	18.49	20.31
Syllidae sp. SG	6.52	15.56	*Brania spp.*	8.08	18.78	*Brania spp.*	5.96	9.11	*Streblospio benedicti*	5.80	8.05	*Streblospio benedicti*	5.47	8.23
Naididae sp. NE	4.05	10.01	*Naididae sp. NE*	3.56	7.67	*Naididae sp. MO*	3.96	5.17	*Lumbrineris spp.*	4.63	6.33	*Syllides sp. B NE*	6.08	7.63
Capitellid sp. C	2.70	7.27	*Nereis grayi*	2.60	5.55	*Syllides sp. B NE*	3.68	5.03	*Ostracods*	6.10	6.31	*Naididae sp. MO*	6.19	7.04
Naididae sp. MO	3.85	6.97	*Capitellid sp. C*	2.50	5.38	*Nereis grayi*	2.97	4.77	*Syllides sp. B NE*	4.82	6.19	*Clymenella torquata*	4.38	6.96
Gemma gemma	2.40	5.85	*Syllides sp. B*	3.16	5.00	*Clymenella torquata*	2.32	4.44	*Clymenella torquata*	3.35	5.36	*Exogone sp.*	4.46	6.66
Ostracods	3.09	5.57	*Naididae sp. MO*	2.77	3.83	*Naididae sp. NE*	3.25	4.27	*Exogone sp.*	3.87	5.28	*Syllides sp. B*	5.12	6.58
			Ostracods	3.43	3.72	*Lumbrineris spp.*	2.88	4.25	*Naididae sp. MO*	3.88	5.10	*Lumbrineris spp.*	4.69	5.53
			Gemma gemma	1.98	3.31	*Ostracods*	4.88	4.17	*Nereis grayi*	3.38	4.72	*Nereis grayi*	3.57	5.39
			Clymenella torquata	1.31	3.00	*Exogone spp.*	2.83	3.91	*Syllides sp. B*	3.27	4.14	*Brania spp.*	5.41	5.29
						Streblospio benedicti	3.23	3.80						

Table 3. SIMPER analysis for groups in which *C. torquata* is absent (n=28), low (n=23), moderate (n=27), high (n=11) and very high (n=10). Species are listed in descending order of contributing percent. The cutoff percentage for contributing variables was 80. Average abundance and contributing percent are calculated per the specified level. Average similarity for the group where *C. torquata* is absent is 60.82. Average similarity for the group where *C. torquata* is low is 60.62. Average similarity for the group where *C. torquata* is moderate is 63.33. Average similarity for the group where *C. torquata* is high is 71.82. Average similarity for the group where *C. torquata* is very high is 65.38.

Low			Moderate			High			Very High		
Species	Average Abund.	Contrib. Percent	Species	Average Abund.	Contrib. Percent	Species	Average Abund.	Contrib. Percent	Species	Average Abund.	Contrib. Percent
Brania spp.	8.27	19.43	*Syllidae sp. SG*	13.40	23.31	*Syllidae sp. SG*	16.12	24.61	*Syllidae sp. SG*	18.21	30.39
Syllidae sp. SG	11.76	19.08	*Brania spp.*	6.79	14.41	*Streblospio benedicti*	5.26	7.87	*Exogone sp.*	4.28	7.30
Naididae sp. NE	3.45	6.79	*Naididae sp. NE*	3.60	7.39	*Syllides sp. B NE*	4.56	6.60	*Syllides sp. B NE*	5.27	7.21
Naididae sp. MO	3.81	6.30	*Ostracods*	4.86	6.02	*Ostracods*	6.40	6.23	*Brania spp.*	5.10	6.50
Capitellid sp. C	2.45	5.32	*Nereis grayi*	2.79	5.91	*Brania spp.*	4.16	6.22	*Lumbrineris spp.*	4.28	5.84
Nereis grayi	2.37	5.15	*Naididae sp. MO*	3.85	5.69	*Syllides sp. B*	3.51	5.44	*Naididae sp. MO*	3.84	5.00
Ostracods	3.52	4.81	*Capitellid sp. C*	2.38	5.11	*Naididae sp. MO*	4.08	5.39	*Clymenella torquata*	2.95	4.90
Gemma gemma	2.41	4.73	*Syllides sp. B*	2.53	3.79	*Lumbrineris spp.*	3.85	5.27	*Naididae sp. NE*	3.30	4.33
Syllides sp. B	2.61	3.34	*Gemma gemma*	1.98	3.75	*Naididae sp. NE*	3.45	5.04	*Ostracod WS*	5.76	4.27
Syllides sp. B NE	1.94	3.16	*Syllides sp. B NE*	2.94	3.69	*Capitellid sp. C*	2.49	4.30	*Nereis grayi*	2.78	4.05

