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The influence of plankton composition and water quality on hard clam (*Mercenaria mercenaria* L.) populations across Long Island's south shore lagoon estuaries (New York, USA)

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Abstract

We conducted a two-year study to assess how plankton composition and water quality impacts the distribution, densities, condition, growth, biochemical composition and reproductive success of juvenile and adult *Mercenaria mercenaria* (L.) in Long Island's south shore estuaries (LISSE). Juvenile and adult hard clams were placed in suspended cages at 10 locations ranging from the ocean inlets to locations furthest from inlets in Shinnecock Bay (SB), the eastern-most barrier island estuary of LISSE, and Great South Bay (GSB), the western-most barrier island estuary of LISSE. Phytoplankton community composition, temperature, salinity, dissolved oxygen, and clam growth and condition were monitored bi-weekly. A benthic survey of *M. mercenaria* densities in both estuaries was also conducted. In both 2004 and 2005, juveniles in central bay locations had significantly faster growth rates, lower mortality rates, and higher lipid content relative to sites closest to the inlets. Adult hard clams closest to the Fire Island inlet also had significantly lower condition indexes compared to mid-bay stations and densities of wild *M. mercenaria* populations in both estuaries were lower near inlets compared to locations further from inlets. In addition to substantial spatial differences within each estuary, differences were also observed between the embayments as juvenile clams in SB grew approximately twice as fast as those in GSB and adults in SB had significantly greater condition indexes than clams in GSB. Instantaneous juvenile growth rates were highly correlated to temperatures below 24 °C ($p<0.0001$) and were also significantly correlated with several indicators of suspended food quantity and food quality (centric diatoms, phytoplankton cells >5 μm, and dinoflagellates (inverse correlation)) which co-varied independently of temperature. In sum, these results suggest tidal exchange in LISSE promotes a water quality regime (cold water, with low food concentration) which would reduce the growth of juvenile clams and the overall reproductive success of adult hard clams located near newly-formed ocean inlets. However, increased exchange for regions furthest from inlets could enhance juvenile clam growth rates by reducing summer peak temperatures (>24 °C) and densities of poor food sources (dinoflagellates).
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Keywords: Great South Bay; Hard clam; Lagoon estuaries; *Mercenaria mercenaria*; Phytoplankton; Shellfish growth; Shinnecock Bay

1. Introduction

There are more than 2200 coastal lagoons or barrier island estuaries in the world (Pilkney, 2003) and the United States is bordered by a series of barrier island lagoons stretching from New England south through the

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Gulf of Mexico. Barrier island estuaries tidally exchange ocean waters via inlets, a process which can influence many aspects of water quality including temperature, salinity, water clarity, nutrient levels, and plankton composition. Low rates of tidal exchange in many lagoonal estuaries allow them to accumulate nutrients from freshwater sources, and in turn, support an abundance of life (Kjerfve and Magill, 1989). However, the precise impact of tidal exchange on many components of estuarine food webs is not completely understood.

The south shore of Long Island, New York, is comprised of a series of continuous barrier island estuaries including Great South Bay (GSB) to its western most extent, Moriches Bay in its mid-section, and Shinnecock Bay (SB) to the east (Fig. 1). Long Island's south shore estuaries (LISSE) have experienced a series of barrier island breaches during the past century which have substantially increased ocean tidal exchange. While some breaches have been ephemeral, lasting for weeks or months (i.e. 1992 breach in Moriches Bay), others have been stabilized and made permanent (i.e. Moriches and Shinnecock Bay inlets). LISSE have been some of the most productive estuaries in the United States with regard to both primary productivity and the past harvest of shellfish (Ryther, 1954; Lively et al., 1983; Kaufman et al., 1983; COSMA, 1985).

The most successful shellfishery in LISSE has been that of the northern quahog or hard clam, *Mercenaria mercenaria* (L.). During the 1970s, two out of every three hard clams consumed on the east coast of the US came from LISSE, representing the top grossing fishery in the history of New York State (McHugh, 1991). During the 1980s and 1990s, overharvesting and chronic brown tide blooms greatly diminished hard clam abundances (COSMA, 1985; Gobler et al., 2005). The current inability of *M. mercenaria* populations in LISSE to recover, despite significantly reduced harvesting pressure and the cessation of brown tides this decade, suggests other factors may be preventing the optimal growth of hard clams in LISSE.

The success of *in situ* populations of shellfish is a function of multiple biological and environmental factors (Kraeuter and Castagna, 1989). In addition to physical factors such as temperature, salinity, and oxygen, food quality and quantity can also influence the growth of hard clams (Laing et al., 1987; Bass et al.,

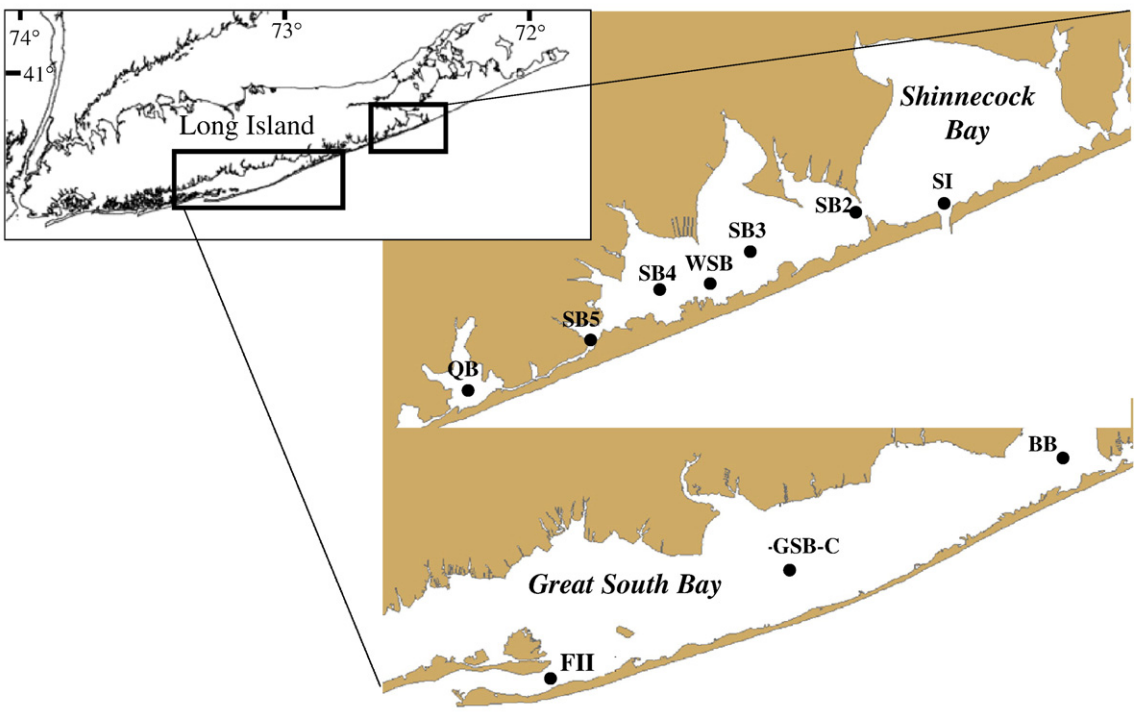

Fig. 1. Study sites in Shinnecock Bay and Great South Bay. In 2004, sampling locations were Shinnecock Bay inlet (SI), sites in western Shinnecock Bay (SB2–SB5), and Quantuck Bay (QB). In 2005, sampling locations were in Great South Bay inlet (FII), central Great South Bay (GSB-C), and Bellport Bay (BB), while Shinnecock Bay stations were SI, western Shinnecock Bay (WSB), and QB.

