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The ability of the gastropod *Crepidula fornicata* to suspension-feed in the presence of cultured and wild populations of the brown tide alga, *Aureococcus anophagefferens*.

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Abstract of the Thesis

The ability of the gastropod *Crepidula fornicata* to suspension-feed in the presence of cultured and wild populations of the brown tide alga, *Aureococcus anophagefferens*.

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The American slipper limpet (*Crepidula fornicata*) is a protandrous, hermaphroditic gastropod native to the Atlantic coast of North America, including some estuaries on Long Island, NY. An important characteristic of *C. fornicata* that may contribute to its ecological success is its ability to consume efficiently and retain particles as small as 1μm in size. Slipper limpets also maintain robust filtration rates even under extraordinarily high particle loads. The Peconic Estuary in NY formerly supported a multi-million dollar bay scallop fishery (*Argopecten irradians*) which collapsed with the onset of harmful brown tides (*Aureococcus anophagefferens*) during the late 1980s and early 1990s. This estuary, however, supports a large population of *C. fornicata* and unlike other NY estuaries, brown tides have not returned to this system since 1995. Brown tides continue to plague Great South Bay (GSB) where the northern quahog or hard clam (*Mercenaria mercenaria*) was once the largest fishery in New York, and where densities of *C. fornicata* are currently low. Landings of *M. mercenaria* in GSB have declined by 99% since the early 1980's, due to the combined effects of overharvesting and the sensitivity of this species to brown tides. In this study, rates of suspension-feeding by *C. fornicata* and *M. mercenaria* in the presence of different strains of *A. anophagefferens* and wild brown tide blooms of varying densities were quantified. Slipper limpets were capable of clearing all strains of *A. anophagefferens* at biomass specific rates similar to an ideal food source (*Isochrysis galbana*), whereas clearance rates of *M. mercenaria* fed toxic clones of *A. anophagefferens* were significantly lower than those of *I. galbana* ($p < 0.01$). During brown tide blooms (10^4 - 10^6 cells ml^{-1}) on the south shore of Long Island during 2008 and 2009, clearance rates of *C. fornicata* fed *A. anophagefferens* were an order of magnitude greater than those of *M. mercenaria* ($p < 0.001$). Finally, during mesocosm experiments, environmentally realistic abundances of *C. fornicata*

significantly reduced bloom densities of *A. anophagefferens* by an order of magnitude in 3 – 4 days, whereas densities of *A. anophagefferens* in mesocosms stocked with equal or greater biomasses of *M. mercenaria* were unchanged. These results demonstrate that *C. fornicata* can actively feed in the presence of elevated densities of *A. anophagefferens*.

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INTRODUCTION

The American slipper limpet (*Crepidula fornicata*) is a suspension-feeding gastropod native to the North American east coast. The species is considered invasive in Washington State and along Western European coasts, including France where it has dramatically increased in abundance since its introduction at the end of WWII (Blanchard 1995). The slipper limpet is a protandrous hermaphrodite and typically forms stacked chains consisting of large females at the bottom of stacks with intersexed individuals layered above and small males at the top of chains (Orton 1952), all of which rely upon suspension-feeding for nutrition.

The species has received attention within Europe because of its rapid spread into oyster beds. There has been much debate regarding its impact on oyster growth and habitat modification (Orton 1926; Werner 1948; Korringa 1952; Ehrhold et al. 1998; de Montaudouin et al. 1999; Thieltges et al. 2006; Decottignies et al. 2007; Leloup et al. 2008). One of the important characteristics of *Crepidula* that may have promoted its success is its remarkable ability to consume a vast array of particle sizes (Orton 1912; Jørgensen et al. 1984; Barillé et al. 2006) as well as its ability to process particles on the gill continuously, even at high particle concentrations (Barillé et al. 2006). This is largely due to the mucus net which the animal secretes across its gill to capture particles as small as 1 μm in size (Jørgensen et al. 1984). Unlike other species of the genus, suspension-feeding has been observed in all age classes of *C. fornicata*, including small juveniles (Eyster and Pechenik 1988).

There have been many changes to native shellfish populations in waters of Long Island, NY, USA, during the past 40 years. During the 1970's, two out of every three northern quahogs (=hard clam, *Mercenaria mercenaria*) eaten on the east coast of the

United States came from Great South Bay, on the south shore of Long Island (McHugh 1991). These large harvests were followed by a >99% decline in landings (NYSDEC 2008) due in part to over harvesting (Kraeuter et al. 2008). Despite restoration efforts and reduced harvesting pressure in recent decades, landings and recruitment of *M. mercenaria* in Great South Bay continue to be minimal (NYSDEC 2008).

The Peconic Estuary, located on the eastern end of Long Island, experienced a collapse in populations of the bay scallop (*Argopecten irradians*) during the 1980s. This estuary does, however, continue support a large population of *C. fornicata*. Surveys of the Peconic Estuary conducted in the mid-1990's reported maximal abundances of *C. fornicata* of 600 ind. m^{-2} and sizable populations throughout the system (Lewis et al. 1997). Distributions of this species in other Long Island estuaries have not been reported.