Table 4. SIMPER analysis for groups in which Chl-*a* µg cm^{-3} is low (n=40), moderate (n=37), high (n=16) and very high (n=10). Species are listed in descending order of contributing percent. The cutoff percentage for contributing variables was 80. Average abundance and contributing percent are calculated per the specified level. Average similarity for the group where Chl-*a* is low is 58.77. Average similarity for the group where Chl-*a* is moderate is 56.67. Average similarity for the group where Chl-*a* is high is 59.53. Average similarity for the group where Chl-*a* is very high is 63.27.

References

Bolam, S.G. and T.F. Ferndandes. 2003. Dense aggregations of tube-building polychaetes: response to small-scale disturbances. Journal of Experimental Marine Biology and Ecology **269**: 197 – 222.

Callaway, R. 2006. Tube worms promote community change. Marine Ecology Progress Series. **308**: 49 – 60.

Campbell, B. R. 2012. Effects of injury and nutrition on sediment disturbance by a marine polychaete, *Clymenella torquata*. (Unpublished master thesis). The University of Maine, Orono, Maine 04469.

Clarke, K.R. 1993. Non-parametric multivariate analyses of changes in community structure. Australian Journal of Ecology **18**: 117 – 143.

Clarke, K.R., and R.N. Gorley. 2015. PRIMER v7: User Manual/Tutorial. PRIMER-E, Plymouth, 296pp.

Craig, N. 1998. Sediment bioengineering and resource availability in a dense assemblage of the deep head down deposit-feeding polychaete *Clymenella torquata*. (Unpublished doctoral dissertation). Stony Brook University, Stony Brook, NY 11790.

Dobbs, F.C. 1981. Community ecology of a shallow subtidal sand flat, with emphasis on sediment reworking by *Clymenella torquata* (Polychaeta: Maldanidae). (Unpublished masters thesis). Stony Brook University, Stony Brook, NY 11790.

Dobbs, F. C., Whitlatch, R. B., 1982. Aspects of deposit-feeding by the polychaete *Clymenella torquata.* Ophelia **21**: 159 – 166.

Dubois, S., C. Retiere and F. Olivier. 2002. Biodiversity associated with Sabellaria alveolata (Polychaete: Sabellariidae) reefs: effects of human disturbances. J. Mar. Biol. Assoc. UK. **82**: 817 – 826.

Du Clos, K. T., S. M. Lindsay and P. A. Jumars. 2013. Spatial distribution of *Alitta virens* and *Clymenella torquata* with respect to rigid boundaries in mud and sand. Journal of Marine Research **71**: 211 – 226.

Dufour, S. C., C. White, G. Desrosiers and S. K. Juniper. 2008. Structure and composition of the consolidated mud tube of *Maldane sarsi* (Polychaeta: Maldanidae). Estuarine, Coastal and Shelf Science **78**: 360 – 368.

Featherstone R.P and M. J. Risk. 1977. Effect of tube-building polychaetes on intertidal sediments of the Minas Basin, Bay of Fundi. Journal of Sedimentary Petrology **47**(1): 446 – 450.

Forster, S. and G. Graf. 1995. Impact of irrigation on oxygen flux into the sediment: intermittent pumping by *Callianassa subterraneana* and 'piston-pumping' by *Lanice conchilega*. Marine Biology **123**: 335 – 346.

Fuller, C.M. 1994. Effects of porewater hydrogen sulfide on the feeding activity of the subsurface deposit-feeding polychaete, *Clymenella torquata*, Leidy. Journal of Marine Research **52**: 1101 – 1127.

Gage, J. 1966. The mode of life of *Montacuta elevate*, a bivalve 'commensal' with *Clymenella torquata*. Canadian Journal of Zoology **46**: 877 – 892.

Hylleberg, J. 1975. Selective feeding by *Abarenicola pacifica* with notes on *Abarenicola vagabunda* and a concept of gardening in lugworms. Ophelia **14**: 113 – 137.

Jones, C.G., Lawton, J.H. & Shachak, M. 1994. Organisms as ecosystem engineers. Oikos **69**: 373 – 386.

Kenny, R. 1969. Effects of temperature, salinity and substrate on distribution of *Clymenella torquata* (Leidy), Polychaeta. Ecology **50**(4): 624 – 631.

Kristensen, E., G. Penha-Lopes, M. Delefosse, T. Valdemarsen, C. O. Quintana, and G. T. Banta. 2012. What is bioturbation? The need for a precise definition for fauna in aquatic sciences. Marine Ecology Progress Series **446**: 285 – 302.