1990; Wikfors et al., 1992; Bricelj et al., 2001; Greenfield et al., 2005). Since temperature, salinity, nutrient, and chlorophyll *a* concentrations near ocean inlets are markedly different than within-estuary sites in LISSE (SCDHS, 1976–2005), ocean tidal exchange is likely to play a pivotal role in the success of hard clam populations.

For this study, we sought to determine how various physical and biological parameters across a range of estuary-to-ocean locations in Shinnecock Bay and Great South Bay of LISSE influenced the success of *M. mercenaria* populations. We evaluated the growth and biochemical composition of juvenile *M. mercenaria* as well as the distribution, densities, and condition of adult *M. mercenaria*. We concurrently assessed water quality (salinity, temperature, dissolved oxygen) and characterized the plankton assemblages with regard to biomass, size distribution, and species composition. Finally, we combined these data sets to elucidate the influence of water quality and plankton communities on the growth, condition, and distribution of adult and juvenile *M. mercenaria* in LISSE.

2. Materials and methods

2.1. Field sampling and water collections

In 2004, six stations across an estuary-to-ocean gradient (Shinnecock inlet (SI) to Quantuck Bay (QB)) were sampled in Shinnecock Bay (Fig. 1) biweekly from June through November. In 2005, we expanded our study to include three sites in GSB ranging across an estuary-to-ocean gradient (Fig. 1) which were sampled biweekly from April through November ($n>12$). Sampling via small boats was conducted irrespective of tidal state. The frequency of sampling assured that each site was sampled during both tidal extremes several times during each season. During each individual sampling event, triplicate surface water samples from each site were processed and analyzed for size-fractioned chlorophyll *a* (whole, <5 μm, <2 μm) and suspended particulate organic carbon and nitrogen (POC, PON). The shallow, well-mixed nature of LISSE (Wilson et al., 1991) ensured that sample water collected was representative of the entire water column at each station. Chlorophyll samples were fluorometrically analyzed according to Parsons et al. (1984). POC and PON samples were analyzed on a CE Instruments Flash 1112 elemental analyzer (Cutter and Radford-Knoery, 1991). To quantify microplankton (>20 μm) to the genus level, Lugol's iodine preserved samples were collected and analyzed using settling chambers and an inverted microscope (Hasle, 1978). Paraformaldehyde-preserved samples were also 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 measured with a YSI Environmental Model 556 proof included water temperature, salinity, and dissolved oxygen. Measurements of these parameters at surface and at depth throughout this study confirmed the absence of stratification in this system (Wilson et al., 1991).

2.2. Bivalve growth, biochemistry, and condition index

In 2004, juvenile *M. mercenaria* ($n=1800$; 11.18±1.04 mm shell length) were supplied by Cornell Cooperative Extension of Southold, NY. Clams were placed in screened (2 mm pore size) 1 m×1 m×20 cm experimental cages that were suspended 0.5 m above the sediment via a buoy. Cages were stabilized via a bottom weight and weights on the bottom of the cage. Triplicate cages were deployed at each site from June to November, 2004. Water temperature of each site was measured every minute through this period using *in situ* temperature loggers (Onset©). In April 2005, juvenile *M. mercenaria* ($n=2000$; 14.45±0.60 mm shell length) were supplied by Easthampton Town Shellfish Hatchery of Easthampton, NY. Clams were placed in rigid, plastic mesh bags (9 mm openings) which were placed in 1 m×3m×60 cm cages which were heavily weighted and suspended about 0.5 m above the sediment. Triplicate cages with temperature loggers were deployed at each site from April to November, 2005, except in Shinnecock Inlet (SI) where cages were lost in late August. Experiments in 2005 utilizing both the 2004 and 2005 cages simultaneously yielded growth rates of juvenile hard clams which were nearly identical and not statistically different.

During both years, length, a measurement from the posterior to anterior end of the shell (Kraeuter and Castagna, 1989), was recorded biweekly in tandem with water column sampling. A mean initial stock was determined by measuring fifty clams, while mean shell length was determined for each sampling period by randomly measuring 25 clams from each cage ($n=3$). To estimate an initial mean ash-free dry weight (AFDW), one hundred clams were selected from the initial set and clam bodies were dried at 70 °C for at least 24 h and then ashed at 450 °C for an additional 4 h (Gabbott and Walker, 1971; Bass et al., 1990). A mean AFDW per cage ($n=3$ per site) was determined by removing eight or more clams per cage

during each sampling period. A final cumulative absolute growth rate of clams (GR) was calculated each year by using the equation: $GR=(L_2-L_1)/(t_2-t_1)$, where GR is the absolute growth rate (per day), L_2 and L_1 represent the final and initial AFDW (milligrams) and t_2 and t_1 represent the final and initial time (days; Grizzle et al., 2001). Instantaneous shell length-based growth rates of clams (μ) were also calculated between collection intervals and was 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 (millimeters) at times t_2 and t_1 (days; Grizzle et al., 2001).

In 2005, total protein and lipid content was measured on juvenile hard clams ($n>10$) obtained at all locations during the final collection (November). Pooled hard clams for each cage from each site were dried (60 °C), weighed, and homogenized according to Zarnoch (2006). Three sub-samples of this powder were then used for each biochemical assay. As such, reported variance is methodological, rather than variability among cages. 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 using the gravimetric, chloroform extraction method of Folch et al. (1957).

In 2005, we also examined the condition index (CI) of adult *M. mercenaria* experimentally placed in GSB and SB. Adult *M. mercenaria* ($n=1000$; mean=63.07±13.05 mm; range 26.62–176.55 mm) were obtained from a common site (Coecles Harbor, NY) during early spring and were placed at each experimental site in the same cages as the juvenile cages in separate rigid, plastic mesh bags. The rigid nature of the bags held the adult clams firmly in place. Forty adult clams were analyzed from the initial stock to determine a mean initial condition index while 15 clams from each site were randomly measured during each collection period. Upon collection, clams were cleaned and placed in seawater tanks to encourage pumping for at least 2 h. A series of shell measurements were taken (length, width, and height) as well as live whole weight. As clams were shucked, water was drained but all body tissues were collected. Clam bodies and shells were desiccated at 75 °C for at least 7 d and then reweighed. CI is a gravimetric measurement that expresses the amount of soft tissue per unit shell and is an index of the nutritive status and recent stress of the bivalve under a given set of ambient environmental conditions: CI=(dry soft tissue wt (g)×1000)/internal shell cavity capacity (Crosby and Gale, 1990).

