



Assessing the Response of Juvenile and Adult Hard Clams to the New Breach in Great South Bay

Post-Hurricane Sandy study

Natural Resource Report NPS/NCBN/NRR—2017/1505



**ON THIS PAGE**

Photograph of researchers departing from the New Inlet in Narrow Bay from a boat after a full day of sampling.
Photograph courtesy of Alexandra Stevens, School of Marine and Atmospheric Sciences, Stony Brook University.

ON THE COVER

Photograph of Graduate Student (Alexandra Stevens) marine biologists sampling juvenile hard clams from a boat in Central Great South Bay, NY.
Photograph courtesy of Alexandra Stevens, School of Marine and Atmospheric Sciences, Stony Brook University.

Assessing the Response of Juvenile and Adult Hard Clams to the New Breach in Great South Bay

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Abstract

The south shore of Long Island (NY, USA) is lined by barrier islands that have been breached by ocean waters dozens of times during the past 300 years. On October 29, 2012, Hurricane Sandy created a new breach in eastern Great South Bay (GSB) that has had a strong effect on the circulation and salinity. The effects of the breach on resident hard clam communities are, however, currently unknown. This study conducted experiments to understand how the New Inlet in GSB may be impacting the growth and condition of resident hard clam communities. Juvenile and adult hard clams were placed in cages across GSB from spring through fall of 2014. The length- and weight-based growth of the clams were quantified along with their biochemical composition. The reproductive condition of adult hard clams was also assessed seasonally. The concurrent assessment of plankton community composition and general water quality permitted a statistical assessment of the extent to which these parameters influenced the performance of clams. The findings of this study were directly compared to a nearly identical study performed nine years ago prior to the formation of the New Inlet. Throughout this study, juvenile hard clams grew fastest and adult clam condition was best in regions closer to the ocean inlets. Juvenile clam growth rates were negatively correlated with quantities of *Aureococcus anophagefferens* (brown tide) and positively correlated with temperature. The poorer performance of clams within central Great South Bay was related to a brown tide that occurred in the fall. The brown tide in GSB was most intense in central GSB, but was lowest in areas near inlets, suggesting that ocean flushing minimized occurrences of brown tide. The central GSB location attained higher and lower than optimal temperatures during the summer and fall, respectively. In contrast to similar experiments performed prior to the New Inlet, which observed slower growth in Bellport Bay near the New Inlet and the fastest growth in central GSB, during this study the pattern reversed. Although the sporadic occurrence of brown tides complicates the ability to draw long-term conclusions, the sum of the findings of this study suggests that the New Inlet will benefit hard clam populations by minimizing the negative effects of harmful algae and fostering ideal temperatures for growth for a longer period during the summer and fall.

Introduction

There are more than 2,200 coastal lagoons in the world (Pilkney 2003) and in the United States, lagoons are found along more than 75 percent of the East and Gulf Coasts. Barrier island lagoon estuaries tidally exchange with ocean waters via inlets, a process that can influence many estuarine properties such as temperature, salinity, water clarity, and nutrient levels. Low rates of tidal exchange in many lagoonal estuaries allow them to accumulate nutrients from freshwater sources, and in turn, support highly productive food webs (Kjerfve and Magill 1989). Long Island's (NY, USA) south shore is composed of a series of bar-built lagoonal estuaries formed nearly 10,000 years ago by glacial activity that collectively stretch from the Nassau-Queens county line to the middle of Southampton Town, encompassing over 278 square kilometers (Bokuniewicz 1991; Sirkin 1995). These estuaries are protected by long narrow stretches of land that act as barriers between the enclosed bays and the northern coastal Atlantic Ocean. Fire Island is the longest continuous barrier island (51 km) and protects all Great South Bay (GSB) and part of Moriches Bay. Due to the delicate and ephemeral nature of barrier islands, many lagoonal estuaries, including GSB and Moriches Bay, are prone to large-scale disturbances by tropical storms and hurricanes (Paerl et al. 2001; Bales 2003; Peierls et al. 2003). Major storms can create breaches of the protective barrier islands resulting in the formation of inlets, which allows for enhanced coastal ocean exchange. The effects of newly formed inlets can result in alterations of phytoplankton assemblages within the estuary, through changes in circulation, temperature, and nutrient availability (Valiela et al. 1998; Gobler et al. 2005).

GSB is the largest of the barrier island estuaries on Long Island, with the major saltwater influence historically coming through the Fire Island Inlet located at the western tip of Fire Island. Over the last 300 years, it has been estimated that a total of 28 inlets have temporarily been created within GSB as a result of Fire Island being breached by storms (Leatherman 1985). During October of 2012, Super Storm Sandy created a barrier island breach within the eastern extent of GSB (Bellport Bay) in a location commonly referred to as 'Old Inlet' as there was an inlet present in this region during the early 1800s. This new breach has been shown to have a major impact on the ocean exchange and salinity in eastern GSB which has risen from ~24 to >30 ppt. While this radical change is likely to impact many aspects of this ecosystem, there are currently only a few studies underway to assess the biological impacts of the breach on this system.

Great South Bay was once well known for its robust hard clam (*Mercenaria mercenaria*) fishery but intense harvesting led to a tremendous decline in the population through the late 1970's and early 1980's (Kraeuter et al. 2005). In addition, since 1985, GSB has experienced brown tide events caused by the pelagophyte, *Aureococcus anophagefferens*, that are thought to have further decimated the resident clam populations (Bricelj et al. 2001; Greenfield and Lonsdale 2002; Gobler et al. 2005). To date, there has yet to be a rebound of this commercially important population.

Prior research of hard clam populations in GSB have emphasized the impact of water quality on the performance of hard clams. Weiss et al. (2007) examined the growth and condition of hard clams across GSB in 2005. Juvenile clams in central GSB had significantly faster growth rates, lower mortality rates, and higher lipid content relative to sites closest to the inlets. Adult hard clams nearest

the Fire Island inlet also had significantly lower condition indexes compared to mid-bay stations. Instantaneous juvenile growth rates were positively correlated to temperatures below 24°C ($p < 0.0001$) and were also significantly correlated with several indicators of suspended food quantity and quality (positive correlation with centric diatoms and phytoplankton cells $> 5 \mu\text{m}$; negative correlation with dinoflagellates) which co-varied independently of temperature. As such, enhanced tidal exchange associated with the new breach is expected to have a significant effect on the growth of juvenile clams and the success of adult hard clams.

The goal of this study is to determine how various physical and biological parameters across a range of estuary-to-ocean locations in GSB influence the success of *M. mercenaria* populations. We evaluated the growth and biochemical composition of juvenile *M. mercenaria* as well as the condition of adult *M. mercenaria* experimentally placed at the New Inlet in Bellport Bay, the middle of GSB, and the Fire Island Inlet. We concurrently assessed water quality (salinity, temperature, dissolved oxygen) and characterized the plankton assemblages with regards to biomass, size distribution, and species composition. Finally, these data sets were used to elucidate the influence of water quality and plankton communities on the growth, and condition of adult and juvenile *M. mercenaria*. The experimental design of this study mimicked a study performed nine years ago (Weiss et al., 2007) prior to the formation of the New Inlet. This facilitates a direct comparison and assessment of how the creation of the New Inlet may affect the performance of hard clams in this ecosystem.

Methods

Field sampling and water collections

Three sites in GSB ranging across an ocean to estuary gradient (Fig. 1) were sampled biweekly in 2014 from May through November ($n=13$): the United States Coast Guard station (USCG) located near the eastern end of the Fire Island Inlet (Latitude = $40.626196^{\circ}\text{N}$, Longitude = $-73.259259^{\circ}\text{W}$), the Bellport station was located at the Bellport Yacht Club ($40.753513^{\circ}\text{N}$, $-72.932468^{\circ}\text{W}$) north of the New Inlet, and the Central Great South Bay (CGSB; $40.687081^{\circ}\text{N}$, $-73.111354^{\circ}\text{W}$) site located between the other sites. These three sites matched those utilized by Weiss et al (2007) and thus were used for comparison of pre- and post-New Inlet conditions.

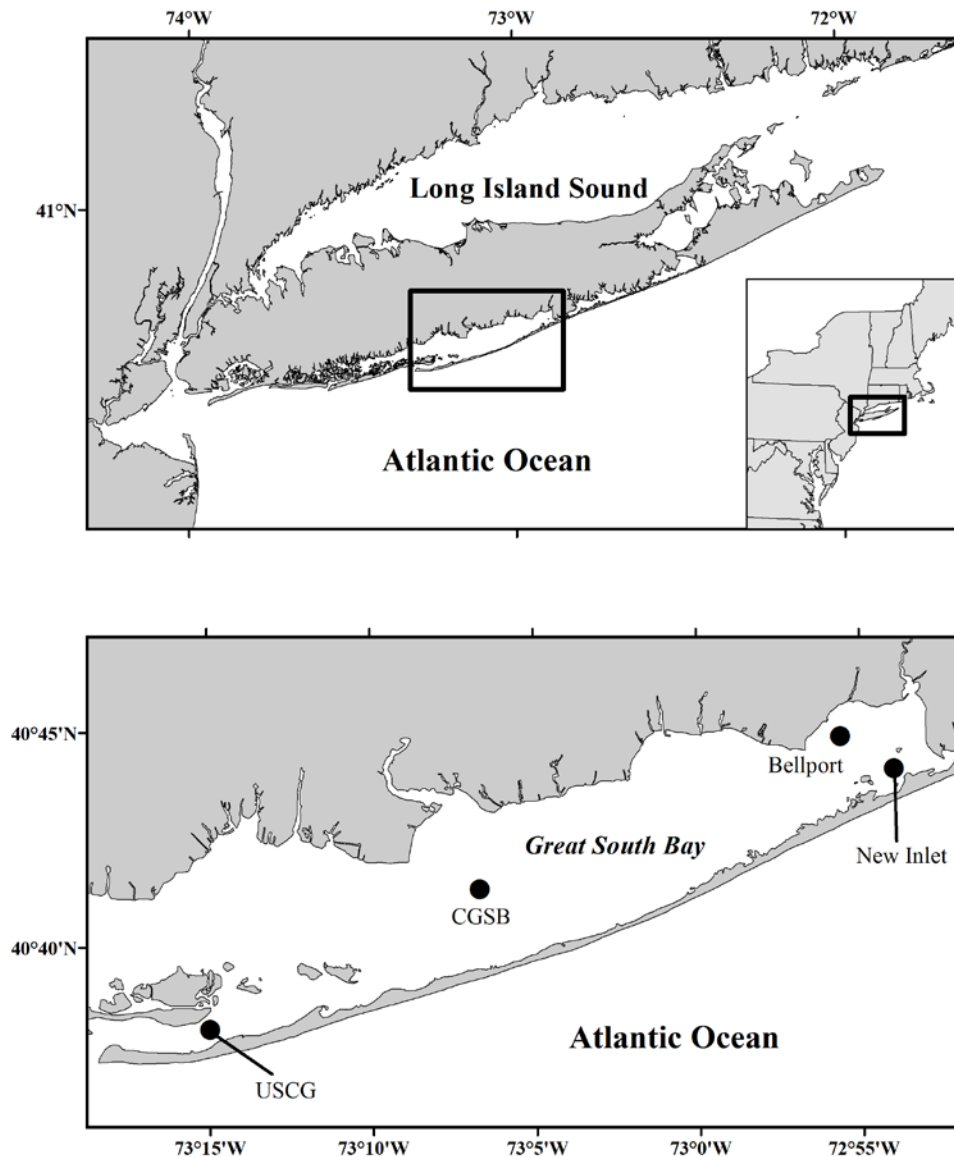


Figure 1. Study sites in Great South Bay in 2014: Fire Island inlet (USCG), central Great South Bay (CGSB), Bellport Bay, and New Inlet.