Some of the changes in shellfish populations on Long Island have been caused by persistent brown tide blooms of the picoplanktonic (~2 μm) pelagophyte, *Aureococcus anophagefferens* (as reviewed by Bricelj and Lonsdale 1997 and Gobler et al. 2005). Blooms of this species have also been documented on the US east coast from Rhode Island south to Virginia, and in South Africa (Sieburth et al. 1988; Tracey 1988; Cosper et al. 1989; Probyn et al. 2001; Gastrich et al. 2004; Trice et al. 2004). In waters surrounding Long Island, blooms have occurred sporadically within south shore estuaries since 1985, but occurred in the Peconic Estuary on eastern Long Island from 1985 through 1995 only (Bricelj and Lonsdale 1997; Gobler et al. 2005). Cell concentrations as high as $3x10^6$ cells mL^{-1} have been documented during blooms (Nuzzi and Waters 1989) and the detrimental effect of these brown tides on shellfish and eelgrass beds has been significant (Dennison 1988; Bricelj et al. 1989; Gallager et al. 1989; Bricelj and Lonsdale

1997). Large blooms effectively shade the benthos causing reduction in eelgrass beds which are important for shellfish recruitment, as well as providing habitat for juvenile fish (Cosper et al. 1987; Dennison 1988). Brown tide caused recruitment failure and starvation in bay scallop populations (Bricelj et al. 1989). High rates of mortality in bivalves during blooms (Greenfield and Lonsdale 2002) have generally been attributed to cessation of feeding and starvation (Bricelj et al. 2001). At concentrations exceeding $5x10^4$ cells mL^{-1}, *A. anophagefferens* can significantly reduce the ability of *M. mercenaria* to filter feed (Gainey and Shumway 1991; Bricelj et al. 2001). Some effects on bivalves have been attributed to an unknown dopamine-mimetic bioactive compound associated with the outer polysaccharide layer of *A. anophagefferens* (Gainey and Shumway 1991).

Brown tides typically develop in late May, peak during June or July, and wane in late summer when water temperatures exceed 25°C (Gobler et al. 2005). If a particularly strong bloom has occurred in June or July, blooms recur in the fall when waters begin to cool (Gobler et al. 2005). Preliminary experiments have demonstrated that the *C. fornicata* can filter a wide range of particles ≥ 1 μm and at very high concentrations (> 10^6 cells mL^{-1}) (Jørgensen et al. 1984; Shumway, unpubl.), including *A. anophagefferens* strain CCMP1784 (Shumway, unpubl.). However, the ability of *C. fornicata* to feed in the presence of other strains or blooms of *A. anophagefferens* has not been reported.

This study sought to compare the feeding rates of *C. fornicata* and *M. mercenaria* when fed diets comprised of cultures or natural blooms of *A. anophagefferens*. Each mollusc was offered diets of three different strains of *A. anophagefferens* and an ideal

food source (*Isochrysis galbana*), as well as water from NY estuaries with varying concentrations of *A. anophagefferens*. Finally, the ability of the molluscs to filter feed during brown tides was examined within large volume mesocosm experiments.

METHODS

Assessment of *C. fornicata* distribution in Long Island Estuaries

In the Peconic Estuary, *C. fornicata* was found at moderate densities as of 1995 (Lewis et al. 1997). Small populations have been observed in Great South Bay (Larson 2000). Shinnecock Bay, which has no historical record available for reference, was surveyed for *C. fornicata* abundance in this study. Near-shore surveys to a depth of 2 meters were conducted with SCUBA or snorkel and fin using 0.25 m^2 quadrat sampling. Ten-meter-long-line transects were established randomly from shore and divided into 10 randomized sub-sections which randomized subsamples (quadrats) into segments along each transect. All individual *C. fornicata* and size classes were counted in each quadrat and three transects were conducted along the north, south, east, and west shores of Shinnecock Bay for a total of 12 transects (Weiss et al. 2007).

Culturing phytoplankton

Phytoplankton cultures were grown in GSe medium (Doblin et al. 1999) made with 0.2 μm filtered seawater (FSW) collected from Shinnecock Inlet during flood tide (salinity ~ 29) and maintained in an incubator at 21°C on a 14:10 light:dark cycle (Gobler et al. 1997). Multiple strains of *A. anophagefferens* were grown and used in experiments including CCMP1984 which is the axenic clone of strain CCMP1784 which was originally isolated from Great South Bay, NY, in 1986 and has been reported as being not

toxic to *M. mercenaria* (Bricelj et al. 2001; Bricelj et al. 2004). Strain CCMP1850 was isolated from Great South Bay, NY, in 1998 and has been shown to be highly toxic to copepod nauplii (Smith et al. 2008), but has not been studied with regard to bivalve feeding. Finally, strain CCMP1794 was isolated from Barnegat Bay, NJ, in 1997 and its toxicity has not been reported. The haptophyte *Isochrysis galbana*, Tahitian strain (T-Iso), was cultured as an idealized food source for shellfish under the same conditions described for *A. anophagefferens.* The size range for all *A. anophagefferens* cultures (CCMP1984, 1850, 1794) was 2 – 3µm while *I. galbana* was 3 – 5µm. The similar sizes of these algae allowed a comparison of shellfish clearance rates irrespective of particle size (Bricelj et al 2001).

Collection of bloom water

Water from brown tide blooms was collected from sites within Great South Bay and Quantuck Bay, NY during 2008 and 2009 (Fig. 1). Water was collected 0.5 m below the surface for use in clearance rate and mesocosm experiments. Physical parameters (temperature, salinity and dissolved oxygen) were recorded at each site using an YSI 556 MPS probe. In addition, secchi depth, bottom depth and GPS location were recorded. In July 2008, bay water was collected from six locations across Long Island's south shore bays (Great South Bay and Quantuck Bay) whereas in 2009 water was collected from Quantuck Bay on multiple dates in June and July (Fig. 1).