2.3. Statistical analyses

Comparisons of characteristics of hard clams among sites were made via one-way ANOVAs, followed by Tukey's multiple comparison tests to elucidate sites which were significantly different from each other. For all juvenile clam parameters, with the exception of biochemical analyses (see above), cages represented replicates ($n=3$ per site). For adult hard clams, for which the total sample size was smaller, there were no statistical differences in the condition index of individuals between cages at each site during each sampling period. Therefore, individual adult clams at each site were pooled on each date ($n=15$) for statistical comparison of condition indexes among sites.

Relationships between shell-based instantaneous growth of juvenile hard clams, adult condition indexes, and environmental data were examined via Spearman's coefficient of rank correlations. Environmental parameters examined specifically included temperature determined with temperature loggers, salinity, size-fractionated chlorophyll *a* (<2, 2–5, >5 μm), flow cytometric-based phytoplankton cell densities (cells <2, 2–5, >5 μm), total eukaryotic phytoplankton cell densities, *Synechococcus* sp. cell densities, total diatoms, centric diatoms, pennate diatoms, dinoflagellates, particulate organic carbon (POC), particulate organic nitrogen (PON), POC:PON ratio, and five photopigments which are found exclusively in single classes of phytoplankton (peridinin=dinoflagellates, alloxanthin=cryptophytes, lutein=chlorophytes, zeaxanthin=cyanobacteria, fucoxanthin=diatoms and some chrysophytes; Wright et al., 1991). The complete set of environmental data can be found in Curran (2006). The construction of correlations between instantaneous growth rates or adult condition indexes and environmental variables over multiple time periods through the study was made with the assumption that successive growth rates of populations at each site were independent of prior growth rates. Linear regressions were also used to compare final cumulative absolute AFDW growth with total mean environmental data to assess the variability in observed differences in growth rates.

2.4. Benthic surveys

In 2004 and 2005, a stratified random sampling design was used to identify ~200 sites throughout Great South Bay and Shinnecock Bay. At each site, ten haphazard quadrats (0.25 m^2) were used to sample frequency, density, and abundance of *M. mercenaria* by hand to a depth of 20 cm allowing clams 20 mm and

larger to be quantified. Point data of hard clam densities were used to produce continuous maps within each estuary. A krigging algorithm (Watson, 1992) was used to interpolate between the random point data. A spatial analysis program (SURFER, Golden Software, Golden, CO, USA) was used to compute areas of each parameter from these interpolated surfaces.

3. Results

3.1. Juvenile hard clam mortality, 2004

By mid-June 2004, we observed elevated levels of mortality at stations SI and SB2 (mean±SE=4.33±3.79% and 10.67±6.66%), compared to other sites (0.67–1.33%; Fig. 2) although differences were not statistically significant. By November, cumulative clam mortality was not significantly different between the Shinnecock Bay sites (Fig. 2). Mortality ranged from 11.00±1.00% to 14.33±1.45% with those clams in SB3 and QB experiencing the greatest final percentages and clams in SB4 and SB5 experiencing the lowest total mortality.

3.2. Growth of juvenile clams, 2004

Clam weights continuously increased during the 2004 growing season but differed among sites (Fig. 3). At the start of the experiment (4 June), the mean initial AFDW of clams was 13.4±4.70 mg. By the end of the study (4 November), clams in SB3 (361.8±97.0 mg) were significantly heavier than clams located at all other sites while clams in SI were significantly lighter than individuals located at all other sites (Tukey test, $p<0.05$; Fig. 3). This trend was also seen in cumulative AFDW-based growth rates with clams in SB3 having the greatest tissue-based growth (2.28 mg d^{-1}) and

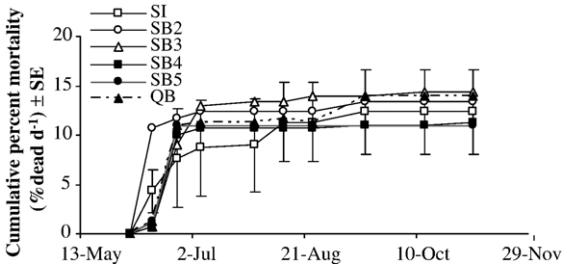

Fig. 2. Cumulative percent mortality ±SD in juvenile hard clams in Shinnecock Bay during May and November, 2004 for Shinnecock inlet (SI, open square, solid line), SB2 (open circle, solid line), SB3 (open triangle, solid line), SB4 (closed square, solid line), SB5 (closed circle, dashed line), Quantuck Bay (QB, closed triangle, dashed line). See Fig. 1 for station locations.

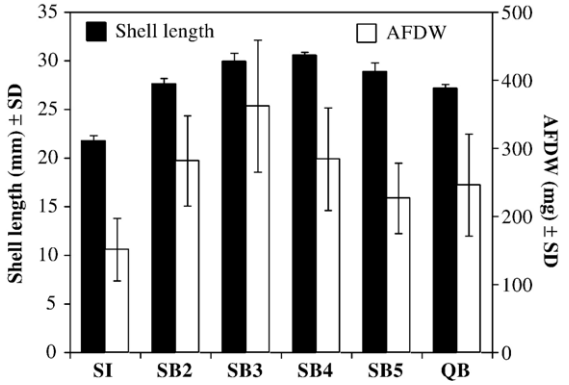

Fig. 3. Final shell length (mm; black bars) ±SD and final AFDW (mg; white bars) ±SD for juvenile clams in November 2004.

clams in the inlet having the slowest overall tissue growth (0.90 mg d^{-1}). Differences in final ADFW were paralleled by clam lengths as by November, clams at SB3 and SB4 achieved lengths (29.91±0.86 mm and 30.56±0.32 mm) which were significantly greater than SI, SB2, and QB (Tukey test, $p<0.004$; Fig 3). Additionally, clams at the inlet site were significantly shorter (21.74±0.57 mm) than all other sites (SB2–QB; Fig. 3; Tukey test, $p<0.001$).

Instantaneous growth rates varied spatially and temporally across sites. Throughout June, the highest instantaneous growth rates were achieved by clams located in sites furthest from the inlet (SB4–QB) while the slowest growing clams were found in sites closest to the inlet (SI–SB3) (Fig. 4). Throughout July and early August, the greatest instantaneous growth occurred in clams found at central bay sites including SB3 (0.010 mm d^{-1}) and SB4 (0.011 mm d^{-1}). During late summer, clams in back-bay sites sustained the lowest growth rates (0.001–0.004 mm d^{-1}) while clams in central locations continued to have the greatest instantaneous growth rates (0.005–0.006 mm d^{-1}; Fig. 4). By the fall (October–November), clams closest to the inlet had the greatest shell growth compared to clams found in sites furthest from the SI which had minimal growth (Fig. 4).