An additional site in Narrow Bay located east of the New Inlet (40.731115°N, -72.889127°W) was used along with the other three locations for a second experiment performed from September through November 2014 designed to assess whether the Bellport Bay site a previously studied site by Weiss et al. (2007) was representative of conditions closer to the breach. Sampling via small boats was conducted irrespective of tidal state. The frequency of sampling assured that each site was sampled during both high and low, incoming and out-going tides several times during each season.

This project was performed in parallel with on-going characterization of plankton communities in GSB by the Gobler Laboratory (Gobler et al., 2017). From that project, the following samples and analyses were used to interpret the results of our clam experiment described below. During each individual sampling event, triplicate surface water samples from each site were processed and analyzed for size-fractionated chlorophyll *a* (total, < 5 µm, < 2 µm) and were fluorometrically analyzed according to Parsons et al. (1984). To quantify plankton (>10 µm) to the genus level, Lugol's iodine preserved samples (5% v/v) were collected and analyzed using settling chambers and an inverted microscope (Hasle 1978). Paraformaldehyde-preserved samples (1% v/v) were collected to quantify densities of nanoplankton (2 - 20 µm), picoeukaryotes (< 2 µm) and densities of picocyanobacteria (i.e. *Synechococcus* sp.) via flow cytometry (Olson et al. 1991). Additional physical parameters were measured with a YSI Environmental Model 556 sonde including water temperature, salinity, and dissolved oxygen. In addition, densities of brown tide were quantified with flow cytometrically via use of a specie-specific, fluorescently labeled antibody (Stauffer et al., 2008). Finally, accessory pigments of phytoplankton filtered onto glass fiber filters were analyzed via high performance liquid chromatography as described by Jeffrey et al (1999).

Bivalve growth, biochemistry, and condition index

Two cohorts of hatchery raised juvenile *M. mercenaria* (cohort 1, small juveniles: n=300; 9.02±1.03 mm shell length and cohort 2, large juveniles: n=300; 16.79±0.91 mm shell length) were supplied by Cornell Cooperative Extension of Southold, NY, and placed in rigid, plastic mesh bags (5 – 15 mm openings depending on the size of clams) and placed in triplicate, 1m x 1m x 0.6 m wire, within aquaculture cages that were weighted and placed on the bay bottom. In addition, a third cohort of 100 adult *M. mercenaria* (~ 60 mm) from Northport Bay, NY, and were placed in the same cages as the juvenile clams in separate rigid, plastic mesh bags at each experimental site (33 per triplicate cage). The rigid nature of the bags held the adult clams firmly in place. Shelves within cages allowed the bags to be placed horizontally and separately ~ 0.1 - 0.5 m above the benthos. Triplicate cages were deployed at each site from May to November 2014. Water temperature and dissolved oxygen of each site were measured every 15 minutes throughout this period using *in situ* dissolved oxygen (DO) loggers (Onset®). These deployments of juvenile and adult hard clams match nearly exactly the deployments performed by Weiss et al. (2007) with regard to the locations, timing of deployment, clams per bag, clams per cage, and size of clams allowing direct comparisons to be made. The single exception is that the juvenile clams used by Weiss et al. (2007) were 11mm when experiments began whereas the two cohorts of juveniles clams used in these experiments were 9mm and 17mm, respectively.

A second experiment was initiated in the late summer and fall of 2014 with a fourth cohort of juvenile *M. mercenaria* (cohort 4, juveniles: $n=200$; 15 ± 2.10 mm in length supplied by the East Hampton shellfish hatchery, Montauk, NY). The juveniles were deployed in separate shelves of the same cages described for the first experiment. Triplicate cages were also deployed at the fourth site, in close proximity to the New Inlet in Narrow Bay, for the second experiment that went from September through November of 2014.

Length, a measurement from the posterior to anterior end of the shell (Kraeuter and Castagna 1989), was recorded for all juvenile clams biweekly in tandem with water column sampling. A mean initial length was determined by measuring fifty clams, while mean shell length was determined for each sampling period by measuring the entire set of juvenile hard clams in all cages and bags. Instantaneous shell length-based growth rates of clams (μ) were calculated between collection intervals and were determined by using the equation: $\mu = (\ln x_2 - \ln x_1) / (t_2 - t_1)$, where μ is the instantaneous growth rate (per day), x_2 and x_1 represent the shell lengths (mm) at times t_2 and t_1 (days; Grizzle et al., 2001). A final cumulative absolute growth rate of clams (GR) was calculated by using the equation: $GR = (L_2 - L_1) / (t_2 - t_1)$, where GR is the absolute growth rate (mm per day), L_2 and L_1 represent the final and initial length (mm) or dry tissue weight (g) and t_2 and t_1 represent the final and initial time (days; Grizzle et al. 2001). To estimate an initial mean dry tissue weight, one hundred clams were selected from the initial set and clam tissues were dried at 55-60° C for at least one week. A final dry tissue weight per cage ($n = 3$ per site) was determined by the end of the experiment. These were the same measurements made by Weiss et al. (2007).

Total protein and lipid content was measured in juvenile hard clams obtained at all locations during the final collection in November. Pooled hard clams ($n > 10$) from each each cohort and cage were dried (75°C for 24 h), weighed, and homogenized according to Zarnoch (2006). Sub-samples of this homogenate were then used for each biochemical assay. The determination of protein content was in triplicate using the coomassie blue method of Bradford (1976). A calibration curve was constructed using bovine serum albumin as a standard. Total lipid content was quantified in triplicate gravimetrically after extraction with chloroform as described by Folch et al. (1957).

The condition index (CI) of adult *M. mercenaria* used in experiments was assessed. Fifty adult clams were analyzed from the initial stock prior to deployment to determine a mean initial condition index. During spring prior to spawning (before water temperatures reached 20°C in mid-June), at the end of summer, and again at the end of the fall, ~30-32 clams were removed from each site for each collection. Upon collection, clams were cleaned and placed in flowing seawater tanks to encourage pumping for at least 2 hrs. A series of shell measurements were made (length, width, and height) along with quantification of whole weight including shell. As clams were shucked, water was drained but all tissues were collected. Clam tissues and shells were desiccated at 60° C for at least 7 d and then reweighed. CI is a gravimetric measurement that expresses the amount of soft tissue per unit shell weight and is an index of the general condition of the bivalve under a given set of ambient environmental conditions: $CI = (\text{dry soft tissue weight (g)} \times 100) / [(\text{whole weight (g)} - \text{shell weight (g)})]$ (Crosby and Gale 1990). These same measurements were made by Weiss et al. (2007) thus allowing for comparisons.

Statistical Analyses

Comparisons of characteristics of hard clams among sites and environmental conditions among sites were made via one-way ANOVAs using Sigma Plot v11, followed by Tukey's multiple comparison tests to elucidate which sites were significantly different from each other using an alpha of <0.05 to indicate significant differences. For all juvenile clam parameters, cages represented replicates ($n = 3$ per site). Relationships between shell-based instantaneous growth of juvenile hard clams, adult condition indexes, and the biochemical composition of clams were combined with the environmental data collected by our plankton characterization study and were examined via Spearman's rank order correlations using Sigma Plot v11. Environmental parameters examined included temperature and dissolved oxygen determined with *in situ* loggers, salinity, size-fractionated chlorophyll *a* (< 2 , $2 - 5$, $> 5 \mu\text{m}$), flow cytometric-based phytoplankton cell densities (eukaryotic cells < 2 , $2 - 5$, $> 5 \mu\text{m}$, as well as total eukaryotic cells, cyanobacterial cell densities), brown tide cell densities, and algal pigments. Mortality data was fit with a generalized linear model (GLM) and then analyzed via an ANOVA on the model using R-Studio. Step-wise multiple linear regressions models of instantaneous growth rates of the small and large juveniles clams deployed May through November with water quality parameters were made using a forward stepwise selection in Sigma Plot (F to enter $p < 0.05$; F to remove $p > 0.10$; Sokal and Rohlf 1995).

Historical comparisons and analyses

The cage experiments being described in this proposal were identical to those performed by Weiss et al (2007) in a study of GSB that was performed in 2005 when there was only one ocean inlet in GSB. As such, this study permitted both a comparison among sites in 2014 as well as a comparison of each site between 2005 and 2014. Such an assessment was made for each individual clam parameter via two-way ANOVA where site and year are the main effects, which were further, assessed via Tukey's multiple comparison tests on Sigma Plot.

Results

Juvenile hard clam mortality

Mortality of the small juvenile clam cohort deployed in 2014 was highest at the sites closest to the inlets (37-38%) as the Central Great South Bay (CGSB) site experienced significantly the lower total small juvenile mortality ($25 \pm 0.17\%$) throughout the experiment (Fig. 2A; $p < 0.05$; Tukey test). USCG experienced the highest cumulative percent mortality ($38 \pm 0.30\%$) although overall differences among sites were not statistically significant. Mortality of the large juvenile clam cohort was lower than small juveniles and, again, sites closest to an inlet (USCG, Bellport) had higher cumulative mortality than CGSB although differences were not statistically significant (Fig. 2B). Clams at CGSB experienced a sharp increase in mortality towards the end of October (Fig. 2B).

For juvenile clams in the second fall experiment, during September and October there was little to no mortality at New Inlet and Bellport, whereas CGSB and USCG experienced greater mortality. The lowest total mortality took place near Fire Island Inlet (USCG) ($11 \pm 0.32\%$). The highest total mortality was observed in Bellport ($19 \pm 0.57\%$) with most of the mortality occurring in mid-October (Fig. 2C).