Clearance rate experiments

To establish the rate at which *C. fornicata* could remove *A. anophagefferens* from suspension, clearance rates of this species in the presence of wild and cultured populations of brown tide were measured according to the "clearance method" as

outlined by Riisgård (2001) which is based upon the indirect clearance method of Fox et al. (1937) and calculations of the exponential decline of particles in a known amount of water with time (Coughlan 1969). Since *M. mercenaria* was formerly the most abundant shellfish in Great South Bay and is currently the largest fishery in New York State (NMFS 2008), parallel clearance rates of *M. mercenaria* on the same diets were also measured. To evaluate the potential effect *A. anophagefferens* has on naïve populations; shellfish were collected from the north shore of Long Island where there has been no historical occurrence of brown tide. Hard clams (49 ± 6.9 mm shell width) were obtained from Frank M. Flowers and Sons, Inc., a shellfish hatchery in Oyster Bay, NY. Stacks of *C. fornicata* were collected from West Meadow Beach, Old Field, NY (Lat: 40° 56' 41" N, Lon: 73° 8' 39" W). For clearance rate experiments in 2009, individual *C. fornicata* (40 ± 2.9 mm shell length) were separated from the stack according to the method described by Newell and Kofoed (1977) leaving one individual snail attached to the empty shell or substrate below the individual. After collection, animals were held at experimental temperatures (~21°C) at the Stony Brook - Southampton Marine Station wet lab facility in a re-circulated temperature controlled sea table. Water in the sea table was changed every 2 days and replaced with fresh FSW. Animals were cleaned of any macroalgae, epiphytes, and/or detritus and fed Instant Algae® Shellfish Diet 1800® according to the manufacturer's recommendations until the day of the experiment which was typically within a week after collection. For each algal strain used in this study, parallel clearance rate experiments for both *C. fornicata* and *M. mercenaria* were performed.

On the day of the experiment, *C. fornicata* and *M. mercenaria* were placed in 0.2 μm FSW under gentle aeration for at least one hour (Shumway et al. 1985; Riisgård 2001; Barillé et al. 2006). Thirteen numbered beakers (volume = 1L) were filled with one liter of treatment water and placed under gentle aeration to maintain a mixed suspension. Cultures requiring dilution to obtain the desired algal biomass (see below) were diluted with 0.2 μm FSW of the same temperature and salinity. Once under aeration, samples were retrieved from all beakers for enumeration of phytoplankton cell densities. For clearance rate experiments using natural populations of *A. anophagefferens*, a 4.5 mL sample of water from each beaker was placed in individual glass culture tubes and preserved with 500 μL of 10% glutaraldehyde solution. Glutaraldehyde preserved samples were stored refrigerated at 4°C for later quantification. For clearance rate experiments using cultures, samples were preserved in Lugol's iodine solution (Throndsen 1978) and stored in the dark for later quantification.

Once initial samples were removed, animals were gently placed in the numbered beakers. Ten beakers were used for animal treatments and three beakers served as controls to account for changes in cell densities not due to animal filtration. Slipper limpets were allowed to feed for 1 hour from the time they were placed in the beaker, whereas *M. mercenaria* were allowed to feed for 1 hour from the time the animals were observed to open and extend their siphon. Samples were obtained every 15 minutes from each beaker according to methods described above until the end of the feeding time and preserved according to the methods described above. Cell counts before and after the known lengths of time were used to determine a clearance rate for each individual according to the formula:

$$Clearance\ Rate\ (L\ hr^{-1}) = \left(\frac{volume\ (L)}{time\ (hr.)}\right) \times \left[\ln\left(\frac{C_i}{C_f}\right) - \ln\left(\frac{C'_i}{C'_f}\right)\right]$$

Where C_i is the initial cell count (cells mL^{-1}) value, C_f is the final cell count (cells mL^{-1}) value, C'_i is the initial control cell count (cells mL^{-1}) and C'_f is the final control cell count (cells mL^{-1}) (Coughlan 1969). Cell counts from control beakers (three for each experiment) were randomly distributed between animal treatments (ten for each experiment) for clearance rate calculations. Random numbers were generated using the RAND function in Microsoft Excel (version 12.0.6425.1000). For random numbers between 0.00 & 0.333, control 1 was assigned; for random numbers between 0.333-0.667, control 2 was assigned, and so on. Once the experiment was concluded, animals were removed and frozen for 24 hours. The soft tissue was then removed and placed in a pre-weighed tin, weighed using an analytical balance (Mettler Toledo AG204), dried at 60°C and weighed again to determine tissue dry weight (DW). Animals were of a narrow size range (1.93 ± 0.16 g for *C. fornicata* and 2.19 ± 0.16 g for *M. mercenaria*) which allowed weights to be used to normalize clearance rates to tissue weight rather than to individual yielding clearance rates in units L hr^{-1} g^{-1}, and thus facilitating a weight specific comparison between the two species.

Diets for clearance rate experiments included natural field assemblages from Long Island estuaries with varying densities of *A. anophagefferens* and unialgal cultures described above. For culture clearance rate experiments, treatments included three strains of *A. anophagefferens* (CCMP1984, 1850, and 1794), fed to two shellfish species at 10^5 and 10^6 *A. anophagefferens* cells mL^{-1}, the observed range of concentrations in NY estuaries during blooms of brown tides (Gobler et al. 2005; including this study).