3.3. Juvenile hard clam mortality, 2005

During the first six weeks of 2005 (21 April–8 June), juvenile *M. mercenaria* in SI experienced significantly higher mortality than all other sites (mean±SE=47.0±9.20%; $p<0.05$; Tukey test; Fig. 5). From April to November, juveniles in all three GSB sites experienced lower mortality (Fire Island inlet (FII): 24%, central GSB (GSB-C): 12%, and Bellport Bay (BB): 9%) than

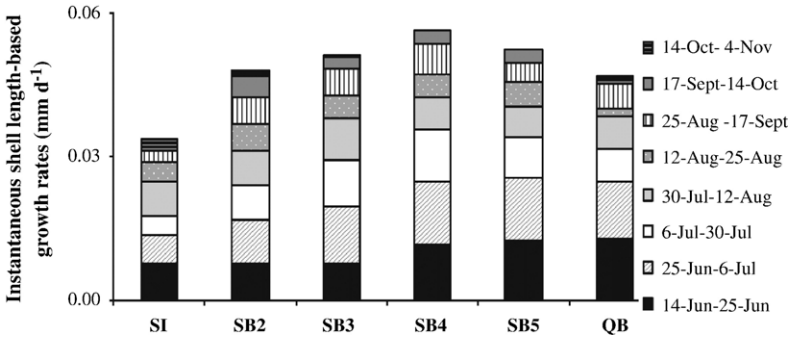

Fig. 4. Instantaneous shell length-based growth rates (mm d^{-1}) for Shinnecock Bay in 2004.

clams in SI (49%), Western Shinnecock (WSB) (26%) and QB (32%; Fig. 5). However, juvenile mortality in FII was significantly greater than mortality in both GSB-C and BB ($p<0.05$; Tukey test; Fig. 5B).

3.4. Growth of juvenile clams, 2005

The weight of juvenile clams increased substantially at all locations in 2005 (Fig. 6). At the start of the experiment, the mean initial AFDW was 17.40±3.13 mg. However, by November, clams in WSB (483.00±51.00 mg) had the heaviest mean AFDW with a cumulative AFDW-based growth rate of 2.29 mg d^{-1} while clams in FII were the lightest (162.09±7.77 mg; SI clams not available) and had a cumulative growth rate of 0.74 mg d^{-1} (Fig. 6). Within GSB, clams in GSB-C (255.61±64.28 mg) were significantly heavier than both FII and BB (162.09±7.77 mg and 194.76±42.39 mg; Tukey test, $p<0.001$; Fig. 6). Cumulative tissue-based growth was also greater in GSB-C (1.22 mg d^{-1}) than both FII (0.74 mg d^{-1}) and BB (0.90 mg d^{-1}). Final shell lengths followed a pattern similar to AFDW with clams in WSB (32.63±3.16 mm) having significantly longer shell lengths than clams in QB (25.9±2.96 mm), FII (21.32±1.71 mm), GSB-C (25.64±2.02 mm), and BB (24.92±2.02 mm; Tukey test, $p<0.001$; Fig. 6). All clams in non-inlet locations (WSB, QB, GSB-C, and BB) were significantly longer than clams found in FII (Tukey test, $p<0.001$; SI clams not available).

Instantaneous growth rates differed significantly among sites through 2005 (Fig. 7). During April and May, clams furthest from both inlets had the largest growth rates while clams in SI and FII showed little to no growth (0.0004 and 0.0003 mm d^{-1}, respectively; Fig. 7). During early summer (June–early August), all clams away from the inlets, particularly clams located in central bay sites sustained the greatest growth rates (0.004–0.009 mm d^{-1}) while the growth of clams near the inlets was consistently lower (0.000–0.005 mm d^{-1};

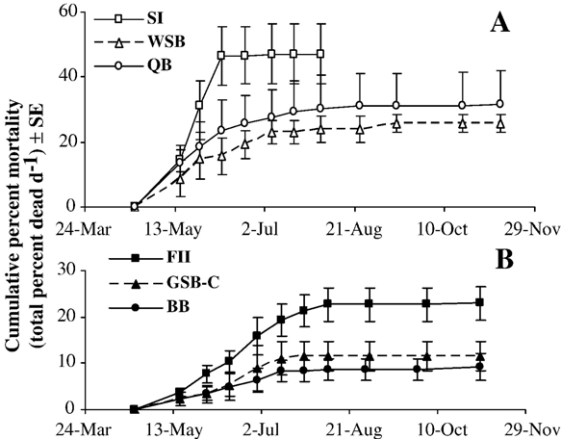

Fig. 5. Cumulative percent mortality ±SD in juvenile hard clams in (A) Shinnecock Bay and (B) Great South Bay during 2005 for Shinnecock inlet (SI, open square), western Shinnecock Bay (WSB, open triangle), Quantuck Bay (QB, open circle), Fire Island inlet (FII, closed square), central Great South Bay (GSB-C, closed triangle) and Bellport Bay (BB, closed circle).

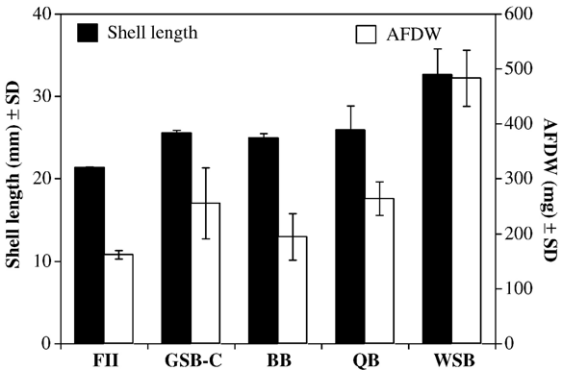

Fig. 6. Final shell length (mm; black bars) ±SD and AFDW (mg; white bars) ±SD for juvenile clams in both Shinnecock Bay and Great South Bay during November 2005.

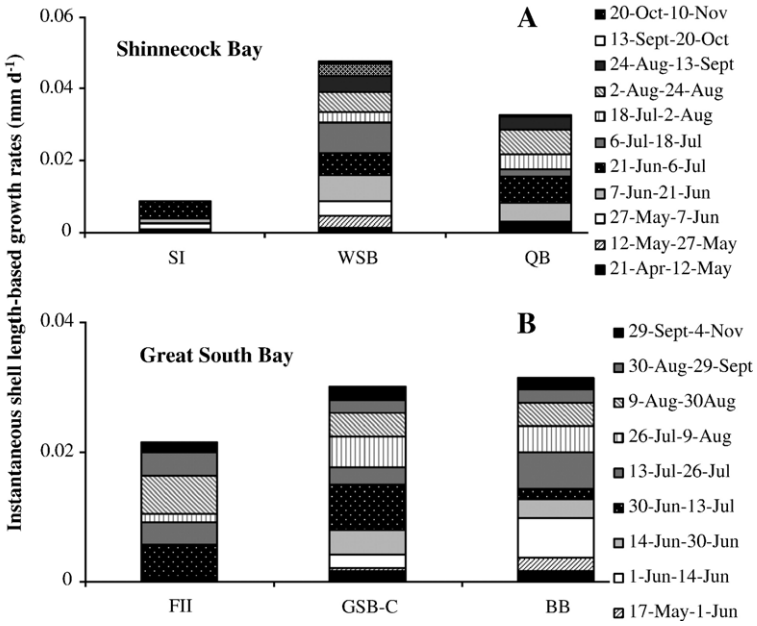

Fig. 7. Instantaneous shell length-based growth rates (mm d^{-1}) for both Shinnecock Bay and Great South Bay.

