The Hard Clam Research Initiative:

Factors Controlling *Mercenaria mercenaria* Populations in South Shore Bays of Long Island, NY

Prepared for New York Sea Grant by V. Monica Bricelj, Ph. D.
Institute of Marine and Coastal Sciences
Rutgers University, New Brunswick, NJ, USA

Sea Grant
New York

NYSGI-T-09-001
February 2009

Acknowledgements

This hard clam synthesis report was funded under award NOAA NA16FL2699 from the National Marine Fisheries Service to the Research Foundation of State University of New York on behalf of New York Sea Grant. The statements, findings, conclusions, views, and recommendations are those of the author and do not necessarily reflect the views of any of those organizations. The five Hard Clam Research Initiative (HCRI) projects were funded under award numbers NOAA NA96FL0279 and NA16FL2699.

The author acknowledges the assistance of Cornelia Schlenk and Barbara Branca from New York Sea Grant in the preparation of this report, and Loriann Cody for her help with design, layout and graphics. The author also thanks HCRI investigators for their input and response to specific questions during the course of writing, for helpful discussions, and in some cases for preparing graphs of their data. This report also benefited from reviews and comments from HCRI researchers and members of the HCRI Advisory Board of an earlier version, and from review of the final draft by James Ammerman, Director of New York Sea Grant. New York Sea Grant thanks two additional, external peer reviewers for their assessment of and valuable comments on the final draft: Dr. Roger L. Mann (Virginia Institute of Marine Sciences, VA) and Dr. Victor S. Kennedy (Horn Point Laboratory, MD).

Preface

This synthesis report was commissioned by the New York Sea Grant Institute and is intended to summarize key results of five research projects funded through New York Sea Grant's Hard Clam Research Initiative (HCRI) between 1999 and 2008. These projects and their principal investigators are listed below as are the co-sponsoring partners.

The main goal in the preparation of this report is to achieve improved, science-based understanding of the factors controlling hard clam, *Mercenaria mercenaria*, populations in Long Island, New York's south shore estuaries, and thereby contribute towards better management and potential enhancement of a once highly productive regional resource. Particular emphasis is given in this synthesis to findings that have direct implications for management of these populations.

The report is thus not intended to provide a comprehensive summary of knowledge about hard clam populations in Great South Bay or other south shore areas, nor can it reflect the views of all participants in the HCRI. Material outside the scope of the five projects, and results of projects funded by other sources have, however, been included where they contribute information directly relevant to the findings of the projects supported by the HCRI. Other funding sources are duly acknowledged throughout this report.

The main sources of information for this report include: a) publications, b) manuscripts in preparation or in press kindly provided by the investigators of these projects, c) project progress reports submitted to New York Sea Grant, and d) material presented at a 2-day workshop sponsored by the New York Sea Grant Institute August 11 and 12, 2008, at the School of Marine and Atmospheric Sciences, Stony Brook University, to summarize findings of the HCRI among the participating investigators, and present these to the HCRI Advisory Committee and stakeholders. Some of the results of the HCRI await final analysis, write-up and publication in peer-reviewed journals and are thus included in their preliminary form as available.

Titles and Principal Investigators of Projects funded through the Hard Clam Research Initiative

Relationships between the timing of reproduction, fecundity, and egg composition to declines in hard clam recruitment
(PIs: R.I.E.Newell, S. Tettelbach, C. Gobler)

The trophic interaction between hard clams and natural assemblages of phytoplankton
(PIs: R. Cerrato, D. Lonsdale, G. Lopez, R. Flood, R. Amstrong, J. Levinton)

Modeling hard clam growth, survival and environmental interactions: what are the controlling factors?
(PIs: E. Hofmann, V. M. Bricelj, R. Grizzle, J. Klinck, J. Kraeuter, E. Powell, S. Buckner)

The effects of brown tide and plankton quality on hard clam larval growth and survivorship
(PIs: D. Padilla, C. Gobler)

A modeling study of the growth, survival and recruitment of hard clam (Mercenaria mercenaria) *larval and post-settlement populations*
(PIs: E. Hofmann, V.M. Bricelj, S. Buckner, J. Klinck, J. Kraeuter, E. Powell)

Funding Co-Sponsor Partners

- NOAA National Marine Fisheries Service
- Port Authority of New York and New Jersey
- South Shore Estuary Reserve
- New York Sea Grant

Additional Projects Cited

Supported by New York Sea Grant core federal funds:
- *Impact of predation by the ctenophore* Mnemiopsis leidyi *on larval mortality of* Mercenaria mercenaria (PIs: D. Lonsdale, R. Cerrato)
- *Influence of ocean exchange on nutrients, plankton assemblages, submerged aquatic vegetation and shellfish within Long Island's South Shore Estuaries* (PIs: C. Gobler, B. Peterson)

Supported by NOAA-Ecology and Oceanography of Harmful Algae (ECOHAB) funds, grant #NA04NOS4780275:
- *The importance of blooms of brown tide,* Aureococcus anophagefferens*, in coastal lagoonal systems: coupling numerical simulation modeling and experiments to determine population effects on hard clam,* Mercenaria mercenaria*, individuals, cohorts and populations* (PIs: J. Kraeuter, V.M. Bricelj, E. E. Hofmann, J. Klinck, E. Powell, E. Ward)

Supported by the National Science Foundation (funding allocation to D. Padilla via the Intergovernmental Personnel Act)
- Research that led to the publication Przeslawski et al. 2008.

The Hard Clam Research Initiative:

Factors Controlling *Mercenaria mercenaria* Populations in South Shore Bays of Long Island, NY

Table of Contents

Executive Summary

This report, *The Hard Clam Research Initiative: Factors Controlling* Mercenaria mercenaria *Populations in South Shore Bays of Long Island, NY,* provides a synthesis of results from studies funded via the Hard Clam Research Initiative (HCRI) and related studies funded from other sources. The studies addressed the downward trend in hard clam populations in Long Island's south shore bays, an issue of both environmental and economic interest to the region.

The precipitous decline in abundance of hard clams, *Mercenaria mercenaria*, in Great South Bay (GSB) from the 1970s to the mid-1980s can now be clearly attributed to overfishing. A population dynamics model developed for hard clams in GSB determined that a sustained harvest rate greater than approximately 25 percent of the historical standing stock (a harvest level exceeded in the 1980s), either as proportional fishing or selective fishing for littleneck clams, would rapidly drive these populations to extinction. This model also predicted that the recovery time of the current clam population to maximum historical densities, following release of all fishing pressure, would take on the order of a decade or more.

The causes for the continued population decline during the 1990s, despite the greatly reduced fishing effort, have not been fully resolved, but potential contributing factors were identified by the HCRI. Some of these factors include: the occurrence of brown tide (BT) blooms, reduced reproductive success associated with low clam densities and/or reduced food quality, and predation.

- **Occurrence of brown tide.** Clam recruitment dropped and remained below the 1979-2003 mean starting in the mid-1990s, coinciding with a period of relatively frequent BT blooms of the toxic picoplankter, *Aureococcus anophagefferens*. Waning of blooms between 2002 and 2006, however, did not lead to population recovery; thus BT cannot be the only factor causing this later decline.

- **Reduced reproductive success.** A spawner-recruit relationship for hard clams was established, indicating that a minimum threshold density of spawning stock (exceeding approximately 0.8 clams per square meter) is necessary to sustain recruitment. Although refinement of this relationship is needed, mean densities of adult clams decreased to this level from the mid-1990s onwards. In addition, from 1996 onward the number of recruits per adult was about half that of earlier years. Recruitment failure may thus be due to limited gamete fertilization success at these low densities which would reduce larval numbers, and/or reduced larval quality and metamorphic/post-metamorphic success. Low fecundities of clams in GSB relative to other mid-Atlantic south shore estuaries were documented by the HCRI in 2001.

- **Predation.** Analysis of long-term predator surveys showed that the decline in hard clam abundance could not be attributed to changes in the abundance of mud crabs, the dominant predator in GSB. The role of other predators that are poorly surveyed, e.g., blue crabs, cannot be excluded as a factor contributing to the more recent population decline.

HCRI research also examined the relationship between hard clam reproduction and food supply in south shore bays. The timing of peak reproductive condition and spawning in GSB did not differ between 2001 (a year of low or no BT depending on location) and 1979 (a pre-brown tide year), and were comparable among south shore estuaries (SSE) in NY, and Sandy Hook Bay, NJ. The estimated clam reproductive output varied greatly in 2001: it was highest in western bays (Sandy Hook and Middle Bay), intermediate in Shinnecock Bay (SB) and lowest within GSB. These differences could not be explained by differences in the total algal biomass as measured by Chlorophyll *a* (Chl *a*). **Reproductive effort was generally inversely related to the percent contribution of small phytoplankton species (less than 5 µm) to total Chl *a* and positively related to the condition index of clams the previous fall.** The occurrence of BT and the fall food supply before the temperature drops in one year may thus influence reproductive success the following year.

Strong spatial gradients in growth rates of juvenile hard clams in SSE were also documented. In both GSB and SB growth was maximal at mid-bay locations, where Chl *a* attained only intermediate levels. Growth was least near inlets where food quantity was presumably limiting, and at inner bay sites where algae smaller than 5 µm made the greatest contribution to algal biomass. Present conditions for clam growth and reproduction were superior in SB compared to GSB. **Overall, experimental data and model simulations generated by the HCRI indicated that food quantity, as measured by total Chl *a*, is a poor predictor of clam production for all life history stages, whereas differences in food availability (size-fractionated Chl *a*) and food quality (gross biochemical composition and/or algal species composition) have major effects on larval and juvenile growth, and adult condition.**

Small algae (smaller than 5 µm) clearly dominate phytoplankton biomass in GSB during intense BT outbreaks. Yet even in non-BT years (e.g. 2005) or at locations where intense BT did not occur (e.g. western GSB in 2001) small algae dominated the total summer phytoplankton standing stock in GSB. Juvenile and adult clams poorly retain this size fraction and many of its constituent species, such as green algae and cyanobacteria, are known to be a poor food source for hard clam larvae and juveniles. Pennate diatoms and dinoflagellates were also associated with a poor food supply for hard clams. **Improved characterization of the food supply for hard clams was identified as a critical research need by the HCRI.**

Model simulations, supported by experimental data, showed that the effect of BT on growth is inversely related to clam size, indicating that juveniles are more vulnerable to negative effects of BT than adults. Additionally, the main period of hard clam larval production in GSB as determined in a pre-BT year (1979) and in 2001, a non-BT year, occurred in June-July. This coincides with the typical mid-summer occurrence of BT, which poses a threat to larvae that are actively feeding on the plankton at this time. **Laboratory studies demonstrated that toxic BT cells in late exponential or stationary growth phase caused concentration-dependent reduction in growth of hard clam larvae.** At high BT concentrations, this will likely lead to a longer development period for the free-swimming larvae in the plankton, and thus result in greater risk of predatory mortality under field conditions. Larvae fed BT in the laboratory also accumulated very low levels of lipid reserves and showed individual variability in their response to BT. Effects of BT on larval recruitment success and the consequences of reduced larval recruitment on the adult population remain to be determined in the field.

Ecosystem-level changes have also been documented in SSE. The decline of hard clams in Long Island shallow bays and the absence of other benthic suspension-feeding macrofauna, documented in GSB, indicate that grazing pressure on the phytoplankton has shifted from the benthos to the zooplankton. Marked spatial variation in the abundance and composition of zooplankton throughout GSB was also documented. Preliminary evidence suggests that ctenophores (commonly known as comb jellies), a gelatinous zooplankter and a major predator of bivalve larvae, have increased in abundance in GSB. Preliminary experiments also suggest that the presence of actively feeding adult clams may, under some conditions, alter the phytoplankton community and thereby enhance juvenile clam growth, but interpretation of these data remains questionable.

Conclusions from the HCRI are somewhat constrained by the relatively short (1- to 1.5-year) experimental period of the funded studies. Improved understanding and prediction of factors influencing the hard clam resource can come only with multi-year studies and the maintenance of long-term, decadal-scale monitoring programs. Management strategies, including nutrient management of the watershed to reduce the frequency and intensity of BT, and hard clam stock enhancement to enable or accelerate population recovery, critically depend on such long-term data. The documented high spatial variability in the food supply that promotes clam growth and reproduction, as well as in the occurrence of BT in SSE, provide an opportunity to exploit these habitat differences and optimize the siting of population enhancement efforts. **Continued critical evaluation of ongoing hard clam population enhancement efforts, their goals and cost-effectiveness, is essential.**

Abbreviations Used in this Report

AFDW	Ash-free dry weight
BB	Bellport Bay
BT	Brown tide
Chl *a*	Chlorophyll *a*
CR	Clearance rate
DIN	Dissolved inorganic nitrogen
DOC	Dissolved organic carbon
DOM	Dissolved organic matter
DON	Dissolved organic nitrogen
DOP	Dissolved organic phosphorus
DW	Dry weight
GSB	Great South Bay
HCRI	Hard Clam Research Initiative
k	Daily instantaneous growth coefficient
QB	Quantuck Bay
R	Respiration
RE	Retention efficiency
SB	Shinnecock Bay
SL	Shell length
SSE	South shore estuaries
SSR	Spawning stock-recruit
TSS	Total suspended solids
WW	Wet weight

1. Background

The south shore of Long Island, NY, is comprised of a series of bar-built, shallow, well-mixed estuaries referred to as the South Shore Estuary (SSE). This ecosystem includes from west to east: Hempstead Bay, Great South Bay (GSB), the largest bay (40 km long, mean depth of 1.5 m, area of 223 km^2 and tidal range < 0.25 m), Moriches, Quantuck and Shinnecock Bay (SB) (Nuzzi and Waters 2004).

Northern quahogs, hereafter referred to as hard clams, *Mercenaria mercenaria*, historically supported a large, commercially important fishery in GSB, NY. This fishery supplied ~50% of total US east coast landings, 90% of the harvest in New York State and contributed a landed value exceeding $16.7M at peak abundance (Lively et al. 1983, McHugh 1991). Landings peaked in the mid-1970s and declined dramatically in the 1980s (Fig.1). This decline is independently reflected in the decline in clam densities of this species, based on bottom surveys conducted by the Towns of Babylon, Brookhaven and Islip, NY in their respective portions of the bay (not shown, Kraeuter et al. 2008). This led to a parallel decline in fishing effort as measured by the number of commercial and recreational licenses issued (Fig. 2).

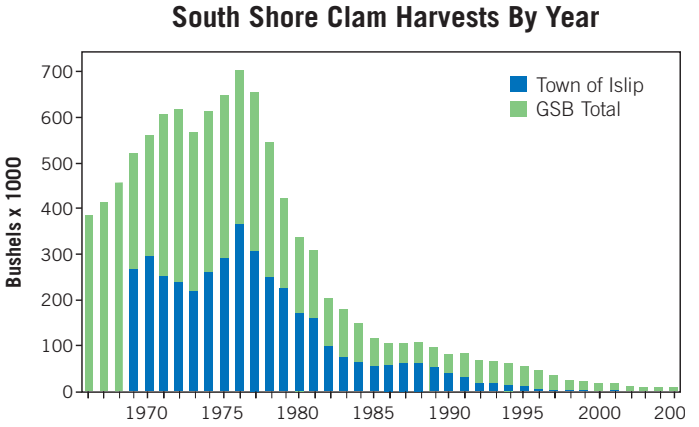

Figure 1. Hard clam (*Mercenaria mercenaria*) commercial landings from Great South Bay (GSB) and those limited to the Town of Islip, NY (modified from Kraeuter et al. 2008).

The precipitous decline of hard clams in GSB also resulted in closure in 2001 of the Blue Points Co., which historically harvested clams from 1/3 of the bay bottom, and has led to renewed interest in restoration efforts. Spawner transplants as a hard clam enhancement method traditionally involve transplanting adult clams from cooler northern waters to warmer waters, in an attempt to extend the spawning period and thus increase the probability that some of the larvae will encounter favorable environmental conditions. The validity of this practice was challenged by

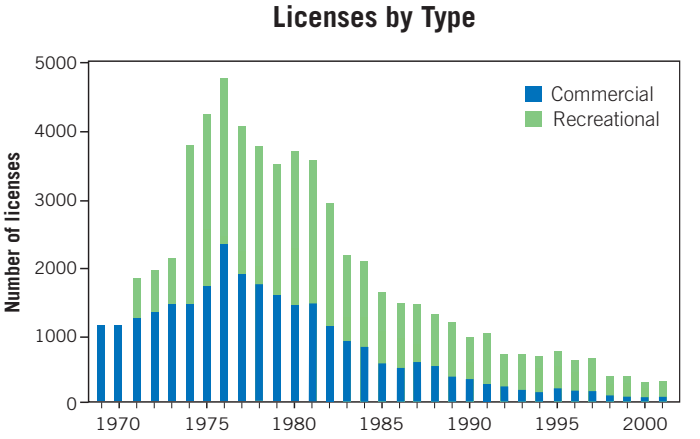

Figure 2. Hard clam (*Mercenaria mercenaria*) commercial and recreational licenses issued by the Town of Islip, NY (modified from Kraeuter et al. 2008).

Kassner and Malouf (1982) who found that transplanted clams spawned at the same time as native clams. Transplanting of adult hard clams to establish spawner sanctuaries has been conducted by the Town of Islip since 1974 within a relatively large portion of GSB (~ 20,000 acres). Annual monitoring of the population indicates that these efforts have met with little or no success (with success defined as recruitment into the harvestable fishery) (S. Buckner, pers. comm.). In addition, the Bluepoints Co. conducted 13 years of spawner transplants from 1973 to 1985, planting over 12 million clams, with little or no success (C. Strong, pers. comm.). Extensive dye study data were used in both programs to site spawner sanctuaries and identify likely areas of larval setting.

Seeding of hatchery-produced hard clam seed, as an alternative management tool to supplement natural recruitment, was critically evaluated by Malouf (1989). The

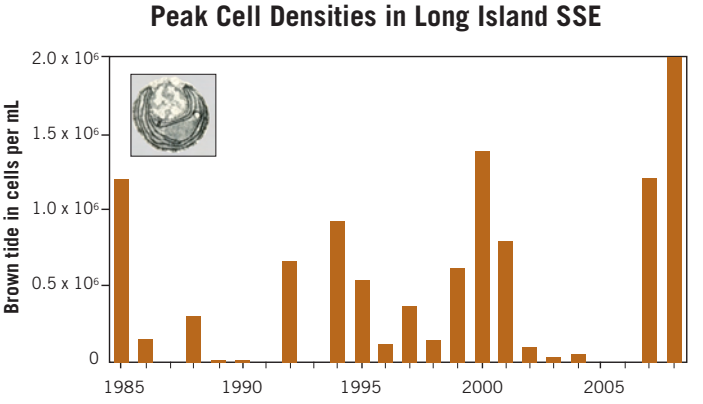

Figure 3. Maximum cell density (in cells per mL) of *Aureococcus anophagefferens* (causative agent of brown tides) in Long Island's south shore estuaries between 1985 and 2008 (monitoring data from the Suffolk County Department of Health Services, SCDHS, NY; graph courtesy of Chris Gobler). Inset shows a transmission electron micrograph of this alga (2 µm in diameter) from Cosper et al. (1987).

potential contribution to hard clam landings from seed plantings conducted in Long Island in the 1980s was deemed insignificant at the scale being conducted at the time, although the value of this practice was recognized as part of an integrated management program to address specific objectives. Based on the lack of results from spawner sanctuaries, the Town of Islip changed the focus of its enhancement efforts in the late 1980s to grow seed clams to larger sizes (~15 to 25 mm) and bypass the early life history stages that suffer the greatest losses from natural predation (S. Buckner, pers. comm.). To address the problem of scale, the Town constructed the first municipally operated hatchery on Long Island combined with further grow-out of clams in land-based and field nursery systems prior to release. Annual targeted production (which was often exceeded) is 40 million clams of the notata variety. Results are monitored by tracking annual changes in the notata population in Islip waters, and show that the notata population has increased from <1% to more than 20% of the natural population. The Town's data also suggest that the hard clam population has stabilized, albeit at low levels, since natural recruitment has continued to decline. This also suggests that hatchery production has contributed toward this stabilization, and that shellfish culture can assist in the recovery of the GSB hard clam population (S. Buckner, pers. comm.), although a cost-return economic analysis remains to be conducted.

Hard clam spawner transplants are being conducted by The Nature Conservancy (TNC), NY, on privately owned GSB bottomlands (Doall et al. 2008). The goals of these current enhancement efforts have changed considerably, however, as a result of the low levels attained by hard clam populations in GSB, and conditions in SSE have also changed relative to those experienced at the time of peak hard clam abundance. Recent surveys indicate that seeding of adult clams over the past four years in TNC harvest-free waters has led to an increase in juvenile recruitment in 2008 (*New York Times*, Long Island section, Dec. 12/2008).

Overharvesting of the fishery was attributed the major role for the earlier decline of hard clam stocks in GSB (Buckner 1984), and confirmed by model simulations undertaken as part of the HCRI (sec. 2). Brown tides of the picoplanktonic alga, *Aureococcus anophagefferens* (2 µm in diameter) first appeared in Long Island, NY, south shore bays in 1985, and have recurred intermittently since (Gobler et al. 2005) (Fig. 3); thus they may have played a contributing role to the continuing decline of hard clam stocks (sec. 8). Despite the marked reductions in the intensity and occurrence of brown tides between 2002 and 2006, and despite reduced fishing pressure in recent years, recovery of hard clam populations in GSB has been very slow. Since there has been, and continues to be, considerable investment in hard clam restoration efforts in GSB, it is critical to undertake a rigorous evaluation of factors that currently affect this species.

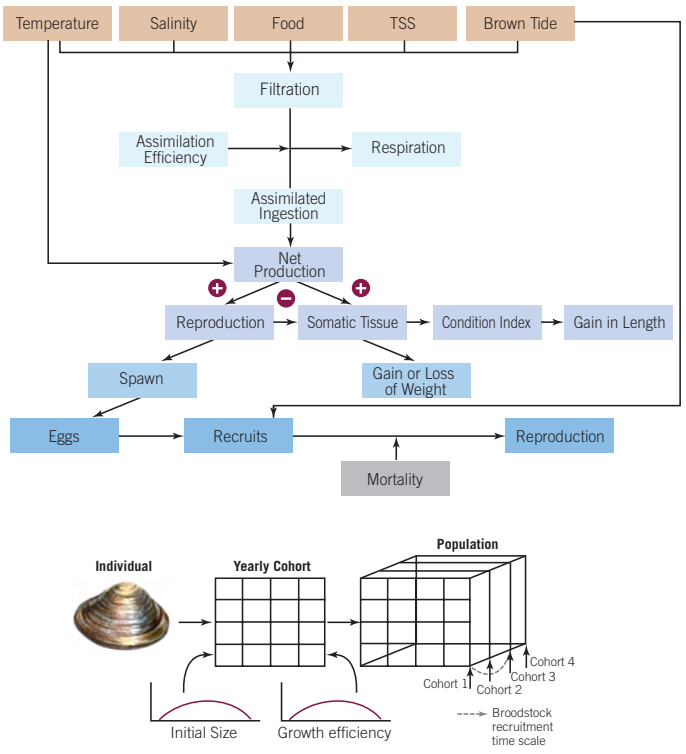

Figure 4. Schematic of the processes and transfers included in the individual-based hard clam model (upper), and scaling allowing individuals to be incorporated into a population model (lower) (modified from Hofmann et al. 2006a).

Multiple cohorts composed of individuals with varying initial size and genotype-dependent growth efficiency, described by Gaussian probability distributions, comprise a population. TSS = total suspended solids. Positive net production (+) results in formation of reproductive and somatic tissue; negative production (-) results in resorption of tissue.

2. Impact of fishing and population dynamics of hard clam populations: model simulations

An individual-based numerical model was developed for *Mercenaria mercenaria* to simulate the growth and population dynamics of the hard clam in response to environmental variables (Fig. 4; Hofmann et al. 2006a). The model was implemented for GSB and was used to simulate the interplay of factors (environmental forcing and fishing) responsible for the decline of clam populations in GSB, as well as to identify areas of research needed to explain and potentially reverse the patterns observed. An important feature of the model, adapted from one developed for the Pacific oyster, *Crassostrea gigas*, is that it allows for individual genotypic or phenotypic variation associated with varying initial size and food absorption efficiency (Fig. 4). Additionally, growth of shell and soft tissues can be independently simulated to allow description of animal condition, and length and age can be tracked

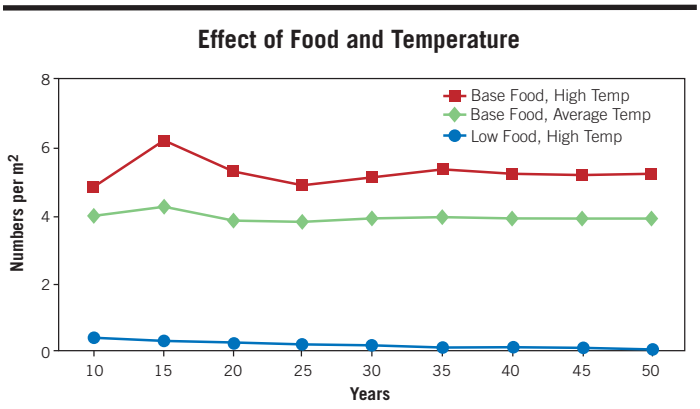

Figure 5. Simulated model output for clam densities in numbers of individuals per m² under various combinations of temperature and food levels (modified from Kraeuter et al. 2008).

Base and Low Food = average and low food conditions from Quaglietta (1987); Average Temperature = as measured in 1978, a year with a typical cool winter (Bricelj 1979); High Temperature = as measured in 1998 (Nuzzi & Waters 1999) a year with a typical warm winter.

independently. A seasonal decrease in hard clam condition (i.e. amount of tissue per unit shell size) can result from food limitation or from spawning activity. Over the lifespan of the species, the modeled condition index declines with increasing clam age. This prediction may not be supported by recent empirical data (Newell et al. 2009); further analysis is required to reconcile model and empirical data, as different measures of condition index have been used in these studies. Model simulations were run for a minimum of 10 years to allow stabilization of results, and are started with 2-yr-old clams as the Town of Islip survey did not provide quantitative counts of younger clams (see below). Outputs of the model are provided in units of clam abundance (numbers per m²) as well as biomass per m², but only numbers are provided in this report.

Environmental variables explicitly included in the model are temperature, salinity, food quantity and quality, concentration of total suspended solids (TSS) and brown tide (BT, concentration, duration). Baseline environmental time series for GSB were used as input to the model, based on typical/average conditions of food and temperature (cool winter) (Fig. 5; Hofmann et al. 2006a). Food levels are based on empirical time series of phytoplankton standing stock as measured by chlorophyll *a* (Chl *a*) concentration, corrected by the addition of a non-algal food supply (detailed in Hofmann et al. 2006a). Addition of this term resulted in simulated hard clam growth rates that matched those reported in Wallace (1991) whereas Chl *a* alone underestimated observed clam growth.

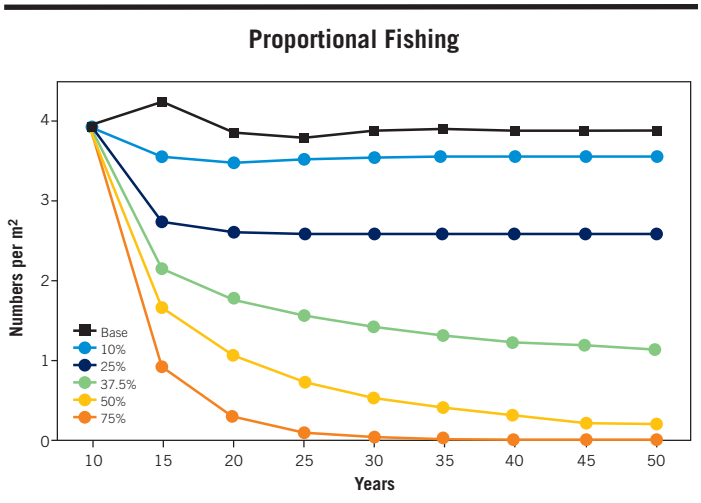

Figure 6. Simulated effects of proportional fishing in Islip Town, NY, waters, on clam numbers per m², in which clams of each size class are harvested in proportion to their abundance (modified from Kraeuter et al. 2008).