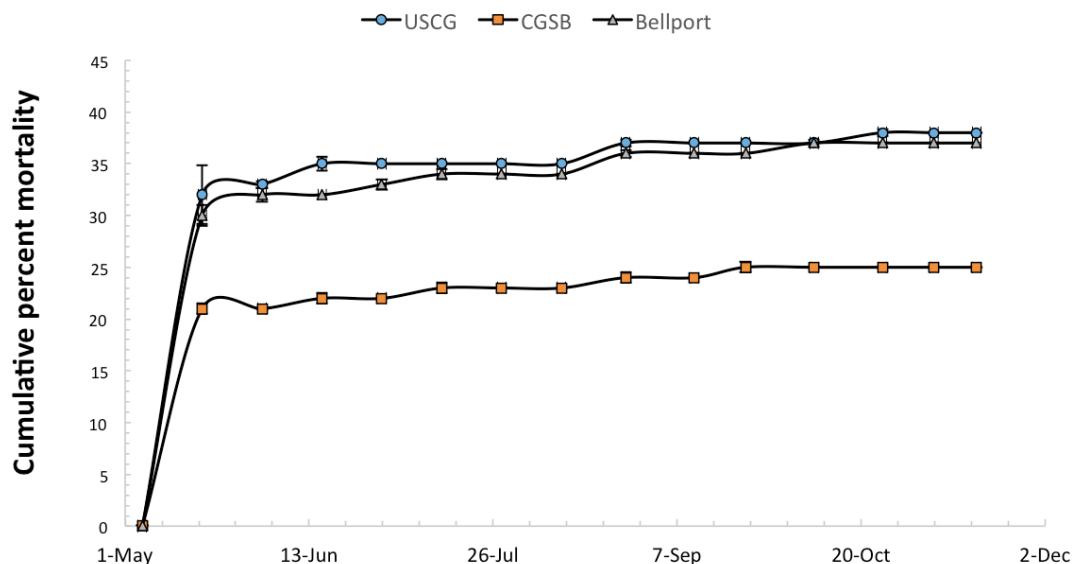


Figure 2A. Cumulative percent mortality (% of total) $\pm$ SE in small juvenile hard clams in Great South Bay during May and November, 2014 for Fire Island inlet (USCG, closed circle), central GSB (CGSB, closed triangle), and Bellport (closed square).

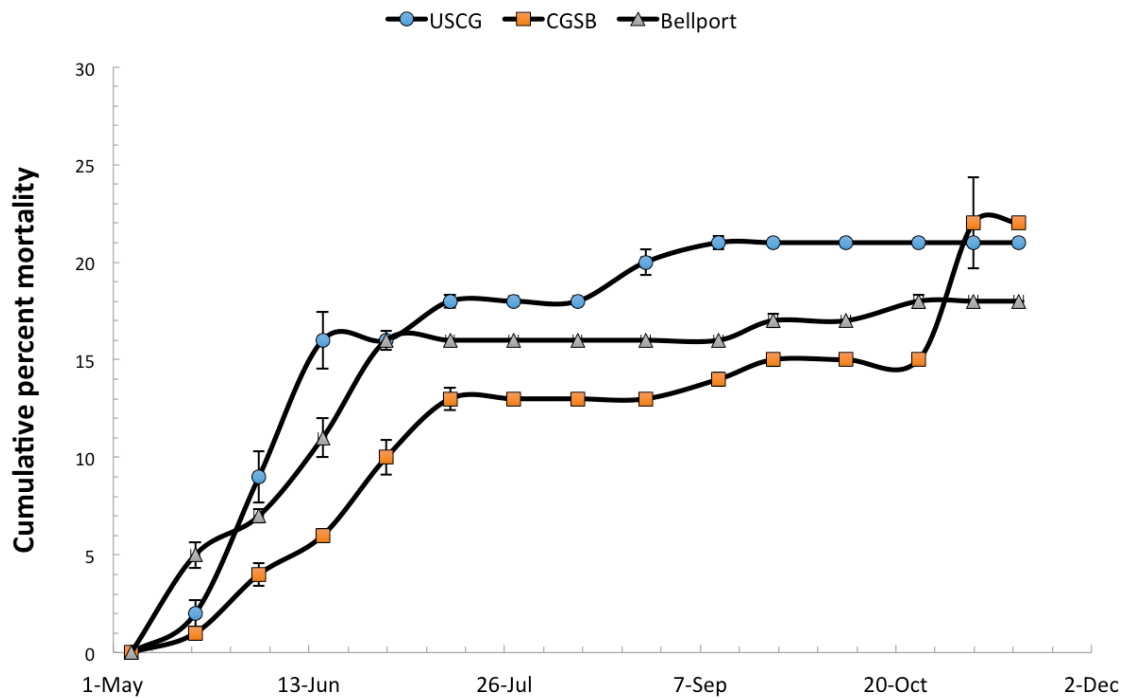


Figure 2B. Cumulative percent mortality (% of total) $\pm$ SE in large juvenile hard clams in Great South Bay during May and November, 2014 for Fire Island inlet (USCG, closed circle), central GSB (CGSB, closed triangle), and Bellport (closed square).

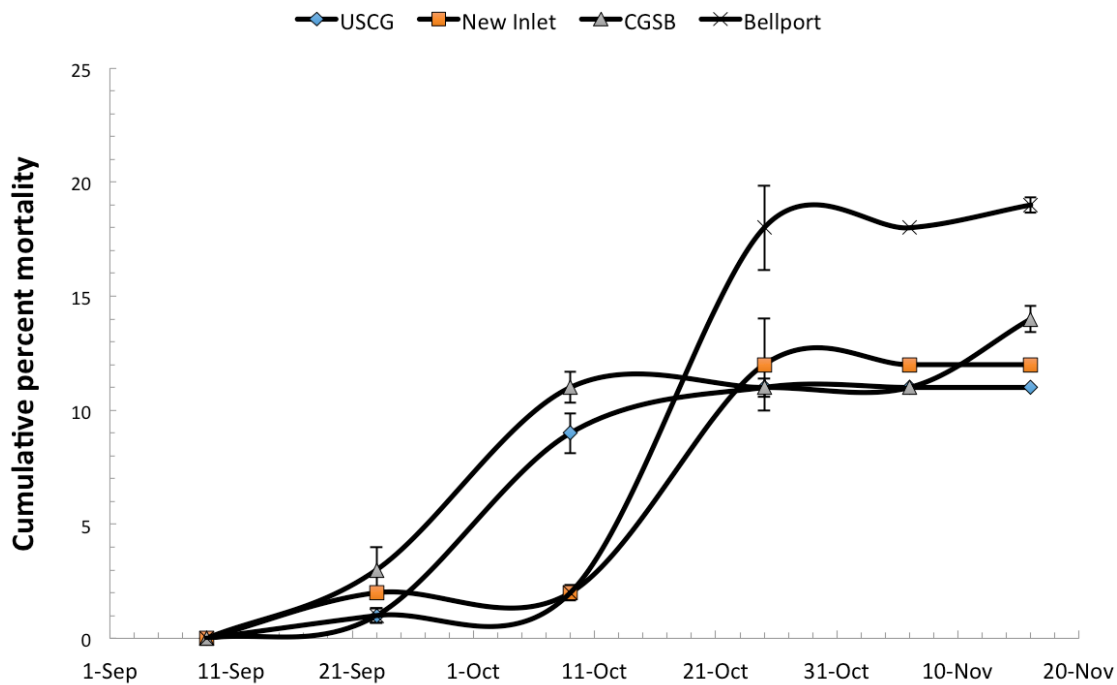


Figure 2C. Cumulative percent mortality (% of total) $\pm$ SE in juvenile hard clams in Great South Bay during September and November, 2014 for Fire Island inlet (USCG, closed circle), New Inlet (closed square) central GSB (CGSB, closed triangle), and Bellport (solid line).

Growth of juvenile hard clams

Over the course of study, small juvenile hard clams in Bellport achieved a significantly greater shell length (25.20 ± 2.49 mm) and dry weight (0.19 ± 0.05 g) compared to individuals deployed at CGSB ($p=0.002$, $p<0.001$, respectively) and USCG ($p=0.014$, $p=0.002$, respectively) (Tukey's test; Fig 3A). In contrast, CGSB clams had the smallest shell length (19.17 ± 1.89 mm) and the lightest dry weight (0.065 ± 0.02 g; Fig 3A). Small juveniles had similar trends regarding growth rate, with the highest growth rate observed in Bellport (length-based; 0.076 ± 0.001 mm d⁻¹; weight-based; 0.186 ± 0.012 g d⁻¹) and the lowest growth rate in CGSB (length-based; 0.048 ± 0.001 mm d⁻¹; weight-based; 0.065 ± 0.002 g d⁻¹; $p<0.001$; one-way ANOVA). Small, juvenile clams showed a similar trend in growth rate, with the highest growth in Bellport (length-based; 0.0589 ± 0.006 mm d⁻¹; weight-based; 0.402 ± 0.076 g d⁻¹) and the lowest growth rate in CGSB (length-based; 0.043 ± 0.002 mm d⁻¹; weight-based; 0.174 ± 0.01 g d⁻¹; $p<0.001$; one-way ANOVA). In manner paralleling the small juveniles, the larger juvenile clams deployed in Bellport achieved a significantly greater shell length (30.01 ± 3.27 mm) and dry weight (0.402 ± 0.12 g) than clams in CGSB which had the smallest shell length (26.60 ± 1.91 mm) and the lightest dry weight (0.17 ± 0.04 g) (Tukey's test, $p<0.05$; Fig. 3B). Hard clams at Bellport and USCG were also significantly heavier than those at CGSB (Tukey's test, $p<0.05$; Fig. 3B).

For the fall experiment, juvenile hard clams deployed at USCG, New Inlet, and Bellport reached similar final lengths (21.12 ± 1.50 mm, 20.58 ± 1.90 mm, and 20.39 ± 1.28 mm, respectively) and dry weights (0.113 ± 0.021 g, 0.113 ± 0.032 g, and 0.106 ± 0.022 g, respectively; Fig. 3C). In contrast, juvenile clams deployed within CGSB were significantly smaller (17.73 ± 1.35 mm, $p<0.001$) and lighter (dry weight 0.061 ± 0.013 g, $p<0.005$; Tukey's test, $p<0.050$; Fig. 3C).

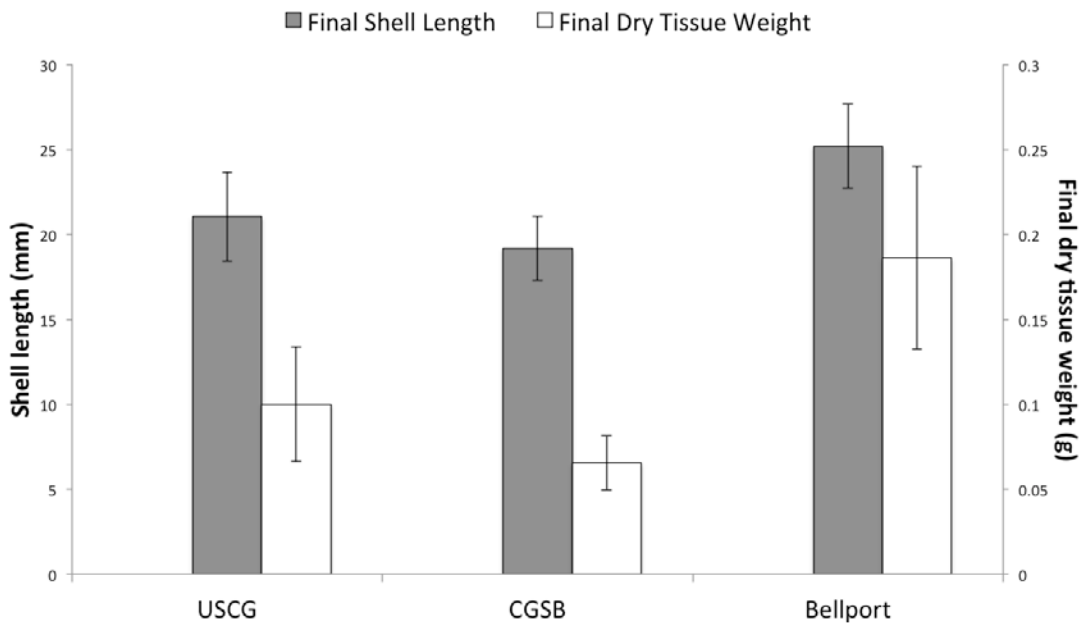


Figure 3A. Final shell length (mm; gray bars) $\pm$ SD and final dry tissue weight (g; white bars) $\pm$ SD for small juvenile clams deployed in the Fire Island Inlet US Coast Guard Station (USCG), Central Great South Bay (CGSB), and Bellport Bay (Bellport) May - November 2014.