Fig. 7). In late summer, these spatial trends began to reverse, as clams within most back-bay stations (WSB, GSB-C, BB) displayed slowed or no growth while clams at the FII site experienced increased growth rates (0.004–0.006 mm d^{-1}; Fig. 7). During the fall, clams in GSB sustained higher instantaneous growth rates than SB (0.000–0.001 mm d^{-1}) with clams in all three GSB sites experiencing nearly identical shell growth (0.002 mm d^{-1}; Fig. 7).

At the end of the study, clams in WSB had a significantly higher lipid content (9.20±0.09%) than clams in FII (6.75±1.22%; Tukey test, $p<0.05$) and also had greater lipid content than BB (8.64±1.37%), GSB-C (7.99±1.35%), and QB (8.43±1.01%) clams, although these differences were not statistically significant (Fig. 8). Protein content of clams did not differ significantly between sites.

3.5. Condition index of adult clams

At the start of the experiment (22 April), mean initial condition index of adult clams placed at each experimental site was 8.85±0.22 (mean±SE). During late June and early July and again during the beginning of August, the CI of adult clams in WSB, QB, and GSB-C were significantly greater than the CI of clams in FII (Tukey test, $p<0.05$; Fig. 9). Between mid-July and early August, the CI of SI clams were also significantly greater than those in the FII (Tukey test, $p<0.05$), while the CI of clams from other sites were similar. By the end of the summer, only clams in WSB (11.86±0.23) and GSB-C (11.93±0.16) had significantly greater CI than clams in FII (10.16±0.42). By early fall (15 September), clams in QB (12.47±0.20) had the greatest CI value which was significantly greater than the CI of both FII (10.16±0.42) and WSB (10.89±0.27) clams (Tukey test, $p<0.05$; Fig. 9).

3.6. Water quality

Mean annual temperature increased with distance from the Shinnecock inlet during 2004. SI had a mean

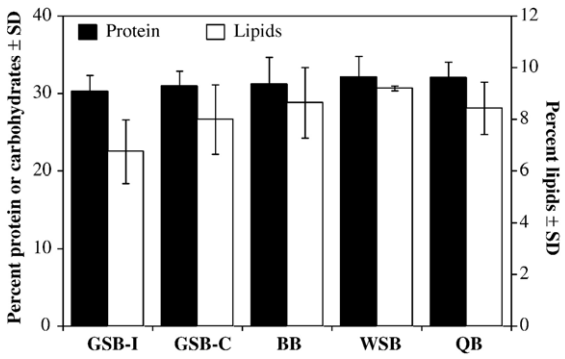

Fig. 8. Percent protein (black) and lipid (white) content ±SD in dried juvenile hard clams from Shinnecock Bay and Great South Bay November, 2005.

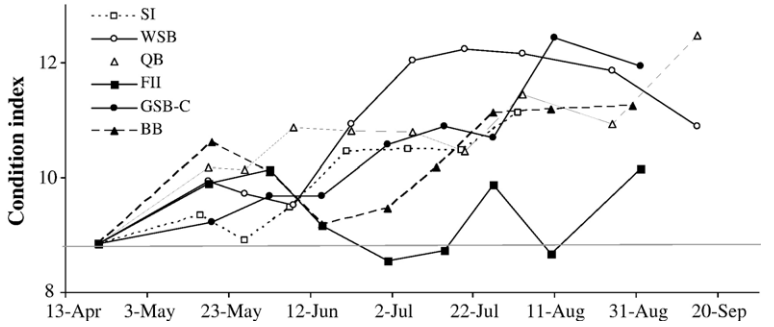

Fig. 9. Mean condition index for adult hard clams in both Shinnecock Bay and Great South Bay during 2005 for Shinnecock inlet (SI, open square, dashed line), western Shinnecock Bay (WSB, open circle, solid line), Quantuck Bay (QB, open triangle, solid line), Fire Island inlet (FII, closed square, solid line), central Great South Bay (GSB-C, closed circle, solid line), Bellport Bay (BB, closed triangle, dashed line) and initial condition index (solid gray line).

temperature of 18.11 °C ± 0.98 (mean ± SE) while QB (21.47 °C ± 1.34) was, on average, approximately 3 °C warmer (Table 1). All SB sites peaked in water temperature during mid-August with maximums ranging from 23.25 to 24.76 °C (Table 1).

In 2005, Great South Bay sites were warmer than Shinnecock Bay sites throughout the sampling season (Table 1). Fire Island inlet (20.02 °C ± 1.67) was, on average, more than 3 °C warmer than SI (16.93 °C ± 1.20) while GSB-C and BB (21.35 °C ± 1.69 and 21.72 °C ± 1.92) were about 1 °C warmer than WSB and QB respectively (20.04 °C ± 1.55 and 20.54 °C ± 1.74). GSB sites also had higher peaks in water temperature than SB sites (Table 1). Peak temperature in GSB-C (29.18 °C) and BB (29.77 °C) during August were slightly warmer than WSB (29.03 °C) and QB (29.21 °C), respectively. Dissolved oxygen levels during both years displayed trends which were generally the opposite of temperature, and were always >5 mg l^{-1}.

In a manner opposite of temperature, salinity decreased with distance from the inlets (Table 1). In 2004, mean salinity ranged from 31.28 ± 0.10 at the SI to 27.52 ± 0.41 in QB, while in 2005 salinities were somewhat lower in SB (SI: 30.11 ± 0.26; WSB: 28.03 ± 0.26; QB: 26.49 ± 0.52). Mean salinities were lower in GSB (FII: 29.32 ± 0.37; GSB-C: 26.31 ± 0.50; BB: 22.26 ± 1.25; Table 1).