Base: base condition with no harvest. Percentages indicate the percent of the stock removed annually for the number of years indicated.

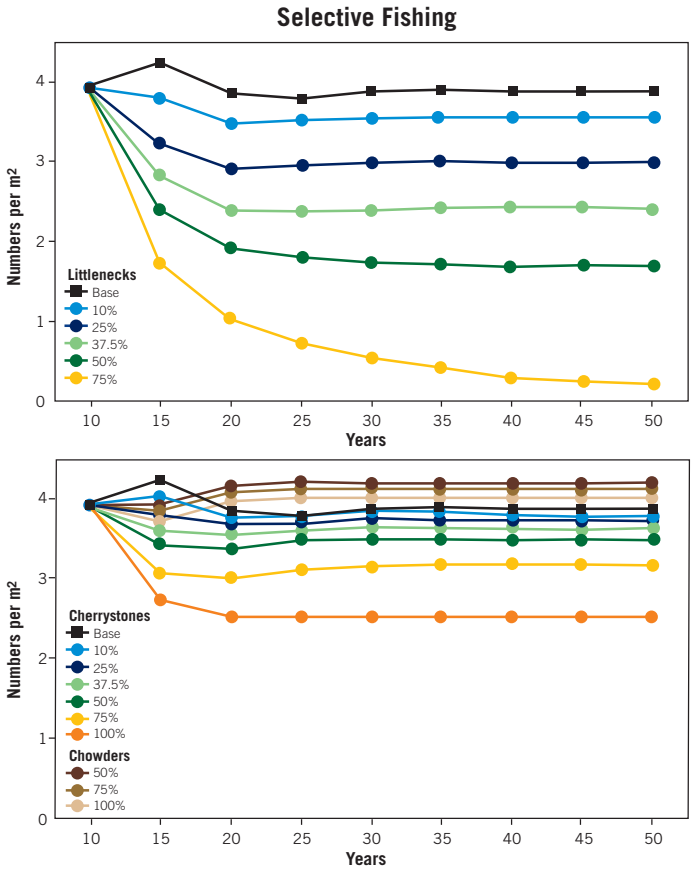

Figure 7. Simulated effects of selective fishing in Islip Town, NY, waters, on clam numbers per m² (modified from Kraeuter et al. 2008).

Upper: only littleneck-sized clams are harvested; lower: only cherrystone or chowder-sized clams harvested; percentages as in Fig. 6.

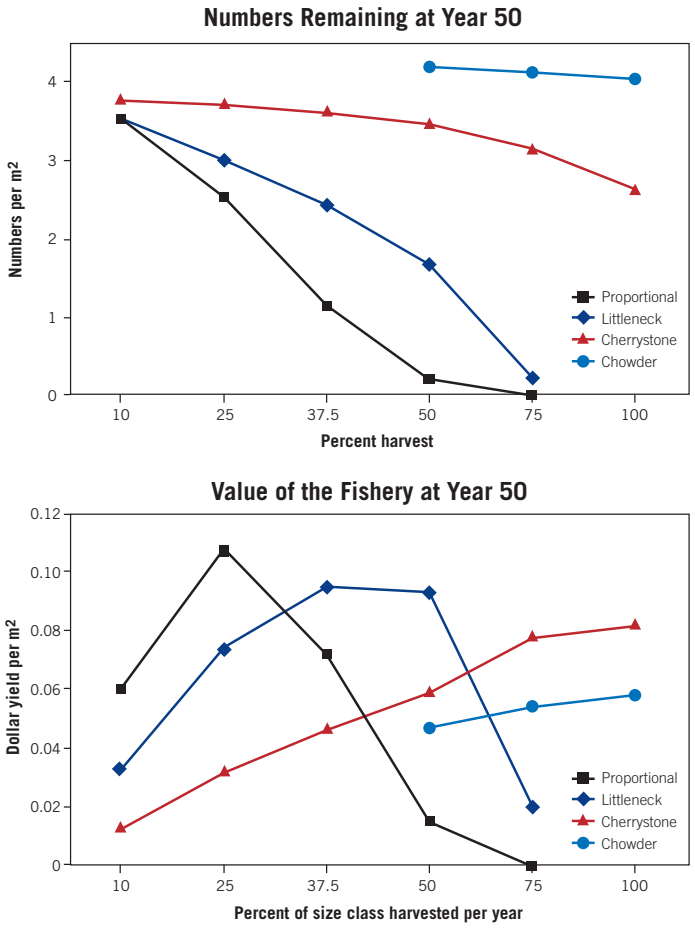

Figure 8. Simulated effects of fishing on various components of the hard clam population after 50 years (modified from Kraeuter et al. 2008): number of clams remaining per m² (upper graph) and their monetary yield (lower graph). Note that connecting lines are to facilitate comparisons across fishing rates and do not imply a linear change in abundance or value.

Model simulations focused especially on the effects of changes in temperature and food supply, since salinity and TSS generally do not vary markedly within GSB. **An important outcome of these model simulations, as illustrated in Fig. 5, was the finding that clam populations were more sensitive to changes in food levels than temperature, although an increase in overall temperature under average food conditions led to a slight increase in clam abundance.**

The model was also used to assess the relative impacts on hard clam populations of varying harvesting strategies and fishing intensities (Kraeuter et al. 2008). Hard clams are harvested in three market size classes: littlenecks (the smallest, 25.4 to 36.4 mm shell width, and most valuable), cherrystones (36.5-41.3 mm) and chowders (>41.3 mm). Outcomes of simulations on the effect of proportional fishing, in which all marketable size classes are harvested in proportion to their abundance with increasing rates of removal from 10 to 75%, are shown in Fig. 6. No large declines in population density occurred until simulated proportional fishing mortality increased from 10 to 20%. Proportional fishing at levels > 25% to 37.5% of the total population caused rapid and continuing decline in stocks.

The effects of selective fishing by size class are shown in Fig. 7 (see Kraeuter et al. 2008 for details). If only littleneck clams, the prime market size, are harvested, the standing stock is incrementally reduced with each successively higher rate of exploitation. As with proportional fishing, increasing exploitation at levels ≥ 25% substantially reduces population levels, and fishing littlenecks at rates > 50% leads to long-term decline in stocks (Fig. 7). In contrast, when selective fishing for large size classes, either cherrystones or chowders, occurs at exploitation rates of 10 to 37.5%, model simulations show that after an initial decline the population recovers to baseline levels and fishing can continue at these levels indefinitely (Fig. 7). Fishing for these larger size classes at levels > 37.5% causes only modest population decline. Furthermore, yields using this strategy remain relatively constant over time. **The model predicts that high exploitation rates can be maintained only if selective fishing is restricted to the largest size classes. It also predicts that harvesting the adult population either proportionally or for littleneck clams at rates that exceed ~25 to 37.5% of the population standing stock would lead to reduction of the population from historical levels.**

Although either proportional fishing or selective fishing for littlenecks leads to a marked decline in the stock with increasing exploitation rates over the long term (e.g. by year 50), the decline in terms of monetary yield is even more precipitous using these two harvesting strategies

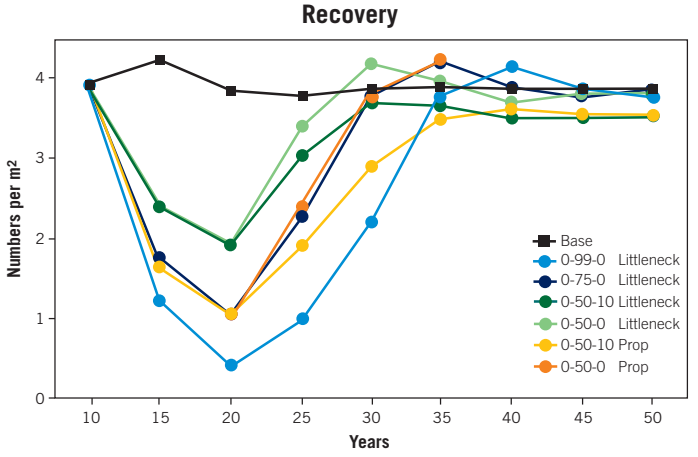

Figure 9. Simulated recovery curves for a hard clam population fished at 50, 75 or 99% of littleneck-sized clams for 10 years and then allowed to recover with no fishing (0 fishing) (modified from Kraeuter et al. 2008). Effects on a proportional (prop) fishery are also shown. Base = base conditions with no fishery.

(Fig. 8). In contrast, the value of the fishery actually increases over the years when cherrystones or chowders are selectively harvested. This results from the higher market value of littlenecks. **The model predicts that proportional fishing at a removal rate of 25% would provide the highest economic value per m². Harvesting only littleneck clams at 37.5 to 50% of their population abundance would provide nearly the same economic yield per unit area, but would require raking larger areas of the bay.**

The model also allowed investigation of the capacity and time frame for recovery of a heavily fished population, either using proportional or size-selective fishing (Fig. 9). Population recovery rates were simulated assuming either a total ban on hard clam fishing, or a limited percent removal. Simulations were run for 10 years of fishing (year 10 to 20) followed by a recovery period. **Irrespective of the fishing strategy employed, model simulations indicate that recovery times to initial levels (historical peak abundance) for the hard clam populations are on the order of a decade or more.**

The model uses a spawning stock-recruit (SSR) relationship to determine recruitment to the population, that was based on a long-term data set collected by the Town of Islip, NY, in GSB waters (Fig. 10; Kraeuter et al. 2005). It is based on 1 m² annual samples sieved through a 6.4 mm mesh (which was reduced to 3.2 mm after 1985) over ~ 6,000 hectares of bay bottom. Only logarithmic and polynomial functions were selected to describe the SSR relationship as they provided a good fit to these data

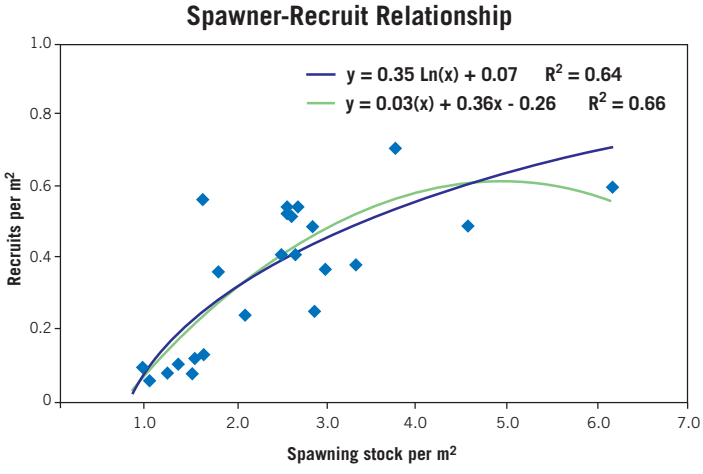

Figure 10. Relationship between the *Mercenaria mercenaria* spawning stock and recruiting year classes (2-yr-old clams) in numbers m⁻² for the Islip Town portion of Great South Bay, NY (modified from Kraeuter et al. 2005).

The curves represent the best fit for Log (blue) and 2nd order polynomial (green) function models, which provided the most realistic fit to the data (linear and power functions were excluded as they led to unrealistic predictions). The fitted equations and coefficients of determination (R^2) are indicated.

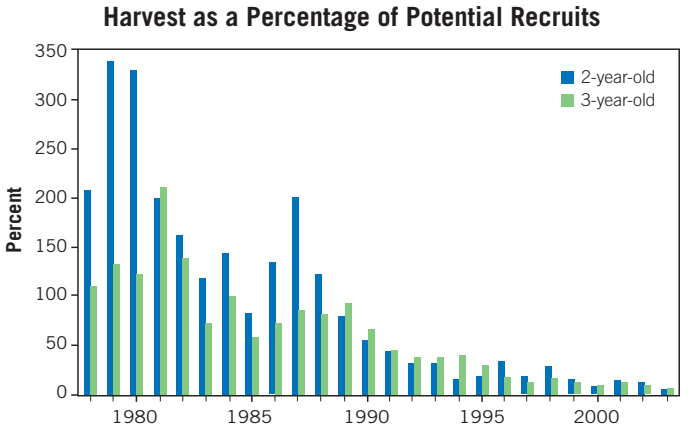

Figure 11. Harvest (clams of all marketable sizes) as a percentage of potential recruits, defined as clams that have reached their first (2-year-old) or second year (3-year-old) in the field (modified from Kraeuter et al. 2008).

while also leading to realistic predictions when extrapolated beyond the locally available data. **Both of these models intercepted the broodstock abundance axis between 0.73 and 0.82 adults m⁻² (Fig. 10), indicating a density-dependent effect on recruitment. Numbers of adults below this threshold are insufficient to provide a sustainable population. This is the first time that a SSR relationship has been described for *M. mercenaria*. The polynomial model also suggested a carrying capacity of ~5 adult clams m⁻², as negative density-dependent factors become important above this density level.** Since the shape of the SSR relationship was based on limited data, and discrimination between the two most likely functions fitted was not possible,

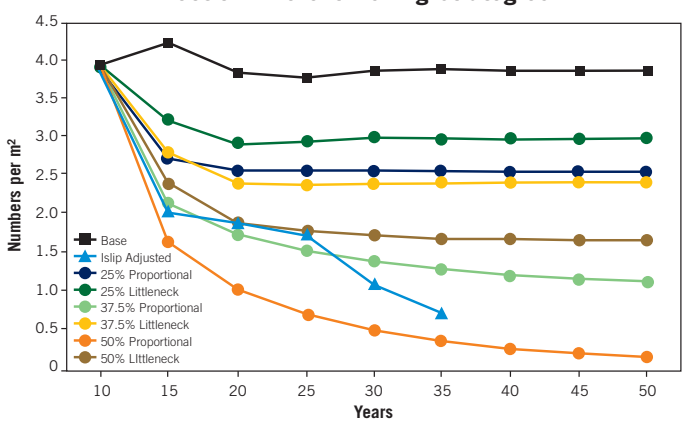

Figure 12. Simulated effects of a fishery that removes clams in proportion (proportional) to the abundance of various size classes in the population at various fishing intensities (25 to 50%) (from Kraeuter et al. 2008). Town of Islip landings data (Islip adjusted) for the 1978-2003 period were adjusted to the base model case of 4 market sized clams per m² to facilitate comparisons (see text).

sensitivity analysis was conducted to determine the effect of variation in the function used (Kraeuter et al. 2005).

Historical data in which the harvest is expressed as a percent of potential recruits (2- or 3- yr-old, sublegal-sized clams) indicate that in most years from the middle 1970s to at least the late 1980s fishing exceeded 75% of recruitment, and at times exceeded 100% of recruitment (Fig. 11). It was not until the mid-1990s that fishing began to remove < 25% of the recruitment level.

The Islip Town fishery-independent surveys of clam abundance began in 1977 with adult densities of 4.7 m^{-2} and these declined to levels of 0.92 clams m^{-2} by 2000. This rate of decline, adjusted to an initial base density of 3.94 clams m^{-2}, was used to compare the actual decline observed with that predicted by the model (Fig. 12). **The actual decline experienced by clam populations during the first 15 years could be predicted by the model using either annual 37.5% proportional or 50% littleneck fishing strategies. In later years, however, the predicted decline diverged, i.e. was greater than that actually measured (Islip-adjusted line in Fig. 12), indicating that a factor other than fishing was accelerating population decline.** In this context, the number of recruits per adult hovered around the time-averaged value calculated between 1979 and 2003, but decreased steadily and remained below this mean from 1995 to 2001, a period of relatively frequent brown tides (Fig. 13). The occurrence of BT in any one year was also typically followed by a reduction in recruitment the following year. It is important to note that in Fig. 13 the recruit per adult data correspond to the Town of Islip section of GSB, and that the occurrence of BT is for all SSE, throughout which there is considerable spatial patchiness in the magnitude and duration of BT. **While no direct cause-effect between BT and recruitment can be inferred from these data, they suggest that BT may be a contributing factor to this later decline.**

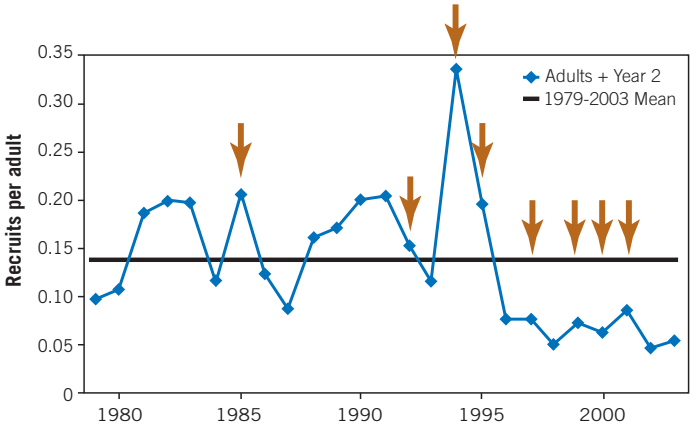

Figure 13. **Temporal changes in the number of recruits per adult between 1979 and 2003. Horizontal line indicates the 1979-2003 mean for recruits per adult (modified from Kraeuter et al. 2008). Adults = clams ≥ 2 year old. Arrows mark years of intense brown tides (≥ 400,000 cells mL^{-1}) (see Fig. 3).**

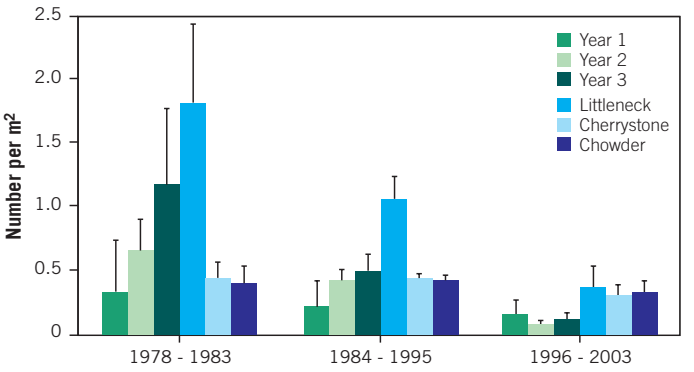

Figure 14. **Temporal change in the abundance of hard clams of three commercial size classes, littleneck, cherrystone and chowder, and year 1 and year 2 recruits between 1978 and 2003 (Kraeuter et al. unpubl.).**

Smaller clams (< 20 mm in shell length) are typically the most vulnerable to mortality factors such as overwintering stress (Bricelj et al. 2007) and predation (Kraeuter 2001). Thus, as expected, the decline in densities from the period 1978-1983 to the period 1996-2003 was greater for littleneck clams than for cherrystones and chowders (Fig. 14). Surprisingly, however, the percent reduction in 1-yr-old clams was less than that of 2- and 3-yr-old clams during this period. This observation remains unexplained, although it is possible that the smallest clams were underestimated during earlier years (note the reduction in sieve mesh size starting in 1985).

Conclusions. Model simulations indicate that a combination of recruitment overfishing (i.e. when removal by fishing occurs faster than recruitment to the fishery) and harvesting rates exceeding 40% of adult clams are the most likely cause of the early decline of *Mercenaria mercenaria* in GSB, especially from the mid-1970s to the mid- or late 1980s. Although recruitment overfishing continued until the late 1980s, other factors appear to have become increasingly important in the late 1990s and into the 2000s. Recruitment has been greatly reduced since the mid-1990s. Repeated brown tides of high densities from ~1994 to 2001, reduced fecundities (as reported by Newell et al. 2009, sec. 3.1.) and/or decreased fertilization at current low clam densities are all possible causes of the later continued decline. Fishing effort directed to the densest portions of the population may have further aggravated the latter effect.

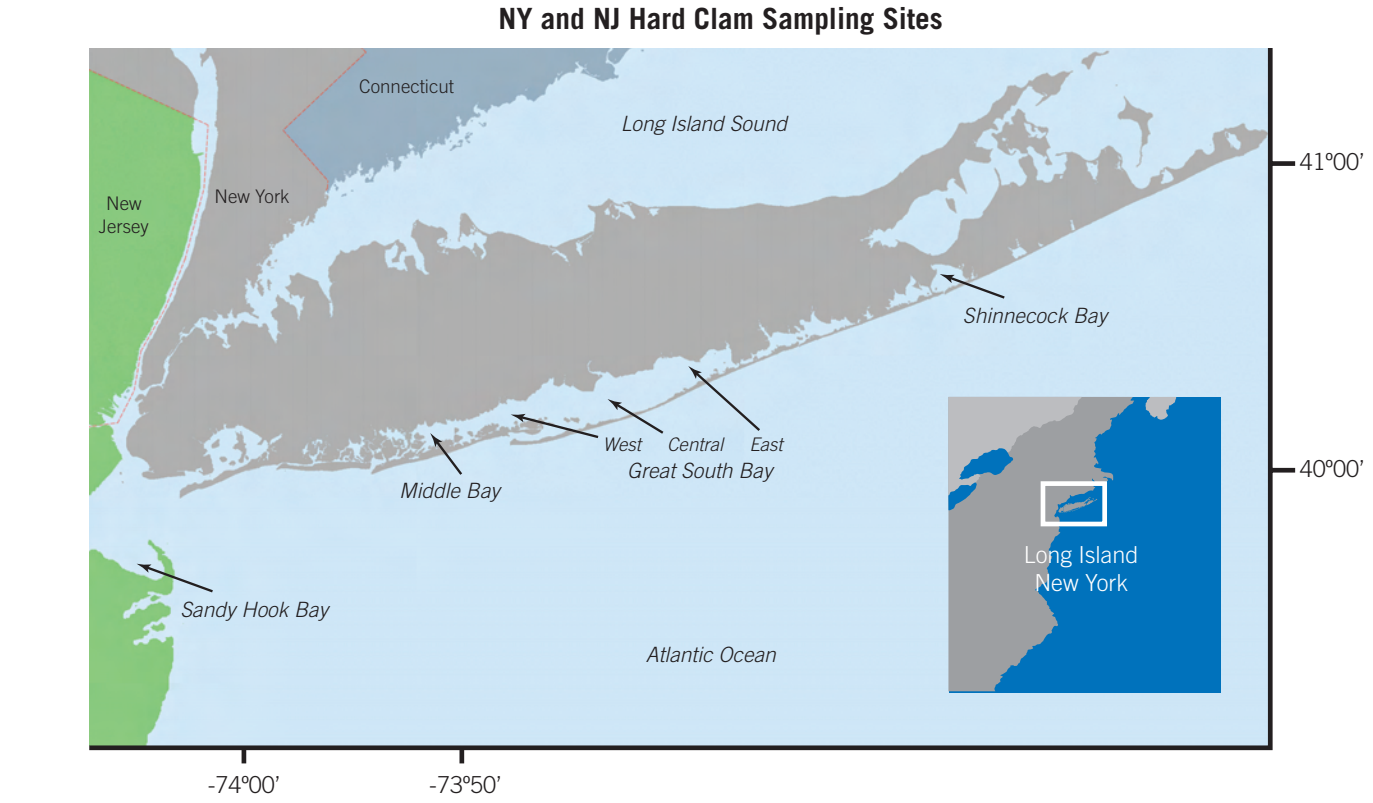

Figure 15. **Map of Long Island, NY, showing sampling sites for the study on reproduction of hard clams in Long Island south shore bays and control sites in Sandy Hook/Raritan Bay, NJ (from Newell et al. 2009).**

3. Reproduction of hard clams in Long Island south shore estuaries

3.1. Hard clam reproductive cycle and performance

The seasonal reproductive cycle of hard clams was determined by sampling adults [mean shell length (SL) 54 to 87 mm] between October 2000 and September 2001 at five sites in southern Long Island Bays along a west to east spatial gradient: Middle Bay in the central portion of Hempstead Bay; western, central and eastern GSB; and Shinnecock Bay (SB), NY (Newell et al. 2009, Tettelbach et al. 2003, Fig. 15). Additionally, two control sites were selected in Sandy Hook Bay, New Jersey (NJ), an area with an established, commercially harvested hard clam population that has not experienced the decline in clam abundance observed in GSB.

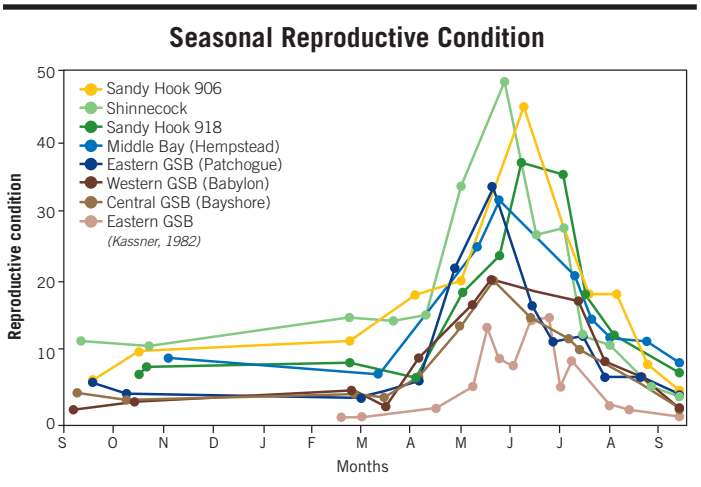

Figure 16. **Seasonal reproductive condition (expressed as percent gamete volume fraction, see text) of hard clams in Long Island south shore estuaries (SSE) and control sites in Sandy Hook/Raritan Bay, NJ (from Newell et al. 2009), compared to data obtained from Kassner (1982). Note that the latter were obtained for a smaller clam size class (see text).**

Several parameters were measured to characterize the clams' reproductive performance, including their condition index reflecting the seasonal buildup of both gonad and somatic tissues, and the relative reproductive output (RRO) was calculated from the following equation:

$$RRO = [\text{condition index (CI)}] \times [\%\ \text{gamete volume fraction}],$$

$$\text{where: } CI = \frac{\text{Total tissue DW}}{\text{Total live WW} - \text{Shell DW}} \times 100$$

and DW and WW = dry weight and wet weight respectively, and the volume fraction was determined using stereological methods.

These parameters were then related to environmental conditions (food, temperature, brown tide) at these sites. Analyses of archived histological sections from a

study on hard clam reproduction conducted in 1979 (Kassner 1982), prior to occurrence of brown tide in these estuaries, were conducted to allow comparisons with current data. These earlier data are useful to compare the timing of reproduction, but cannot be used to compare reproductive output, as the clams collected by Kassner (1982) were considerably smaller (30 to 48 mm in SL) than those collected in the current study.

A key finding of this study was that the timing of seasonal reproduction, i.e. of peak gonad buildup and spawning, was comparable among sites the year of the study (2001), and occurred during the same window of time described in the 1970s (Fig. 16). It is important to note that this comparison is based upon only two years (1979 and 2001) and that longer-term data series are needed to evaluate historical trends in reproductive patterns. Spawning across a range of environmental conditions/sites thus occurs primarily in mid-summer, in June and July. The amplitude of the reproductive cycle, and thus the synchrony in reproductive development and spawning, was also similar among sites and comparable to that described for clams collected in 1979. **In contrast, large variability was found among sites in the magnitude of peak reproductive condition (Fig. 16), and in the calculated reproductive output, which showed 3-fold maximum variation (Fig. 17).** Reproductive effort was lowest within GSB, highest at the western sites (Sandy Hook and Middle Bay) and intermediate in Shinnecock Bay. **Thus low reproductive output of clams in GSB, if a recurring phenomenon over a number of years, may be a contributing factor to the slow recovery of hard clam populations in the past decade.** Geographic/spatial variability in clam reproductive output should be considered in the potential siting of spawner sanctuaries.