Additionally, for each strain-shellfish-density combination, parallel clearance rates were performed using an ideal food source (*I. galbana*) at equivalent biovolumes (1 *I. galbana* cell = ~ 8 *A. anophagefferens* cells) with each species of shellfish and each biovolume concentration. Each algal composition and concentration experiment with each shellfish species consisted of 10 replicate beakers with animals and 3 control beakers without animals. Therefore, each *A. anophagefferens* strain experiment combination involved 8 experiments (2 shellfish species x 2 algal species x 2 food concentrations). Cultures were counted prior to experiments using a hemacytometer and appropriate dilutions were made with 0.2µm FSW. All clearance rates generated for field and culture experiments involving *A. anophagefferens* were expressed as *A. anophagefferens*-specific clearance rates. Clearance rates involving cultured *I. galbana* are expressed as *I. galbana*-specific clearance rates.

Quantification of *Aureococcus anophagefferens*

To quantify *A. anophagefferens* cell densities, two methods were employed depending on the sample source. Samples from the field were quantified using a monoclonal antibody (MAb) technique which has been adapted to a colorimetric, enzyme-linked immunosorbent assay (ELISA) format performed in a 96-well plate (Caron et al. 2003). This technique provides more accurate and rapid detection of *A. anophagefferens* cells in mixed algal samples over both the immunofluorescent staining with a polyclonal antibody (PAb) method and traditional microscopy techniques since *A. anophagefferens* is small and non-distinct making it impossible to distinguish from other picoplankton in field samples (Sieburth et al. 1988; Anderson et al. 1989; Caron et al. 2003; Gobler et al. 2005). This assay yielded a 95.5 ± 15.9% recovery of samples spiked

with known amounts of *A. anophagefferens*, a methodological relative standard deviation of 8.1 ± 6.6%, and a mean detection limit of 3.6 ± 2.1 x 10^3 cells mL^{-1}. Dense bloom samples were diluted to fall between the detection limit and the highest standard with a solution of 0.2 µm filtered seawater in 1% glutaraldehyde.

For unialgal culture experiments, cells were enumerated following the methods of Bricelj et al. (2001). Samples of both *A. anophagefferens* and *I. galbana* were counted using a Beckman Coulter Multisizer™ 3 Coulter Counter® with a 50µm aperture. Stock cultures of both species were verified microscopically with a hemacytometer (Bricelj et al. 2001). This counting method yielded a mean relative standard deviation of 5.9 ± 2.7% for both species.

Mesocosm experiments

Two mesocosm experiments were conducted during June 2008 to assess the ability of *C. fornicata* and *M. mercenaria* to suspension-feed during natural blooms of *A. anophagefferens*. Experiments were carried out in 70 L polyethylene tubs (depth = 42 cm, inside top diameter = 50 cm, inside bottom diameter = 42 cm) maintained under ambient light and temperature conditions. Hard clam densities used in the experiments (29 and 22 individuals m^{-2}) were chosen to match *C. fornicata* densities on a biomass-specific basis (see below). Hard clam densities were larger than historical average densities of the species (7.76 individ. m^{-2}, Kraeuter et al. 2008), but lower than patch densities in NY during the 1970's (50-100 individuals m^{-2}, Cerrato et al. 2004). For *C. fornicata*, densities of >100 individuals m^{-2} have been reported for some regions of the Peconic Estuary (Lewis et al. 1997) and numbers as high as 1,400 individuals m^{-2} have been observed in Shinnecock Bay (this study) which is similar to numbers documented in

the Bay of Brest, France (Chauvaud et al. 2000). For these experiments, densities were purposely similar to those found in the higher populated areas of the Peconic Estuary, (188 - 245 individuals m^{-2} *C. fornicata*). Since *C. fornicata* naturally occurs in stacks, mesocosm experiments followed the methods of Barillé et al. (2006) and *C. fornicata* used in these experiments were in stacks of 6 to 8 individuals, matching median stack sizes observed during field surveys. Additionally ash-free dry weights (AFDW) were used in place of dry weight for clearance rate calculations. Both *M. mercenaria* and *C. fornicata* were placed in numbered tin weigh boats, frozen for 24 h, dried at 60°C for 24 h, weighed using an analytical balance (Mettler Toledo AG204), combusted at 450°C for 4 h, and weighed again to determine the ash-free dry weight (AFDW) of their tissues.

For all experiments, replicates for each treatment were placed among the array of mesocosms using a randomized block design (Sokal and Rohlf 1995) to minimize any effects due to placement of the mesocosms. Bloom water was collected from Great South Bay and Quantuck Bay and transported back to the Stony Brook - Southampton Marine Station following the methods described above. Water circulator pumps (Rio® 180 Mini Aqua Pump, pumping rate: 456 L h^{-1}) were then added to ensure adequate mixing of the water column. To commence experiments, initial parameters were measured within the mesocosms included temperature, salinity, dissolved oxygen and chlorophyll *a* (GFF glass fiber filter). In addition, samples were preserved in glutaraldehyde for later quantification of *A. anophagefferens* according to the methods described above. After initial samples were processed, *C. fornicata* and *M. mercenaria* were gently placed in the bottom of the mesocosms in trays. Nutrients (5 μM ammonium and 0.31 μM orthophosphate) were added daily to mimic a nutrient loading rate similar to NY estuaries

(Wall et al. 2008). Initial measurements were repeated daily until the end of the experiment (3-4 days).

At the end of each mesocosm experiment, clearance rates by *C. fornicata* and *M. mercenaria* on the phytoplankton (chlorophyll *a*) and *A. anophagefferens* in the control mesocosms were determined as described above. After processing all samples, remaining water in the mesocosms was sterilized using a combination of bleach and sodium thiosulfate to ensure *A. anophagefferens* cells were not released into the surrounding waters.