During both years and in both bay systems, total chlorophyll *a* values were maximal during summer months (Table 1). Mean chlorophyll levels substantially increased with distance from both inlets where concentrations were typically <5 μg l^{-1}. In contrast, locations furthest from inlets (WSB, QB, BB, GSB-C) averaged >10 μg chlorophyll *a* μg l^{-1} (Table 1). With

Table 1
Mean *in situ* temperature (from in situ temperature loggers; °C) ± SD, maximum seasonal temperatures (from in situ temperature loggers; °C), mean salinities (biweekly) ± SD, mean total chlorophyll *a* (biweekly) ± SE (μg L^{-1}) and size-fractioned chlorophyll *a* (>5, 2–5, and <2 μm; biweekly) ± SE (μg L^{-1}) for both 2004 and 2005 sampling seasons

	Mean temp	Max. temp	Mean salinity	Mean whole Chl *a*	Mean Chl *a* >5 μm	Mean Chl *a* 2–5 μm	Mean Chl *a* <2 μm
2004							
SI	18.11 ± 0.98	23.25	31.28 ± 0.10	4.18 ± 1.65	1.98 ± 1.21	0.74 ± 0.39	1.53 ± 0.33
SB2	19.34 ± 1.04	24.60	31.24 ± 0.17	5.25 ± 0.83	2.61 ± 0.63	0.77 ± 0.31	2.47 ± 0.56
SB3	19.51 ± 1.13	23.97	30.56 ± 0.18	7.85 ± 1.57	3.95 ± 1.12	0.51 ± 0.24	3.63 ± 1.10
SB4	20.66 ± 1.20	24.69	29.38 ± 0.33	10.17 ± 2.26	3.99 ± 1.23	2.72 ± 0.95	5.31 ± 1.19
SB5	21.30 ± 1.34	25.46	28.29 ± 0.36	11.10 ± 2.72	3.87 ± 1.51	2.03 ± 0.88	5.81 ± 1.31
QB	21.47 ± 1.34	25.37	27.52 ± 0.41	12.93 ± 2.69	3.14 ± 1.29	3.84 ± 1.67	6.06 ± 1.63
2005							
SI	16.93 ± 1.20	28.83	30.11 ± 0.26	3.00 ± 0.52	1.28 ± 0.34	0.47 ± 0.23	1.53 ± 0.36
WSB	20.04 ± 1.55	29.03	28.03 ± 0.32	14.68 ± 3.06	3.63 ± 0.89	2.83 ± 0.88	8.37 ± 2.20
QB	20.54 ± 1.74	29.21	26.49 ± 0.47	16.69 ± 3.07	3.02 ± 1.08	4.39 ± 1.45	9.67 ± 1.91
FII	20.02 ± 1.67	27.44	29.32 ± 0.37	5.84 ± 1..79	3.63 ± 1.51	0.50 ± 0.16	1.81 ± 0.35
GSB-C	21.35 ± 1.69	29.18	26.31 ± 0.50	9.94 ± 2..38	5.80 ± 2.04	0.92 ± 0.72	3.95 ± 0.90
BB	21.72 ± 1.92	29.77	22.26 ± 1.25	11.22 ± 2.21	5.43 ± 1.57	1.19 ± 0.33	4.92 ± 0.92

regard to the size distribution of chlorophyll, stations furthest from the inlets (QB, BB) had the greatest mean abundance of smaller phytoplankton in each bay, while mid-bay sites had a greater mean abundance of larger phytoplankton relative to other sites, especially stations near inlets (Table 1). Patterns in total chlorophyll *a* were generally reflected in other parameters such as POC, PON, and total phytoplankton cell densities which were lower near inlets and higher within back-bay locations (data not shown).

3.7. Benthic surveys

In 2004, a benthic survey of Shinnecock Bay revealed the presence of *M. mercenaria* at 61% of the sites at 94 random sites sampled. The greatest densities of hard clams were found between SB3 and SB4 where densities reached 5 clams m^{-2} (Figs. 1 and 10). Densities in eastern Shinnecock Bay were generally low (<1 m^{-2}; Fig. 10) while densities in far western Shinnecock Bay and Quantuck Bay were modestly higher (~1 m^{-2}; Fig. 10).

The densities of hard clams collected in our Great South Bay survey were substantially lower than Shinnecock Bay random sites. Hard clams were found at 36% of sites with densities ranging from 0.4 to 2 individual m^{-2} (Fig. 10). Spatially, we did not find hard clams in most of the bay. The greatest densities of hard clams (>1 m^{-2}) were found in patches near the central and eastern portions of the bay (Fig. 10).

4. Discussion

This study documented substantial spatial variability of hard clam growth, densities, and conditions across Shinnecock Bay and Great South Bay. In both 2004 and 2005, juveniles in central bay locations (SB3, SB4, WSB, GSB-C) had significantly faster growth rates, lower mortality rates, and higher lipid content relative to sites closest to the inlets (SI, SB2, FII; Figs. 2–8). Adult hard clams nearest FII had significantly lower CI compared to mid-bay stations (Fig. 9) and densities of wild *M. mercenaria* populations in both estuaries were highest at mid-bay stations (Fig. 10), a result consistent with juvenile clam growth rates. This study also documented substantial differences in hard clam growth and population characteristics between Shinnecock Bay and Great South Bay. Juvenile clams in SB grew approximately two times faster in terms of AFDW than those in GSB (Fig. 6) and adults in SB had significantly greater condition indexes than clams in GSB (Fig. 9). Mean densities of hard clams were also substantially higher in Shinnecock Bay compared to GSB (Fig. 10). In conjunction with our environmental data, these findings provide a refined understanding of the factors which regulate populations of *M. mercenaria* in estuarine ecosystems.

4.1. Factors regulating growth of juvenile hard clams

Hard clam growth can be a function of a variety of environmental parameters including temperature,

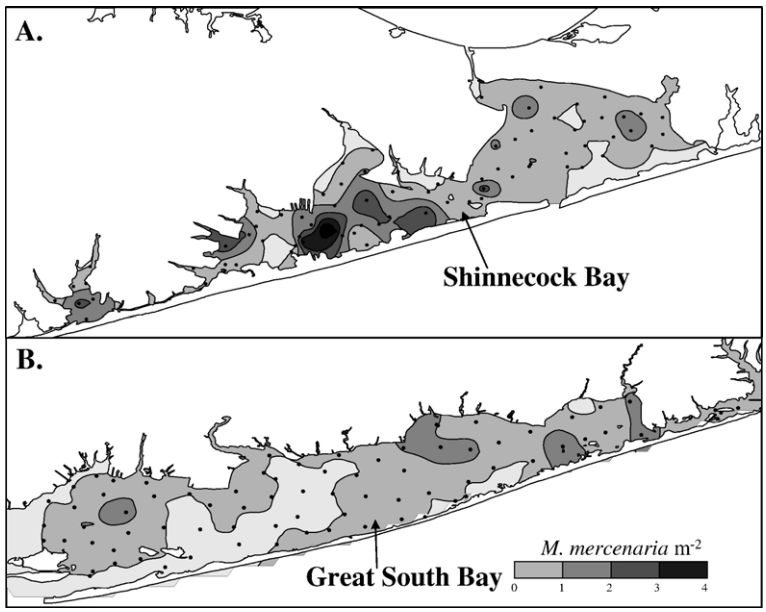

Fig. 10. Densities of *Mercenaria mercenaria* within Shinnecock Bay (n=94) and Great South Bay (n=79).