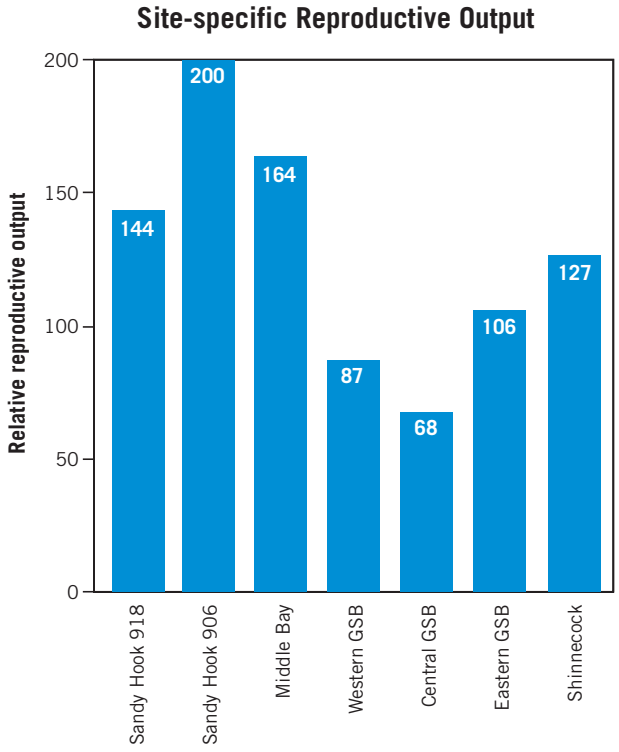

Figure 17. Total relative reproductive output (total RRO, see text) of hard clams in Long Island, NY, south shore estuaries and control sites in Sandy Hook Bay, NJ in 2001 (from Newell et al. 2009). Total RRO was calculated by integration of the RRO over time during the reproductive period.

Model simulations (Hofmann et al. 2006a) were unable to reproduce the typical cessation of spawning of hard clams in GSB via a change (drop) in temperature, as was used for the eastern oyster model. In order to allow spawning to cease in the fall, a relationship had to be introduced in the hard clam model based on the number of days with temperatures between 20 and 27ºC (day-degrees). This implies that the processes (endogenous and external) that terminate hard clam spawning are not fully understood, and consequently mechanistically-based parameterizations of this process are not possible. Therefore, this *ad hoc* approach was used to adequately simulate field observations (Hofmann et al. 2006a).

3.2 Association between reproductive performance and environmental variables. Historical salinity averages showed relatively limited variation across sites (25 to 28 in GSB, 25 in Sandy Hook Bay and 30-31 in SB and Middle Bay). Therefore the large variability in relative reproductive output (RRO) could not be attributed to differences in salinity. Differences in mean spring, summer and fall temperatures among sites were also unable to explain the observed variation in reproductive output. Furthermore, the latter could not be ascribed to differences in food quantity as measured by total chlorophyll *a* (Chl *a*), total organic carbon or nitrogen during the study period. Thus central and eastern GSB and Sandy Hook Bay had the highest Chl *a*, organic carbon and nitrogen levels, yet the two GSB sites showed the lowest RRO. Analysis of historical data revealed that, as expected, there was high inter-annual variability in Chl *a* levels between sites, but corroborated that eastern and central GSB and Sandy Hook Bay had the highest Chl *a* levels (Table 1). The condition index of clams in the previous fall/early winter (Nov.-Dec, 2000) differed considerably among sites, and was ~30% lower in GSB where RRO was also lowest compared to all other sites. These differences in condition were maintained throughout the winter and early spring. **This suggests that the food supply and condition attained by clams the previous fall may be an important factor in predicting their reproductive performance the following spring and summer.** A significant correlation between the condition index of hard clams at the end of the fall and the peak in condition the following

spring has been described for clams transplanted into GSB over a 4-year study period (Doall et al. 2008).

Results presented by Newell et al. (1990) suggest that food quality (phytoplankton composition) is more important than food quantity and temperature in controlling the reproductive output of clams in these bays. Unlike bivalve larvae, juvenile and adult hard clams, in common with many other suspension-feeding bivalves, show a steep decline in gill retention efficiency (RE) for particles < 3-4 µm in size (Riisgård 1988), such that *M. mercenaria* retains 2 µm particles with only ~50% efficiency. At high densities, however, this may be sufficient to support clam growth if the algae are of high nutritional value. Thus the contribution to clam nutrition of algae below the size threshold for 100% RE will depend on their size, cell density and nutritional quality. A number of small green algae (chlorophytes) such as *Nannochloris/Chlorella/Nannochloropsis* (= *Stichococcus*) spp. and cyanobacteria such as *Synechococcus* spp., are known to be poorly absorbed and to support poor growth of juvenile clams (Bricelj et al. 1984, Bass et al. 1990) and larvae (Tiu et al. 1989). *Synechococcus* is often an important constituent of the smaller phytoplankton size fraction in SSE (Caron et al. 2004, Sieracki et al. 2004). Thus, even if partially retained by the gills on the basis of size, algal species comprising this size fraction may not contribute effectively to the nutrition of clams. **In this context, Newell et al. (2003 and 2009 data) found that the relatively low reproductive output measured in eastern and central GSB was associated with the highest contribution of picoplankton (0.2 to < 2 µm), and of the < 5 µm size fraction to total Chl *a* (Fig. 18). Middle Bay had the highest RRO compared to all other Long Island bays and was characterized by the lowest contribution of "small forms". This and other information presented elsewhere in this report indicate that size-fractionation of the food supply is important to characterize the food available for hard clams. Routine environmental monitoring by the counties and townships typically only quantifies total Chl *a*, so including such size characterization would provide valuable additional information.**

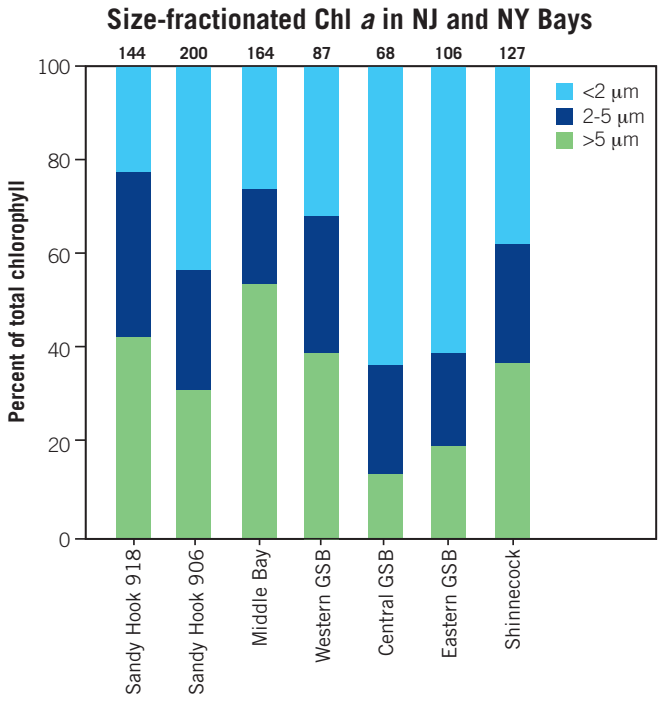

Figure 18. Percent annual mean chlorophyll *a* in three size classes in Long Island, NY, south shore bays and control sites in Sandy Hook Bay, NJ, in 2001 in relation to the hard clams' Relative Reproductive Output (RRO) values shown above each bar (modified from Newell et al. 2009).

Changes in phytoplankton size structure, however, could not adequately explain all the site-related differences in reproductive output observed. Thus, the phytoplankton in western GSB did not differ greatly from other sites characterized by a relatively high RRO, such as Sandy Hook and Middle Bay. High concentrations of *Aureococcus anophagefferens* did not occur in 2001, the year of Newell's study (Table 2). However, concentrations at the three GSB locations at times exceeded the 35,000 cells mL^{-1} threshold known to inhibit bivalve feeding (sec. 8.1) and thus cannot be ruled out as a contributing factor, via its toxic effects, to the low RRO obtained at these sites. A maximum concentration of ~773,000 *A. anophagefferens* cells mL^{-1} was measured in Central GSB in late June, after the peak in gonad condition was attained (Table 2). This was the only site with a relatively extended brown tide, with levels exceeding the threshold level lasting ~2 mo (early June through early August). Detectable levels of *A. anophagefferens* were never found in Middle Bay and Shinnecock Bay. Additionally, high levels of *A. anophagefferens*, attaining ~ 689,000, 1.4 million and 357,000 cells mL^{-1} were reported in eastern, central and western GSB respectively in the previous year (2000; Table 2). Analysis of longer term data indicated that BT is a more frequent annual occurrence in eastern and central GSB than in western GSB or SB, and have not yet been recorded in Middle Bay, a relatively well flushed estuary (Newell et al. 2009).

Long Island estuaries may have experienced a historical shift in the composition of the phytoplankton assemblage leading to a greater contribution of "small forms" (< 5 µm) that are detrimental to hard clams and other commercially important suspension-feeding bivalves. This remains speculative, however, as there are limited historical data to determine long-term trends. Blooms of "small forms" occurred in the 1950s and Ryther (1954) hypothesized that they were a major cause of the demise of eastern oyster populations in GSB. This was a transient phenomenon, however, related to the nutrient release of duck farm effluent that caused an increase in the phos-

		Spring mean ± SD	n	Summer mean ± SD	n	Autumn mean ± SD	n
Sandy Hook	Historical	11.1 ± 10.6	9	14.8 ± 11.1	17	23.8 ± 33.8	5
	This study	34.8 ± 32.2	4	37.2 ± 22.6	10	20.5 ± 3.5	2
Middle Bay	Historical	11.7 ± 10.7	64	11.5 ± 11.2	66	6.2 ± 6.4	63
	This study	2.0 ± 0.2	2	11.2 ± 10.7	6	2.7 ± 2.3	2
Western GSB	Historical	6.8 ± 5.9	56	11.5 ± 15.9	62	4.7 ± 3.7	58
	This study	2.5 ± 0.8	3	5.6 ± 1.8	7	2.6 ± 1.0	3
Central GSB	Historical	9.0 ± 5.3	50	17.4 ± 8.1	74	13.7 ± 6.9	55
	This study	4.7 ± 1.0	2	14.6 ± 6.9	7	8.1 ± 3.6	3
Eastern GSB	Historical	10.7 ± 8.2	48	19.3 ± 10.9	73	20.4 ± 9.5	54
	This study	9.1 ± 4.0	2	11.7 ± 4.0	6	7.3 ± 0.9	3
Shinnecock	Historical	4.3 ± 2.9	62	9.2 ± 7.7	89	9.4 ± 7.2	72
	This study	2.2 ± 0.4	2	3.0 ± 3.5	6	2.9 ± 2.2	3

Table 1. Mean (± standard deviation, SD) chlorophyll *a* concentrations (µg Chl *a* L^{-1}), for all sites from historical monitoring data and from sampling conducted in 2000 and 2001 as part of the HCRI (see Newell et al. 2009). Spring includes data from March, April, and May; Summer includes June, July, and August; and Autumn includes September, October, and November, pooled data for 2000 and 2001; n = sample size.

phorus to nitrogen ratio and high levels of ammonia and uric acid. In a study conducted in 1972, "small forms" were estimated to contribute only 5 to 35% of total biomass (Cassin 1978 in Lively et al. 1983) and were estimated to contribute ~ 50% of total phytoplankton biomass by volume in 1979/1980 (Lively et al 1983). It is noteworthy, however, that enumeration of phytoplankton was only conducted three times seasonally in this study and that the value reported was based on calculations, as the < 5 µm Chl *a* size fraction was not measured directly.

Studies conducted in the last decade (e.g. Lonsdale et al. 1996, Sieracki et al. 2004) do show that microalgae < 5 µm ("small forms") are often the dominant fraction of the total chlorophyll biomass during the summer in Long Island SSE (as illustrated in Figs. 18 and 23B from two HCRI studies). **We can conclude that present conditions in GSB, including the present nutrient regime, are favorable for the summer dominance of "small forms".** Changes in environmental conditions, especially nutrient ratios (e.g. organic and inorganic N:organic and inorganic P:Si or micronutrients), in these bays need to be evaluated, and especially their role in favoring "small forms" or particular algal species that inhibit hard clam feeding, are indigestible, or otherwise detrimental to hard clam growth.

4. Trophic interactions between hard clams and natural phytoplankton and zooplankton assemblages in SSE

4.1. Background. A benthic survey in Patchogue Bay conducted by Cerrato et al. (unpublished) in 2002 indicated the absence of any major assemblages of suspension-feeders, other that serpulid worms (*Hydriodes dianthus*) found encrusting oyster shell bottom. An earlier survey conducted in the spring and summer of 1999 in eastern GSB had shown an extensive population of the coot clam, *Mulinia lateralis*, at densities of up to 50,000 m^{-2}, that exerted strong grazing pressure in the bay, but these populations are transient (Nuzzi and Waters 2004). The historical decline of hard clam populations in GSB, and the absence of other major macrofaunal suspension-feeders to occupy their ecological niche, has led to a shift from a community dominated by benthic grazers to one dominated by zooplankton grazers. Benthic macrofauna, including hard clams, can also influence the flux of nutrients from the sediment, and mesocosm studies showed that grazing by hard clams at low *A. anophagefferens* densities (< 5,000 cells mL^{-1}) could play a role in preventing brown tide development (Cerrato et al. 2004; sec. 6.1). Therefore, a reduction in the biomass of benthic macrofaunal suspension-feeders may be expected to result in associated changes in the biomass, size structure and/or composition of the natural phytoplankton and zooplankton community, and in the flux and recycling of nutrients in this shallow and relatively well-mixed bay.

To investigate these potential food web interactions, Streck (2003) and Cerrato et al. (2003) determined the growth of juvenile hard clams (2-4 mm initial SL) over 2-4 wks under ambient conditions (hung off the side from moored platforms in a mesh pouch) and in experimental tanks, with and without the addition of adult clams, at three sites along a west to east gradient in GSB: Copiague, Babylon and

Mean Date	Shinnecock	Eastern GSB	Central GSB	Western GSB	Middle Bay
13-Apr-00	ND	60,892	**142,094**	17,702	ND
27-Apr-00	<20	**267,976**	**143,656**	ND	ND
17-May-00	ND	**647,764**	**61,945**	30,308	ND
24-May-00	ND	**296,571**	**85,850**	215	ND
8-Jun-00	ND	**689,344**	**221,153**	**161,017**	ND
20-Jun-00	ND	ND	**1,357,309**	**304,083**	ND
28-Jun-00	14,298	**216,304**	**601,006**	ND	ND
5-Jul-00	ND	ND	**145,698**	6,264	ND
10-Jul-00	7,232	ND	**371,000**	ND	ND
18-Jul-00	ND	ND	**259,825**	ND	ND
1-Aug-00	ND	ND	**160,558**	ND	ND
15-Aug-00	25,029	ND	**36,798**	ND	ND
6-Sep-00	ND	15,495	ND	ND	ND
21-Nov-00	ND	ND	19,336	251	ND
15-Mar-01	0	546	955	501	ND
3-Apr-01	137	0	0	532	137
23-Apr-01	137	1,092	1,229	355	0
18-May-01	0	819	1,138	1,065	683
5-Jun-01	0	**63,336**	**159,332**	3,924	137
24-Jun-01	137	5,392	**773,283**	**59,645**	0
8-Jul-01	ND	273	**35,580**	1,065	410
15-Jul-01	0	ND	**87,005**	177	273
24-Jul-01	137	6,893	**69,596**	887	0
7-Aug-01	273	**76,713**	**115,813**	1,065	137
28-Aug-01	410	3,890	20,263	1,775	683
17-Sep-01	0	0	15,015	177	0

Table 2. ***Aureococcus anophagefferens*** **cell concentrations (modified from Newell et al. 2009). Data from April – Nov. 2000 were provided by the Suffolk County Department of Health Services; data from 2001 are means obtained from Newell et al. (2009). Boldfaced values mark cell concentrations > 35,000 cells mL^{-1}, the concentration above which toxic effects on hard clams are manifest (Fig. 34). ND = not determined.**

Patchogue. Experimental tanks were deployed in moored, floating platforms (Fig. 19) that allowed the tank water to remain under ambient light and temperature conditions. An air pump supplied vertical mixing of tank water, which was exchanged with ambient water once a day by bucket at a rate of 10% per day. Juvenile clams were sufficiently small and their numbers sufficiently low that their grazing was deemed negligible, yet their growth response provided a measure of food quality. Two weeks were allowed for establishment of plankton communities within the tanks prior to the addition of juveniles.

Treatments with added adult clams were intended to identify potential positive or negative feedback interactions on the phytoplankton community and ultimately on the food supply for juvenile clams. The addition of 6 adults per tank simulated the grazing (clearance rate) expected in the 1970s prior to the decline of hard clam stocks (at 40% day^{-1}).

Additionally scope for growth (SFG) was determined for adult clams during the last week of the experiment by measuring individual clearance rate (CR), absorption efficiency (AE) and respiration (R), where SFG = [(CR x food concentration) x AE] – R. These parameters were measured under ambient conditions and in experimental tank suspensions that were diluted at all sites to attain comparable Chl *a* concentrations. Physiological measurements were obtained from short-term exposure (a few hours) to ambient or tank water that was collected at the end of the experiment at each site and are therefore not directly comparable to the integrated growth measurements obtained for juveniles. It is also important to note that due to logistic reasons the experiments with and without addition of adult clams were not run concurrently at the three sites, but were staggered over several weeks during the summer of 2002. Therefore statistical comparison among sites was not attempted. Statistical analysis was restricted to comparing treatments with and without adults for each parameter measured (juvenile growth, AE and SFG) following Gurevitch and Hedges (1993).

4.2. Juvenile and adult growth. Growth rates of juvenile hard clams under ambient conditions decreased along a west to east gradient in GSB (Fig. 20A). The same spatial pattern was observed in experimental tanks without added adult clams, except that growth rates were reduced at all sites, reflecting the more limited flow exchange and thus food limitation in the enclosed system (Fig. 20B). **The addition of adults, however, resulted in increased growth of juveniles relative to untreated tanks at two out of three sites (central and eastern GSB) where juvenile growth was moderate to poor (Fig. 20B).** In contrast, at the westernmost location, where growth under ambient conditions was high, juvenile growth was reduced by 57% in the treatment with adults, suggesting that juve-

Experimental Setup

Figure 19. View of moored platforms deployed in the field during the spring and summer of 2002 (Streck 2003 and Cerrato et al. unpublished). The 2.4 x 6.7 m (8' x 22') platform had a center walkway and held 12 fiberglass cylindrical tanks containing 400 L seawater, suspended from each side (also shown in the inset), covered with screened doors.

niles and adults were competing for food. **This indicates that adult clams exerted a positive feedback at sites (two out of three) where the food supply supported lowest juvenile growth. At the third site, the presence of adult clams exerted a negative feedback on juvenile growth.**

Growth of adult clams, as measured by the scope for growth (SFG), was highest at the western GSB site (Fig. 21A), as observed for juveniles. Again growth was reduced in all experimental tanks relative to ambient conditions, and was negative at the western GSB site indicating food limitation due to the limited water exchange. The presence of adult clams had a significant positive effect on SFG at all sites ($p = 0.04$; Fig. 21B). Absorption efficiency [(organic matter absorbed/ingested) x 100] under ambient conditions was lowest at the western GSB site where juveniles grew best (Fig. 22A). The presence of a detrital food component, not measured by Chl *a*, was suggested as a possible explanation for this unexpected result. **Absorption efficiency in short-term experiments was enhanced at all three sites in tanks that experienced addition of adults (Fig. 22B),** indicating that intense adult

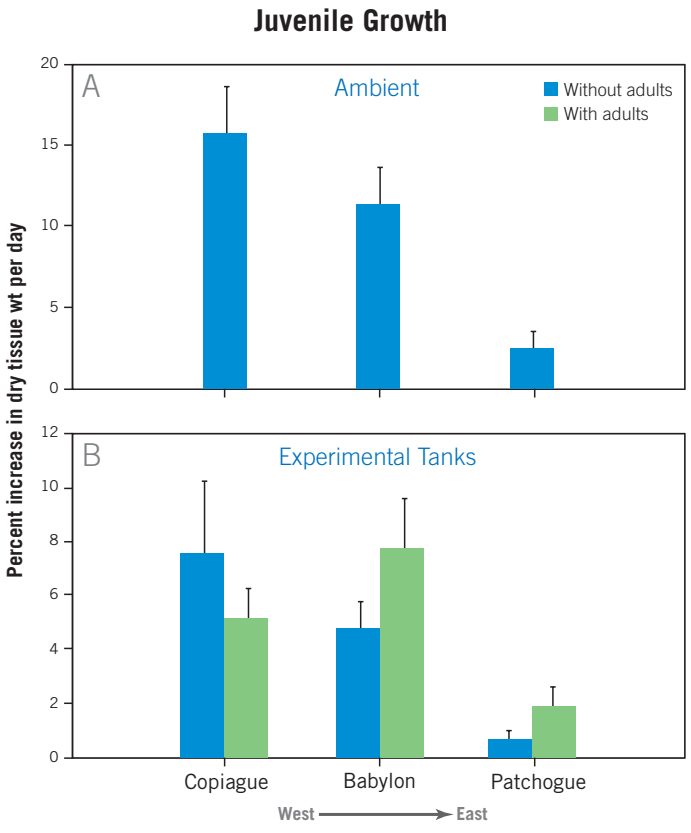

Figure 20. **Growth rate of soft tissues (mean ± SE) of juvenile hard clams (*Mercenaria mercenaria* 2-4 mm initial shell length) held at ambient conditions (A) or within the experimental tanks for 3 to 4 wks, without and with adult clams added (B), at three sites along a west to east gradient in GSB (from Streck 2003). Growth expressed as the daily instantaneous growth coefficient (k) = (lnWf – lnWi)/t x 100 where Wi and Wf are initial and final weight respectively and t = time interval.**

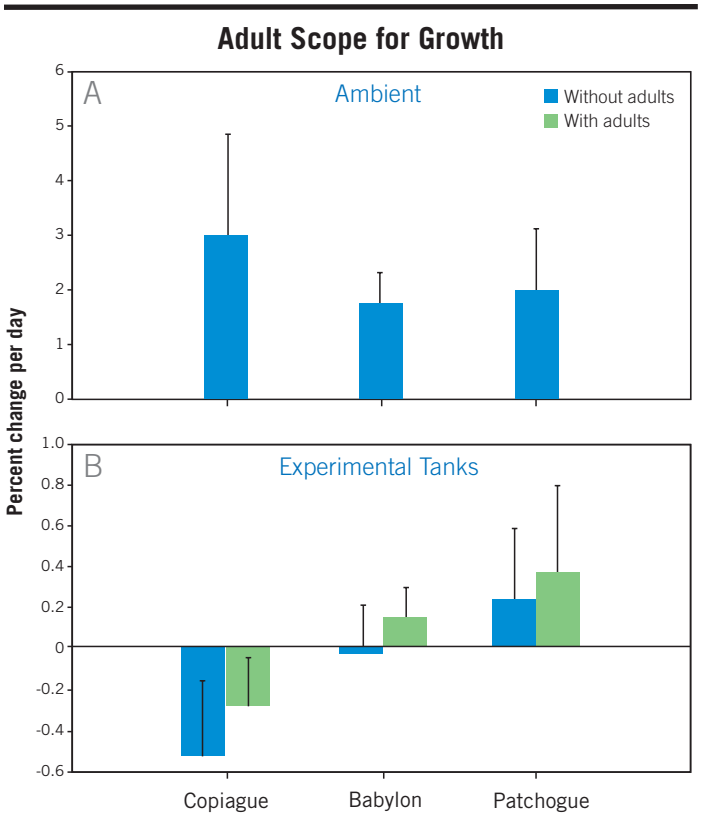

Figure 21. **Scope for growth (SFG, mean ± SE), calculated from individual physiological data (see text) as percent change (increase or decrease) per day, of adult hard clams (*Mercenaria mercenaria*) under ambient conditions (A) and within the experimental tanks, without and with adult clams added (B), at three sites along a west to east gradient in GSB (from Streck 2003).**

Results were standardized for a clam 1 g in dry tissue weight. Note that SFG and the absorption efficiency (Fig. 22) were determined from measurements taken during the last week of the experiment. Thus the time scale does not match that of Fig. 20.

grazing activity improved food quality/digestibility by some unknown mechanism. This could be due to removal via adult grazing of a detrimental factor, or addition of a factor that contributed positively to the quality of the food supply. In summary, the effects of adult clam addition were statistically significant for all three parameters measured ($p<0.04$ for juvenile growth and SFG, and $p<0.01$ for absorption efficiency; Cerrato, pers. comm.).

Ambient Chl *a* concentrations showed no clear relationship with growth of juvenile clams exposed to ambient conditions (Fig. 23A; Streck 2003). As found by Newell et al. (sec. 3.2) the < 5 µm size fraction made the dominant contribution to the total ambient Chl *a* biomass at all three sites, ranging from 65 to 85%. The > 5 µm size phytoplankton size fraction, known to be retained with high efficiency by the clam gills, decreased along a west to east gradient (Fig. 23B), and was positively related to juvenile growth. Conversely, small (2-3 µm) nanoplank-

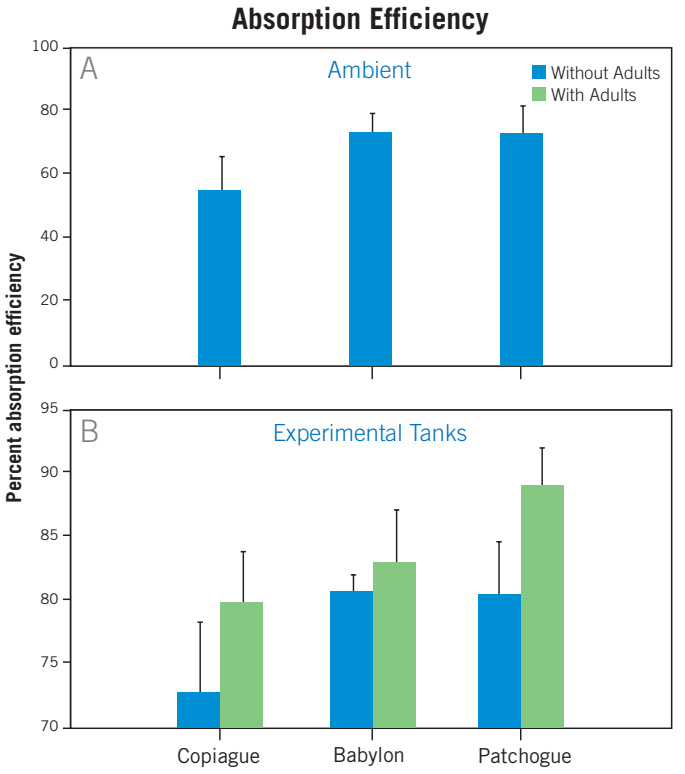

Figure 22. **Percent absorption efficiency (mean ± SE) of *Mercenaria mercenaria*, measured by the Conover's ash ratio method (1966) under ambient conditions (A) and within the experimental tanks, without and with adult clams added (B), at three sites along a west to east gradient in GSB (from Streck 2003).**

ton, a size fraction that is inefficiently retained by the clam gills, increased from west to east. These results again point to the importance of size-fractionated characterization of the food supply to explain differences in *Mercenaria mercenaria* growth, as described in sec. 3.2. Brown tide did not occur the year of this study (2002) and therefore did not contribute to the < 5 µm fraction. Lower juvenile growth in eastern GSB could not be attributed to the prevalence of dinoflagellates, as their ambient concentration was lowest at this site (Fig. 24A). Total ambient, pennate diatom concentrations, however, increased along a west to east gradient and were thus inversely related to juvenile growth. Species identification, once completed, may help to explain this pattern. All copepod stages in the ambient mesoplankton (200-2000 µm size fraction) also increased markedly from west to east (Fig. 24B). Dilution experiments showed that zooplankters were the dominant grazers at all three GSB sites.