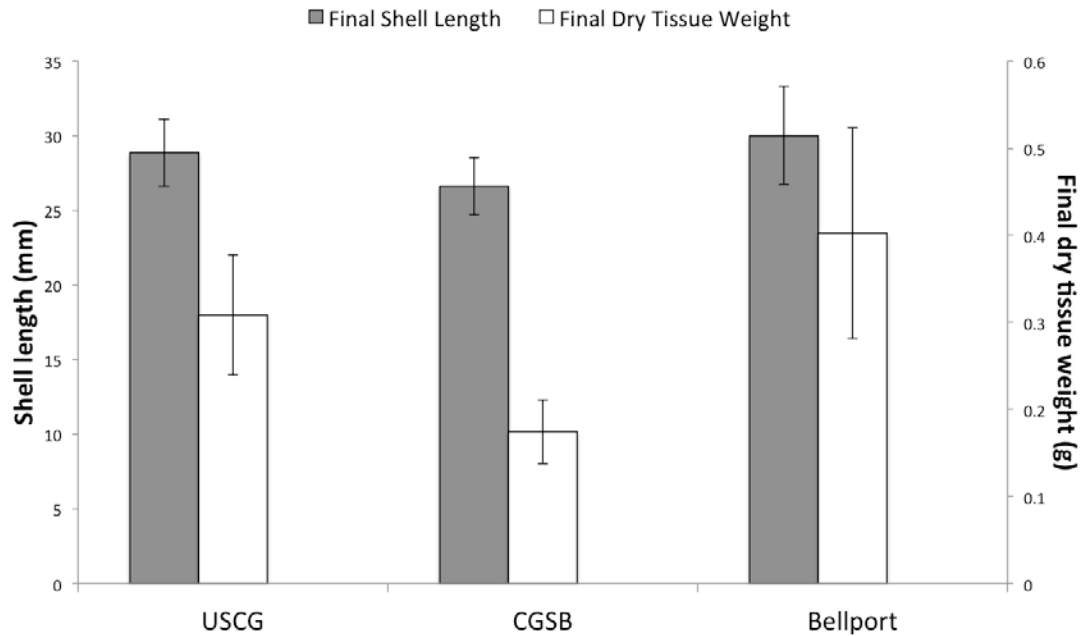


Figure 3B. Final shell length (mm; gray bars) $\pm$ SD and final dry tissue weight (g; white bars) $\pm$ SD for large juvenile clams deployed in the Fire Island Inlet US Coast Guard Station (USCG), Central Great South Bay (CGSB), and Bellport Bay (Bellport) May - November 2014.

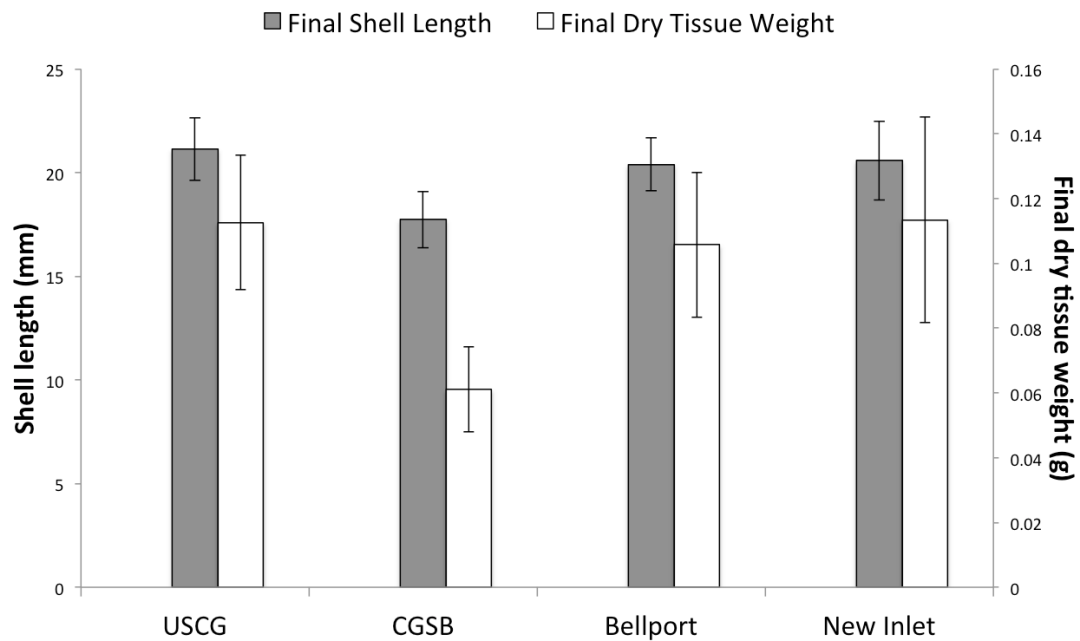


Figure 3C. Final shell length (mm; gray bars) $\pm$ SD and final dry tissue weight (g; white bars) $\pm$ SD for second experiment juvenile clams deployed in the Fire Island Inlet US Coast Guard Station (USCG), Central Great South Bay (CGSB), and Bellport Bay (Bellport) September - November 2014.

Throughout the study instantaneous shell length-based growth rates varied spatially and temporally across sites and size classes. During the beginning of the experiment (late May - early June) small juvenile clams in CGSB had the highest growth rate ($0.12 \pm 0.02 \text{ mm d}^{-1}$) through the end of June. In contrast, the sites closest to inlets had lower growth rates, with Bellport being the lowest ($0.03 \pm 0.02 \text{ mm d}^{-1}$; Fig. 4A). Starting in the beginning of July, these patterns reversed and the site closer to New Inlet (Bellport) experienced faster growth rate ($0.12 \pm 0.02 \text{ mm d}^{-1}$) than the central part of the bay (CGSB) ($0.07 \pm 0.06 \text{ mm d}^{-1}$), a trend that continued throughout the late summer months and into the fall (October-November; Fig. 4A). The greatest instantaneous growth rate occurred in Bellport during late September - early October, 0.14 mm d^{-1} (Fig. 4A). In contrast, CGSB had little to no growth (0 to 0.01 mm d^{-1}) during late August into November. For the entire study (May – November), the instantaneous shell length-based growth rates at Bellport were significantly greater than rates at USCG ($p < 0.005$; Tukey's Test) and CGSB ($p < 0.001$; Tukey's Test).

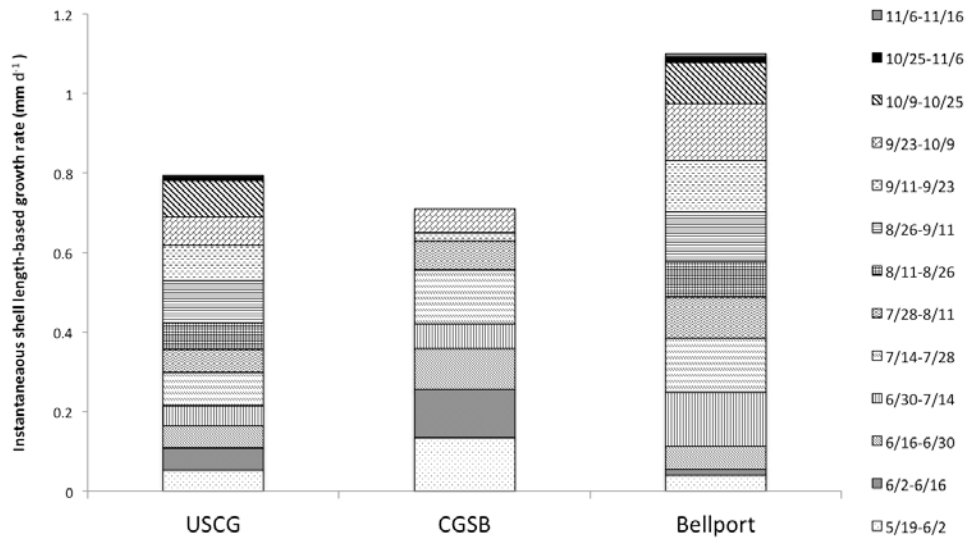


Figure 4A. Instantaneous shell length-based growth rates (mm d^{-1}) for Great South Bay in 2014 for small juvenile hard clams deployed in the Fire Island Inlet US Coast Guard Station (USCG), Central Great South Bay (CGSB), and Bellport Bay (Bellport) May - November 2014.

Larger juveniles grew in a manner that paralleled the small juveniles. During late spring (May - mid June), the large juvenile clams from CGSB had the highest growth rate ($0.10 \pm 0.01 \text{ mm d}^{-1}$) and the sites closer to inlets had lower growth rates, with USCG being the lowest ($0.06 \pm 0.02 \text{ mm d}^{-1}$; Fig. 4B). In summer, clams deployed near inlet sites (USCG, Bellport) displayed growth rates (0.08 ± 0.01 , $0.11 \pm 0.01 \text{ mm d}^{-1}$) faster than individuals within the central part of the bay (CGSB) ($0.06 \pm 0.05 \text{ mm d}^{-1}$), a trend that continued throughout the summer and fall (Fig. 4B). The greatest instantaneous growth rate occurred in Bellport during late June-early July (0.12 mm d^{-1} ; Fig. 4B). Bellport maintained the highest overall instantaneous growth rates throughout the experiment ($0.08 \pm 0.03 \text{ mm d}^{-1}$) compared to the other sites, until the clams began slowing their growth towards the end of October-early November. In contrast, clams within CGSB showed little to no growth from September through November with overall growth rates within CGSB being significantly slower than Bellport and USCG ($p < 0.05$; Tukey's Test; Fig. 4B).