salinity, food quality, and food quantity (Grizzle et al., 2001). To better understand the degree to which various environmental factors influenced trends in juvenile hard clam tissue (AFDW) and shell growth, we conducted a Spearman's coefficient of rank correlation test using concurrent water quality data. Of all the parameters examined, water temperature was the most strongly correlated with instantaneous shell-based growth in juvenile clams (shell: $p<0.001$; Table 3), a finding in agreement with a wealth of prior studies of hard clams. Ansell (1968) showed a strong relationship between growth and ambient temperature with maximal growth rates occurring within the optimal temperature range of 20–24 °C. Temperatures outside this range can result in slowed growth (10–20 °C; >24 °C) or no growth when temperatures are <10 °C (Loosanoff, 1939; Pratt and Campbell, 1956; Ansell, 1968; Kennish, 1980; Grizzle and Lutz, 1988; Arnold et al., 1991; Greenfield et al., 2005). Consistent with this concept, instantaneous shell-based juvenile hard clam growth rates were more strongly correlated with temperatures ≤24 °C ($R=0.410$) than all temperatures ($R=0.314$; Table 2). Moreover, growth rates which occurred when temperatures exceeded 24 °C were inversely correlated with temperature, demonstrating the negative impact of higher temperatures on growth (Table 2; Ansell, 1968; Hamwii and Haskin, 1969; Greenfield et al., 2005).

Many of the other parameters that were significantly correlated with hard clam instantaneous growth rates were also correlated with temperature (data not shown). Since it is likely this correlation was caused by temperature, these factors were not considered further. However, there were several potential food sources that were significantly correlated with shell-based instantaneous growth rates and cumulative AFDW-based absolute growth which were independent of temperature. For the entire study (all sites and years) instantaneous clam growth rates were significantly and positively correlated with temperature ($p<0.001$), phytoplankton cells >5 μm ($p<0.001$), and centric diatoms ($p=0.05$), and were negatively correlated with dinoflagellates densities ($p<0.001$; Table 3).

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

Variable	n	R	Slope	P
All temperature	108	0.314	0.0005	<0.001
≤24 °C	90	0.410	0.0003	<0.001
>25 °C	18	0.0994	−0.0002	0.685

Positive correlations between growth rates of juvenile hard clams with phytoplankton quantity (phytoplankton cells >5 μm, centric diatoms; Table 3) is in agreement with a host of research which has shown that bivalve growth rates increase with increasing algal biomass until an optimal concentration (Walne, 1970; Tenore and Dunstan, 1973; Winter, 1978; Bayne, 1993; Coutteau et al., 1994). The specific correlation with larger phytoplankton (>5 μm) may reflect an inability of hard clams to retain small particles (Mohlenberg and Riisgard, 1978; Bass et al., 1990; Riisgard, 1991; Malouf, 1991; Grizzle et al., 2001). For example, Riisgard (1991) showed that *Mercenaria mercenaria* retained 5 μm particles with 100% efficiency but experienced decreasing particle retention with decreasing particle size below this threshold.

The positive correlation between juvenile hard clam growth rates and centric diatom densities (Table 3) is in agreement with prior studies which have reported that diatoms support robust growth in *M. mercenaria* (Walne, 1970; Epifanio, 1979; Persoone and Claus, 1980; Bass et al., 1990; Wikfors et al., 1992; Laing et al., 1987). Greenfield et al. (2005) reported that centric diatoms supported better juvenile clam growth than pennate diatoms which were considered a low quality food source due to poor clearance rates of these cells. During the present study, the primary centric diatoms were *Skeletonema costatum* and *Chaetoceros* sp. (unpublished data) which have been reported as supporting rapid quahog growth (Epifanio, 1979; Bricelj et al., 2001; Wikfors et al., 1992; Greenfield et al., 2005).

Large dinoflagellates (>10 μm) were found to be significantly and inversely correlated with shell growth (Table 3), a finding consistent with literature identifying dinoflagellates as a poor source for clams (Bricelj et al., 1991; Wikfors et al., 1992; Lesser and Shumway, 1993; Wikfors and Smolowitz, 1993; Greenfield et al., 2005; Table 3). It is notable that some of the high densities of dinoflagellates recorded in back-bay locales (QB and BB) were blooms of toxic or harmful algae such as *Karlodinium veneficum* (Wang et al., 2005) and *Prorocentrum minimum* (Wikfors et al., 1992) which may further account for the negative relationship between clam growth and dinoflagellates.

Regression analysis of mean environmental parameters and final cumulative AFDW-based growth each year indicated some specific components of suspended food particles were significantly correlated with tissue growth (Table 3). Specifically, cumulative tissue-based growth rates compared with environmental data showed an inverse correlation between both POC and dinoflagellates

Table 3
Significant correlations between shell length-based instantaneous growth rates (mm d^{-1}) and environmental parameters: temperature (°C), dinoflagellates (cells ml^{-1}), phytoplankton cells >5 μm (cells ml^{-1}) and centric diatoms (cells ml^{-1}) determined by Spearman's coefficient of rank correlation for both 2004 and 2005 data combined (R=correlation coefficient)

Variable	Growth (shell)	Growth (AFDW)	
	R	R	P
Temperature	0.38		<0.001
Dinoflagellates	−0.35		<0.001
Phytoplankton cells >5 μm	0.30		0.001
Centric diatoms	0.19		0.05
Dinoflagellates		−0.79	0.002
POC		−0.67	0.02

Significant parameters that were also auto-correlated with temperature were not included. Also, significant regressions between cumulative AFDW-based growth rates (mm d^{-1}) and total mean environmental parameters (POC; μM) and dinoflagellates (cells ml^{-1}) determined by linear regressions for both years and all sites.

with tissue growth ($p<0.05$) (Table 3). This finding emphasizes the negative impact of dinoflagellates on clam growth (Bricelj et al., 1991; Wikfors et al., 1992; Lesser and Shumway, 1993; Wikfors and Smolowitz, 1993; Greenfield et al., 2005). The inverse correlation with POC may also be driven by dinoflagellates blooms in back-bay stations which represented the highest levels of POC during this study.

Clearly, the growth of juvenile hard clams in Long Island's south shore estuaries is influenced by multiple factors (Table 3). To model the importance of individual variables measured during this study on juvenile hard clam growth rates (both instantaneous shell growth and cumulative AFDW-growth), a series of multivariate linear regression models were constructed. For instantaneous shell growth, the best model was highly significant ($p<0.001$), explained 59% of the variance in the data, and included temperature, centric diatoms, phytoplankton larger than 5 μm, and dinoflagellates: instantaneous shell growth (mm d^{-1}) $=-0.004+(4.4\times10^{-4}*$temperature (°C)$)+(5.9\times10^{-7}*$phytoplankton cells >5 μm $ml^{-1})+(8.7\times10^{-7}*$centric diatoms $ml^{-1})-(7.7\times10^{-7}*$dinoflagellates $ml^{-1})$. Of the individual parameters, temperature was the most significant ($p<0.001$), although each phytoplankton group was also highly significant (centric diatoms: $p=0.002$, phytoplankton larger than 5 μm: $p=0.002$, dinoflagellates: $p=0.003$). For cumulative AFDW-growth, the best three-parameter model and explained 94% of the data and included centric diatoms, phytoplankton larger than 5 μm, and temperature of the variability in the data: cumulative AFDW growth (mg d^{-1}) $=1.7+(0.0017*$centric diatoms $ml^{-1})+(0.0011\times$phytoplankton cells >5 μm $ml^{-1})+(0.065\times$temperature (°C)). Of the individual parameters, centric diatoms and phytoplankton larger than 5 μm were marginally significant ($p<0.1$) but temperature was not, perhaps because mean annual temperatures are not a good proxy for the actual influence of seasonal changes in temperature on growth (see discussion above).