There was no apparent effect of the addition of adult clams on total Chl *a* concentrations (not shown). Contrary to expectation (see sec. 5), the addition of adults did not lead to a reduction in the density of copepod eggs and early life history stages relative to untreated tanks, but rather to their increase at all three sites (not shown). Effects of the addition of adult clams on other components of the microzooplankton and mesozooplankton were generally not consistent at the three sites, and are not

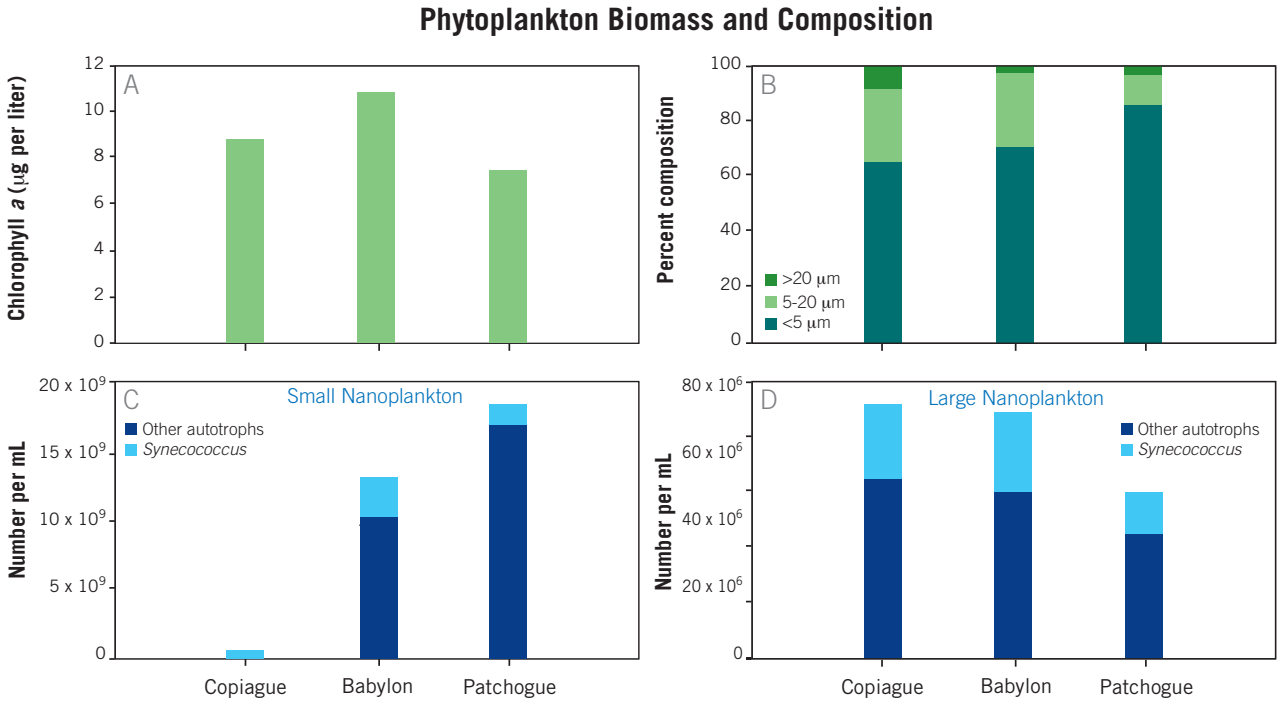

Figure 23. **Ambient total chlorophyll *a* concentration (A), size-fractionated Chl *a* (B), and concentration and composition of small nanoplankton, 2-3 µm size fraction (C), and large nanoplankton, 3-20 µm size fraction (D) at three sites along a west to east gradient in GSB (from Streck 2003 and Cerrato et al. unpubl.). Autotrophs = photosynthetic organisms; *Synechococcus* = small (1 µm) blue-green alga or cyanobacterium. Note that no brown tide (*Aureococcus anophagefferens*) was detected in 2002, the year of the study (see text).**

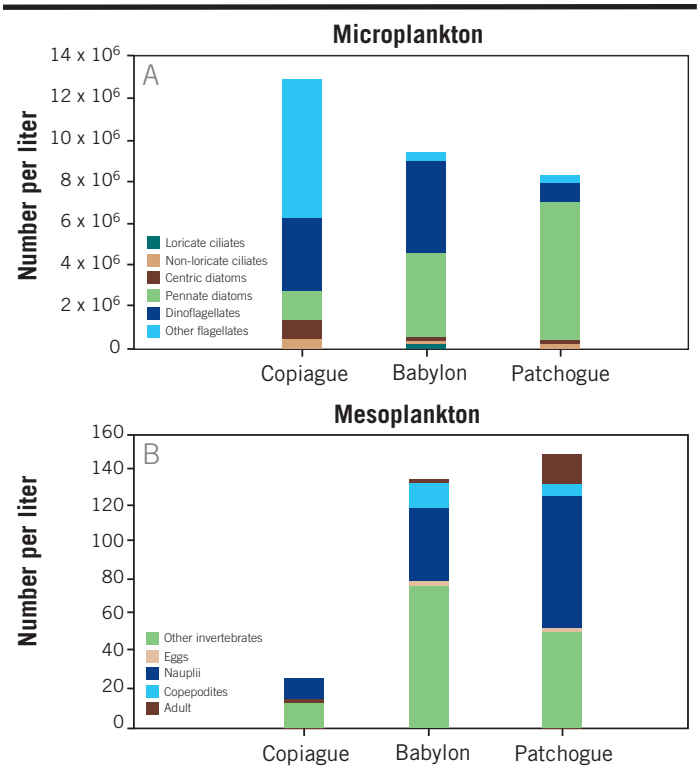

Figure 24. Ambient concentration and composition of the microplankton, 20 to 200 µm size fraction (A), and mesoplankton, 200 to 2000 µm size fraction (B) at three sites along a west to east gradient in GSB (from Streck 2003).

reported here as they await analysis and interpretation.

Conclusions. Although it is difficult to draw definitive conclusions on the complex trophic interactions involved from the available data, results indicate that there are major differences among GSB sites along a west to east gradient in the size structure, abundance and composition of the phytoplankton and zooplankton, and in the environment's ability to support growth of juvenile clams. There is thus considerable spatial heterogeneity in the food supply controlling growth rates that needs consideration in stock enhancement efforts. Additionally, intense grazing by adult hard clams was suggested to exert a positive feedback on juvenile growth at two of the three sites (Babylon and Patchogue) where juvenile growth was lowest. The authors interpreted this positive feedback as resulting from improvement of the food supply by the presence of adults, as reflected in increased absorption efficiency measured over the short term in tanks that contained adult clams relative to untreated tanks, but the mechanism involved remains speculative. Additionally, absorption efficiency measurements were not repeated over time throughout the period of juvenile growth experiments. These results must therefore be considered preliminary and interpreted with caution until any proposed underlying mechanisms can be tested and confirmed.

4.3. Effect of inlet proximity to hard clam growth and survival. The SSE bays are characterized by relatively low flushing rates and tidally exchanged ocean waters via inlets. Some of these inlets have been ephemeral but others such as Fire Island Inlet and Moriches and Shinnecock inlets have been stabilized and made permanent.

Spatial variability in growth rate of juvenile clams from west to east in southern Long Island bays, as described in the previous section, was also demonstrated by Weiss et al (2007) and related to the proximity to the inlets and associated greater tidal exchange. Juveniles were held in suspended cages off-bottom, protected from predators. Adults were also suspended in 2005 to determine their condition index. Study sites in Shinnecock Bay and GSB are shown in Fig. 25.

Overall, in both GSB (in 2005) and SB (in 2004) lowest clam growth rates were found near inlet locations and maximum growth rates observed in mid-bay sites where flushing rates and total Chl *a* levels were intermediate (Fig. 26). Total Chl *a* attained lowest values at sites closest to the inlets in both SB and GSB. In SB, where the spatial resolution was greatest, an inverse relationship was found between total Chl *a* and distance from the inlet (Fig. 27A). Thus poor growth at near-inlet locations may be related to limitation in total phytoplankton biomass. There was also a spatial pattern in size-fractionated Chl *a*, as illustrated for SB in Fig. 27B. **The contribution of the < 5 µm size fraction increased progressively with increasing distance from the inlet in both SB and GSB. Therefore the relatively poor clam growth determined at the innermost bay locations, characterized by lowest flushing rates, can be associated with the dominance of "small forms," despite high total Chl *a* levels.**

Mortalities of juvenile clams occurred mostly in late April-early June and were significantly higher at inlet sites in both bays in 2005 but not in 2004 (Fig. 28). During extended periods of temperatures < 5ºC clams stop feeding and use carbohydrate reserves to meet their metabolic demand (Zarnoch and Schreibman 2008, Bricelj et al. 2007). Therefore high spring mortalities in 2005 were attributed to food limitation experienced by clams at inlet locations during the spring when juveniles recover from overwintering stress. The food supply in the fall was found to be a factor influencing the magnitude of these subsequent winter and spring mortalities in juvenile hard clams (Zarnoch and Schreibman 2008). Unintentional (e.g. via storms) or intentional breaching of inlets in Long Island's south shore bays is thus expected to have pronounced effects on hard clam populations.

Inter-bay differences were also observed by Weiss et al. (2007): Shinnecock Bay (SB) supported higher juvenile growth rates, higher condition of adults, and higher clam densities than GSB (Fig. 26). This is consistent with results of Newell et al. (2009) showing that reproductive condition was greater in SB than in GSB.

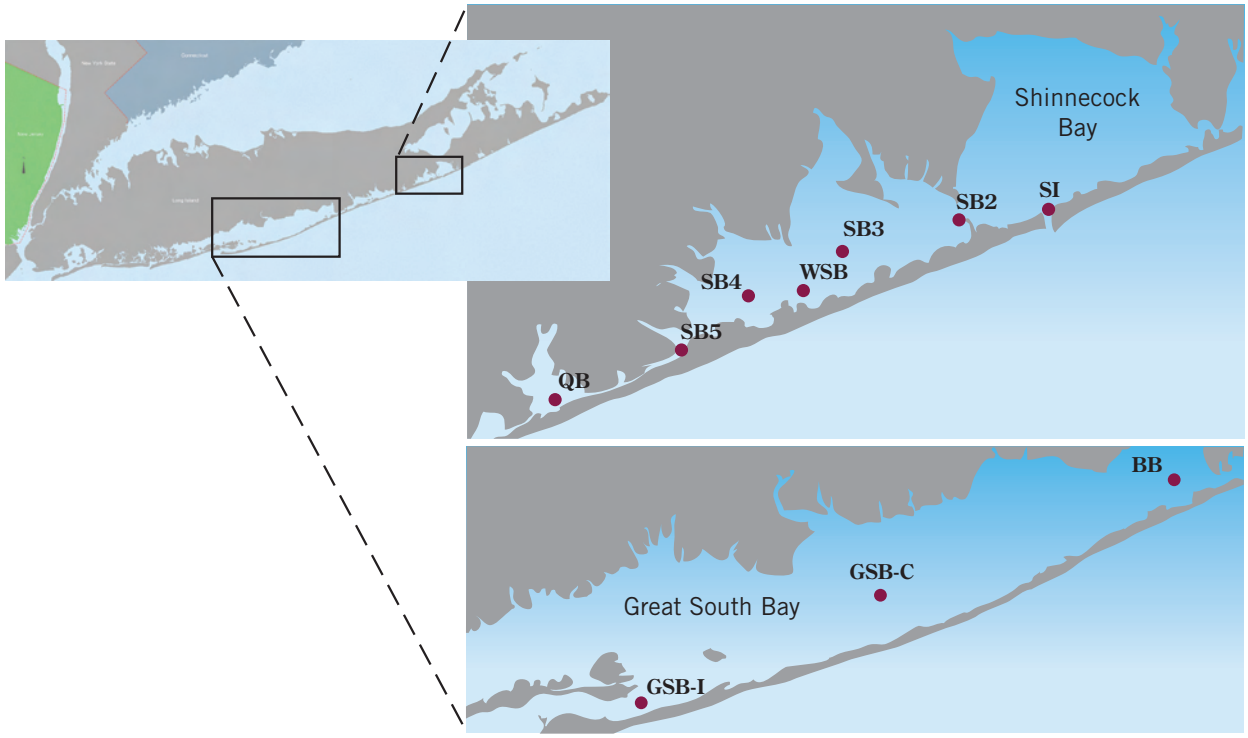

Figure 25. Study sites in Shinnecock Bay, SB, (2004, 2005) and Great South Bay, GSB, (2005) (redrawn from Weiss et al. 2007). In 2004, sampling locations were SB inlet (SI), sites in western SB (SB2–SB5), and Quantuck Bay (QB). In 2005, sampling sites were in GSB inlet (GSB-I), central GSB (GSB-C), and Bellport Bay (BB), while SB stations were SI, western SB (WSB), and QB (data for these 3 sites are not shown in this report).

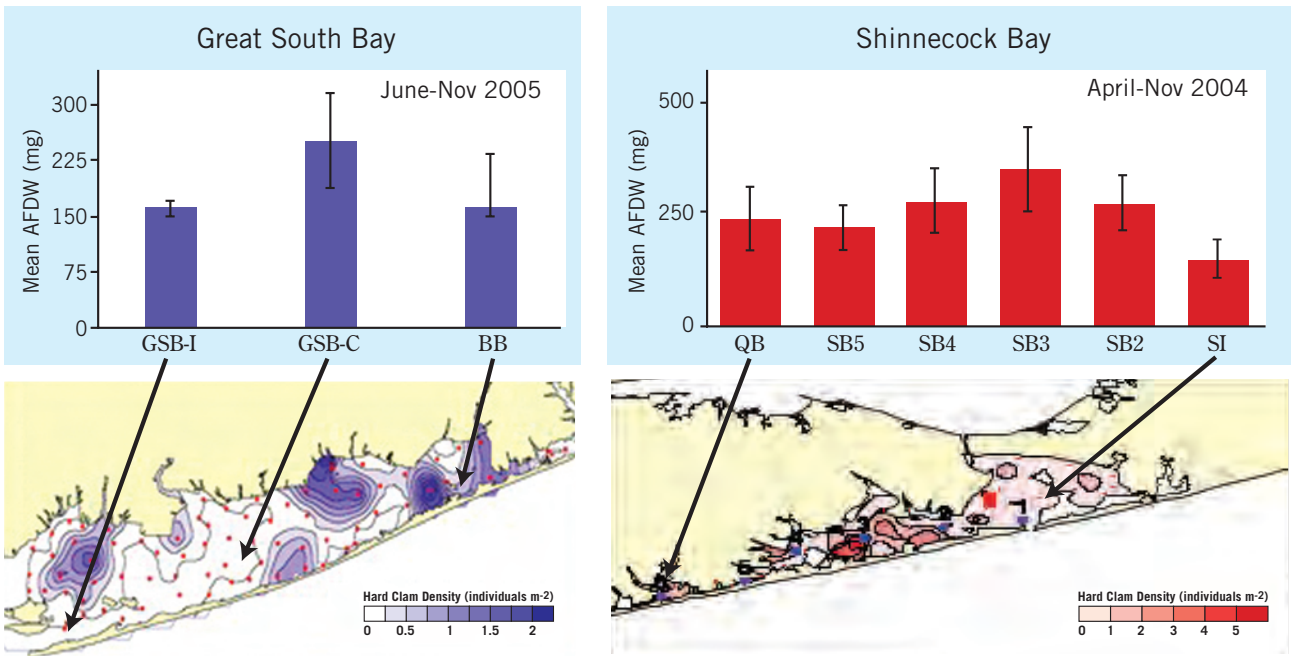

Figure 26. Final ash-free dry weight (AFDW) of juvenile hard clams (11 to 14 mm initial shell length, SL) deployed with predator protection in two Long Island south shore bays throughout the growing season, illustrating the spatial variability in growth along a west to east gradient (modified from Weiss et al. 2007; work funded outside the HCRI; site abbreviations as in Fig. 25). Note lowest growth rates at inlet locations (GSB-I and SI) and highest growth rates at mid-bay locations. Deployment sites and natural densities of hard clams (≥ 20 mm SL) shown in the bottom graphs.

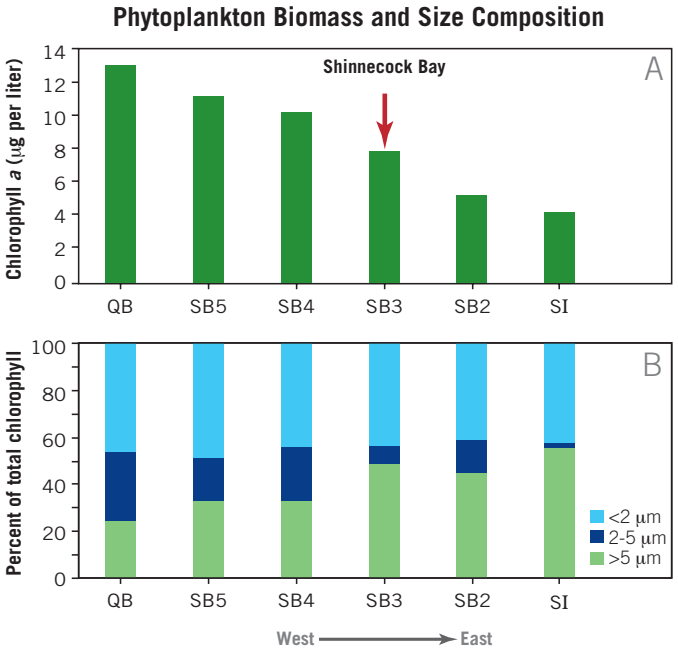

Figure 27. **Mean total chlorophyll *a* (A) and size-fractionated Chl *a* (B) in Shinnecock Bay, NY, along a west to east gradient during the 2004 growing season (refer to Fig. 25 for site locations; plotted from data tabulated in Weiss et al. 2007).**

Note the inverse relationship between total Chl *a* and distance from the inlet (SI). The red arrow marks the site where juvenile hard clams attained the highest growth rate in terms of shell length. This site was characterized by intermediate levels of mean total Chl *a* yet showed the highest percent contribution of the > 5 µm size-fraction, except for SI, where the total phytoplankton biomass was presumably limiting. (Note that growth in tissue ash-free dry weight was maximized at SB4).

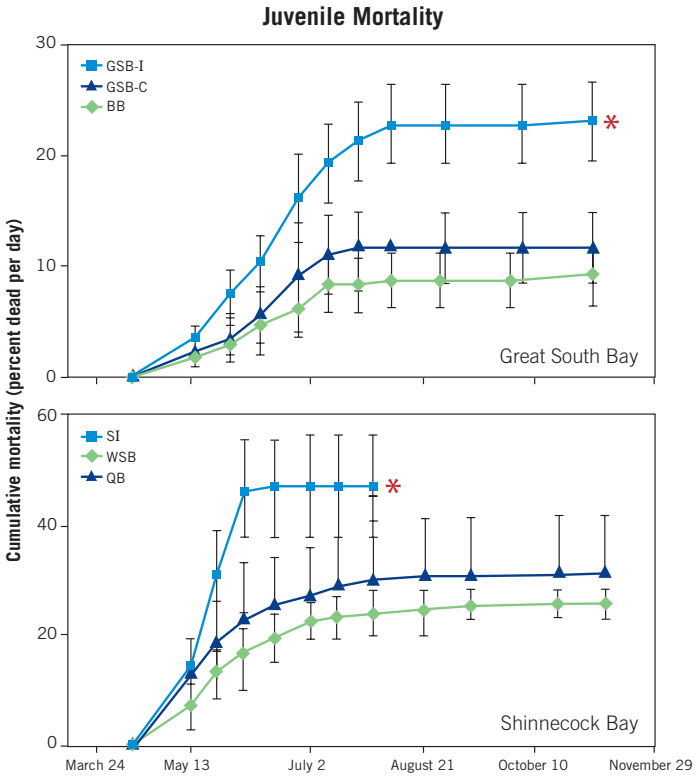

Figure 28. **Cumulative mortalities (mean ± SD) of juvenile hard clams in southern Long Island bays in 2005 (modified from Weiss et al. 2007).**

Note significantly higher mortalities, indicated by the asterisk, at inlet locations (GSB-I and SI) within each bay; site abbreviations as in Fig. 25.

Both studies thus indicate that SB may provide more favorable conditions at present for hard clams than GSB.

Seasonal environmental parameters were also measured by Weiss et al. (2007) in GSB and SB in 2004 and 2005. Peak temperatures occurred during the summer, coinciding with the months of highest Chl *a*. Optimum growth occurred at 20 to 24ºC, and declined above and below this range, as previously reported for *M. mercenaria* (reviewed by Grizzle et al. 2001). Growth was positively correlated with temperatures below 24ºC, but negatively correlated with temperatures exceeding 24ºC. Temperature had the most significant effect on growth of all individual parameters measured. The condition index of adult clams was positively correlated with total Chl *a* as well as with total diatom density.

Multivariate analysis showed that growth of juvenile clams was positively and significantly correlated with the > 5 µm Chl *a* size fraction (but not with total Chl *a*), and with the density of centric diatoms, whereas, a significant negative correlation was observed with the density of dinoflagellates. This supports previous results of Greenfield et al. (2005) that associated lower hard clam juvenile growth rates in West Sayville, GSB during a non-BT year (1999) with a greater dominance of pennate diatoms (especially *Nitzschia closterium*) relative to centric diatoms, and greater contribution of the < 5 size fraction compared to Oyster Bay, on the north shore of Long Island.

5. Copepod-hard clam grazing interactions

Recent studies indicate that suspension-feeding bivalves can consume zooplankton as well as phytoplankton as part of their diet (e.g. Wong et al. 2003). Mesocosm studies also showed an inverse relationship between the abundance of hard clams introduced in the system and that of copepod nauplii, copepodites and adults (Lonsdale et al. 2007). This inverse relationship, however, could result from direct consumption of zooplankton eggs and early life history stages by hard clams, and/or competition for the food supply. Copepods and their life history stages are often the dominant component of the mesozooplankton in Long Island estuaries (as illustrated in Fig. 24B for GSB). Therefore, laboratory experi-

ments were conducted as part of the HCRI to investigate the potential of hard clams to graze on early life history stages of the copepod *Acartia tonsa*, the dominant copepod in GSB during the summer (Lonsdale et al. 1996).

Preliminary analyses indicate that *M. mercenaria* (22-35 mm in SL) were able to remove both eggs (~ 70 µm in diameter) and nauplii (100-140 µm) of *Acartia tonsa* when each was offered in a mixed suspension with the alga *Rhodomonas salina* (6x12 µm) (Marzec 2003). Nauplii were cleared at a lower rate than algae offered in the mixed suspension. Clearance rates of copepod eggs were greater than those of nauplii, although these rates were not directly comparable as they were obtained from separate experiments. This difference may result from swimming avoidance of nauplii leading to reduced entrainment in clam feeding currents. It may also reflect the fact that although equal numbers of eggs or nauplii were added, the latter are larger and contribute a higher biomass, and hard clam CR is typically inversely related to biomass concentration of suspended particulates. Selective rejection of copepod eggs and nauplii in clam pseudofeces was not quantified in this study, although qualitative observations indicated that only *R. salina* (but no copepod eggs or nauplii) were found in pseudofeces. No eggs or nauplii were found in feces suggesting that those ingested were digested following gut passage. **Thus it is possible that hard clams benefit nutritionally from consumption of copepod eggs that are high in lipid and protein content, although this was not tested.**

Conclusions. Results of this study and calculations of the turnover time of bay water by clams during peak abundance and at present densities (Kassner 1993, Bricelj et al. 2001), suggest that the sharp decline of hard clams in GSB in past decades may have released zooplankton, such as early copepod life history stages, from benthic grazing pressure. The significance of these laboratory results in nature remains to be determined as, contrary to predictions, no impact on copepod eggs and early life history stages was found following addition of adult clams to experimental tanks by Cerrato et al. (sec. 4.2).

6. Potential impacts of climate change on clam populations

Climate change may lead to changes in temperature and salinity, but may also have more subtle effects on the food supply via changes in the timing of the phytoplankton blooms and changes in phytoplankton species composition. Temperature changes were assessed by Weiss et al. (2007) to predict the **effects of climate change on clam growth. They predicted that effects of warming would be site-specific within SSE. Sites near inlets would likely benefit from climatic warming, whereas sites furthest from inlets, where peak summer temperatures are highest, and could exceed the 24ºC threshold for maximum clam growth, would likely lead to detrimental effects on growth.** Weiss et al. (2007) also suggested that higher winter temperatures resulting from overall warming of these bays may benefit clam populations by reducing winter/spring mortalities. Temperatures that fluctuate or remain around a threshold that induces a prolonged period of low clearance rates insufficient to meet metabolic demands (e.g. around 7ºC), may, however, be more detrimental than lower temperatures that induce complete valve closure (Bricelj et al. 2007) leading to uncertainties in predicting the impacts of long-term warming on these mortalities. Effects of climate change on mortalities of juvenile clams during and following overwintering stress need to be investigated further via empirical studies and model simulations.

Potential effects of climate change were also examined via modeling simulations by Grizzle et al. (2003 and unpubl. results) as part of the HCRI. Simulations involved: a) changes in the temperature regime, e.g. overall warming from the present regime in GSB to that experienced in North Inlet, South Carolina waters, and b) changes in the timing of the main spring and fall phytoplankton blooms, as these were most likely to influence clam growth. When bloom times were held constant, long-term warming resulted in increased growth and the predicted rates matched published values for clams from each area from which water temperature data were used. **Model simulations revealed that clam population abundance in terms of biomass or numbers (Fig. 29) was extremely sensitive to changes in the timing of phytoplankton blooms. This suggests that year-**

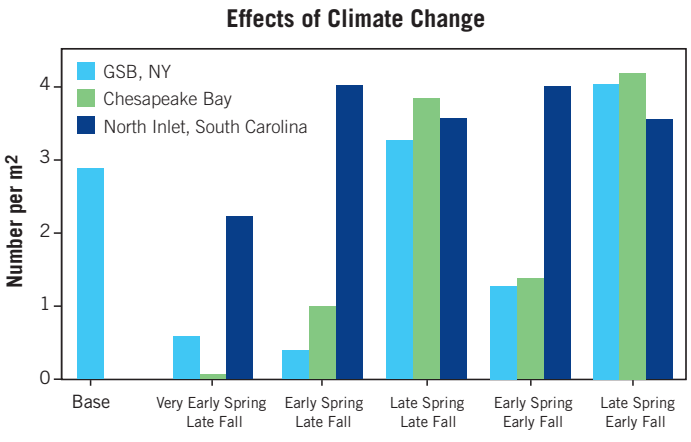

Figure 29. Model simulations on the effects of seasonal climate change on hard clam populations (Grizzle et al. unpubl.).