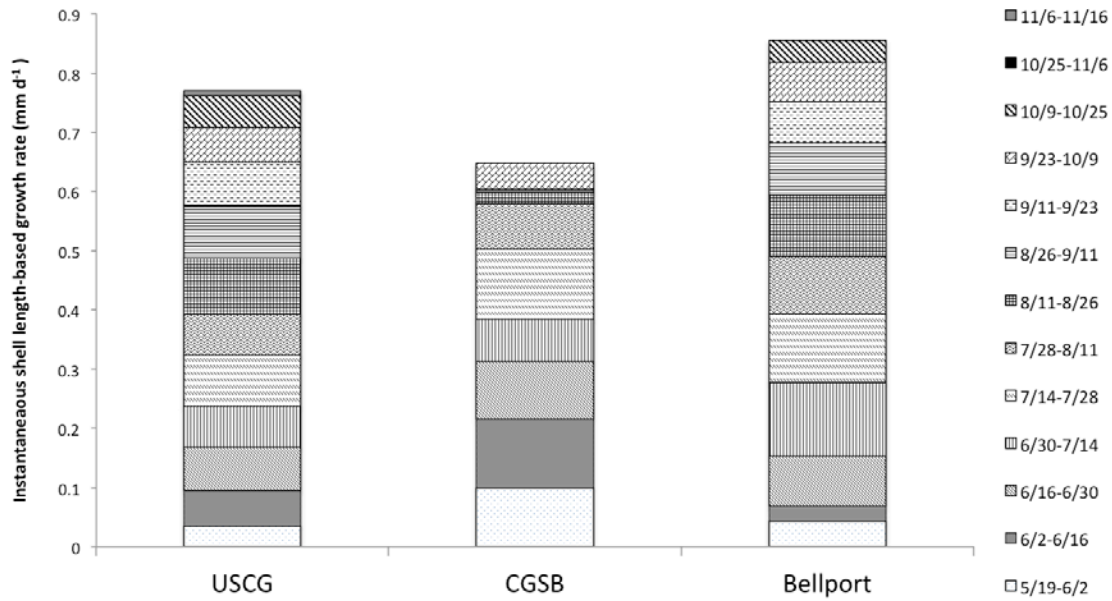


Figure 4B. Instantaneous shell length-based growth rates (mm d^{-1}) for Great South Bay in 2014 for large juvenile hard clams deployed in the Fire Island Inlet US Coast Guard Station (USCG), Central Great South Bay (CGSB), and Bellport Bay (Bellport) May - November 2014.

For the fall only experiment with juvenile clams, individuals at the CGSB grew significantly slower ($0.03 \pm 0.05 \text{ mm d}^{-1}$) than clams placed closer to the inlets (USCG ($p < 0.05$), Bellport ($p < 0.038$), and the New Inlet ($p = 0.07$) ($0.07 \pm 0.08 \text{ mm d}^{-1}$ mean for the three sites; Tukey's Tests; Fig. 4C). Bellport and New Inlet had nearly identical growth rates, thus demonstrating the Bellport was, in fact, representative of New Inlet. The greatest instantaneous growth rate occurred at Bellport during the month of October (0.25 mm d^{-1} ; Fig. 4C).

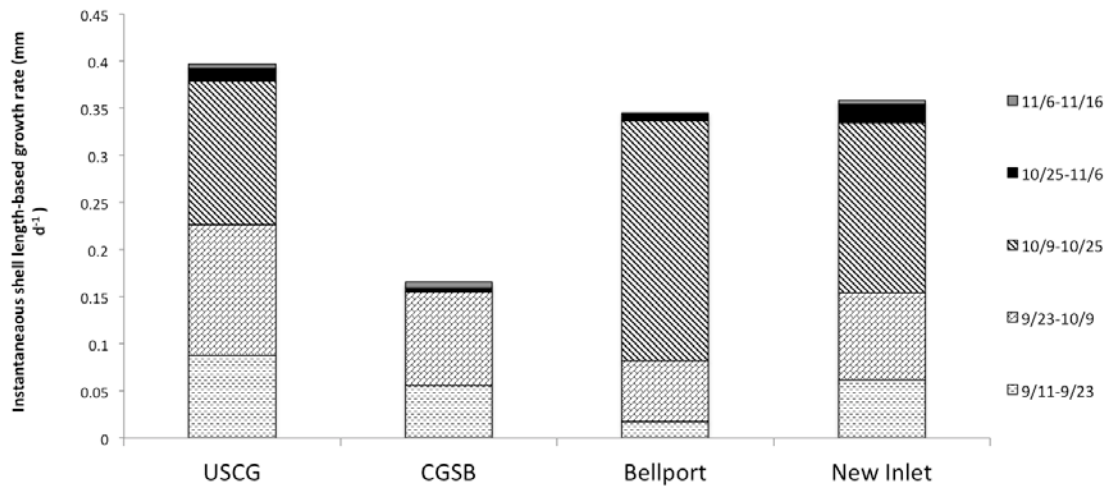


Figure 4C. Instantaneous shell length-based growth rates (mm d^{-1}) for Great South Bay in 2014 for juvenile hard clams in the second experiment deployed in the Fire Island Inlet US Coast Guard Station (USCG), Central Great South Bay (CGSB), and Bellport Bay (Bellport) September - November 2014.

Lipid and protein analysis was performed on all juvenile hard clams' tissue. Small juvenile clams in USCG contained the highest percentage of lipids ($5.46 \pm 0.43\%$) and proteins ($22.2 \pm 2.84\%$; Fig. 5A). Clams at CGSB had lowest percentage of proteins ($22.1 \pm 2.20\%$) while Bellport has the overall lowest percentage of lipids ($5.03 \pm 0.50\%$; Fig. 5A). Large juvenile hard clams within CGSB had the highest percentage lipids ($4.27 \pm 0.18\%$) and the lowest overall percentage proteins ($16.3 \pm 3.29\%$; Fig. 5B). The second experiment showed that sites closest to inlets (New Inlet, USCG) had the highest percentage of lipids (9.01 ± 3.34 , $7.91 \pm 0.97\%$) and the site with the highest percentage of proteins ($17.37 \pm 1.86\%$) located in the central part of the bay (CGSB; Fig. 5C). Tissue analyses was not performed on juveniles from the fall only experiment or on adult clams.

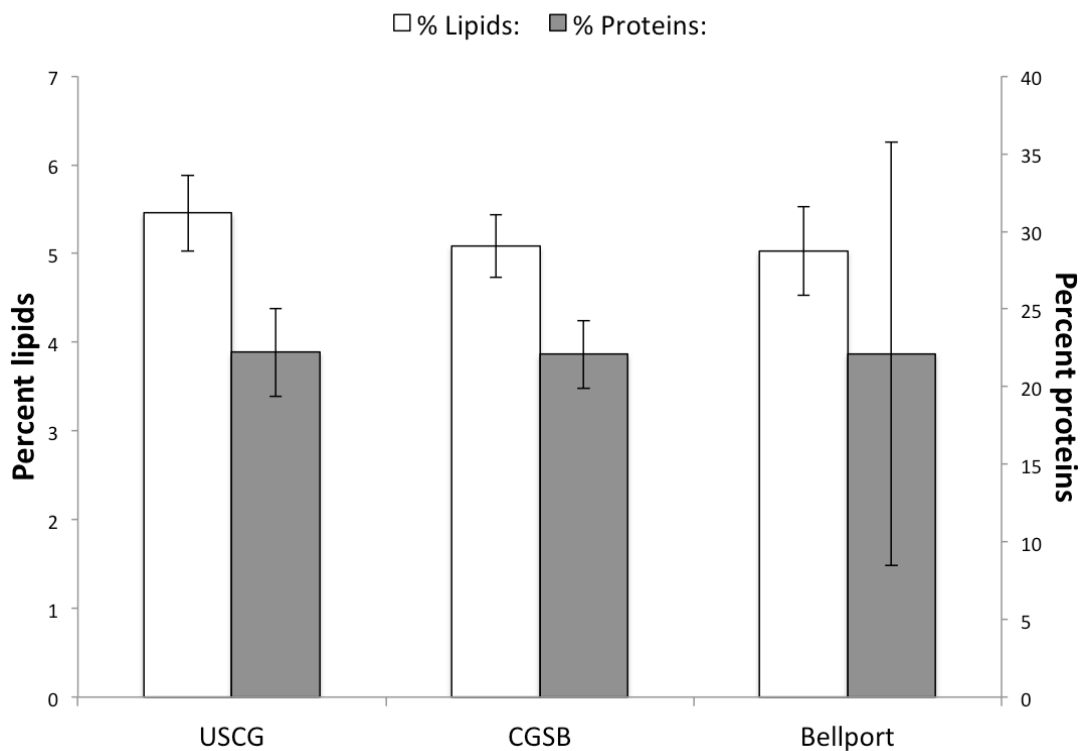


Figure 5A. Percent protein (gray) and lipid (white) content $\pm$ SD in dried small juvenile hard clams from Great South Bay deployed in the Fire Island Inlet US Coast Guard Station (USCG), Central Great South Bay (CGSB), and Bellport Bay (Bellport) September - November 2014.

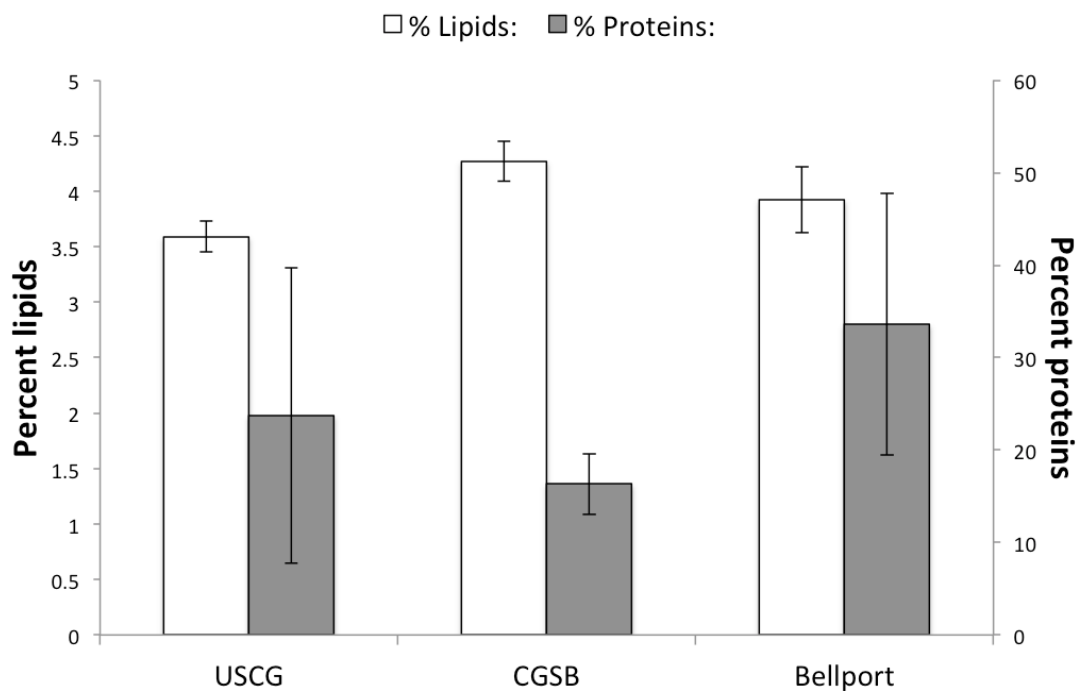


Figure 5B. Percent protein (gray) and lipid (white) content $\pm$ SD in dried large juvenile hard clams from Great South Bay deployed in the Fire Island Inlet US Coast Guard Station (USC), Central Great South Bay (CGSB), and Bellport Bay (Bellport) September - November 2014.