4.2. Biochemical content of juvenile hard clams

Biochemical analysis of juvenile hard clams indicated that clams near ocean inlets were food-limited or slower growing compared to those in central bay locations. Dietary protein and lipids are often positively correlated with clam growth and represent an indicator of a clam's physiological condition (Gallager et al., 1986; Wikfors et al., 1992). Although protein levels did not significantly differ between sites, juveniles in SB in general, and WSB in particular, not only grew the fastest but also had higher lipid levels compared to GSB locations (Fig. 8). Greater lipid contents were likely indicative of a more nutritious food source in WSB and poorer food source in sites such as FII (Caers et al., 2000).

4.3. Spring mortality of juvenile hard clams

During extended periods (>8 weeks) of low temperatures (<5 °C) in winter, juvenile hard clams cease feeding and consequently utilize their energy stores for metabolism (Zarnoch, 2006). In this compromised physiological state, massive spring mortality can occur if temperature and metabolic demands increase while food levels remain low (Zarnoch, 2006). During this study, the greatest percentage of early spring mortality in 2005 occurred at inlet sites (SI: 46%, 21 April–8 June; FII: 10%, 21 April–14 June) where mortality was significantly greater than the other SB and GSB sites ($p<0.05$; Figs. 2 and 5). Interestingly, all juveniles used in the 2005 study were over-wintered in ambient waters that had >8 weeks of temperatures <5 °C (SCDHS, 1976–2005) and chlorophyll *a* levels were low during the spring at both inlets sites (<4 μg l^{-1}; Table 1) suggesting that mortality was associated with food limitation at this time (Zarnoch, 2006). In 2004, the later deployment of clams (June) likely prohibited us from observing this seasonal phenomenon.

4.4. Condition of adult hard clams

During this study, adult hard clams placed near the FII had a lower CI than those placed further away from

inlets, such as WSB (Fig. 9). In addition, adult hard clams in SB had a significantly greater CI than those in GSB during the period of June to August (Tukey test, $p<0.001$, $n=500$; Fig. 9) indicating clams in SB had a higher nutritive state than those clams in GSB (Crosby and Gale, 1990). This finding is consistent with work by R.E.I. Newell (unpublished data) who also found that clams in SB had significantly higher CI (2×) than clams in GSB. To better understand the degree to which various environmental factors influenced the trends observed in CI of adult clams, we conducted a series of linear regressions using the mean CI of adults during the June–August period and concurrent water quality data. Higher CI seemed to be associated with sites having greater food quantity as CI was most significantly correlated with whole chlorophyll *a* ($p<0.001$) and total eukaryotic phytoplankton densities ($p=0.002$). CI were also correlated with total diatoms ($p=0.07$) suggesting that adult clams found in SB, particularly WSB supported a high level of tissue growth due to a higher quality food source (diatoms) as well as greater concentration of potential food particles relative to clams in GSB (Wikfors et al., 1992). Interestingly, the CI of adult *M. mercenaria* were also significantly correlated with both AFDW ($p=0.006$) and shell ($p<0.001$) growth of juveniles, a finding similar to a study of juvenile bay scallops (*Argopecten irradians*) in Massachusetts which found adult CI to significantly increase with increasing tissue growth (Shriver et al., 2002). This finding suggests the same food sources which promote higher CI in adult clams also foster rapid growth of juveniles.

4.5. Potential impacts of climate change and estuarine breaches on hard clams

Temperature was the single most influential factor on the shell growth of juvenile hard clams during this study. Climatic warming is impacting many aspects of coastal ecosystems (Kennedy et al., 2002), and this study demonstrated that such warming is likely to impact the success of *M. mercenaria* populations in temperate estuaries. During this study, sites which were the furthest from ocean inlets (QB, BB) rapidly warmed to a temperature within the optimal range for hard clams during the spring and concurrently displayed the fastest growth rates (Figs. 3 and 7; Table 1). However, growth within these locations quickly slowed when temperatures exceeded 24 °C and did not increase until temperatures cooled later in the fall (Figs. 3 and 7). Conversely, clams near the inlets did not grow appreciably until summer months (July–September; Figs. 3 and 7) when inlet water temperatures approached 20 °C. As future estuarine temperatures rise, one might expect the lower growth seen at back-bay sites (QB, BB) at higher temperatures to occur within a larger portion of estuaries. At the same time, clams located closer to inlets should experience annual growth which exceeds current rates.

An increase in water temperatures earlier in the season could also influence juvenile spring mortality. We found that high levels of spring mortality occurred in juveniles following a winter that had temperatures <5 °C lasting for greater than 8 weeks when spring chlorophyll *a* levels were low. However, others have documented negligible mortality occurred in juveniles when temperatures were <5 °C for less than 4 weeks and when spring chlorophyll *a* levels were high (Zarnoch, 2006). Higher winter water temperatures associated with climatic warming would shorten the period of temperatures <5 °C and consequently may reduce spring juvenile clam mortality.

Reproductive patterns will also change with increasing temperatures. Increases in spring temperatures could cause adult hard clams to spawn earlier in the season (Grizzle et al., 2001), potentially impacting future stocks and distribution within LISSE. Since temperature is one of the most important environmental factors driving clam growth and sustaining populations, future restoration efforts and aquaculture facilities must pay particular attention to seasonal temperature changes. Such efforts should choose clam transplantation sites that have the greatest duration of time at optimal clam temperatures (in LISSE, mid-bay sites).

Both unintentional and intentional breaching of barrier islands occurs along all coasts of the United States. When unintentional, barrier island breaches are problematic, while, if purposeful, breaches can reduce flooding potential, improve navigation, and promote environmental restoration (Kraus and Wamsley, 2003). Within LISSE, many of the current ocean inlets (Shinnecock Inlet, Moriches Inlet) were formed by storm-associated barrier island breaches. Clearly, this study has shown the presence of these inlets strongly influences *M. mercenaria* populations in LISSE by bringing in cold, food-poor water into estuaries which decreases clam growth rates and lipid content, and increases juvenile mortality. Moreover, hard clam densities within LISSE were minimal and often undetectable near ocean inlets in GSB and SB (Fig. 10). Negative changes associated with barrier island breaches may be offset by increases in growth of clams in regions furthest from inlets which might experience cooler temperatures during the peak of

summer and lower densities of phytoplankton associate with poor clam growth (dinoflagellates).

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