Variable scenarios for the timing of the spring and fall phytoplankton blooms are tested in three temperature regimes: baseline conditions for GSB, NY, an intermediate temperature regime (Chesapeake Bay) and a higher temperature regime (North Inlet, SC).

to-year variations in the timing of blooms may be more important than overall long-term temperature trends. Earlier occurrence of the spring phytoplankton bloom, irrespective of the timing of the fall bloom, caused the most severe reduction in clam growth relative to present conditions in GSB. Conditions of a late spring and early fall phytoplankton bloom resulted in greatest growth enhancement relative to current average conditions modeled for GSB (Fig. 29, Grizzle unpublished data).

7. Effects of environmental variables on hard clam larvae: larval model simulations

A biochemically-based larval model was developed for *Mercenaria mercenaria* as part of the HCRI and expanded via ECOHAB-supported research to test the effects of environmental variables, primarily temperature, food quality and quantity, and brown tide, on larval recruitment (Hofmann et al. 2006a). This model was adapted from a larval model developed for the Pacific oyster *Crassostrea gigas* (Bochenek et al. 2001). It is important to note, however, that much less information is available on biochemical changes during early development in hard clams than in oysters.

An important characteristic of the model is that it is bio-

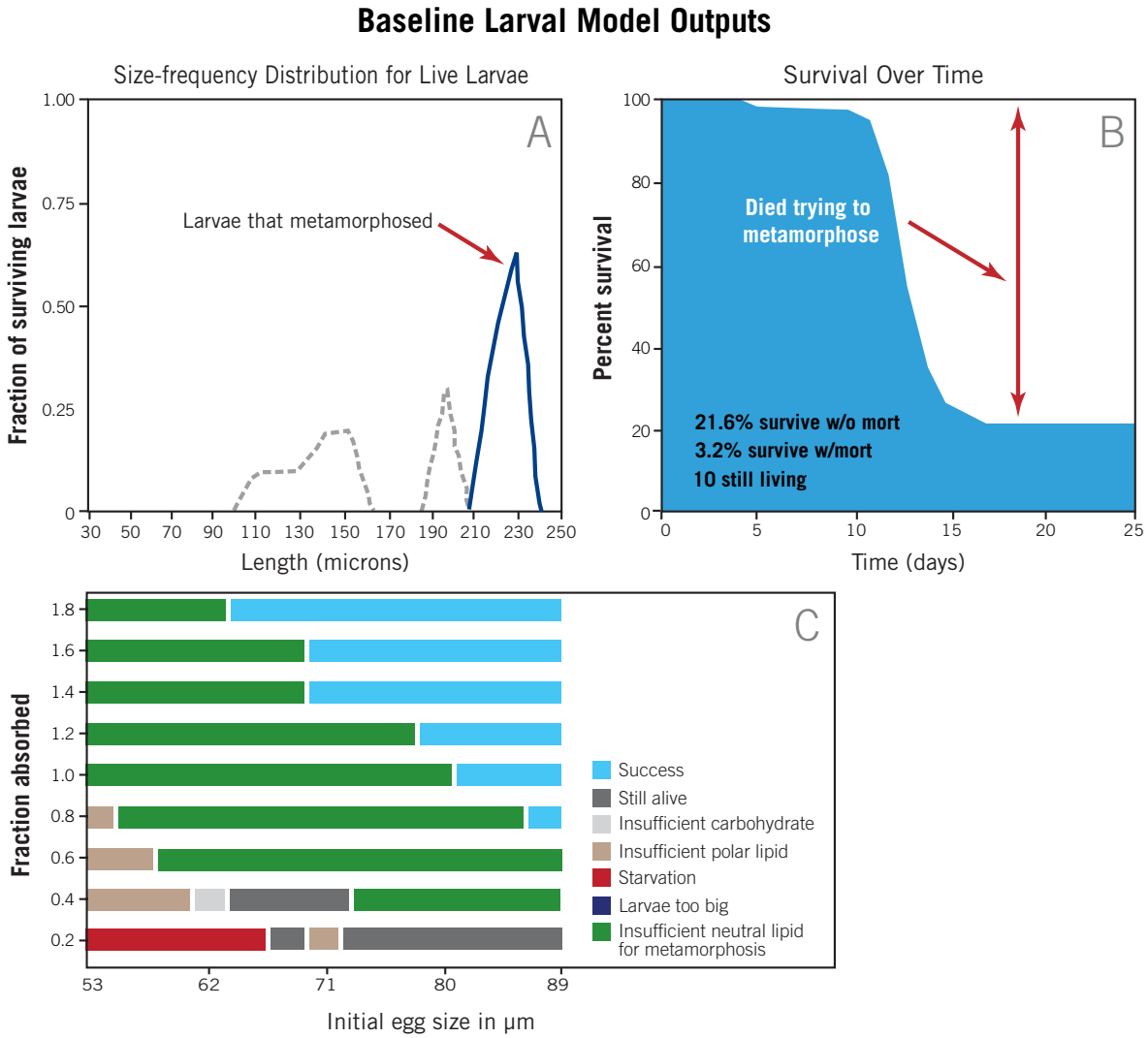

Figure 30. Outputs of the hard clam larval model for baseline or reference conditions: temperature = 18ºC, food = 1 mg dry weight (DW) L^{-1}; food biochemical composition as a proportion of organic weight = 0.38 protein, 0.078 polar lipid, 0.052 neutral lipid, 0.48 carbohydrate (Hofmann et al. unpubl.).

A: Larval size-frequency distribution: solid line indicates the distribution of larvae that successfully metamorphosed, and dashed line that of live larvae that have not metamorphosed; B: percent survival without and with added external mortality factor, e.g. predation; C: relationship between larval absorption efficiency and egg size, with explanatory end codes indicating the causes of metamorphic success or failure.

chemically-based, thus allowing a test of the effects of food quality or biochemical composition (proportion of protein, carbohydrate, neutral lipids and structural or polar lipid) and also allowing assessment of the causes/mechanisms of development success or failure. It also allows for genetic variability among individuals, introduced via variation in initial egg size and absorption efficiency. Brown tide was incorporated into this model via density- and toxicity-dependent inhibition of larval filtration rate, based upon experimental results of Bricelj et al. (2007). Outputs of the model include: a) size-frequency distributions of live larvae, b) survivorship over development time resulting from both intrinsic mortality factors (e.g. loss of lipid reserves) and externally applied mortality (e.g. predation), and c) plots of absorption efficiency as a function of egg size that provide a spectrum of possible larval outcomes, from successful metamorphosis to metamorphic failure. These diagnostics are illustrated in Fig. 30 for baseline or average GSB conditions.

A key outcome of larval model simulations was that variation in food quality (i.e. biochemical composition) had much greater effects on larval metamorphic success than changes in temperature and food quantity (Hofmann et al. 2006b and unpubl. results). Bivalve larvae are highly dependent on lipid reserves (neutral lipids) to support metamorphosis. Therefore, model simulations were conducted to investigate the effect of varying lipid content of the food supply (Fig. 31). A marked reduction (e.g. 50%) in the total lipid content relative to reference conditions caused a marked reduction in survival to metamorphosis, down to 1%. Additionally, a much greater fraction of the larvae failed to complete metamorphosis due to the accumulation of insufficient lipid reserves from the diet. Only a very narrow spectrum of larvae originating from very large eggs or with genotypes characterized by very high absorption efficiency were able to complete metamorphosis. In contrast, much less pronounced effects were observed when the temperature was increased by 2ºC (from 18 to 20ºC) and total food quantity was reduced by 50% from baseline levels (from 1 to 0.5 mg dry weight L^{-1} (Fig. 32). Survival to metamorphosis under these conditions of increased temperature and reduced food quantity remained relatively high, at 43%.

Conclusions. These results suggest that changes in available food quality experienced in GSB may be a contributing factor to low recruitment of hard clam larvae. Long-term data on recruitment of hard clam larvae in GSB are not available to test this hypothesis, and are notori-

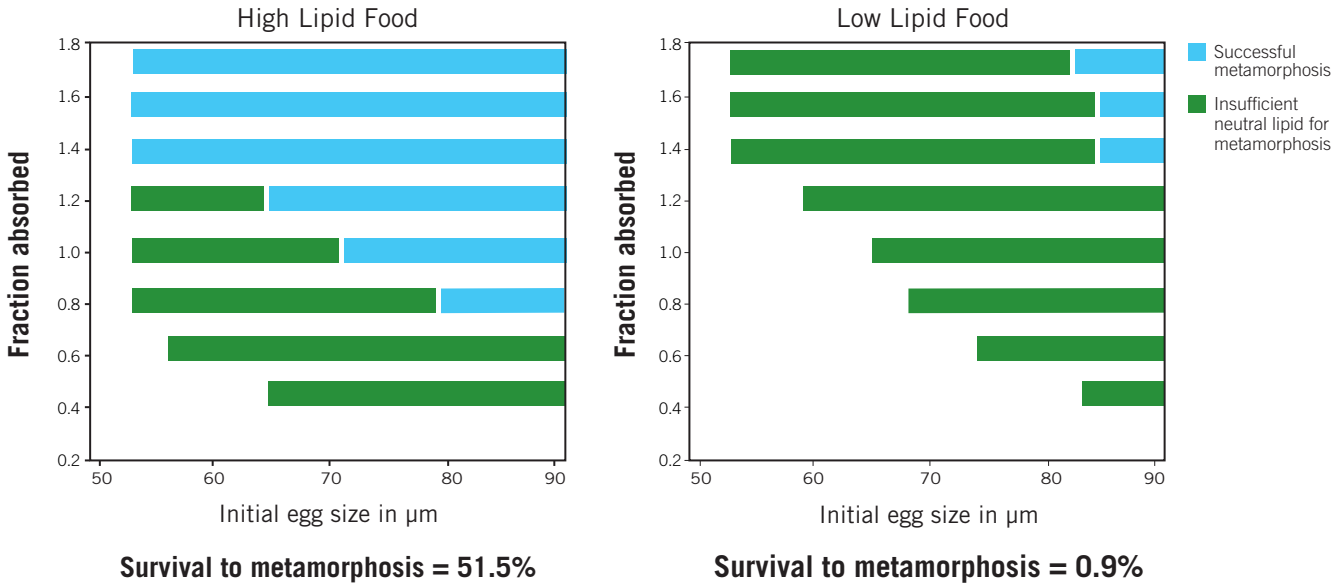

Figure 31. Plots of larval absorption efficiency vs. egg size obtained from larval model simulations for a high quality diet (high lipid) vs. a low quality diet (low lipid) (Hofmann et al. unpubl.).

High lipid food composition: 0.337 protein: 0.104 polar lipid: 0.069 neutral lipid: 0.48 carbohydrate; low lipid food composition = 0.446 protein: 0.039 polar lipid: 0.025 neutral lipid: 0.48 carbohydrate (numbers indicate the proportion of total organic matter). Note the reduction in the spectrum of conditions that lead to successful larval metamorphosis as indicated by the blue horizontal bars (see text). Percent survival to metamorphosis without additional, external mortality is indicated below each plot.

ously difficult to generate. Known reductions in density of hard clam broodstock may also be a factor leading to poor fertilization success in species that broadcast their gametes. Finally, low fecundities of individual clams, as described in GSB during 2001 (Newell et al. 2009), may also influence larval abundance. Predatory mortalities during postlarval and juvenile stages, before a size refuge is attained, are generally considered the single most important factor controlling bivalve recruitment success, as bivalves produce large numbers of gametes. The synergistic effects of poor-quality food, reduction in broodstock density below a threshold level that impinges on fertilization success, and reduced individual fecundities and/or gamete quality could, however, play a role in the slow recovery of hard clam stocks. Model simulations could provide useful information in this context.

8. Effects of brown tide on hard clams

8.1. Background. Brown tides caused by *Aureococcus anophagefferens* (Pelagophyceae) typically occur in shallow estuaries with long residence times and high salinities (> 25) (Gobler et al. 2005). Since their first appearance in Narragansett Bay, Rhode Island, brown tides have extended southward to other estuaries, including Barnegat Bay, NJ, Delaware bays (Little Assawoman Bay), and Maryland and Virginia bays (Chincoteague Bay). Brown tide has no known human health effects, or known direct effects on finfish, but severely affects suspension-feeding bivalves, including mussels, bay scallops and hard clams, as well as several components of the zooplankton (reviewed by Bricelj and Lonsdale 1997). Brown tide also negatively affects eelgrass beds, *Zostera marina*, via its effects on light attenuation. A review of the factors that promote brown tides is outside the scope of this report, as it was not the subject of the HCRI and has been extensively studied elsewhere (reviewed by Gobler et al. 2005). In general, blooms are favored by a low light regime, a nutrient environment with high dissolved organic matter (DOM), low dissolved inorganic nitrogen (DIN), with dominance of the dissolved N pool by reduced forms (ammonium, urea, amino acids, DON), elevated dissolved organic carbon (DOC):DON ratios and reduced DON:dissolved organic phosphorus (DOP) ratios. Bloom proliferation is also promoted by the lack of grazing top-down control.

8.2. Effects of brown tide on hard clam juveniles and adults. Brown tide (BT), caused by *Aureococcus anophagefferens,* is known to cause severe, density-

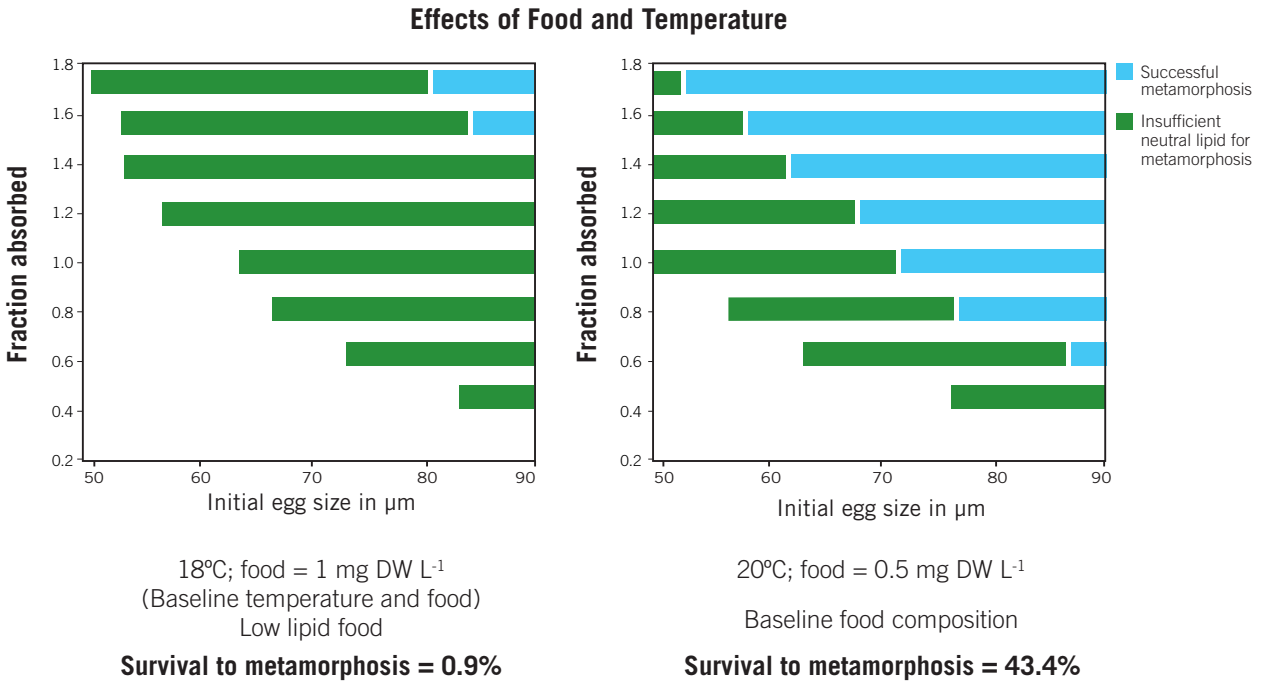

Figure 32. Plots of larval absorption efficiency vs. egg size obtained from larval model simulations for baseline temperature and food levels compared to a lower food quality diet as reflected in lower lipid content (left panel), relative to a higher temperature and lower food level but baseline food biochemical composition (right panel) (Hofmann et al. unpubl.).

Note that the effect of food quality has much more pronounced effects on metamorphic success than a change in temperature or food concentration (compare with baseline conditions in Fig. 30C).

dependent inhibition of growth in juvenile hard clams. This was shown in field studies under conditions of natural BT in Maryland waters (Wazniak and Glibert 2004), and in the laboratory using toxic and non-toxic strains of *A. anophagefferens* (Fig. 33) (Bricelj et al. 2004). Growth of juveniles ~ 7 mm in initial SL was completely suppressed at ≥ 400,000 cells mL^{-1} of a toxic *A. anophagefferens* isolate and led to tissue weight loss comparable to that of non-fed controls. Addition of non-toxic cells of the control alga *Isochrysis galbana* to BT at 400,000 cells mL^{-1} did not mitigate the negative effects of BT on growth. A non-toxic *A. anophagefferens* strain, however, supported relatively good growth of juveniles, only 18% less than that of clams fed *I. galbana* at volume equivalent concentrations (Fig. 33). This small reduction could be attributed to the lower retention efficiency of this picoplanktonic alga (2 µm). **These results clearly indicated that *A. anophagefferens* was toxic rather than nutritionally inadequate for juvenile clams.**

The mechanism of action of toxic BT is via inhibition of the beat of lateral cilia, involved in the generation of feeding currents in juvenile and adult bivalves, as determined from *in vitro* studies using excised gills (Gainey and Shumway 1991). Ciliary inhibition required contact with toxic cells (was not induced by algal filtrates) and was attributed to a dopamine-mimetic effect, i.e. an effect similar to that of the neurotransmitter dopamine but that differed in the time frame of induced response. Inhibition of feeding (clearance rate of particles from the suspension) by toxic *A. anophagefferens* was demonstrated *in vivo* in juvenile clams, and occurred when BT surpassed a concentration of ~35,000 cells mL^{-1} (Fig. 34; Bricelj et al. 2001) and was also demonstrated during a natural BT in adult hard clams (Tracey 1988). Demonstration that a threshold concentration of *A. anophagefferens* needs to be exceeded before feeding is inhibited explains the fact that the addition of adult clams in mesocosm experiments could curtail the development of BT (Cerrato et al. 2004). Calculations made in this study and by Bricelj et al. (2001) indicated that the grazing pressure exerted by hard clam populations in GSB during peak abundance in the 1970s would be sufficient to prevent brown tide development.

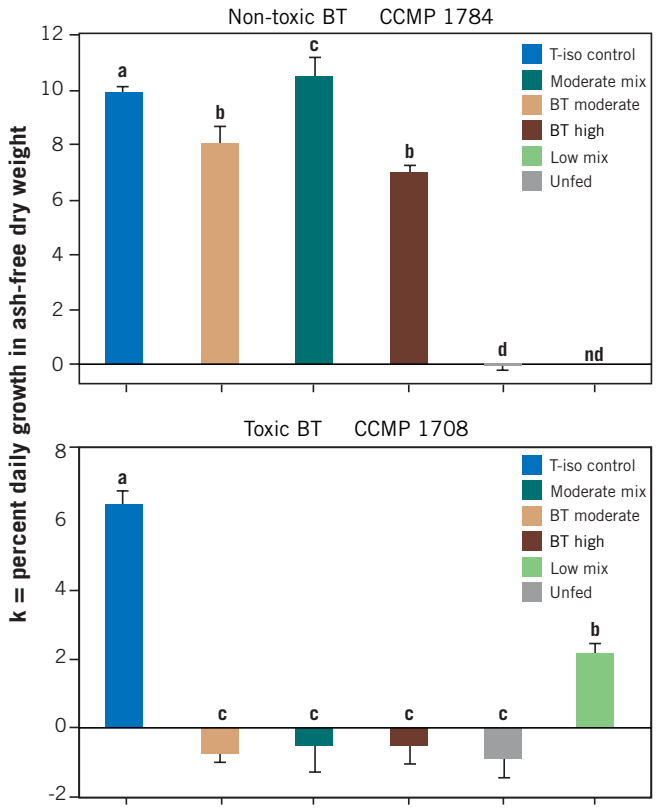

Figure 33. **Effects of *Aureococcus anophagefferens* on growth of juvenile hard clams (modified from Bricelj et al. 2004, work funded outside the HCRI).**

Growth measured by the instantaneous growth coefficient (k, percent change in total organic or ash-free dry weight per day, mean ± SE) of clams (7.4 mm initial shell length) exposed for two wks to various experimental diets. Diets: *Isochrysis galbana* (clone T-iso) control at 60,000 cells mL^{-1}, unialgal diets of moderate and high brown tide (BT) at 400,000 cells mL^{-1} and 1,000,000 cells mL^{-1} respectively, and two mixed suspensions, moderate mix and low mix, containing 60,000 *I. galbana* plus either 400,000 or 80,000 *A. anophagefferens* cells mL^{-1}. Upper graph shows results using a non-toxic *A. anophagefferens* strain, and lower one using a toxic strain, as verified by the mussel feeding bioassay. Different letters indicate statistically significant differences.

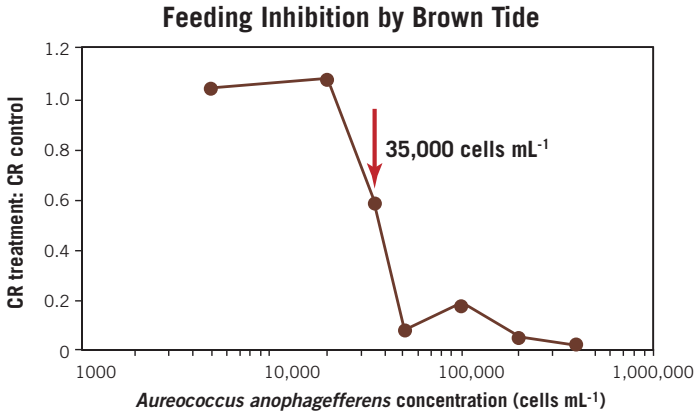

Figure 34. **Effects of toxic *Aureococcus anophagefferens* (strain CCMP 1708) on short-term feeding rates of juvenile hard clams *Mercenaria mercenaria* 10 mm in shell length (data from Bricelj et al. 2001; work funded outside the HCRI).**

The arrow indicates the approximate threshold concentration of *A. anophagefferens* above which significant feeding inhibition occurs. [Feeding rates expressed as the ratio of clearance rate (CR, volume cleared of particles per unit time) of clams exposed to a suspension of 60,000 cells mL^{-1} of non-toxic *Isochrysis galbana* (clone T-Iso, control) spiked with increasing concentrations of *A. anophagefferens*, relative to CR on a suspension containing only *I. galbana* at 60,000 cells mL^{-1}].

Whereas Bricelj et al. (2004) found that 7 mm juveniles experienced no mortalities after 3 wks of exposure to BT, Greenfield and Lonsdale (2002) found that smaller (~ 2 mm) juveniles suffered high mortalities at comparable cell densities and durations of exposure during a naturally occurring brown tide in GSB (Fig. 35). This led to the suggestion that the effects of BT on juveniles were highly size-specific. A pre-recruit mortality function, based on the Greenfield and Lonsdale (2002) data was incorporated in the hard clam population model as an externally forcing function. Model simulations indicated that the combined effects of overfishing and brown tide induced-juvenile mortality caused a marked decline in stocks relative to the effects of overfishing alone (not shown).

Indeed, simulations conducted using the hard clam model as part of the HCRI showed that **the reduction in scope for growth induced by brown tide was inversely related to clam size between 18 and 87 mm (Fig. 36).** This finding may explain why Laetz (2002) found no measurable effects of BT on shell growth of adult hard clams (30 to 50 mm in shell height) planted in GSB during a year when *A. anophagefferens* attained $1x10^6$ cells mL^{-1}. Using shell sectioning, this author also found that archived shells of adults (40 to 50 mm height) showed comparable growth rates between BT and pre-BT years. Brown tide causes starvation of both juvenile and adult clams. Small individuals, however, have a higher metabolic rate per unit tissue mass than large ones and are therefore expected to suffer a greater percent weight loss per unit time, and to be more vulnerable to starvation than adults. **Adverse effects of BT on growth are thus more likely to be observed in smaller, juvenile clams, or reflected in lower condition index or fecundities of adults rather than in their shell growth. Potential long-term changes in larval and juvenile growth rates in SSE need to be evaluated, as these are the most sensitive to BT and non-BT changes in the food supply.**

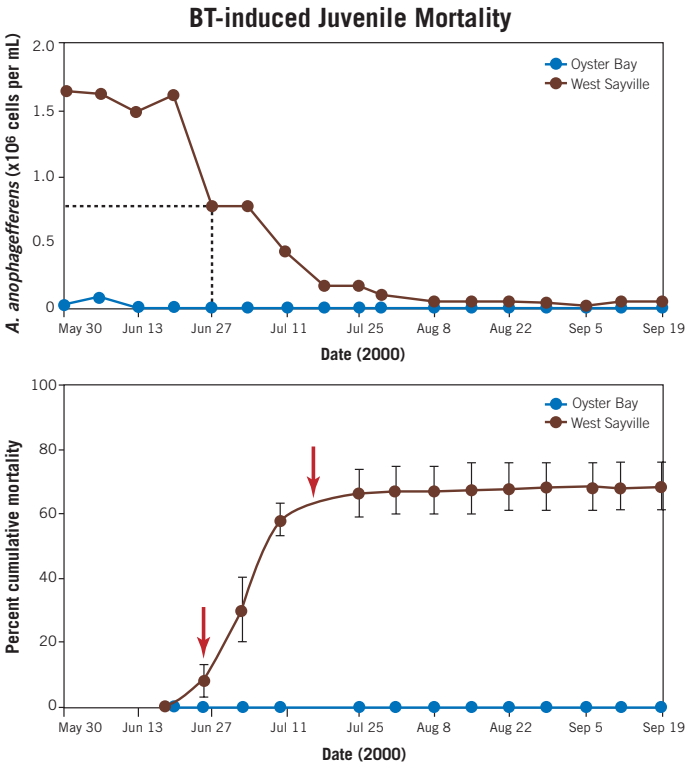

Figure 35. Cumulative mortalities of juvenile hard clams (2.2 mm initial shell length) (lower graph) exposed with predator protection to naturally occurring brown tide in GSB, compared to those in Oyster Bay, on the north shore of Long Island, where BT does not occur. The corresponding seasonal concentrations of *A. anophagefferens* are shown in the upper graph (from Greenfield & Lonsdale 2002; work funded outside the HCRI).

8.3 Effects of brown tide on hard clam larvae. Brown tide in Great South Bay, NY, typically occurs during mid-summer. Peak abundance of *A. anophagefferens* in June-July generally coincides with the main period of spawning and thus larval development of hard clams in GSB, as determined during pre-BT years by Kassner and Malouf (1982; Fig. 37). A secondary, lower peak of *A. anophagefferens* can occur in the fall. Newell et al. (2009) found that the timing of hard clam spawning has not changed in recent, post-BT years (sec. 3.1). Brown tide typically lasts one to two months in mid-summer (Fig. 37) and the duration of hard clam larval development can range from 10 to 23 days at GSB summer temperatures (cited in Przeslawski et al. 2008). This overlap between the timing of BT and the typical period of hard clam spawning and thus larval occurrence in the water column (Figs. 16 and 37) first suggested that hard clam larval recruitment might be significantly affected during BT years. Additionally, hard clam larvae, unlike juveniles and adults, can efficiently capture picoplanktonic cells (Gallager et al. 1994) and can therefore be expected to be directly affected by consumed BT cells.