The first mesocosm experiment was carried out from 6 June 2008 to 9 June 2008. Nine mesocosms were each filled with 60 liters of bloom water obtained from Great South Bay in Long Island, NY (Lat: 40° 41' 34.98" N, Lon: 73° 9' 15.9" W) with 4.7 x 10^5 *A. anophagefferens* cells mL^{-1} and ambient chlorophyll *a* of 20.5 μg L^{-1}. Treatments involved three mesocosms as controls which contained no animals, three mesocosms which contained four *M. mercenaria* (29 individuals m^{-2}, 11.5g AFDW), and three mesocosms with four stacks each (26 individuals) of *C. fornicata* (188 individuals m^{-2}, 5.3g AFDW). The second mesocosm experiment was carried out from 12 June 2008 to 16 June 2008. In this experiment, water was collected from Quantuck Bay in Long Island, NY (Lat: 40° 48' 21.66" N, Lon: 72° 37' 13.74" W) with 9.5 x 10^5 *A. anophagefferens* cells mL^{-1} and ambient chlorophyll *a* of 37.0 μg L^{-1}. Treatments included three control mesocosms, three mesocosms with three *M. mercenaria* each (22 individuals m^{-2}, 7.0g AFDW), and three mesocosms with four stacks each (34 individuals) of *C. fornicata* (245 individuals m^{-2}, 6.7g AFDW).

Statistical analyses

Clearance rates of algal cultures by *C. fornicata* and *M. mercenaria* were analyzed using a two-way analysis of variance (ANOVA) where the composition and concentration of food were the main effects. Post-hoc multiple comparisons were performed with Student-Newman-Keuls tests. Data sets which did not meet the assumption of normality or heterogeneity of variance were log transformed. For experiments using wild populations of plankton, mean clearance rates of each mollusc were analyzed using t-tests or Mann-Whitney Rank Sum tests for non-normal data. A Spearman rank correlation was used to assess the relationships between *A. anophagefferens* densities of field populations and clearance rates for each shellfish. For mesocosm experiments, changes in levels of chlorophyll *a* and *A. anophagefferens* cell densities were analyzed using a one-way ANOVA with post-hoc multiple comparisons made via Student-Newman-Keuls tests. Statistical analyses were performed with SigmaStat (Version 3.5, Build 3.5.0.54).

RESULTS

Survey of *Crepidula fornicata*

Densities of *C. fornicata* within eastern Shinnecock Bay varied greatly. Slipper limpets were most abundant on the southeastern shore of Shinnecock Bay where densities ranged from 0 to 1,496 individuals m^{-2} and averaged 776 individuals m^{-2} (Table 2). Along the northern shore of this basin, a similar range of densities was found and densities averaged 182 individuals m^{-2}. Other locations consisted of sandy bottoms and hosted lower densities of *C. fornicata*, with means ranging from 6 to 124 individuals m^{-2} (Table 2).

Clearance Rates of Algal Monocultures

For experiments with *A. anophagefferens* clone CCMP1794, clearance rates of *C. fornicata* were greater at the 10^5 cells mL^{-1} level (1.17 ± 0.10 L $hr.^{-1}$ g^{-1}) than at the 10^6 cells mL^{-1} level (0.59 ± 0.09 L $hr.^{-1}$ g^{-1}; $p < 0.05$; Student-Newman-Keuls). When fed *I. galbana*, clearance rates of *C. fornicata* were similar at both algal densities and similar to those of *M. mercenaria* at the same food densities, averaging 0.76 ± 0.24 L $hr.^{-1}$ g^{-1}. Additionally, clearance rates of *C. fornicata* when fed CCMP1794 at 10^6 cells mL^{-1} (0.59 ± 0.09 L $hr.^{-1}$ g^{-1}) were significantly lower than when fed *I. galbana* at equivalent biovolume (1.12 ± 0.11 L $hr.^{-1}$ g^{-1}; $p < 0.05$; Student-Newman-Keuls). Due to differences in clearance rates of *C. fornicata* in the presence of differing levels of clone CCMP1794, but not differing levels of *I. galbana,* there was an interaction between diet composition and concentration for *C. fornicata* ($F = 4.650$, $df = 39$, $p < 0.05$; Two-way ANOVA). For *M. mercenaria*, both diet composition and concentration were significant treatment factors ($F(1) = 5.972$, $df = 29$, $p < 0.05$; $F(2) = 26.490$, $df = 29$, $p < 0.001$, Two-way ANOVA). Clearance rates of *M. mercenaria* fed clone CCMP1794 were significantly lower than rates of individuals fed *I. galbana* at both biovolume levels ($p < 0.05$; Student-Newman-Keuls). Additionally, clearance rates of *M. mercenaria* fed *I. galbana* at 10^6 cell equivalents mL^{-1} (1.06 ± 0.14 L hr^{-1} g^{-1}) were significantly greater than those when fed *I. galbana* at 10^5 cell equivalents mL^{-1} (0.69 ± 0.14 L hr^{-1} g^{-1}; $p < 0.05$; Student-Newman-Keuls)

For clearance rates of *C. fornicata* fed *A. anophagefferens* clone CCMP1850, neither diet composition nor diet concentration were significant treatment effects, although there was a significant interaction between diet composition and concentration