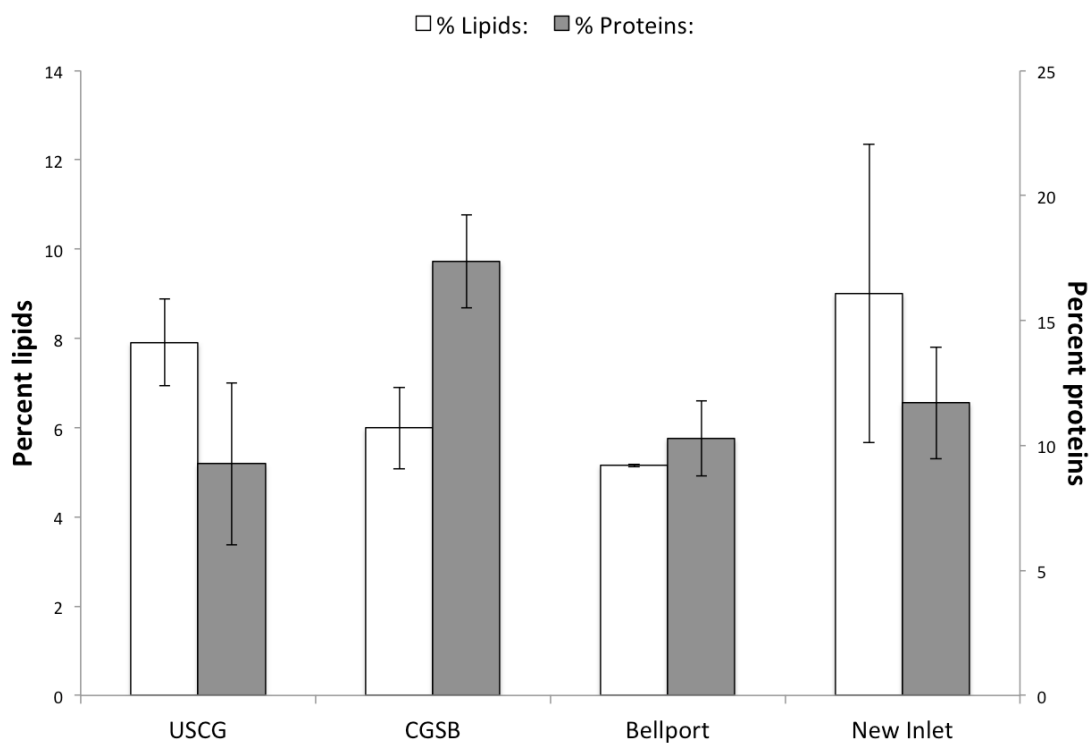


Figure 5C. Percent protein (gray) and lipid (white) content $\pm$ SD in dried juvenile hard clams from Great South Bay November, 2014.

Condition index of adult clams

The mean initial condition index (CI) at the start of the experiment (13 May) of all adult clams placed at each experimental site was 10.05 ± 0.88 (Fig. 6). In late spring CGSB had the highest CI (10.07 ± 1.17) compared to the other sites (Fig. 6). By early September, the CI for adult clams in Bellport (9.26 ± 1.77) was significantly higher than clams in CGSB (8.06 ± 0.90 ; $p=0.031$; Tukey's test; Fig. 6). By November, clams in Bellport (10.23 ± 1.34) and USGC (9.41 ± 1.25) had high CI, while clams at CGSB (7.32 ± 0.68) had significantly lower CI than clams at sites closer to inlets ($p<0.05$; Tukey's test; Fig. 6).

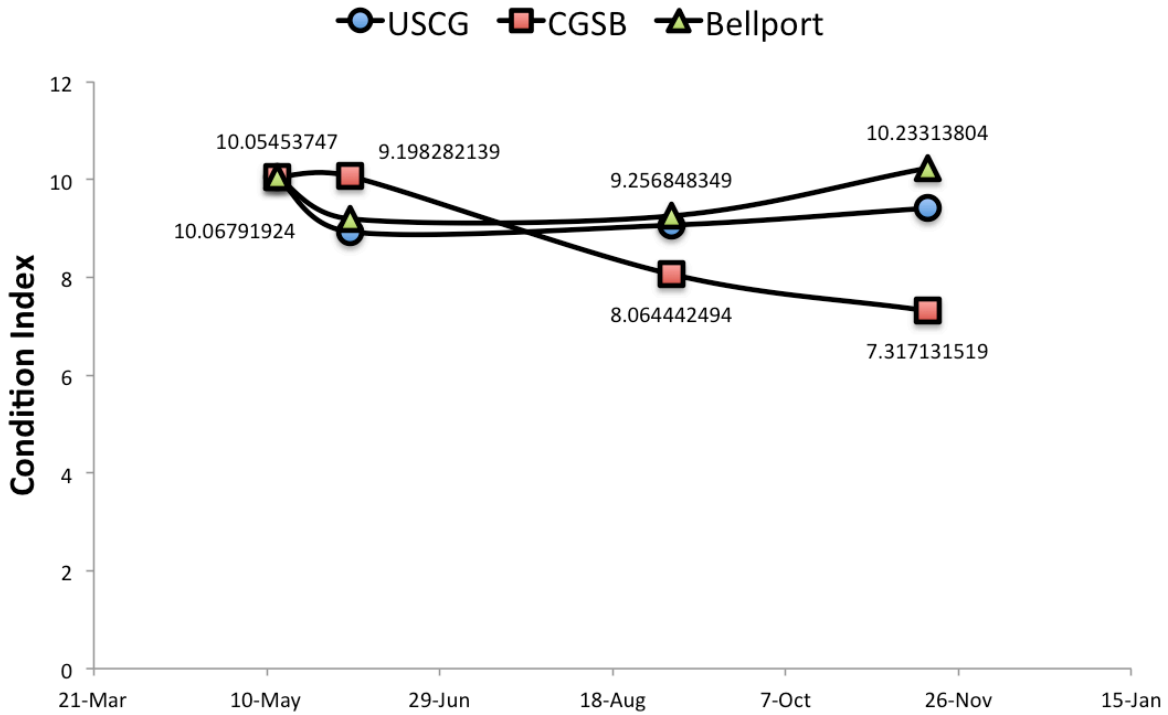


Figure 6. Mean condition index for adult hard clams in Great South Bay during 2014 for Fire Island Inlet (USGC, open circle), central Great South Bay (CGSB, open square), and Bellport (open triangle).

Water quality

Mean annual temperature increased with distance from both the Fire Island and New Inlet in Great South Bay in 2014. All the sites in Great South Bay varied slightly in temperature with CGSB experiencing the peak highest temperature (25.28°C) in June and remained warmest throughout the experiment ($20.30 \pm 5.37^{\circ}\text{C}$). Bellport was $0.15 \pm 0.10^{\circ}\text{C}$ cooler. Meanwhile, the USGC mean water temperature was significantly lower ($18.94 \pm 4.12^{\circ}\text{C}$) than the other sites and reached a maximum temperature of 23.23°C (Table 1). All sites experienced a seasonal decline in water temperature from September through the end of the experiment (16 November). Salinity decreased with distance from the inlets in the bay. The lowest mean salinity was at CGSB at 27.98 ± 0.92 PSU and the highest mean salinity was closest to New Inlet at the Bellport site (30.84 ± 1.69 PSU; Table 1). For the second experiment, the highest salinity readings were from New Inlet (31.51 ± 0.47 PSU).

The highest total chlorophyll *a* was present during late summer into early fall. The mean chlorophyll *a* showed a trend of higher levels found within CGSB ($9.33 \pm 2.35 \mu\text{g L}^{-1}$) compared to the inlets ($4 - 5 \mu\text{g L}^{-1}$; Table 1). The dominant size fraction near the inlet (Bellport) was $>5 \mu\text{m}$ ($3.88 \pm 1.34 \mu\text{g L}^{-1}$) and for USCG was $<2 \mu\text{m}$ ($4.23 \pm 1.19 \mu\text{g L}^{-1}$) (Table 1). Among all sites, the central area of GSB had the highest amount of total, 2-5 and $<2 \mu\text{m}$ chlorophyll *a* (Table 1). A brown tide began in Great South Bay in September and continued through the end of the experiments in November.

Aureococcus anophagefferens concentrations peaked in November in CGSB with counts averaging at $551,000 \pm 13503 \text{ cells mL}^{-1}$, while USCG ($121,000 \pm 14658 \text{ cells mL}^{-1}$), Bellport ($138,00 \pm 6122 \text{ cells mL}^{-1}$) and New Inlet ($32,000 \pm 4016 \text{ cells mL}^{-1}$) experienced significantly lower averages ($p < 0.05$; Tukey's test; Fig. 7).

Table 1. Mean *in situ* temperature (from in situ temperature loggers; °C) $\pm$ SD, maximum seasonal temperatures (from in situ temperature loggers; °C), mean salinities (biweekly) $\pm$ SD, mean total chlorophyll *a* (biweekly) $\pm$ SD ($\mu\text{g L}^{-1}$) and size-fractioned chlorophyll *a* (>5 , 2-5, and $<2 \mu\text{m}$; biweekly) $\pm$ SD ($\mu\text{g L}^{-1}$) for the 2014 sampling season.