8.3.1. Effects of brown tide on larval growth and survival. Laboratory experiments to determine the effects of *A. anophagefferens* on growth and survival of *M. mercenaria* larvae were conducted by Padilla et al. (2006) as part of the HCRI, and by Bricelj and MacQuarrie (2007) via ECOHAB-funded research. The former study was conducted under the following conditions: larvae were obtained by spawning broodstock collected from GSB and SB, and were reared at very low densities of 0.1 larvae mL^{-1} representative of those found in the field, in 1 L beakers, using cultured *A. anophagefferens* isolate CCMP 1708 (putatively toxic although toxicity was not confirmed via independent bioassays prior to larval experiments). Additional differences in methods employed in experiments conducted by Bricelj and MacQuarrie (2007) are as follows: Padilla et al. reared larvae in the presence of an antibiotic mix (penicillin, streptomycin and neomycin)

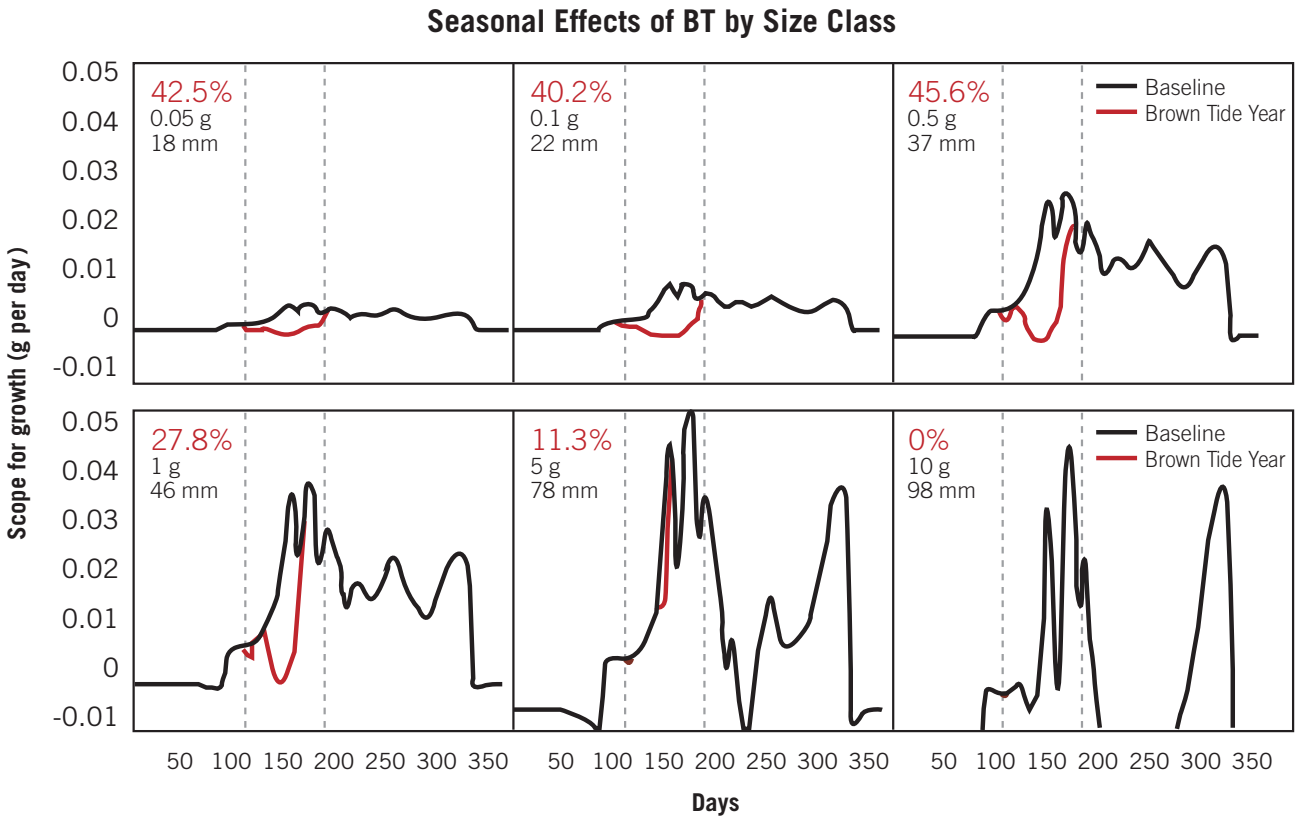

Figure 36. **Size-specific effects of brown tide, BT (peak concentration = 1x10^6 cells mL^{-1} on June 1; 2 month-bloom duration) on seasonal scope for growth (SFG) of clams of different sizes (soft tissue dry weight and shell length indicated in upper, left corner of each panel) (Bricelj et al. unpubl.). The red line shows the reduction in SFG during a BT-year, and the percent reduction relative to baseline conditions is indicated in the upper, left corner of each panel. Vertical dashed lines mark the period of BT.**

to remove bacteria, and high-speed centrifuged their *A. anophagefferens* cultures and resuspended cells in filtered seawater prior to delivery to remove the culture medium. This was done because a preliminary experiment showed that although the addition of *A. anophagefferens* culture medium had no effect on larval growth, it significantly reduced larval survival (by ~9 to 11%) relative to controls with medium removed. Useful information can be obtained by comparing results of these studies which used different experimental approaches and conditions.

An initial trial was also run by Padilla et al. (2006) to determine the effects of antibiotic addition. Although antibiotic treatment had no effect on survival or the percent of larvae that metamorphosed by the end of the experiment, it significantly accelerated the rate of larval development (Fig. 38). Thus, for any given diet, a greater percentage of larvae attained competence (pediveliger stage) in the presence of antibiotics by day 10 (contrast A and B in Fig. 38). Additionally, metamorphosed larvae at the end of the experiment in the mixed diet were significantly larger in antibiotic-treated cultures. Pernet et al. (2006) found that treatment with a different antibiotic

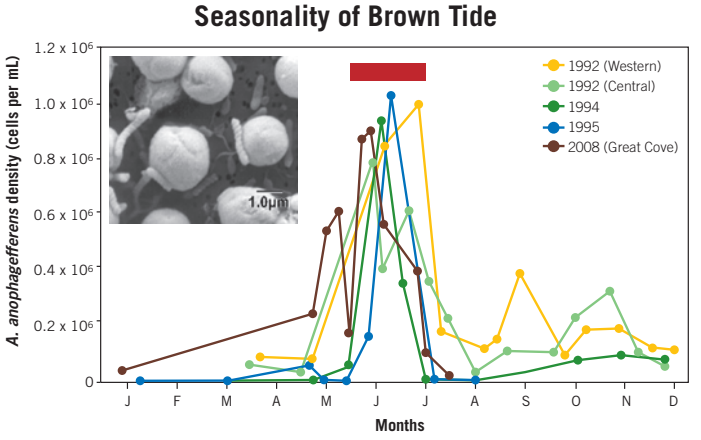

Figure 37. **Seasonal occurrence of *Aureococcus anophagefferens* (brown tide) in GSB, NY, during representative bloom years in the early 1990s, and during recent re-occurrence of brown tide (BT) in 2008 (see text).**

The red horizontal bar marks the timing of major spawning of hard clams in pre-BT yrs (from Kassner & Malouf 1982); note that this has not changed in post-BT years (Newell et al. 2009). The inset shows a scanning electron micrograph of non-axenic *A. anophagefferens* cultures (note bacterial rods) (from Bricelj et al. 2001).

(chloramphenicol) had a significant effect on the rate of development and levels of lipid reserves of sea scallop larvae. Larvae reared with antibiotics showed reduced survival relative to controls with no antibiotic, but reached competence to metamorphose (pediveliger stage) earlier and remained in the plankton showing delayed settlement while continuing to build lipid reserves. Therefore some caution must be exercised in interpreting results obtained with antibiotics. Relative comparisons between diets should remain valid, however, since all subsequent experiments described in Padilla et al. (2006) were compared to controls also cultured with antibiotics.

Padilla et al. (2006) found that a unialgal diet of exponentially growing *A. anophagefferens* at a moderate density (160,000 cells mL^{-1}) had no effect on survival or growth of hard clam larvae relative to *Isochrysis galbana* at an equivalent volume concentration, and all larvae metamorphosed by the end of the experiment (Fig. 38A). A subsequent experiment, however, showed a significant, negative effect of exponentially growing *A. anophagefferens* on larval growth at the same exposure concentration (Przeslawski et al. 2008) (Table 3). Discrepancies between the results of these two studies remain unresolved, although they were run at different temperatures and different larval cohorts may vary in susceptibility to BT. *A. anophagefferens* cultures in stationary phase or slow-growing cultures at 160,000 cells mL^{-1} significantly reduced larval growth rate and increased development time (Padilla et al. 2006, Table 3), such that all larvae remained in the veliger stage at the end of the experiment (23 days). Similarly, late stationary cultures of a toxic strain of *A. anophagefferens* resulted in a greater inhibition of feeding (clearance) of mussels than cultures in mid-exponential phase tested concurrently (Bricelj and MacQuarrie 2007), although both had strong negative effects at bloom levels. **These results suggest that the growth stage of *A. anophagefferens* can influence its toxicity to hard clam larvae.**

Padilla et al. (2006) found that a bloom concentration of exponentially-growing *A. anophagefferens* (10^6 cells mL^{-1}), significantly reduced growth of hard clam larvae but had no negative effect on survival (Fig. 39). Larvae exposed to bloom BT levels reached a significantly smaller size (241 µm SL) than that attained by larvae fed *I. galbana* at the same biovolume concentration at the end of 20 days (297 µm). BT also slowed down development as a greater proportion of larvae remained in the veliger stage than in the *I. galbana* bloom treatment at 20 days (Fig. 39, Table 3).

Larval experiments conducted by Bricelj and MacQuarrie (2007) used the same toxic *A. anophagefferens* isolate

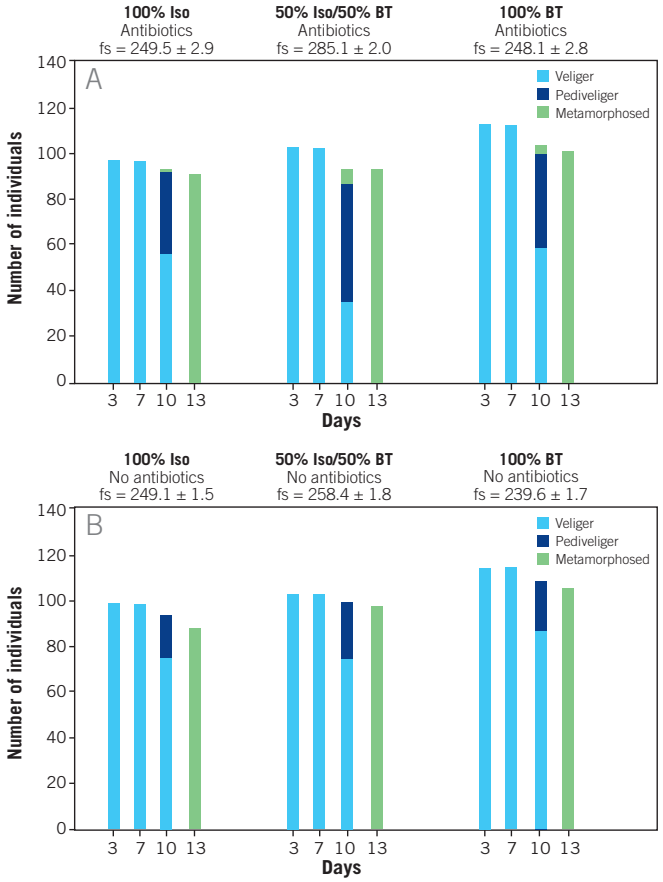

Figure 38. Effects of moderate concentrations of *Aureococcus anophagefferens* (brown tide, BT, clone CCMP 1708) in unialgal and mixed suspensions with *Isochrysis galbana* (clone T-Iso) relative to a unialgal control diet of *I. galbana* at 26ºC (from Padilla et al. 2006).

All diets offered in equal cell volume concentrations: 20,000 *I. galbana* cells mL^{-1}, 80,000 BT cells mL^{-1} + 10,000 *I. galbana* (clone T-Iso) cells mL^{-1}, and 160,000 BT cells mL^{-1}. The effects on larvae reared with (A) and without (B) antibiotics are compared. Days indicate days post-fertilization. Final shell lengths (fs, mean ± SE) are also indicated.

(CCMP 1708) as the above studies, but the toxicity/bioactivity of cultures was tested prior to each experiment using a bioassay based on the inhibitory effects of BT on feeding rates of juvenile mussels (Bricelj et al. 2001). Toxicity characterization using a standardized method is important to interpret discrepant experimental results and to characterize toxicity in the field, as harmful algae can experience marked changes in toxicity depending on culture conditions and over time in the laboratory, even when grown under identical culture conditions. For example, strain CCPM 1784 used as a non-toxic control in BT studies conducted in the early 1990s was highly toxic when first isolated in the mid-1980s (Bricelj et al. 2001). Bricelj and MacQuarrie (2007) used higher lar-

Diet (growth stage/density in cells mL^{-1})	Temperature	Effect on growth (percent change relative to control)	Effect on development time to metamorphosis	Source
Unialgal				
$^{a}BT_{exp}$/160,000	26ºC (Fig. 38A)	No effect	+	Padilla et al. 2006
$^{a}BT_{exp}$/160,000	22ºC (Fig. 43)	– (33%)	nr	Przeslawski et al. 2008
$^{a}BT_{slow\text{-}growing}$/160,000	22ºC	– (38%)	–	Padilla et al. 2006
$^{a}BT_{stat}$/160,000	22ºC	– (56%)	–	Padilla et al. 2006
$^{a}BT_{exp}$/1,000,000	22ºC (Fig. 39)	– (19%)	–	Padilla et al. 2006
$BT_{late\ exp}$/800,000	20ºC	– (90%)	–	Bricelj & MacQuarrie 2007
Mixed diets				
$^{a}BT_{exp}$/80,000 + Iso/10,000	26ºC (Fig. 38A)	+ (14%)	+	Padilla et al. 2006
$^{a}BT_{exp}$/80,000 + Iso/10,000	22ºC (Fig. 43)	– (21%)	nr	Przeslawski et al. 2008
BT_{exp}/80,000 + Iso/10,000	26ºC (Fig. 38B)	+ (4%)	+	Padilla et al. 2006
$BT_{late\ exp}$/100,000 + Iso/50,000	20ºC (Fig. 40)	– (63%)	–	Bricelj & MacQuarrie 2007
$BT_{late\ exp}$/200,000 + Iso/75,000	20ºC (Fig. 41)	– (60%)	–	Bricelj & MacQuarrie 2007
$BT_{late\ exp}$/400,000 + Iso/50,000	20ºC (Fig. 41)	– (79%)	–	Bricelj & MacQuarrie 2007

Table 3. Effects of brown tide (BT, *Aureococcus anophagefferens*) on shell growth and development time of hard clam larvae exposed to unialgal or mixed algal suspensions with *Isochrysis galbana* (see text for differences in experimental protocols among studies).

Effect on growth calculated as a percent of that obtained in the same experiment on a unialgal control diet of *I. galbana* at an ~ equivalent total cell volume concentration. Stage of growth of *A. anophagefferens* cultures = exponential (exp), stationary (stat) and late exponential/early stationary (late exp); algal concentrations are indicated for each diet and the superscript "a" indicates larvae reared with antibiotics. Statistically significant effects are indicated as positive (+) or negative (-); no effect = not statistically significant; nr = not reported. Negative effects on development time indicate longer development time to metamorphosis in treatment relative to control.

val stocking densities (2.5 larvae mL^{-1}), larger rearing containers (50 L) and no antibiotics. They determined growth and survival trajectories by measuring larvae every few days using real-time video-microscopy, but only assessed stage of larval development percentage of larvae in D-stage) at the end of the experiments (~15 days). Larvae were obtained from naïve broodstock that had not previously experienced BT. Algal stocks were dosed without prior removal of the culture medium as initial experiments demonstrated that the culture filtrate at the volumes added had no effect on larval growth or survival (Bricelj and MacQuarrie 2007).

Bricelj and MacQuarrie (2007) found that **toxic *A. anophagefferens* in late exponential-early stationary growth phase consistently and predictably inhibited shell growth of hard clam larvae in a dose- or concentration dependent manner (Figs. 40 and 41).** Larval growth was completely suppressed at *A. anophagefferens* concentrations ≥ 400,000 cells ml^{-1}, and at these high densities most of the larvae were arrested at D-stage of development by day 15 (see micrographs in Fig. 40). Effects of high *A. anophagefferens* densities were comparable

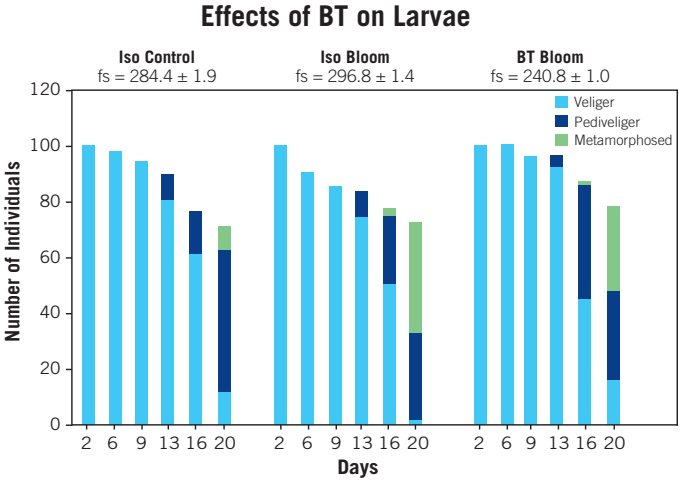

Figure 39. Effects of bloom levels of toxic *Aureococcus anophagefferens* (clone CCMP 1708 at 1x 10^{6} cells mL^{-1}) on survival, development rate and final size of hard clam larvae relative to those fed an equivalent volume concentration (125,000 cells mL^{-1}) of *Isochrysis galbana* (clone T-Iso) and a control diet of 20,000 *I. galbana* cells mL^{-1} (from Padilla et al. 2006).

All larvae were reared with antibiotics at 22ºC. Mean shell length (fs ± SE) at the end of 20 days post-fertilization is indicated for each treatment.

to those of starvation, as previously shown for juveniles. Experiments conducted by spiking a suspension containing an optimum cell density of *I. galbana* with increasing concentrations of *A. anophagefferens* indicated that the presence of a nutritious, non-toxic alga in a mixed suspension did not mitigate the adverse effects of *A. anophagefferens*, at least at high densities. Furthermore, even at a low density of 50,000 cells mL^{-1} *A. anophagefferens* caused significant (13%) growth inhibition of larvae. **Brown tide inhibits larval growth via reduction of larval feeding rates (clearance rates). Epifluorescence measurements of gut fullness showed that larvae exposed to bloom levels of *A. anophagefferens* had empty guts comparable to those of starved larvae, contrasting with full guts observed in controls fed *I. galbana*, thus confirming that larval feeding is compromised by BT (Bricelj and MacQuarrie, 2007).** Exposure of larvae to a constant algal biovolume but increasing proportions of *A. anophagefferens* in a mixed suspension with *I. galbana* also demonstrated that *A. anophagefferens* exerts toxic effects on hard clam larvae that cannot be attributed only to poor nutritional value of this alga (Fig. 41).

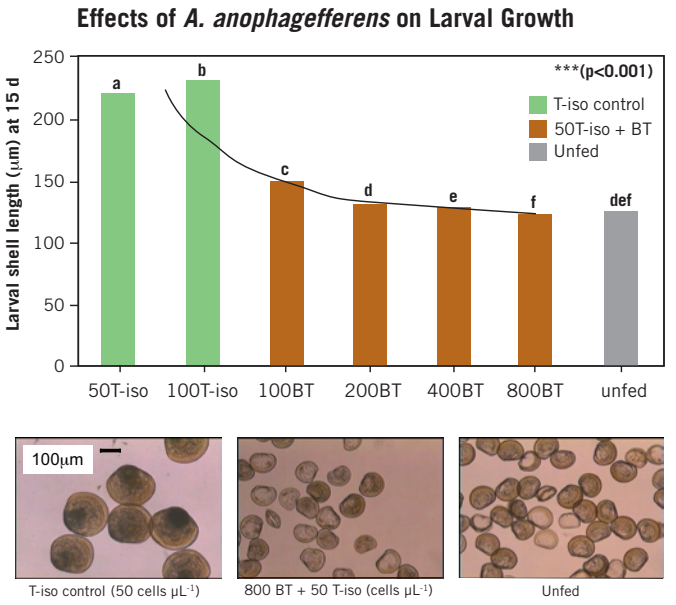

Figure 40. **Concentration-dependent effects of *A. anophagefferens* (brown tide) on growth of hard clam larvae exposed in the laboratory from first-feeding (D-stage at 24 h) to 15 d of development (at 20ºC). Video micrographs illustrate the differences in final size and stage of development of larvae from the 3 treatments (modified from Bricelj and MacQuarrie, 2007; ECOHAB-funded research). Algal concentrations from 50 to 800 are given in cells per µL (= 50,000 to 800,000 cells per mL).**

Larvae were fed a baseline diet of 50,000 *I. galbana* (clone T-iso, CCMP 1324) in cells mL^{-1}, spiked with increasing concentrations of *A. anophagefferens* (BT) from 100,000 to 800,000 cells mL^{-1}, compared to unfed controls and a control fed only clone T-iso at 50,000 cells mL^{-1}. The treatment at 100,000 *I. galbana* cells mL^{-1} was equivalent in total cell volume concentration to the mixed suspension at the highest density, and was used to rule out confounding inhibitory effects that might result from a high algal biomass rather than addition of toxic cells. Different letters indicate statistically significant differences.

In the above study by Bricelj and MacQuarrie (2007), adverse effects of BT on larval survival varied among experiments, and Padilla et al. (2006) found no adverse effects of BT on survival in trials that used antibiotics, suggesting that BT may negatively affect larval survival via indirect rather than direct effects. Survival rate may also be a function of initial larval condition, which can vary among cohorts. Thus reduced survival may result from secondary bacterial infection of compromised larvae. **Thus, a common finding from these studies is that brown tide negatively affects hard clam larvae primarily through its inhibitory effects on growth, which would lead to more prolonged exposure to predators in the water column and thus indirect mortalities.**

Table 3 provides a synthesis of the various experiments published to date on effects of BT on hard clam larvae. Although treatment effects are expressed relative to the control in each experiment, these trials are not strictly comparable given that they used different protocols, duration and conditions. They provide, however, an integrated snapshot of results that allow drawing of general patterns and conclusions. **Overall, toxic *A. anophagefferens* in late exponential-early stationary growth phase, or in stationary phase at densities ≥ 160,000 cells mL^{-1} resulted in delayed metamorphosis (longer development time).** Bricelj and MacQuarrie (2007) found that the percentage of D-stage larvae at the end of ~ 2 wks decreased with decreasing concentrations of *A. anophagefferens* in the diet. In contrast, exponentially growing *A. anophagefferens* only slowed down development (delayed metamorphosis) at bloom densities (1,000,000 cells mL^{-1}) (Padilla et al. 2006); lower densities (80,000 cells mL^{-1}) in a mixed diet with *I. galbana* elicited the opposite effect, i.e. accelerated metamorphosis (+ effect on development time in Table 3). These results again emphasize the importance of characterizing the growth stage and toxicity of BT cells, as this could vary over the course of a bloom.

There is increasing evidence indicating that individual hard clam larvae vary in their susceptibility to brown tide. For example, Bricelj and MacQuarrie (2007) found that 20% of the experimental larval population could recover following 2 wk-exposure to 400,000 *A. anophagefferens* cells mL^{-1} if they were subsequently fed a good food source of *I. galbana*. Potential genetic differences among larvae in their responses (growth and lipid accumulation) to BT were also suggested by Przeslawski

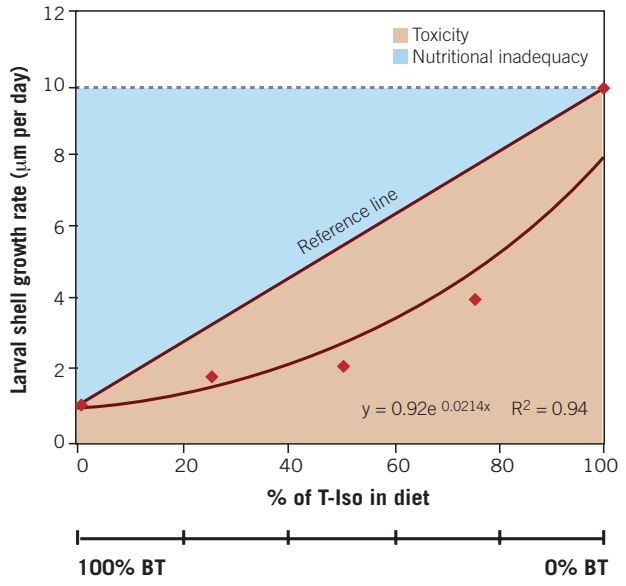

Figure 41. A test of brown tide (BT) toxicity: effects of variable proportions of *A. anophagefferens* (clone CCMP1708) in the diet on growth rates of hard clam larvae (from Bricelj and MacQuarrie, 2007; ECOHAB-funded research).

Note that in contrast to Fig. 38, the total volume concentration of algae remained constant among all experimental treatments. Values below the reference line indicate that *A. anophagefferens* is toxic rather than of poor nutritional value relative to *Isochrysis galbana* (clone T-iso, CCMP 1324). 100% BT and 100% T-Iso equal 800,000 *A. anophagefferens* and 100,000 *I. galbana* cells mL^{-1} respectively.

et al. (2008) (sec. 8.3.2). Larval model simulations (Bricelj et al. unpubl.) also show that BT has the potential to cause changes in the genotypic composition of hard clam larval populations. Thus, a narrower spectrum of larvae, those with higher absorption efficiency, and those derived from larger eggs with higher lipid stores, are predicted to survive exposure to brown tide (not shown). A genetic basis has been demonstrated for differences in susceptibility of softshell clams, *Mya arenaria,* to paralytic shellfish toxins produced by toxic dinoflagellates (Bricelj et al. 2005). **Thus selection for hard clams stocks resistant to brown tide might be possible if genetic adaptation to BT could be demonstrated.**

8.3.2. Effects of brown tide on lipid reserves of hard clam larvae. Neutral lipid reserves are essential to sustain bivalve larvae during metamorphosis, when larvae stop feeding and require lipid reserves to meet their metabolic demand (Gallager et al. 1986; Pernet et al. 2006). Hard clam larvae exposed to BT throughout development are not only significantly smaller, but also attain very low levels of lipid reserves (Figs. 42 and 43). Padilla et al. (2006) noted that larvae fed BT appeared to have lower levels of accumulated lipids than those fed the control diet (Fig. 42). Therefore they followed their initial observations with experiments to determine the size-adjusted neutral lipid accumulation in larvae fed BT using a neutral lipid-specific stain and fluorescence image analysis (Przeslawski et al. 2008). In this study, larvae fed a moderate cell density of *A. anophagefferens* (160,000 cells mL^{-1} in exponential growth phase) had a significantly reduced lipid index by the end of planktonic development than those fed *I. galbana* or a mixed diet of these two algae (Fig. 43). In agreement with these results, quantitative chemical analysis of lipid classes by thin layer chromatography over the course of development demonstrated conclusively that **larvae fed toxic *A. anophagefferens* at bloom levels (400,000 cells mL^{-1} in late exponential/early stationary phase) accumulated extremely low levels of neutral lipid reserves (triacylglycerols) relative to controls fed *I. galbana*** (Bricelj et al. 2008 and unpublished results).

Przeslawski et al. (2008) found that for larvae fed BT there was no apparent trade-off between growth and lipid accumulation. Larvae that grew the largest also had the highest amount of size-adjusted lipid stores, yet this relationship was not observed for larvae fed *I. galbana.* This indicates that some larvae exposed to BT were better able to perform than others. These differences could be attributable to genetic differences among larvae in susceptibility to BT or differences in initial maternal investment.