($F = 13.511$, $df = 22$, $p < 0.05$; Two-way ANOVA). Clearance rates for *C. fornicata* were higher when fed *I. galbana* at 10^6 cell equivalents mL^{-1} (1.40 ± 0.24 L hr^{-1} g^{-1}) than at the 10^5 cell equivalents mL^{-1} (0.60 ± 0.16 L hr^{-1} g^{-1}) ($p < 0.05$; Student-Newman-Keuls). Additionally, clearance rates by *C. fornicata* were lower when fed CCMP1850 at 10^6 cells mL^{-1} when compared to a good food source (*I. galbana*) at the equivalent biovolume ($p < 0.05$; Student-Newman-Keuls). In contrast, for clearance rates of *M. mercenaria*, both diet composition and diet concentration were significant effects ($F(1) = 15.221$, $F(2) = 16.096$, $df = 14$, $p < 0.05$; Two-way ANOVA; Fig. 3). Specifically, mean clearance rates of *M. mercenaria* fed clone CCMP1850 at both food concentrations (0.07 ± 0.03 L hr^{-1} g^{-1}) were five-fold lower than those of *I. galbana* (0.34 ± 0.01 L hr^{-1} g^{-1}; $p < 0.05$; Student-Newman-Keuls). Additionally, similar to *C. fornicata*, clearance rates by *M. mercenaria* when fed *I. galbana* were higher at the 10^6 level (0.62 ± 0.10 L hr^{-1} g^{-1}) than the 10^5 level (0.06 ± 0.01 L hr^{-1} g^{-1}) ($p < 0.05$; Student-Newman-Keuls).

Clone CCMP1984 is the strain of *A. anophagefferens* which has previously been shown to have no inhibitory effects on clearance rates of *M. mercenaria* (Bricelj et al 2001). For clearance rates of *C. fornicata* fed the clone CCMP1984, diet composition was a significant treatment effect whereas diet concentration was not ($F = 8.011$, $df = 39$, $p < 0.05$; Two-way ANOVA). Specifically, clearance rates by *C. fornicata* were significantly higher when fed *I. galbana* at the 10^6 cell equivalents mL^{-1} (1.23 ± 0.15 L hr^{-1} g^{-1}) than those of *I. galbana* at the 10^5 cell equivalents mL^{-1} density (0.80 ± 0.14 L hr^{-1} g^{-1}) ($p < 0.05$; Student-Newman-Keuls). Additionally, clearance rates of *C. fornicata* were significantly higher in the presences of *I. galbana* at 10^6 cell equivalents mL^{-1} (1.23 ± 0.15 L hr^{-1} g^{-1}) than those in the presence of 10^6 CCMP1984 cells mL^{-1} (0.70 ± 0.08 L

hr^{-1} g^{-1}) ($p < 0.05$; Student-Newman-Keuls). Although there was no concentration dependent effect on clearance rates for *C. fornicata*, concentration was a significant factor in clearance rates of *M. mercenaria* whereas composition was not ($F = 33.975$, $df = 30$, $p < 0.001$; Two-way ANOVA). Specifically, clearance rates of *M. mercenaria* were significantly higher in the presence of 10^6 CCMP1984 cells mL^{-1} (1.29 ± 0.24 L hr^{-1} g^{-1}) than at the 10^5 CCMP1984 cells mL^{-1} treatment (0.52 ± 0.08 L hr^{-1} g^{-1}, $p < 0.001$; Student-Newman-Keuls). Additionally, clearance rates of *M. mercenaria* were significantly higher in the presence of *I. galbana* at 10^6 cell equivalents mL^{-1} (1.26 ± 0.13 L hr^{-1} g^{-1}) than those of *I. galbana* at the 10^5 cell equivalents mL^{-1} density (0.43 ± 0.07 L hr^{-1} g^{-1}) ($p < 0.05$; Student-Newman-Keuls; Fig. 4).

South Shore Survey

On 11 July 2008, water was collected from multiple locations across the south shore of Long Island, including Babylon, Bay Shore, Sayville, Patchogue, and Bellport in Great South Bay, and a site in Quantuck Bay (Fig. 1). Brown tide cell densities were high in Quantuck Bay and Sayville (1.07 x 10^6 and 8.11 x 10^5 cells mL^{-1}, respectively), moderate in Bay Shore and Babylon (4.02 x 10^5 and 2.30 x 10^5 cells mL^{-1}, respectively), and lower in Bellport and Patchogue (2.98 x 10^4 and 2.85 x 10^4 cells mL^{-1}, respectively; Table 1). Chlorophyll *a* levels across sites ranged from 7.65 µg L^{-1} (Bellport) to 43.28 µg L^{-1} (Quantuck Bay; Table 1). There was a wide range of *A. anophagefferens*-specific clearance rates (calculated from the change in *A. anophagefferens* cells with time) displayed by each suspension-feeder in 2008, with *C. fornicata* displaying a maximal rate of 2.53 ± 0.45 L $hr.^{-1}$ g^{-1} in Babylon and a minimal rate of 0.25 ± 0.06 L $hr.^{-1}$ g^{-1} in Sayville and *M. mercenaria* displaying a maximal rate of 0.18 ± 0.14 L $hr.^{-1}$ g^{-1} in

Babylon and a minimal rate of 0.04 ± 0.02 L hr.$^{-1}$ g^{-1} in Sayville. On average, *C. fornicata* displayed *A. anophagefferens*-specific clearance rates (1.36 ± 0.46 L hr.$^{-1}$ g^{-1}) which were an order of magnitude greater than those of *M. mercenaria* (0.13 ± 0.03 L hr.$^{-1}$ g^{-1}; $p <$ 0.001; Mann-Whitney Rank Sum Test) (Fig. 5).