Levin, L., N. Blair, D. DeMaster, G. Plaia, W. Fornes, C. Martin and C. Thomas. 1997. Rapid subduction of organic matter by maldanid polychaetes on the North Carolina slope. Journal of Marine Research **55**: 595 – 611.

Lorenzen, C.J., 1967. Determination of chlorophyll and phaeo-pigments: spectrophotometric equations. Limnology and Oceanography **12**: 343 – 346.

Luckenbach, M.W. 1986. Sediment stability around animal tubes: The roles of hydrodynamic processes and biotic activity. Limnology and Oceanography **31**(4): 779 – 787.

Mach, M.E., C.D. Levings, P.S. McDonald, K.M.A. Chan. 2012. An Atlantic infaunal engineer is established in the Northeast Pacific: *Clymenella torquata* (Polychaete: Maldanidae) on the British Columbia and Washington Coasts. Biological Invasions **14**: 503 – 507.

Mangum, C.P. 1964. Studies on speciation in maldanid polychaetes of the North American Atlantic coast. II. Distribution and competitive interaction of five sympatric species. Limnology and Oceanography **9**: 12 – 26.

Precht, E. and M. Huettel. 2003. Advective pore-water exchange driven by surface gravity waves and its ecological implications. Limnology and Oceanography **48**(4): 1674 – 1684.

Reise, K. 2002. Sediment mediated species interactions in coastal waters. Journal of Sea Research **48**: 127 – 141.

Rhoads, D. C. 1967. Biogenic reworking of intertidal and subtidal sediments in Barnstable Harbor and Buzzards Bay, Massachusetts. The Journal of Geology **75**(4): 461 – 476.

Rhoads, D.C. and D.J. Stanley. 1965. Biogenic graded bedding. Journal of Sedimentary Petrology **35**: 956 – 963.

Rhoads, D.C. and D.K. Young. 1970. The influence of deposit-feeding organisms on sediment stability and community trophic structure. Journal of Marine Research **28**(2): 150 – 178.

Rusch, A. and M. Huettel. 2000. Advective particle transport into permeable sediments—evidence from experiments in an intertidal sandflat. Limnology and Oceanography **45**(3): 525 – 533.

Sanders, H. L., E. M. Goudsmit, E. L. Mills and G. E. Hampson. 1962. A Study of the Intertidal Fauna of Barnstable Harbor, Massachusetts. Limnology and Oceanography **7**(1): 63 – 79.

Significant Habitats and Habitat Complexes of the New York Bight Watershed: Shinnecock Bay Complex #12. Retrieved from https://nctc.fws.gov/pubs5/web_link/text/sb_form.html.

Sørensen, T. A. 1948. A method of establishing groups of equal amplitude in plant sociology based on similarity of species content, and its application to analyses of the vegetation on Danish commons. Biol. Skr., K. Danske Vidensk. Selsk **5**(4): 1 – 34.

Tide table: Shinnecock Inlet (ocean), Long Island, New York 40.8383° N, 72.4750° W (2016, October). Retrieved from http://tides.mobilegeographics.com/calendar/month/5816.html.

Waldbusser, G.G., R.L. Marinelli, R.B. Whitlatch and P.T. Visscher. 2004. The effects of infaunal biodiversity on biogeochemistry of coastal marine sediments. Limnology and Oceanography **49**: 1482 – 1492.

Weinberg, J. R. 1984. Interactions between functional groups in soft-substrata: Do species differences matter? Journal of Experimental Marine Biology and Ecology **80**: 11 – 28.

Weinberg, J. R. and R. B. Whitlatch. 1983. Enhanced growth of a filter-feeding bivalve by a deposit-feeding polychaete by means of nutrient regeneration. Journal of Marine Research **41**: 557 – 569.

Wendelboe, K., J.T. Egelund, M.R. Flindt, and T. Valdemarsen. 2013. Impact of lugworms (*Arenicola marina*) on mobilization and transport of fine particles and organic matter in marine sediments. Journal of Sea Research **76**: 31 – 38.

Woodin, S.A., D. S. Wethey, and N. Volkenborn. 2010. Infaunal hydraulic ecosystem engineers: cast of characters and impacts. Integrative and Comparative Biology **50**: 176 – 187.

Zorn, M.E., S. V. Lalonde, M.K. Gingras, S.G Pemberton, and K.O. Konhauser. 2006. Microscale oxygen distribution in various invertebrate burrow walls. Geobiology **4**: 137 – 145.