Bricelj et al. (2008 and unpubl. data) conducted experiments in which hard clam larvae were fed unialgal sus-

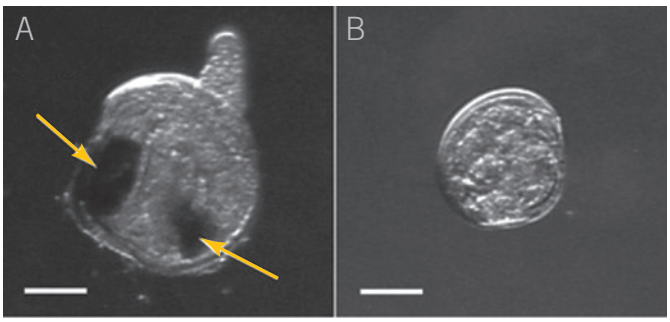

Figure 42. Micrographs of hard clam larvae stained with Nile Red following exposure to (A) a control diet of *Isochrysis galbana* (clone T-iso) at 125,000 cells mL^{-1}, and (B) toxic brown tide [1,000,000 *Aureococcus anophagefferens* (clone CCMP1708) cells mL^{-1}] (from Padilla et al. 2006).

All larvae were treated with antibiotics. Note the conspicuous lipid droplets in (A), absent in (B). Final larval sizes at the end of 20 days averaged 297 and 241 µm respectively. Scale bars = 100 µm.

pensions of clone T-iso, non-toxic *A. anophagefferens* (strain CCMP 1784) or toxic *A. anophagefferens* (strain CCMP 1708) at bloom levels (BT toxicity measured by the mussel feeding bioassay). **Non-toxic BT supported larval growth rates comparable to the *I. galbana* control throughout planktonic development (Bricelj et al. 2008). Yet larvae fed non-toxic BT accumulated low neutral lipid reserves, comparable to those of larvae fed toxic BT.** This reflects the fact that both toxic and non-toxic *A. anophagefferens* isolates are characterized by an extremely low neutral lipid content (Bricelj et al. unpublished data). **Thus larvae fed unialgal suspensions of non-toxic BT throughout development suffered higher mortalities during and immediately following metamorphosis than those fed *I. galbana*, even though they suffered no adverse effects on growth and survival during planktonic development.**

8.3.3. Larval model simulations. Model simulations were conducted to determine the effects of variable *A. anophagefferens* cell toxicity on hard clam larval growth (Bricelj et al. unpublished data). They showed that the effects of BT in the presence of alternate food on larval growth are extremely sensitive to cell toxicity at low *A. anophagefferens* concentrations; the effect of varying cell toxicity becomes less important at high densities (not shown). Simulations were also undertaken to compare the susceptibility of larvae to early (first week of development) vs. late (day 8 onwards) exposure to BT. These demonstrated that late exposure to brown tide in the presence of alternate food, during the period approaching competence, was much more detrimental to the larvae than early exposure, as reflected in reduced survival to metamorphosis, from 71 to 48% (Fig. 44). Late exposure to moderate BT levels was also found to lead to metamorphosis at smaller sizes.

Conclusions. Overall, the above laboratory studies suggest that hard clam larvae are likely to experience se-

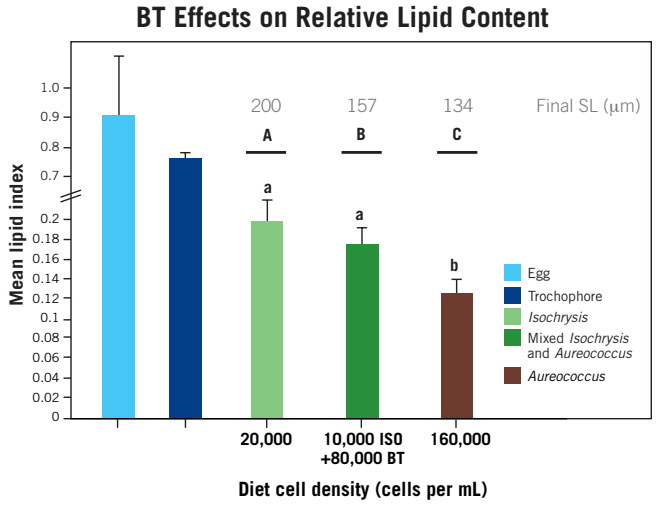

Figure 43. Effects of brown tide (BT) on larval lipid reserves (modified from Przeslawski et al. 2008; work funded outside the HCRI).

Lipid index (mean ± SE) determined using Nile Red fluorescent staining, of hard clam larvae fed 3 experimental diets equal in total cell volume at the end of 2 wks, compared to that of eggs and non-feeding trocophore larvae. Unialgal diets were: 160,000 *A. anophagefferens* (BT) cells mL^{-1}, a control diet of *I. galbana* (Parke, clone CCMP 1323) at 20,000 cells mL^{-1}, and a mixed suspension containing 10,000 *I. galbana* and 80,000 *A. anophagefferens* cells mL^{-1} (22ºC). Different letters indicate statistically different mean final lengths (upper case) and final lipid index (lower case) of veliger larvae in the 3 diet treatments. Lipid index standardized for larval size = fluorescence area of the larval shell/projected area representing lipids.

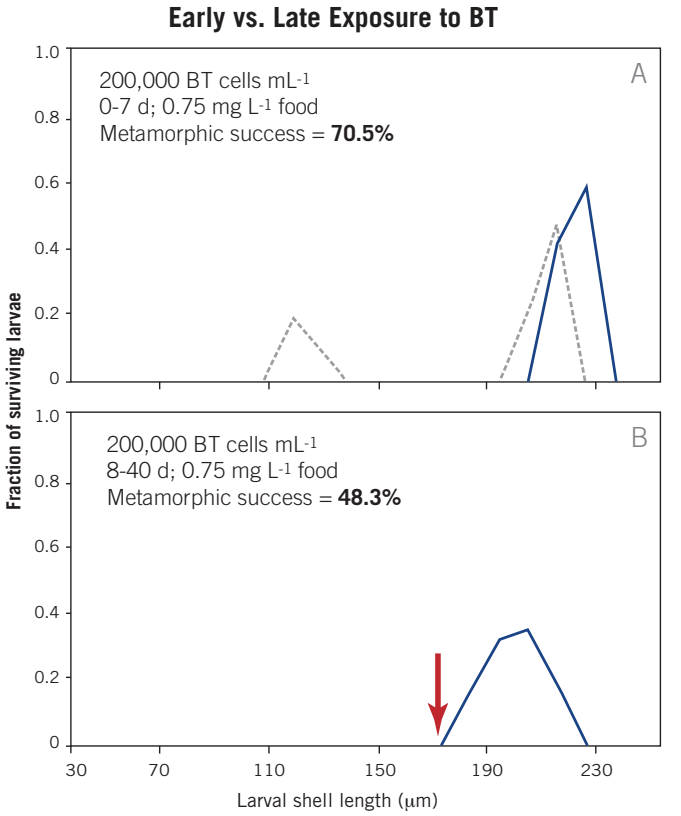

Figure 44. Effects of brown tide (BT) on early vs. late development of hard clam (*Mercenaria mercenaria*) larvae. Size-frequency distribution and metamorphic success of larvae obtained as output of larval model simulations (Bricelj et al. unpubl.).

Larvae were exposed to moderate BT (200,000 *A. anophagefferens* cells mL^{-1}, toxicity = 0.25), in the presence of alternate food (0.75 mg dry weight L^{-1}) during early planktonic development, from first-feeding to 7 days (A), and to the same conditions during late development, from day 8 onwards (B). Solid lines = distribution of larvae that have successfully metamorphosed; dashed lines = that of live larvae that have not metamorphosed. The arrow indicates the minimum shell length for metamorphosis of *M. mercenaria* in the model = 175 µm.

vere detrimental effects (inhibited growth and thus increased predatory risk in the field) from exposure to *A. anophagefferens* blooms exceeding ~100,000 cells mL^{-1} during planktonic development. The annual prevalence and magnitude of these effects will be concentration-dependent and depend on the duration and intensity of BT in a given year and the degree of overlap between BT and larval occurrence. Information is currently lacking on hard clam spawning and larval success during years of intense BT outbreaks. The high fecundities characteristic of bivalves, including *M. mercenaria*, the relatively long lifespan of this species (> 20 yrs) and co-existence of multiple cohorts will tend to buffer *M. mercenaria* from intermittent episodes of recruitment failure caused by BT. This contrasts with short-lived, semelparous species (which generally reproduce once in their lifespan) such as the bay scallop, *Argopecten irradians,* that has undergone restoration efforts in Long Island Peconic bays, which are also affected by BT. The recurrence of BT between 1994 and 2001 has likely contributed to the slow recovery of hard clam populations in GSB despite reduced fishing pressure in recent years.

9. Predation on hard clams in Great South Bay

Increased abundance of predators or changes in the composition of predators has been proposed as a factor contributing to the decline and/or slow recovery of hard clams in GSB. Changes in the food web can lead to a shift of top predators and increased abundance of gelatinous zooplankton in some ecosystems (Purcell 2005). There is evidence that ctenophores have increased in abundance in Long Island bays over the past two decades and may exert significant predation pressure of hard clam larvae (McNamara 2007).

9.1. Predation on hard clam larvae. Concurrent water column sampling of all bivalve veligers and of the ctenophore *Mnemiopsis leidyi* at two sites in GSB during the summer of 2006 showed that the peak in abundance of bivalve veligers coincided with that of this ctenophore species (Fig. 45). The peak in *M. leidyi* abundance occurred 2 to 3 mo. earlier than previously documented in temperate estuaries, including GSB (Quaglietta 1987). Peak ctenophore abundances were an order of magnitude higher in GSB than in Peconic Bay, NY, and peak ctenophore biovolume in GSB was on average 3.6x greater than that recorded in this bay in the mid-1980s by Quaglietta (1987). Large variability in predator abundance was found in 2006, however, between the two GSB sites, and molecular discrimination between *M. mercenaria* and other bivalve larvae was not possible in this study. Analysis of gut contents of ctenophores collected from the field, and laboratory estimates of gut residence times led to calculation of very high consumption rates of veliger larvae by *M. leidyi*. **Current ctenophore populations appear to overlap seasonally with the occurrence of hard clam larvae in GSB and may represent an important source of predatory mortality for clam larvae in this system. Additional spatial coverage is required, however, to determine if this is a bay-wide phenomenon, and longer-term data are also needed. The resolution of the present data is also insufficient to determine whether the peaks of prey and predator abundance were offset in time, as might be expected if *M. leidy* predation were controlling veliger abundance. Ctenophore abundance and impact may thus need to be considered in the establishment of hard clam spawner sanctuaries. This impact will depend on the relative abundance of hard clam larvae relative to other co-occurring prey, including other bivalve larvae.**

9.2. Predation on juvenile and adult hard clams. A variety of crabs are known to be voracious predators of hard clam juveniles. Long-term trends in the abundance of benthic predators were investigated by Polyakov et al. (2007) using observations on the abundance and composition of macropredators conducted by the Town of Islip, NY, in western GSB between 1978 and 2003. These annual surveys, mainly conducted during the summer, in daytime, over a 50 km^2 area, provide the only long-term data set available, although sampling was discontinued between 1982 and 1990. It should also be noted that predators were captured with variable efficiency by the method used (clam-shell bucket with a 6.4 mm sieve). **Mud crabs (Xanthid crabs, primarily *Dyspanopeus sayii*) were the numerically dominant predator in the system, accounting for > 95%**

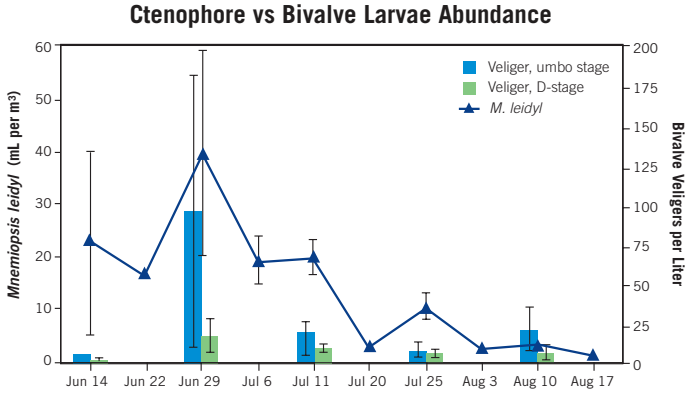

Figure 45. Abundance of bivalve veliger larvae and biovolume of the ctenophore *Mnemiopsis leidyi* (mean ± SE) averaged for two sites in central GSB, NY during 2006 (modified from McNamara 2007, work funded outside the HCRI).

of the total (Fig. 46A). Other hard clam predators occurring in GSB include: blue crabs, lobsters, starfish, whelks, oyster drills and snails. Blue crabs (*Callinectes sapidus)* appeared in this system in the late 1990s, well after the decline in hard clams began. Sampling methods used by the Town of Islip do not adequately sample this highly motile crab species, leading to markedly underestimated abundances, although relative abundances are expected to remain valid. Another important limitation of the sampling is that most of the clams surveyed were > 2.2 cm, yet most predatory losses occur below this size threshold (Kraeuter 2001). Increased predation on recruits should propagate, however, through the larger size classes over time and analysis with a 1 or 2 yr lag time yielded similar results to those with a zero-lag (Polyakov et al. 2007).

Empirical orthogonal function (EOF) analysis of the temporal and spatial patterns of abundance of all predators and of hard clams led to conclude that fluctuations in the abundance of predators were in phase throughout the area surveyed (Fig. 47), and showed large inter-annual fluctuations in predator abundance. Hard clam abundance, also in phase within the survey area, showed a clear decreasing trend over time, i.e. a decline of 44% since the early 1990s (Fig. 46B). **Thus predator distributions and abundance did not change significantly in the survey area since the early 1990s and were similar to those in the late 1970s. Most importantly, the study concluded that there was no strong coupling between hard clams and their predators, thus suggesting that increasing predator abundance was not a primary factor leading to the long-term decline of hard clam populations in the Bay.** It is possible that predation pressure per recruit increased over time concomitantly with the decline in the abundance of hard clams. However, clams are also known to achieve an effective predator refuge at low densities (Peterson et al. 1995).

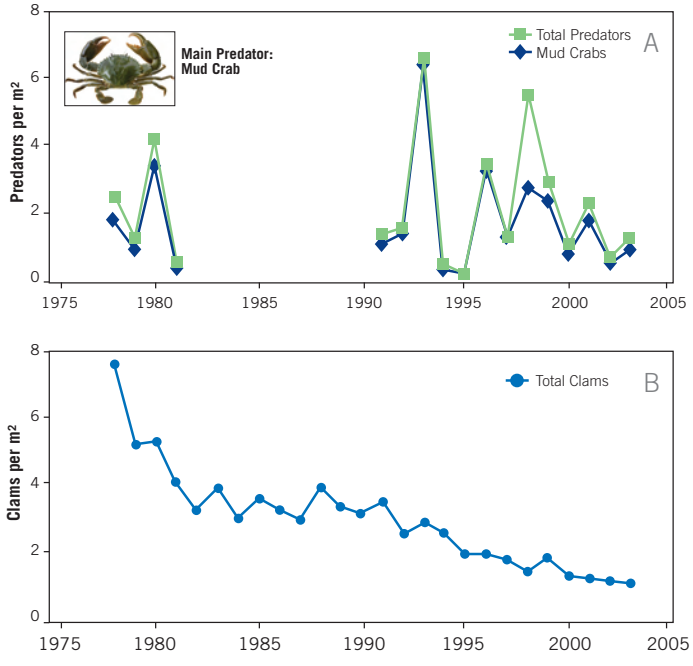

Figure 46. Temporal variability of area-wide averages of (A) total predators (see sec. 9.2) and total mud crabs (primarily *Dispanopeus sayi*), and (B) total hard clams (*Mercenaria mercenaria*) obtained during annual surveys conducted by the Town of Islip, NY (from Polyakov et al. 2007). No predator counts available from 1982 to 1990.

10. Final Conclusions and Recommendations

Specific conclusions and recommendations for management of hard clam populations as well as future research needs were included in each relevant section of this report, and major research outcomes boldfaced throughout. Key conclusions and recommendations derived from integration of all HCRI studies by the author of this report, with input from HCRI participants, however, are highlighted below.

The earlier decline of hard clam populations in GSB through the early 1980s has been clearly established to be caused by overfishing (Buckner 1984, Kraeuter et al. 2008). Other factors appear to have contributed to their continued decline once fishing pressure was markedly reduced. Model simulations showed that the number of recruits per adult consistently remained below the long-term average starting in 1996, and the period between 1994 and 2001 was marked by the reoccurrence of intense brown tide outbreaks, at levels that in most years exceeded the *A. anophagefferens* densities that are detrimental to hard clam early life history stages (larvae and juveniles). The period 2002-2006, however, was marked by a waning of these blooms in SSE, yet hard clam populations have not rebounded. While model simulations predicted a long recovery period from overfishing for *M. mercenaria* natural populations in GSB (a decade or more) without intervention, **BT and other factors (e.g. low fecundities due to poor food quality and/or poor fertilization success resulting from low clam densities) or a combination of these, may be contributing to the delayed recovery and low standing stock during the past two decades.**

There is a clear need to continue long-term monitoring of environmental data and clam populations. Without such long-term surveys, the efficacy of the hard clam model could not have been evaluated. They are required for further fine-tuning of the model where predictions do not match observations, and proved valuable in the interpretation of current HCRI results. They

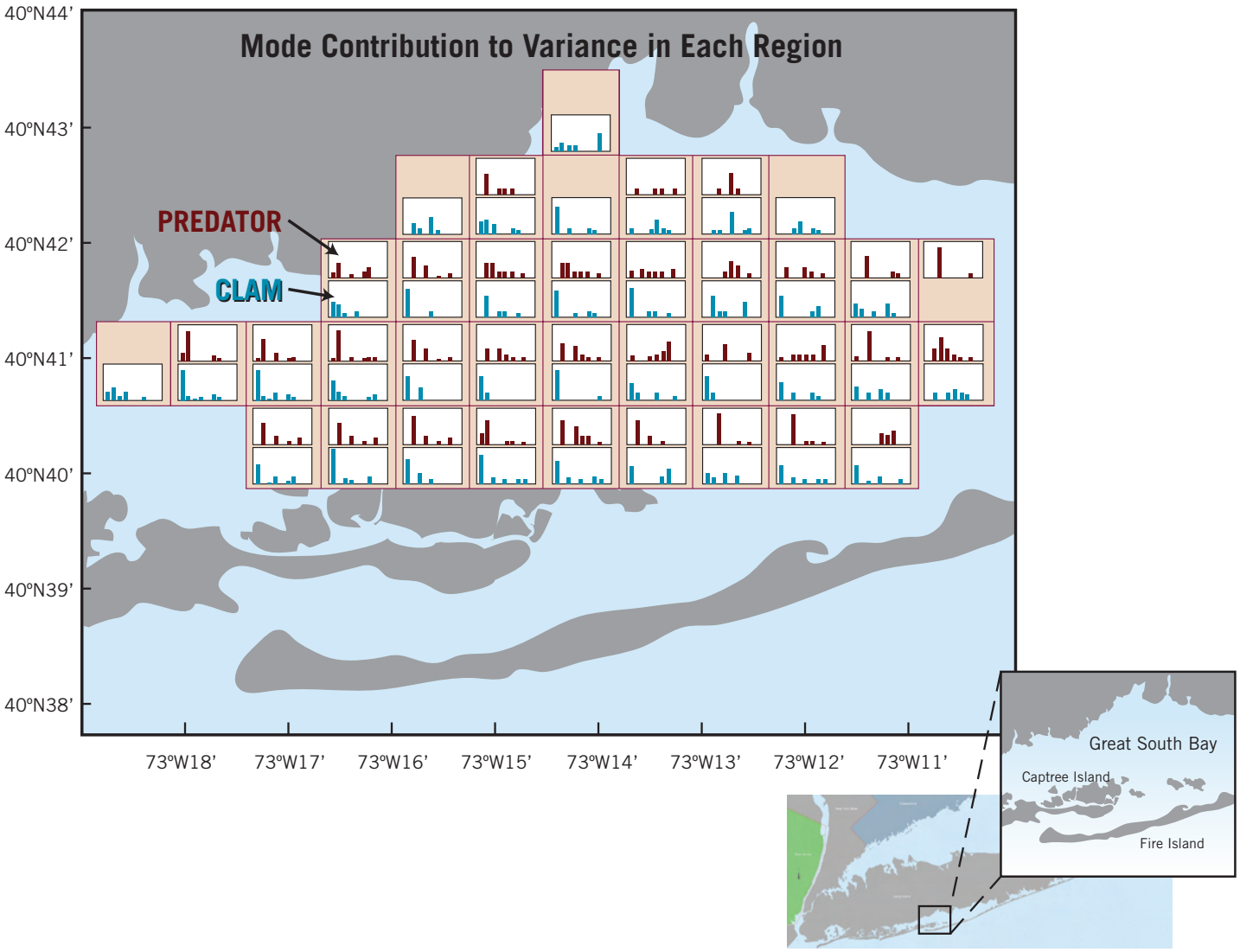

Figure 47. Distribution of the fraction of variance in the predator-prey data explained by the modes calculated by Empirical Orthogonal Function (EOF) analysis, in each grid cell, indicated by heavy lines, calculated from the predator (top) and hard clam (bottom) paired data sets (modified from Polyakov et al. 2007).

The relative height of each bar indicates the contribution of an individual mode to the total variance. Empty cells are indicated where data were insufficient for calculation of the distribution; negative values were set to zero to simplify the plots. Inset map shows the portion of GSB sampled during the Islip Town hard clam survey. Note that most of the variance in both predator and clam data sets was accounted for by one or two primary modes and that these differed between the two data sets, indicating uncoupling or mismatch between predator and prey populations (see text).

are also essential to assess population recovery rates and to identify the environmental changes that may affect this recovery. **Inter-annual variability in temperature and food supply, as well as long-term changes expected as a result of climate change, point to the need for multi-year research studies rather than studies focused on a single year.** The role of predators could at present be evaluated only in a cursory fashion, due to the lack of data on the abundance of major predators, including large, mobile predators such as blue crabs, and those that have experienced a latitudinal shift in their distributions (e.g. green crabs). A better knowledge of the predator field is key to the success of restoration efforts conducted in the absence of predator protection.

The spawner-recruit relationship (SSR) for *Mercenaria mercenaria* was based on limited data, primarily at the upper end of the curve, and was therefore associated with considerable uncertainty at higher stock levels (sec. 2). Continued, long-term monitoring is also required to better describe this relationship for Long Island SSE. The relationship developed to date is, however, fairly robust at the lower end of the SSE curve, and predicts that at an average density of ~0.7 clams m^{-2} the hard clam population will have difficulty recovering. Clams

are known to exhibit an aggregated distribution (Fig. 26, see clam spatial distributions in Islip Town waters between 1992 and 2003 [Polyakov et al. 2007]). The mean clam density data used to develop the SSR relationship were derived from these naturally occurring, non-uniform clam distributions and were used for predictive purposes, yet the error around the mean and the spatial distributions from which it was calculated are of critical biological relevance. It is important to note that even at the threshold mean density at which recruitment is predicted to be near zero (~0.7-0.8 clams per m^2), fertilization success and recruitment may be restricted to localized patches of highest clam density. **Therefore, additional empirical and modeling data are needed on the clam densities that limit fertilization success, and the effects of spatial and year-to-year variability of clam distribution patterns on recruitment success. The finding of a density-dependent effect on recruitment at low clam densities despite the characteristic high-fecundity of *M. mercenaria*, combined with the relatively low fecundities determined by Newell et al. (2009) for GSB clams in 2001 (sec. 3.1) suggest that fertilization success could be compromised at present low population densities.**

Limited information is available on the quality of the larvae produced in these bays. Studies of gamete and larval quality and clam fertilization success at low population densities are thus needed to determine their effect on hard clam reproductive success. The potential contribution of late summer-fall spawning to hard clam larval recruitment, especially in BT years, is also unknown. Similarly, very little is known about post-metamorphosis survival under natural conditions and its role in limiting recruitment under current environmental conditions. Coupling of the larval hard clam model with that on the population dynamics of juveniles and adults could be used to simulate these effects. HCRI research also suggested that the fall condition of adults may affect reproductive success in the subsequent year, a finding supported by recent data on spawner transplants into GSB (sec. 3.2).

A recurring theme throughout this report is that food quality (e.g. as defined by biochemical composition, species composition, size structure of the phytoplankton and alternate food sources) is a critical factor affecting larval and juvenile clam growth, and adult reproduction. This was generally found to be more important than total food concentration, as measured by either Chl *a*, organic carbon or nitrogen. Total Chl *a* was repeatedly found in the HCRI studies to be a poor predictor of the food supply for hard clams. Summer Chl *a* levels during BT years in SSE remain within normal levels (~10 to 25 µg L^{-1} described for these bays prior to the occurrence of BT) and would thus not indicate a poor food supply (Cosper et al. 1987). Model simulations confirmed that Chl *a* alone was inadequate to support hard clam growth, and required introduction of a non-algal food supplement to describe the food supply. **Therefore further characterization of both the algal and non-algal food supply, especially for early life history stages (larvae and juveniles) is needed. Food requirements to support a high reproductive effort of adult clams should also be determined.**

At a minimum, size-fractionated Chl *a* could be incorporated into long-term monitoring efforts, since the HCRI demonstrates its utility in providing improved characterization of the food supply for hard clams. Phytoplankton species composition provides a very useful additional level of resolution, as dinoflagellates (Weiss et al. 2007) and pennate diatoms (Streck 2003) were found to be negatively correlated with juvenile hard clam growth. Furthermore, habitat suitability within GSB, and across SSE, to support clam growth and reproduction, was found to vary greatly along spatial gradients. Therefore, it is important to provide adequate spatial as well as temporal characterization of environmental variables affecting clam production. Adult reproductive output (Fig. 17), adult condition index (Weiss et al. 2007), juvenile growth rates and clam densities (Fig. 26) were all higher in Shinnecock Bay than in GSB. The former is also less prone to BT outbreaks, although unusually high *A. anophagefferens* concentrations (up to 480,000 cells mL^{-1}) were reported in 2008 (SCDHS records).

Long-term analysis of western GSB from 1976 to 2000 indicated that DIN concentrations have decreased significantly over this period, in relation to the use of municipal sewer systems, and low DIN tends to favor *A. anophagefferens* blooms (Gobler et al. 2005). It has been hypothesized that *A. anophagefferens* is only one of the species that can fill a summer picoalgal niche in SSE during the transition from the spring bloom community of diatoms and dinoflagellates to the summer community dominated by "small forms" (Smayda and Villareal 1989, Sieracki et al. 2004). **Furthermore, several HCRI studies suggest that reduced clam growth and reproductive performance along spatial gradients is associated with the dominance of "small forms" (*A. anophagefferens* and other unidentified species).** Although the nutrient conditions and speciation that favor blooms of *A. anophagefferens* have been studied extensively, those that favor other picoplankters that are also detrimental for hard clam production, are less well known and need to be further investigated. **Changes in nutrient loading practices should be explored as a potential management option to reduce the occurrence of such blooms** given that it is well established that human-induced changes in nutrient ratios can cause changes in phytoplankton species composition and that such changes can also be reversed by management of nutrient inputs (Cloern 2001).