Additional experiments were also conducted during the 2009 brown tide bloom in Quantuck Bay with brown tide cell densities ranging from 7.2 x 10^5 to 1.3 x 10^6 cells mL^{-1} during June and July. In these experiments, the filtration rates of individual and stacked *C. fornicata* were explored (Fig. 5). As was observed in 2008, clearance rates of *C. fornicata* fed *A. anophagefferens* were greater than those of *M. mercenaria*, however this difference was not significant ($p > 0.05$; Mann-Whitney Rank Sum Test), although rates for both species were lower than those observed in 2008. Stacks and individual *C. fornicata* had *A. anophagefferens*-specific clearance rates of 0.13 ± 0.04 and 0.11 ± 0.04 L hr.$^{-1}$ g^{-1} respectively, whereas hard clam rates were 0.07 ± 0.03 L hr.$^{-1}$ g^{-1} (Fig. 5).

For all field-based bloom water experiments, both molluscan species displayed an inverse relationship between clearance rates and *A. anophagefferens* abundance. The highest clearance rates (2.53 ± 0.45 L hr.$^{-1}$ g^{-1} for *C. fornicata* and 0.18 ± 0.06 L hr.$^{-1}$ g^{-1} for *M. mercenaria*) were found using water from locations with low *A. anophagefferens* densities (1.8 ± 0.88 x 10^4 cells mL^{-1}, Babylon). The lowest clearance rates (0.04 ± 0.01 L hr.$^{-1}$ g^{-1} for *C. fornicata* and 0.04 ± 0.01 L hr.$^{-1}$ g^{-1} for *M. mercenaria*) were found using water from locations with extremely high *A. anophagefferens* densities (1.3 ± .03 x 10^6 cells mL^{-1} Quantuck Bay). There was significant inverse correlation between clearance rates of *M. mercenaria*. and *A. anophagefferens* densities (Fig. 5; Spearman Correlation, $p < 0.05$), but not for *C. fornicata*.

Mesocosm Experiments

The first mesocosm experiment, performed on 6 June 2008, using bloom water from Great South Bay (4.7 x 10^5 *A. anophagefferens* cells mL^{-1} and ambient chlorophyll *a* of 21 μg L^{-1}) and the *C. fornicata* treatment biomass level (5.3 g AFDW) was less than half of the *M. mercenaria* treatment biomass (11.5 g AFDW). Despite this difference, after three days, chlorophyll *a* levels and *A. anophagefferens* concentrations in the *C. fornicata* treatment were markedly reduced to 3.57 ± 0.43 μg L^{-1} chlorophyll *a* and 2.9 ± 1.6 x 10^4*A. anophagefferens* cells mL^{-1}. In contrast, the control and *M. mercenaria* treatments had chlorophyll *a* and *A. anophagefferens* counts of 19.96 ± 1.05 μg L^{-1} and 2.9 ± 0.4 x 10^5 cells mL^{-1}, and 11.91 ± 3.17 μg L^{-1} and 2.3 ± 0.6 x 10^5 cells mL^{-1}, respectively, levels that were all significantly greater than the *C. fornicata* treatment (F = 10.453, df = 8, $p <$ 0.05; One-Way ANOVA). At the end of the experiment, clearance rates for *M. mercenaria* (0.08 ± 0.03 L $hr.^{-1}$ g^{-1}) were significantly lower than those for *C. fornicata* 0.61 ± 0.06 L $hr.^{-1}$ g^{-1} ($p < 0.001$, t-test; Fig. 6).

The second mesocosm experiment was performed the following week (12 June 2008) using water collected from Quantuck Bay (9.5 x 10^5 *A. anophagefferens* cells mL^{-1} and 37.0 μg chlorophyll *a* L^{-1}). After four days, mesocosms with 7.0 g AFDW of *M. mercenaria* and the control showed almost no change in *A. anophagefferens* levels (9.5 ± 2.2 x 10^5 cells mL^{-1} and 6.1 ± 2.3 x 10^5 cells mL^{-1}, respectively, on day four) or chlorophyll *a* (35.26 ± 3.12 μg L^{-1} and 31.08 ± 2.27 μg L^{-1}, respectively). In stark contrast, in mesocosms containing 6.7 g AFDW of *C. fornicata*, *A. anophagefferens* cell densities (1.1 ± 0.3 x 10^5 cells mL^{-1}) and chlorophyll *a* levels (19.38 ± 6.91 μg L^{-1}) were significantly lower than levels found in the control and *M. mercenaria* treatments (F =

15.306, $df = 6$, $p < 0.05$; One-Way ANOVA). Clearance rates for *M. mercenaria* (0.05 ± 0.04 L $hr.^{-1}$ g^{-1}) were lower than those for *C. fornicata* (0.21 ± 0.08 L $hr.^{-1}$ g^{-1}) however, this difference was not significant ($p > 0.05$, t-test; Fig. 7).

DISCUSSION

Brown tides caused by the harmful pelagophyte *Aureococcus anophagefferens* have had devastating effects on shellfish populations across the northeast United States. In 1985, in Narragansett Bay, Rhode Island, blooms killed a large portion of the blue mussel population, *Mytilus edulis* (Sieburth et al. 1988; Tracey 1988). Similarly, brown tides caused recruitment failure and adult mortality of bay scallops in the Peconic Estuary leading to the demise of this population (Bricelj and Lonsdale 1997). Across the south shore of Long Island waters, brown tide blooms have occurred sporadically since 1985, contributing to the low recruitment and accelerated decline in the hard clam fishery in Great South Bay (Kraeuter et al. 2005; Hofmann et al. 2006). In contrast to resource bivalves such as scallops, hard clams, and blue mussels which have been decimated by brown tides (as reviewd by Bricelj and Lonsdale 1997; Gobler et al. 2005), the American slipper limpet (*C. fornicata*) grazed robustly in the presence of *A. anophagefferens* (both toxic and non-toxic cultured strains as well as wild populations) and maintained high clearance rates when compared to *M. mercenaria*, even at concentrations exceeding 10^6 *A. anophagefferens* cells mL^{-1} (Fig. 2 - 5).