Original Exp.							
Sites	Mean Temp	Max. Temp	Mean Salinity	Mean whole Chl <i>a</i>	Mean Chl <i>a</i> $>5 \mu\text{m}$	Mean Chl <i>a</i> 2-5 μm	Mean Chl <i>a</i> $<2 \mu\text{m}$
CGSB	20.30 ± 5.37	25.48	27.98 ± 0.92	9.33 ± 2.35	1.67 ± 0.35	2.34 ± 0.45	5.32 ± 1.84
USCG	18.94 ± 4.12	23.23	28.90 ± 1.43	4.87 ± 1.10	1.70 ± 0.43	0.71 ± 0.12	2.46 ± 0.73
Bellport	20.15 ± 4.70	25.24	30.84 ± 1.69	3.78 ± 0.87	2.70 ± 0.81	0.50 ± 0.13	0.58 ± 0.47
Second Exp.							
CGSB	16.80 ± 5.60	24.50314416	28.79 ± 0.94	16.86 ± 4.14	2.15 ± 0.62	3.60 ± 0.44	11.11 ± 3.33
USCG	17.64 ± 4.47	23.06237741	30.26 ± 0.90	7.81 ± 1.75	2.71 ± 0.81	0.88 ± 0.12	4.23 ± 1.19
Bellport	17.63 ± 4.92	24.35101859	32.58 ± 0.47	5.68 ± 1.73	3.88 ± 1.34	0.47 ± 0.15	1.33 ± 0.61
New Inlet	17.18 ± 3.75	21.00585106	32.58 ± 0.47	5.68 ± 1.73	3.88 ± 1.34	0.47 ± 0.15	1.33 ± 0.61

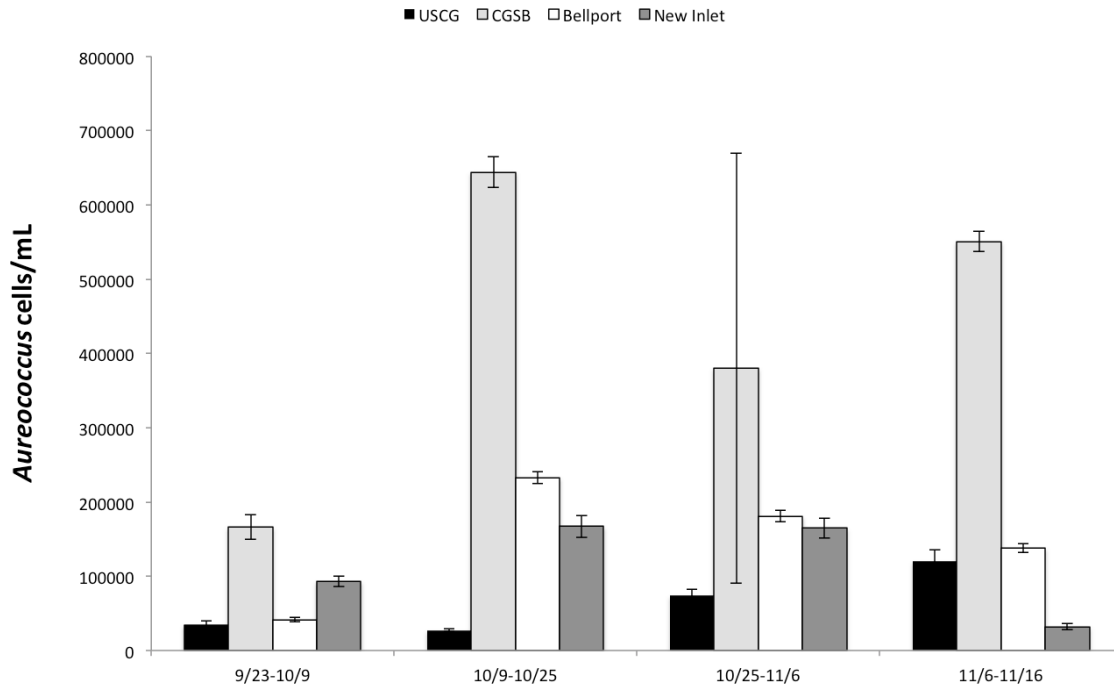


Figure 7. *Aureococcus anophagefferens* cell densities $\pm$ SD. A brown tide took place during experiment in Great South Bay during fall 2014 in central Great South Bay (CGSB, black), Fire Island Inlet (USCG, lite gray), Bellport (white), and New Inlet (dark gray). X-axis labels indicate dates across which samples were collected.

Comparison of 2005 to 2014

Great South Bay has experienced some significant changes since the Weiss et al. (2007) study was conducted in 2005, including the most recent breach (New Inlet) near Bellport Bay and the appearance of brown tide, which did not occur in 2005. Weiss et al. (2007) found that mortality rates of juvenile clams from May-November (2005) within USCG were significantly greater mortality than both CGSB and Bellport Bay (USCG: 24%, CGSB: 12% and Bellport: 9%) ($p < 0.05$; Tukey's test). A similar trend took place for small and large juvenile hard clams in 2014 results; mortality was highest near inlets, being highest at USCG (38%). For the second experiment, however, juvenile hard clams showed an opposite trend, USCG had the lowest mortality (11%).

Weiss et al. (2007) found juvenile clams deployed in CGSB were significantly heavier ($p < 0.001$; Tukey's test) than clams at USCG and Bellport whereas in 2014 small juveniles, CGSB had significantly lower dry tissue weight than USCG and Bellport ($p < 0.05$; Tukey's test). The large juvenile hard clams shared a similar trend in 2014, with CGSB having significantly lower final dry tissue weights (0.174 ± 0.01 g) than USCG (0.308 ± 0.02 g) and Bellport (0.402 ± 0.08 g; $p < 0.05$; Tukey's test).

Weiss et al. (2007) found that the final shell lengths of the hard clams at CGSB and Bellport before the New Inlet were significantly longer than the clams found closer to the inlet (USCG) ($p < 0.001$; Tukey's Test). In contrast, final shell lengths of small, juvenile hard clams for the 2014 experiment showed an opposite trend with sites closer to inlets (USCG, Bellport; 21.12 ± 2.09 mm, 25.25 ± 0.23

mm, respectively) had significantly longer final lengths than CGSB (19.23 ± 0.26 mm; $p < 0.05$; Tukey's test). This 2014 trend was also observed in the large juveniles. Lastly, the final lengths observed in the second experiment also showed that clams at all inlet sites (USCG, Bellport, and New Inlet) were significantly longer than the non-inlet site, CGSB (17.87 ± 1.29 mm).

Growth rates based on length for small juvenile hard clams were different between years ($p < 0.001$) across sites ($p < 0.05$), with a higher average growth rate in 2014 (0.0596 ± 0.013 mm d⁻¹) versus 2005 (0.0459 ± 0.01 mm d⁻¹; Fig. 8). Growth rates based on length for large juvenile hard clams demonstrated the same trend compared to 2005 data, with significantly higher growth rates observed in the 2014 data across all sites (2014; 0.0519 ± 0.008 mm d⁻¹) versus 2005 (0.0459 ± 0.01 mm d⁻¹; $p < 0.001$; two-way ANOVA; Fig. 8). Small and large juvenile clams grew significantly faster in Bellport in 2014 compared to 2005 ($p < 0.05$; Tukey's test; Fig. 8). Small and large juvenile clams grew significantly faster in CGSB in 2005 compared to 2014 ($p < 0.05$; Tukey's test; Fig. 8). Large juvenile clams grew significantly faster in USCG in 2014 compared to 2005 ($p < 0.05$; Tukey's test), whereas there was no difference for the smaller clams (Fig. 8).

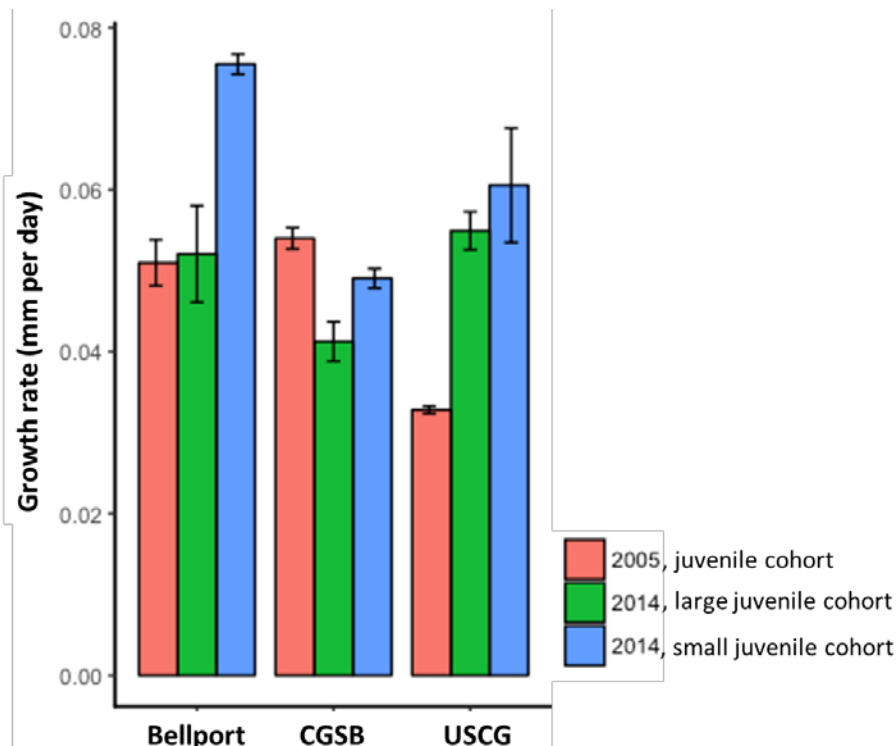


Figure 8. A comparison of length based growth rates of juvenile hard clams deployed in 2005 vs those deployed in the same locations in 2014. Growth rates differed across years and sites for all sites and both cohorts.

Regarding adult clam condition indexes, Weiss et al. (2007) found that by the end of the summer the condition of clams in CGSB (11.93 ± 0.16) was significantly higher than USCG (10.16 ± 0.42), whereas the 2014 condition indexes showed the reverse trend. USCG had a higher condition index (9.07 ± 0.94) than CGSB (8.06 ± 0.9). The CGSB and USCG summer condition indexes for 2005 vs. 2014 were significantly different ($p < 0.001$; one-way ANOVA). Overall, the trends of the main effects of site (CGSB and USCG) and year (2005 and 2014) were significant ($p < 0.006$, $p < 0.001$, respectively; two-way ANOVA).

Water quality differed between 2005 and 2014 in Great South Bay. Water temperatures were significantly warmer in 2005 (CGSB= $21.35^\circ\text{C} \pm 1.69$, USCG= $20.2^\circ\text{C} \pm 1.67$, and Bellport= $21.72^\circ\text{C} \pm 1.92$) compared to 2014 (CGSB= $20.3^\circ\text{C} \pm 5.37$, USCG= $18.9^\circ\text{C} \pm 4.12$, and Bellport= $20.15^\circ\text{C} \pm 4.7$; $p = 0.03543$; $p < 0.05$; two-way ANOVA). The salinity in the GSB in 2014 was significantly lower for USCG (28.09 ± 1.43 PSU) compared to 2005 (29.32 ± 0.37 PSU) but was significantly higher for CSGB and Bellport (27.98 ± 0.92 and 30.84 ± 1.69 PSU) compared to 2005 (26.31 ± 0.5 and 22.26 ± 1.25 PSU). Overall, the trends of the main effects of site and year (2005 and 2014) were significant ($p < 0.001$, $p < 0.001$, respectively; two-way ANOVA). Lastly, the quality and quantity of phytoplankton in GSB differed between 2005 and 2014. The most extreme difference was the appearance of a harmful brown tide in 2014 from September through November at $>100,000$ cells mL^{-1} whereas cell densities in 2005 were three orders of magnitude lower. Regarding total algal biomass, in 2005 the chlorophyll *a* levels peaked during the summer months, with higher concentrations ($>10 \mu\text{g L}^{-1}$) further from the inlet ($<5 \mu\text{g L}^{-1}$). The sites furthest from the inlet (CGSB, Bellport) had the smallest sized phytoplankton abundance, while phytoplankton sizes increased in closer proximity to the inlet (USCG). This overall trend in abundance and size of plankton in 2005 was similar to the water quality in the 2014 experiment. Although, chlorophyll *a* concentrations throughout size fractions (total, >5 , 2-5, $<2\mu\text{m}$ chlorophyll *a*) were significantly lower in Bellport in 2014 compared to 2005 ($p < 0.001$) ($p < 0.05$; one-way ANOVA).