The timing and duration of toxic *A. anophagefferens* blooms coincides with the documented main period of spawning and thus larval production of hard clams in GSB during pre-BT years or a year of low BT (sec. 3.1). **Laboratory studies demonstrated that this algal species inhibits feeding and growth of hard clam larvae in a concentration-dependent manner. High densities of BT are therefore expected to cause recruitment failure of larvae under field conditions, if the occurrence of larvae in the plankton coincides with a BT outbreak, although this remains to be demonstrated.** In contrast, non-toxic *A. anophagefferens* at bloom densities (400,000 cells mL^{-1}), can support relatively good growth of juvenile hard clams as well as excellent shell growth of larvae during planktonic development. Model simulations also show that larval growth is very sensitive to the toxicity of *A. anophagefferens* at low densities. **Characterization of the toxicity of *A. anophagefferens* in the field and its variability among years and sites is sorely lacking.** Chemical markers for toxic cells and rapid bioassays are required to quantify cell toxicity. This will help to interpret differences in experimental results between laboratories as well as identify potential temporal and spatial variability in cell toxicity of *A. anophagefferens* in the field. The HCRI study by Newell et al. (2009) on hard clam reproduction did not coincide with a year of intense blooms of *A. anophagefferens.* Therefore, the effects of BT during spring hard clam gonad buildup and June-July spawning remain unknown. The potential contribution of late summer-fall spawning, once BT has subsided, to hard clam larval recruitment during BT years also needs to be investigated.

There is evidence that hard clams at the time when populations in GSB were relatively abundant exerted profound effects via their grazing pressure in this shallow well-mixed ecosystem. During peak abundance it was estimated that hard clams could filter 40% of the GSB volume per day, and that this has been reduced to only 1-2% at present population levels (Kassner 1993) This ability to exert a strong top-down grazing control has led to interest in hard clam stock enhancement efforts with a view towards ecological restoration. **The decline of clam populations and absence of other benthic macrofaunal suspension-feeders to replace them, however, has led to changes in the food web, and a shift to a system in which grazing is no longer controlled by the benthos.** Clam restoration efforts should take into account that habitat suitability for this species may have changed from the time when this bay supported a major commercial fishery. **Integrated measures of habitat suitability for hard clams based on a number of parameters need to be developed for these estuaries, and for specific locations within them.**

Transplanting of adult hard clams to establish spawner sanctuaries was conducted by the Town of Islip for three decades in GSB with little success (sec. 1). Stocking was conducted with the *M. mercenaria* notata variety that is rare in the native population and allows tracking of transplants. Only chowder clams were planted until 2003, although large littlenecks and cherrystone clams were stocked in 2006 (S. Buckner, pers. comm.). The hard clam model required a reduction in the number of eggs produced per unit weight for large clams to make realistic predictions of annual egg production (Hofmann et al. 2006a). Model simulations also showed that higher food levels were required to initiate a high level of gonad output in larger animals. Thus chowders, despite their low market price, may not be the best candidate for spawner transplants.

Seed plantings to enhance natural recruitment in bays recurrently affected by BT are not recommended, since juveniles are more susceptible to BT effects and predation than larger clams. Planting of cultured seed in areas less prone to BT using predator protection until the clams attain a size refuge from most predators could provide a viable alternative for hard clam population enhancement in areas that support high growth rates. Information from the HCRI can assist in suitable site selection. Existing and novel aquaculture technologies to mass produce high-performing, high-quality clam seed at reduced cost should therefore be encouraged. Careful selection of broodstock will be necessary and identification of genetically-based differences in clam susceptibility to BT could greatly advance this effort. Facilitation of leasing practices for aquaculture in SSE and proper safeguards to prevent poaching would also help to stimulate these aquaculture efforts. **Thus, rigorous evaluation of ongoing and future practices to restore and enhance hard clam populations continues to be a pressing management need.**

Restoration efforts for hard clams should clearly establish at the onset their goals and expectations, and develop realistic time-frames and cost estimates to achieve these. These goals may vary widely, e.g. overall ecosystem function and health, recovery of a commercial fishery, or other social goals, including the maintenance of a traditional local lifestyle or source of local employment. Restoration efforts generally meet with enthusiastic public support, and therefore are often not scrutinized or evaluated as closely as other less popular interventions (Mann and Powell 2007). **Therefore, rigorous evaluation of proposed restoration activities and of their outcomes is an essential component of science-based management of this resource.** Cost-benefit evaluation of various management options, ranging from hard clam enhancement to habitat improvement, should also be considered.

Literature Cited

Bass, AE, R.E. Malouf, S.E. Shumway, 1990. Growth of northern quahogs (*Mercenaria mercenaria* L 1758) fed on picoplankton. J. Shellfish. Res. 9:299-307.

Bochenek, E.A., J.M. Klinck, E.N. Powell, E.E. Hofmann, 2001. A biochemically-based model of the growth and development of *Crassostrea gigas* larvae. J. Shellfish Res. 20:243-265.

Bricelj, V.M., 1979. Fecundity and related aspects of hard clam, *Mercenaria mercenaria*, reproduction in Great South Bay, New York. MS thesis, Stony Brook University, New York, 98 pp.

Bricelj, V.M., A.E. Bass, G.R. Lopez, 1984. Absorption and gut passage time of microalgae in a suspension feeder: an evaluation of the ^{51}Cr:^{14}C twin tracer technique. Mar. Ecol. Prog. Ser. 17: 57 63.

Bricelj, V.M., L. Connell, K. Konoki, S. P. MacQuarrie, T. Scheuer, W. A. Catterall, V. L. Trainer, 2005. Sodium channel mutation responsible for saxitoxin resistance in clams increases risk of PSP. Nature 434: 763-767.

Bricelj, V.M., D.J. Lonsdale, 1997. *Aureococcus anophagefferens*: causes and ecological consequences of brown tides in U.S. mid-Atlantic coastal Waters. Limnol. Oceanogr. 42: 1023-1038.

Bricelj, V.M., S. P. MacQuarrie, 2007. Effects of brown tide (*Aureococcus anophagefferens*) on hard clam, *Mercenaria mercenaria,* larvae and implications for benthic recruitment. Mar. Ecol. Prog. Ser. 331:147-159.

Bricelj, V.M., S. MacQuarrie, R.A. Schaffner, 2001. Differential effects of *Aureococcus anophagefferens* isolates ("brown tide") in unialgal and mixed suspensions on bivalve feeding. Mar. Biol. 139: 605-615.

Bricelj, V.M., S. MacQuarrie, R. Smolowitz, 2004. Concentration-dependent effects of toxic and non-toxic isolates of the brown tide alga *Aureococcus anophagefferens* on growth of juvenile bivalves. Mar. Ecol. Prog. Ser. 282: 101-114.

Bricelj, V.M., C. Ouellette, M. Anderson, N. Brun, F. Pernet, N. Ross, T. Landry, 2007. Physiological and biochemical responses of juvenile quahogs, *Mercenaria mercenaria*, to low temperatures: potential for mitigation of overwintering mortalities. Can. Tech. Report Fish. Aquatic Sci. 2739, 49pp. http://www.dfo-mpo.gc.ca/library/331763.pdf

Bricelj, V.M., H. Robbins, S. MacQuarrie, F. Pernet, 2008. Effects of toxic and non-toxic brown tide on the biochemical composition and metamorphic success of *Mercenaria mercenaria* larvae. J. Shellfish Res. 27(4): 991-992, abstract

Buckner, S.C., 1984. Aspects of the population dynamics of the hard clam, *Mercenaria mercenaria* L., in Great South Bay, New York, Ph.D. dissertation, Stony Brook University, New York, 217 pp.

Buckner, S.V., 1987. Preliminary evaluation of hard clam resource enhancement strategies. Suffolk County Department of Planning Report, Long Island, NY, 30 pp.

Caron, D.A., C.J. Gobler, D.J. Lonsdale, R.M. Cerrato, R.A. Schaffner, J.M. Rose, N.J. Buck, G. Taylor, K.R. Boissonneault, R. Mehran, 2004. Microbial herbivory on the brown tide alga, *Aureococcus anophagefferens:* results from natural ecosystems, mesocosms and laboratory experiments. Harmful Algae 3: 439-457.

Cerrato R., M. Streck, D. Lonsdale, 2003. Trophic interaction between hard clams and natural assemblages of plankton. J. Shellfish Res. 22(1):323 (abstract).

Cerrato, R.M., D.A. Caron, D.J. Lonsdale, J.M. Rose, R.A. Schaffner, 2004. Effect of northern quahog *Mercenaria mercenaria* on the development of blooms of the brown tide alga *Aureococcus anophagefferens*. Mar. Ecol. Prog. Ser. 291: 93-108.

Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. 210: 223-253.

Conover, R.J., 1966. Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11:338-345.

Cosper, E.M., W.C. Dennison, E.J. Carpenter, V.M. Bricelj, J.G. Mitchell, S.H. Kuenstner, D. Colflesh, M. Dewey, 1987. Recurrent and persistent "brown tide" blooms perturb coastal marine ecosystem. Estuaries 10(4): 284-290.

Crosby, M.P., L.D. Gale, 1990. A review and evaluation of bivalve condition index methodologies with a suggested standard method. J. Shellfish Res. 9(1): 233-237.

Doall, M.H., D.K. Padilla, C.P. Lobue, C. Clapp, A.R. Webb, J. Hornstein, 2008. Evaluating northern quahog (= hard clam, *Mercenaria mercenaria* L.) restoration: are transplanted clams spawning and reconditioning. J. Shellfish Res. 27(5): 1-12.

Gainey, L.F., S.E. Shumway, 1991. The physiological effects of *Aureococcus anophagefferens* ('brown tide') on ther lateral cilia of bivalve mollusks. Biol. Bull (Woods Hole) 181: 298-306.

Gallager, S.M., R. Mann, G.C. Sasaki, 1986. Lipid as an index of growth and viability in three species of bivalve larvae). Aquaculture 56: 81-103.

Gallager, S.M., J.B. Waterbury, D.K. Stoecker, 1994. Efficient grazing and utilization of the marine cyanobacterium *Synechococcus* sp. by larvae of the bivalve *Mercenaria mercenaria*. Mar. Biol. 119(2): 251-259.

Gobler, C.J., D.J. Lonsdale, G.L. Boyer, 2005. A review of the causes, effects, and and potential management of harmful brown tideblooms caused by *Aureococcus anophagefferens* (Hargraves et Sieburth). Estuaries 28: 726-749.

Greenfield, D.I., D.J. Lonsdale, 2002. Mortality and growth of hard clams, *Mercenaria mercenaria*, during brown tide. Mar. Biol. 141: 1045-1050.

Greenfield, D.I., D.J. Lonsdale, R.M. Cerrato, 2005. Linking phytoplankton community composition with juvenile-phase growth in the northern quahog *Mercenaria mercenaria* (L.). Estuaries 28(2): 241-251.

Grizzle, R. Bricelj, V.M., S.E. Shumway, 2001. Physiological ecology of *Mercenaria mercenaria*, Chapter 8 In: Kraeuter, J.N., M. Castagna (eds.), Biology of the Hard Clam, Elsevier, New York, pp. 305-382.

Grizzle, R., E.E. Hofmann, J.M. Klinck, E.N. Powell, E.N., J.N. Kraeuter. V.M. Bricelj, S.C. Buckner, 2003. A simulation model of the population growth of the hard clam (*Mercenaria mercenaria*). IV. Effects of climate change. J. Shellfish Res. 22(1), pp. 333 (abstract).

Gurevitch, J., L.V. Hedges, 1993. Meta-analysis: combining the results of independent experiments. In: Scheiner, S., J. Gurevitch (eds.). Design and Analysis of Ecological Experiments, Chapman and Hall, New York, pp. 378-401.

Hofmann, E.E., J.M. Klinck, J.N. Kraeuter, E.N. Powell, R.E. Grizzle, S.C. Buckner, V.M. Bricelj, 2006a. A population dynamics model of the hard clam, *Mercenaria mercenaria*: development of the age- and length-frequency structure of the population. J. Shellfish Res. 25(2): 417-444.

Hofmann, E.E., E.N. Powell, J.M. Klinck, J.N. Kraeuter, R. Marzec, V.M. Bricelj, 2006b. Can hard clam larval survival explain recruitment failure in Great South Bay: a modeling study. J. Shellfish Res. 25(2), p. 739 (abstract).

Kassner, J., 1982. The gametogenic cycle of the hard clam, *Mercenaria mercenaria*, from different locations in the Great South Bay, New York. MS Thesis, State University of New York at Stony Brook, 72 pp.

Kassner, J., 1993. Possible effects of reduced hard clam abundance in Great South Bay. On the Water July/Aug: 4-5, Cornell Cooperative Extension of Suffolk County, Riverhead, NY,

Kassner, J, R.E. Malouf, RE, 1982. An evaluation of "spawner transplants" as a management tool in Long Island's hard clam fishery. J. Shellfish Res. 2:165-172.

Kraeuter, J.N., 2001. Predators and predation, Chapter 11 In: Kraeuter, J.N., M. Castagna (eds.), Biology of the Hard Clam, Elsevier, NY, pp. 441-589.

Kraeuter, J.N., S. Buckner, E.N. Powell, 2005. A note on a spawner-recruit relationship for a heavily exploited bivalve: the case of northern quahogs (hard clams), *Mercenaria mercenaria*, in Great South Bay New York. J. Shellfish Res. 24(4):1043-1052.

Kraeuter, J.N., J. Klinck, E.N. Powell, E. Hoffman, S.C. Buckner, R.E. Grizzle, V.M. Bricelj, 2008. Effects of the fishery on the northern quahog (=hard clam, *Mercenaria mercenaria* L.) population in Great South Bay, New York: A modeling study. J. Shellfish Res. 27(4):653-666.

Laetz, D.A., 2002. Reconstructing the growth of hard clams, *Mercenaria mercenaria*, under brown tide conditions. M.S. Thesis, Stony Brook University, N.Y.

Lonsdale, D.J., R. Cerrato, D.A. Caron, 2007. Zooplankton changes associated with the introduction of hard clams (*Mercenaria mercenaria* L.) to mesocosms. Est. Coast Shelf Sci. 73: 101-110.

Lonsdale, D.J., E.M. Cosper, W.S. Kim, M. Doall, A. Divadeenam, S.H. Jonasdottir, 1996. Food web interactions in the plankton of Long Island bays, with preliminary results on brown tide effects. Mar. Ecol. Prog. Ser. 134: 247-263.

Lively, J.S., Z. Kaufman, E.J. Carpenter, 1983. Phytoplankton ecology of a barrier island estuary: Great South Bay, N.Y. Est. Coastal Shelf Sci. 16: 51-68.

Malouf, R.E., 1989. Clam culture as a resource management tool, Chapter 18 In: Manzi, J.J. and Castagna, M. (eds.), Clam Mariculture in North America, Developments in Aquaculture and Fisheries Sci. 19, Elsevier, New York, pp. 427-447.

Mann, R., E.N. Powell, 2007. Why oyster restoration goals in the Chesapeake Bay are not and probably cannot be achieved. J. Shellfish Res. 26(4): 905-917.

Marzec, R., 2003. Predation on early life stages of the calanoid copepod *Acartia tonsa* (Dana) by the northern quahog (*Mercenaria mercenaria* L.). MS Thesis, Stony Brook University, Stony Brook, NY., 72 pp.

McHugh, J.L., 1991. The hard clam fishery past and present. Pp. 55-64 In: J.R. Schubel, T.M. Bell, H.H. Carter (eds). The Great South Bay, Chapter 7, Albany State University of New York Press, 107 pp.

McNamara, M.E., 2007. Impact of predation by the ctenophore *Mnemiopsis leidyi* on larval mortality of *Mercenaria mercenaria* in Long Island Estuaries. MS Thesis, Stony Brook University, Stony Brook, NY. 89 pp.

Newell, R.I.E, C. Gobler, S. Tettlebach, 2003. Linking hard clam (*Mercenaria mercenaria*) reproduction to phytoplankton community structure: II. Phytoplankton community structure and food composition. J. Shellfish Res. 22(1):347 abstract.

Newell R.I.E., S.T. Tettelbach, C.J. Gobler, and D.G. Kimmel. 2009. Relationships between reproduction in suspension-feeding hard clams, *Mercenaria mercenaria*, and phytoplankton community structure. Mar. Ecol. Prog. Ser. In review. For reprint email rnewell@hpl.umces.edu

Nuzzi, R., R.M. Waters, 1999. Surface water quality monitoring report, II, Data. Suffolk County Department of Health Services, Office of Ecology, Riverhead, NY.

Nuzzi, R., R.M. Waters, 2004. Long-term perspective on the dynamics of brown tide blooms in Long Island coastal bays. Harmful Algae 3: 279-293.

Padilla, D.K., M.H. Doall, C. J. Gobler, A. Hartson, K. O'Boyle, 2006. Brown tide alga, *Aureococcus anophagefferens*, can affect growth but not survivorship of *Mercenaria mercenaria* larvae. Harmful Algae 5: 736-748.

Pernet, F., V.M. Bricelj, S. Cartier, 2006. Lipid class dynamics during larval ontogeny of sea scallops, *Placopecten magellanicus,* in relation to metamorphic success and response to antibiotics. J. Exp. Mar. Biol. Ecol. 329: 265-280.

Peterson, C.H., H.C. Summerson, J. Huber, 1995. Replenishment of hard clam stocks using hatchery seed: combined importance of bottom type, seed size, planting season and density. J. Shellfish Res. 14: 293-300.

Polyakov, O., J. Kraeuter, E.E. Hofmann, S.C. Buckner, V.M. Bricelj, E. Powell, J. Klinck,. 2007. Benthic predators and northern quahog (=hard clam) (*Mercenaria mercenaria Linnaeus*, 1758) populations. J. Shellfish Res.26 (4): 995-1010.

Przeslawski, R., P.E. Bourdeau, M.H. Doall, J. Pan, L. Perino, D.K. Padilla, 2008. The effects of a harmful alga on bivalve larval lipid stores. Harmful Algae 7: 802-807.

Purcell, J.E., 2005. Climate effects on formation of jellyfish and ctenophore blooms: a review. J. Mar. Ass. UK 85:461-476.

Quaglietta, C.E., 1987. Predation by *Mnemiopsis leidyi* on hard clam larvae and natural zooplankton in Great South Bay, NY. MS thesis, Stony Brook University, New York.

Riisgård, H.U., 1988. Efficiency of particle retention and filtration rate in 6 species of northeast American bivalves. Mar. Ecol. Prog. Ser. 45: 217-223.

Ryther, J. H. 1954. The ecology of phytoplankton blooms in Moriches Bay and Great South Bay, Long Island, New York. Biol. Bull. 106:198–209.

Sieracki, M.E., C.J. Gobler, T.L. Cucci, E.C. Their, I.C. Gilg, M.D. Keller, 2004. Pico- and nanoplankton dynamics during bloom initiation of *Aureococcus* in a Long Island, NY bay. Harmful Algae 3: 459-470.

Smayda, T.J., T.A. Villareal, 1989. The 1985 "brown tide" and the open phytoplankton niche in Narragansett Bay during summer, Chapter 10, In: E.M. Cosper, V.M. Bricelj, E.J. Carpenter (eds.), Novel Phytoplankton Blooms: Causes and Impacts of Recurrent Brown Tides and Other Unusual Blooms, Vol. 35. Springer, New York, pp. 159-188.

Streck, A.E. 2003. Feedbacks resulting from changes in *Mercenaria mercenaria* abundance in Great South Bay, New York. MS Thesis, Stony Brook University, New York, 56 pp.

Tettlebach, S., R.I.E. Newell, C.J. Gobler, 2003. Linking hard clam (*Mercenaria mercenaria*) reproduction to phytoplankton community structure: I Clam growth and reproductive cycles. J. Shellfish Res 22(1):357-358 abstract.

Tiu, A.T., D. Vaughan, T. Chiles, K. Bird, 1989. Food value of eurytopic microalgae to bivalve larvae of *Cryptopleura costata* (Linnaeus, 1758), *Crassostrea virginica* (Gmelin, 1791) and *Mercenaria mercenaria* (Linnaeus, 1758). J. Shellfish Res. 8(2): 399-405.

Tracey, G.A., 1988. Feeding reduction, reproductive failure, and mortality in *Mytilus edulis* during the 1985 'brown tide' in Narragansett Bay, Rhode Island.

Wallace, H.V.E. 1991. A comparison of hard clam population characteristics between high and low density regions within Great South Bay. M.S. thesis, Stony Brook University, New York, 67 pp.

Wazniak, C.E., P.M. Glibert, 2004. Potential impacts of brown tide, *Aureococcus anophagefferens*, on juvenile hard clams, *Mercenaria mercenaria*, in the coastal bays of Maryland, USA. Harmful Algae 3: 321-329.

Weiss, M.B., P.B. Curran, B.J. Peterson, C.J. Gobler, 2007. 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). J. Exp. Mar. Biol. Ecol. 345:12–25.

Wong, W.H., J.S. Levinton, B.S. Twining, N. Fisher, 2003. Assimilation of micro- and mesozooplankton by zebra mussels: a demonstration of the food web link between zooplankton and benthic suspension feeders. Limnol. Oceanogr. 48: 308-312.

Zarnoch, C.B. and M.P. Schreibman 2008. Influence of temperature and food availability on the biochemical composition and mortality of juvenile *Mercenaria mercenaria* (L.) during the over-winter period. Aquaculture 274:281-291

About the Author

Dr. V. Monica Bricelj is a nationally and internationally recognized expert in shellfish biology, eco-physiology and aquaculture. She has also conducted extensive research on the effects of harmful algal blooms on commercially important bivalve species and the accumulation of algal toxins by shellfish – a human health concern. She participated in the Hard Clam Research Initiative as a researcher on two of the funded projects. In the last twenty years, Dr. Bricelj has been the author/coauthor of over 60 peer-reviewed journal articles, and several review articles and reports in this field, including a review on brown tide, a chapter on hard clam physiology and an Intergovernmental Oceanographic Commission report on management of shellfish toxins in Hong Kong. A recipient of awards of excellence and outstanding achievement for work published in *Nature* in 2005, she has lectured worldwide and served as a panelist on numerous boards with government agencies and industry. Dr. Bricelj was Associate Professor at the Marine Sciences Research Center at Stony Brook University (now known as the School of Marine and Atmospheric Science) where she received her M.S. in marine environmental sciences and Ph.D. in coastal oceanography, with research focused on *Mercenaria mercenaria* in the GSB. She was an Associate and Senior Research Officer at the Institute for Marine Biosciences of the National Research Council in Halifax, Canada, for a decade and is currently Research Professor at the Institute of Marine and Coastal Sciences at Rutgers University.

Glossary

Absorption efficiency (AE): the proportion of the ingested food (e.g. calories, nitrogen etc.) that is absorbed by the animal and is available to support growth and metabolism or some may be excreted in urine.

Brown tide: a bloom of microalgae that causes visible discoloration of the water to a brown color. In this report it refers specifically to that caused by proliferation of the microalga *Aureococcus anophagefferens*.

Condition Index (CI): a measure of "fatness" or nutritive status of a bivalve under a given set of environmental conditions. There are numerous quantitative expressions of this index (reviewed by Crosby and Gale 1990), e.g.

$$CI = \frac{\text{Total dry soft tissue weight (g) x 100}}{\text{Internal shell cavity capacity}}$$

where shell cavity capacity is measured volumetrically (in mL) from water displacement, or more often gravimetrically (in g) as Total live wet weight – Dry shell weight. (see Sec. 3.1).

D-stage larva: early veliger larva of bivalves (uses a velum as swimming and feeding organ). It represents the first-feeding stage following that of the non-feeding trocophore stage. The D-stage larva typically develops ~24 hours following fertilization of the egg and has a characteristic D-shaped shell.

Exponential and stationary growth phases: in this report refers to two sequential growth stages of algal cultures in the laboratory grown under batch conditions (nutrients only added at time zero). During the exponential phase cells divide actively and thus undergo population growth, i.e. an exponential increase in cell numbers. During the stationary stage algae cease dividing as they become nutrient limited, and population growth = 0. Numerous characteristics (e.g. cell size, biochemical composition, etc.) can change between these two stages.

Empirical orthogonal function (EOF): a statistical method of analysis that decomposes a data set in terms of a series of functions that account for as much of the variance in the data as possible, and is used to find both temporal and spatial patterns.

Larval competence: bivalve (e.g. hard clam) larvae become competent to undergo metamorphosis when they reach a certain minimum size, develop a foot, and accumulate sufficient lipid reserves to sustain them during the non-feeding metamorphosis stage. Once those criteria are satisfied these **pediveliger** larvae (with foot and velum) exhibit distinct behavioral changes (e.g. become negatively phototactic and start crawling and probing the bottom with their foot to find a suitable substrate to complete larval development).

Mesoplankton: particles in the plankton in a size range > 200 to 2000 µm

Metamorphosis: during larval development, the period of transition from life in the water column (planktonic) to that on the bottom (benthic), during which they experience profound morphological, physiological, biochemical and behavioral changes. In bivalves such as the hard clam these changes include secretion of a distinct postlarval shell, temporary cessation of feeding, loss of the velum and thus of swimming capacity, development of the gills as feeding organs, etc..

Microplankton: organisms in the plankton (plant or animal) in a size range > 20 µm to 200 µm (zoomicroplankton refers only to the animal component)

Nanoplankton: organisms in the plankton in a size range > 2 µm to 20 µm.

Neutral lipids: one of the lipid classes (triacylglycerols, TAG) that is used as a reserve or metabolic fuel, in contrast to phospholipids or **polar lipids** that are typically structural components of cell membranes.

Notata: a genetic variety of the hard clam, *Mercenaria mercenaria,* characterized by distinct brown markings, stripes or zigzag, on the shell.

Picoplankton: organisms (microalgae, bacteria, etc) in the plankton that are typically in the size range of ~ 0.2 to 2 µm.

Relative reproductive output (RRO): an estimate of reproductive output calculated (sec. 3.1) by multiplying the clams' mean reproductive condition (percent gamete volume fraction) by the mean condition index for the same time point. To allow comparison of RRO values among sites (Fig. 17), RRO was plotted over time (months of the year) and the area integrated below the fitted curve and above the baseline for each site.

Scope for growth (SFG): the amount of energy per unit time that is available for somatic (non reproductive) and reproductive growth. It is calculated from the energy budget equation by measuring various physiological parameters, rather than measured directly from changes in weight over time, as: SFG = (I x AE) – M, where I = ingestion rate, AE = percent absorption efficiency and M = metabolic rate or respiration.

"Small forms": non-technical term that in this report refers to particles in the plankton less or equal than 5 µm in size.

Stereology, stereological methods: a histological technique that allows calculation of the percentage of a given surface area or volume of a tissue or organ that is occupied by a given component [e.g. gametes, thus percent **gamete volume fraction**, a measure of **reproductive condition** (Fig. 16)]. It is based on superimposing a point grid on a tissue section and calculating the number of points that intersect the component of interest, relative to the total number of points in the grid.

Citation:
Bricelj, V. M. (2009) The Hard Clam Research Initiative: Factors Controlling *Mercenaria mercenaria* Populations in South Shore Bays of Long Island, NY. New York Sea Grant, Report NYSGI-T-09-001, 43 pages.

Photo credits:
Front cover, top row of clam photos: left, right: Cornell Cooperative Extension of Suffolk County.; center: Preston O. Petre courtesy of *Journal of Shellfish Research.* Bottom row: photo of fourth generation GSB clammer Rob Hoek by J. Dlhpolsky; photo of clam larvae, S. MacQuarrie. Background image and back cover: J. Tempelman

This publication was printed on recycled paper using soy-based inks.

Sea Grant
New York

New York Sea Grant
121 Discovery Hall
SUNY at Stony Brook
Stony Brook, NY 11794-5001
Tel: (631) 632-6905
Fax: (631) 632-6917
E-mail: nyseagrant@stonybrook.edu
www.nyseagrant.org

NOAA
NATIONAL OCEANIC AND ATMOSPHERIC ADMINISTRATION
U.S. DEPARTMENT OF COMMERCE