Discussion and Conclusion

During the 2014 experiment, juvenile clams grew faster at sites located closer to inlets compared to the central part of Great South Bay (CGSB) where clams were significantly shorter, lighter, and experienced slower tissue-based growth. Adult clams near the inlets (USCG, Bellport) had significantly larger condition indexes compared to adult clams located further away from ocean inlets (CGSB). This experimental outcome differs from the results from Weiss et al. (2007) who found that clams deployed in CGSB grew fastest and had the highest condition indexes. While the appearance of a brown tide in 2014, but not 2005, was likely to have strongly affected the results, the role of the New Inlet in altering water quality, including brown tide was likely of equal importance in affecting the performance of hard clams.

Factors regulating growth and survival of juvenile hard clams

During the study of hard clams in 2005, their growth and condition was found to be strongly influenced by temperature as well as food quality and quantity. During this study, water temperature was again strongly correlated with instantaneous shell-based growth rate in juvenile clams (Small juveniles $p=0.007$, Large juveniles $p<0.0001$). The optimal temperature range for hard clams is typically between 20-24 °C, while temperatures below (10-20 °C) or above (>24 °C) can result in little to no growth for the clam (Loosanoff, 1939; Pratt and Campbell, 1956; Ansell, 1968; Kennish, 1980; Grizzle and Lutz, 1988; Arnold et al., 1991; Greenfield et al., 2005; Weiss et al., 2007). Consistent with this concept, the growth of large and small juvenile clams was more strongly correlated with cooler temperatures (≤ 24 °C; Small juveniles $R=0.4852$, Large juveniles $R=0.7562$, and second experiment juveniles $R=0.6075$; $p<0.001$ for all) than all temperatures (Table 2). Growth rates with temperatures exceeding 24°C (>25°C) were inversely or poorly correlated (small juveniles $R=-0.2606$, large juveniles $R=0.1272$; Table 2).

Table 2. Correlation (R) of shell length growth rates (mm d⁻¹) with all temperatures (°C), as well as with temperatures less than or equal to 24 °C and greater than 25 °C. Second experiment was conducted during later summer/early fall so temperatures were never greater than 25 °C.

Group	Variable	n	R	Slope	P
Small Juveniles	All temperature	39	0.4269	0.0053	0.0072
	≤ 24 °C	29	0.4852	0.0059	0.0083
	>25 °C	10	-0.2606	0.0232	0.4697
Large Juveniles	All temperature	39	0.6607	0.0063	8.22E-06
	≤ 24 °C	29	0.7562	0.007	4.76E-06
	>25 °C	10	0.1272	0.006	0.7329
Second Exp. Juveniles	All temperature	20	0.6075	0.0098	0.0054
	≤ 24 °C	20	0.6075	0.0098	0.0054

The effect of the New Inlet in regulating temperatures in GSB and, in turn, hard clam growth rates are of importance. Water temperatures during May – October 2014 were cooler than the 2000 – 2015 average for GSB (SCDHS, 2000 – 2016) suggesting that the negative effects of higher summer

temperature would have been even more pronounced during a year with more normal temperatures. Regionally, temperatures have increased by several degrees in recent decades (Gobler et al., 2017) and this rise is expected to continue in the coming decades (I.P.C.C., 2014). Hence, one key role of the New Inlet is likely keeping hard clam growth rates within an optimal range (20 – 24°C) for a greater number of days during summer and fall. While this benefit will not be realized in the spring when cold ocean water limit clam growth rates, regions near the New Inlet will be kept within the ideal region during summer while that region had formerly exceeded the optimal range annually (SCDHS 1976-2016). Further, that range is likely to remain optimal longer in the fall when ocean temperatures exceed those of the more rapidly cooling bay allowing clams to grow faster for longer. Other environmental parameters were also significantly correlated with hard clam growth were also correlated with temperature such as, dissolved oxygen ($p < 0.0001$) and $> 5 \mu\text{m}$ chlorophyll *a* ($p < 0.05$), likely representing collinearity.

One potential negative effect of ocean inlets can be colder temperatures in spring compared to mid-bay locations. Both cohorts of juvenile clams experienced high rates of mortality in spring (May) with rates within the CGSB sites being significantly lower than the ocean inlet sites. During extended periods (> 8 weeks) of low temperatures ($< 5^\circ \text{C}$) in winter, juvenile hard clams cease feeding and consequently utilize their energy stores for metabolism (Zarnoch and Schreiber, 2008). In this compromised physiological state, massive spring mortality can occur if temperature and metabolic demands increase while food levels remain low (Zarnoch and Schreiber, 2008).

Beyond temperature, hard clams in Great South Bay were strongly influenced by plankton groups present in GSB. To model the importance of all environmental factors measured on hard clam populations, step-wise, forward multiple linear models were made using concurrently measured environmental parameters. For small juvenile clams, the best model explained 76% of the variance in their growth rates ($R = 0.76$) and included the pigments (in $\mu\text{g L}^{-1}$) 19'-butanoyloxyfucoxanthin ($p < 0.001$), fucoxanthin ($p < 0.05$), lutein ($p < 0.005$), and temperature (in $^\circ\text{C}$; $p < 0.05$):

$$\text{Small juvenile growth rates (mm d}^{-1}\text{)} = -0.0171 - (0.218 * \text{But-fuco}) + (0.0250 * \text{fucoxanthin}) - (0.0239 * \text{lutein}) + (0.00414 * \text{temperature})$$

For large juvenile clams, the best model explained 71% of the variance in their their growth rates ($R = 0.71$) and included the pigment (i19'-butanoyloxyfucoxanthin (in $\mu\text{g L}^{-1}$; $p < 0.05$) and temperature (in $^\circ\text{C}$; $p < 0.05$):

$$\text{Large juvenile growth rates (mm d}^{-1}\text{)} = -0.0167 - (0.0718 * \text{but-fucoxanthin}) + (0.00407 * \text{temperature})$$

As explained earlier in the discussion, clam growth rates are positively dependent on the association between temperature and the growth of both cohorts of hard clams in the models. As discussed below, brown tide is toxic to juvenile hard clams and 19'-butanoyloxyfucoxanthin is a pigment used to trace the brown tide (Trice et al., 2004) accounting for the negative association with this factor in both models. For the small juvenile hard clams, the positive association with fucoxanthin likely represents the importance of high quality food for clams as this pigment is enriched in diatoms and

chrysophytes, two classes of phytoplankton known to support robust growth in *Mercenaria* (Kraeuter and Castagna, 1989). Finally, lutein is only found in green algae which have formed algal blooms in Great South Bay that were harmful to bivalves (Ryther, 1954), likely accounting for the negative association in the small juvenile clam model.

Brown tides have been shown to be harmful to hard clams (Bricelj et al., 2001; Greenfield and Lonsdale, 2002; Gobler et al., 2005) and the negative effects of the fall 2014 brown tide on clams deployed in Great South Bay seemed clear. The highest brown tide densities were observed at the CGSB station and juvenile clams at this location had a 10% rise in the mortality during the brown tide and all juveniles deployed in this locale showed the slowest growth. Examining the changes in growth rate with time, all three cohorts of juvenile clams stopped growing entirely during the first three weeks of October when the brown tide was most intense. In addition, juvenile clams from the fall-only deployment that were located in CGSB and Bellport had almost extremely low lipid content by the end of the experiment while clams from the inlets had significantly higher levels. Since lipids are considered an energy reserve for early life stage bivalves (Gallager et al., 1986) and since brown tide is known to be a poor food source (Bricelj and Lonsdale, 1997), the lower lipid levels in these clams is likely reflective of these individuals needing to rely on internal lipid stores for metabolism during the brown tide. Finally, while adult clams deployed near the inlets displayed an increasing condition index during the fall, the condition of clams within CGSB declined, indicating brown tide may diminish the reproductive output of hard clam populations (Doall et al., 2008). While brown tides had formerly spread throughout all of Great South Bay (SCDHS 1985-2011), since the formation of the New Inlet the cells densities achieved by brown tide during these events in eastern GSB has been lessened, presumably due to enhanced ocean flushing. Given that the impacts of brown tides on hard clams are dose-dependent (Bricelj et al., 2001), it would seem the ability of the New Inlet to dilute brown tide cell densities is of benefit to hard clams. Since brown tides are harmful to seagrasses, zooplankton, and other bivalves, the New Inlet's ability to mitigate brown tides may benefit the entire marine food web.

Potential interactive effects of temperature and food quality on hard clams

Consistent with prior studies, temperature and food quality had a strong effect on the growth and condition of hard clams in Great South Bay during this study. As with any single year environmental study, the conditions present in a given year will strongly influence the outcome of the experiment and may or may not be reflective of long-term trends. In 2014, there was a brown tide and summer water temperatures were cooler than average. As already discussed, these conditions may have had antagonistic effects on the clams as the temperatures remaining in the optimal range for clams was likely beneficial while the brown tide was detrimental (Gobler et al., 2005; this study). Had a brown tide not occurred in 2014, it is possible that the warmer temperatures and perhaps improved food quality in CGSB may have benefited the clams there and performance of the clams may have improved. During a prior study in GSB, juvenile clam growth rates were negatively correlated with dinoflagellates (Weiss et al., 2007) and a longer term study of the New Inlet has shown that it has led to lower levels of dinoflagellates across GSB and particularly within Bellport Bay (Gobler et al., in prep). Hence, even in the absence of brown tides, it would seem the change in phytoplankton

communities associated with the formation of the New Inlet will have some direct benefits to hard clams.

Over the course of the study, juvenile hard clams grew fastest and adult clam condition was best in regions closer to ocean inlets. The poorer performance of clams within CGSB was partly related to a brown tide that occurred in the fall that was most intense in that region and was minimized near inlets by ocean flushing. Growth rates of clams were positively correlated with temperature for nearly all of the 2014 experiment but the CGSB location attained higher than optimal temperatures during the summer and cooled below optimal temperatures faster in the fall. Although the sporadic occurrence of brown tides complicates the ability to draw long-term conclusions, the sum of the findings of this study suggests that the New Inlet will benefit hard clam populations in the region by minimizing the negative effects of harmful algae and fostering ideal temperatures for a longer period during the summer and fall. Future management schemes could consider leaving newly formed ocean inlets open to benefit resident hard clam populations. To generate a more holistic understanding of the manner in which new inlets affect hard clam populations in GSB, future studies could be longer term and could target additional metrics of hard clams such as larval stages, reproductive output, and whole population models.

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