During experiments with algal cultures, clearance rates of *M. mercenaria* matched or exceeded clearance rates by *C. fornicata* when fed the biomass equivalent of 10^6 cells mL^{-1} of a preferred food source (*I. galbana*; Fig 2 – 3), confirming that under ideal conditions, *M. mercenaria* is an efficient filter feeder and can compete well with *C.*

fornicata. This pattern is, however, reversed in the presence of *A. anophagefferens*. For example, snails cleared the toxic strain CCMP1850 (Smith et al. 2008) at rates more than an order of magnitude greater than those of *M. mercenaria*, but similar to those when fed *I. galbana* (Fig. 3). Similarly, clearance rates of *C. fornicata* fed clone CCMP1794 and *I. galbana* at 10^5 cells mL^{-1} were similar while clearance rates of *M. mercenaria* were significantly reduced when fed *A. anophagefferens* strain CCMP1794 when compared to a diet of *I. galbana* at both food concentrations (Fig. 2). Clone CCMP1984 is clone CCMP1784 without bacteria and this strain has been previously identified as non-toxic to hard clams (Bricelj et al. 2001). Accordingly, clearance rates of clone CCMP1984 were similar to those of *I. galbana* for *M. Mercenaria* at both algal densities. Clearance rates of *C. fornicata*, however, were lower when fed the clone CCMP1984 at 10^6 cells mL^{-1} as compared to that of *I. galbana* at an equivalent biovolume (Fig. 4).

In the presence of wild, bloom populations of *A. anophagefferens* (10^4 to 10^6 cells mL^{-1}), *C. fornicata* consistently displayed clearance rates more than an order of magnitude greater than those of *M. mercenaria* (Fig. 5). These low clearance rates for *M. mercenaria* are consistent with prior research since *A. anophagefferens* densities were at or far above the threshold level known to inhibit *M. mercenaria* clearance rates (Bricelj et al. 2001). In fact, there was a significant reverse correlation between *A. anophagefferens* densities and clearance rates of *M. mercenaria* ($p < 0.05$). A threshold effect of *A. anophagefferens* on *C. fornicata* was not obvious as animals maintained near maximal clearance rates (as observed in this study) even as ambient cell densities approached 10^6 cells mL^{-1}. There were, however, four field-based experiments when *A. anophagefferens* densities were high (10^5 to 10^6 cells mL^{-1}), where clearance rates of *C. fornicata* were

lower than rates observed when feeding on cultures or on some field blooms. Such differences suggest that other members of the plankton community and/or particles in the water column in these regions may impact clearance rates of *C. fornicata* or that there are differences in *A. anophagefferens* field populations which affect clearance rates.

In short term mesocosm experiments with bloom concentrations of *A. anophagefferens* (10^5 to 10^6 cells mL^{-1}), *C. fornicata* significantly reduced chlorophyll *a* and brown tide levels relative to control treatments while equal or greater biomass levels of *M. mercenaria* did not (Fig. 6 & 7). This was most dramatic in the second mesocosm experiment when *C. fornicata* reduced 10^6 *A. anophagefferens* cells mL^{-1} by an order of magnitude in only four days, while a population of *M. mercenaria* at similar biomass levels had no effect on *A. anophagefferens* densities. These results are consistent with the clearance rates by each species measured during experiments which demonstrated that *M. mercenaria* individuals were feeding at very low rates. These experimental results further suggest that at sufficient densities (> 100 m^{-2}) *C. fornicata* could serve as a top down control during brown tides in regions with slow tidal flushing rates.

At high concentrations, *A. anophagefferens* causes a depression of filtration rates or even a complete cessation of feeding in some bivalves which leads to eventual starvation (Tracey 1988; Bricelj et al. 1989; Gallager et al. 1989; Bricelj et al. 2001). This physiological effect has been linked to the dopamine-like inhibitory compound found on the extracellular polysaccharide coating of *A. anophagefferens*. The toxicity of this coating causes a decrease in the activity of the lateral cilia of the gills of numerous bivalve species including *Mytilus edulis*, *Mercenaria mercenaria*, *Crassostrea virginica*, *Ostrea edulis*, and *Modiolus modiolus* (Gainey and Shumway 1991). In contrast to these

bivalves, *C. fornicata* secretes a mucus net across the entrance to the ciliated gill chamber to capture particles (Werner 1951), allowing it to retain small particles efficiently and at high particle loads (Jørgensen et al. 1984; Barillé et al. 2006). This difference in particle capture physiology may account for the ability of *C. fornicata* to filter high densities of *A. anophagefferens* which inhibit some bivalves and the mucus net likely acts to shield the animal from the inhibitory effects of *A. anophagefferens*. Interestingly, there was a statistically significant inverse relationship between *C. fornicata* clearance rates and *A. anophagefferens* densities in natural blooms ($p < 0.05$; Fig. 5). In feeding experiments using monocultures, this relationship was observed in clones CCMP1794, CCMP1984 and CCMP1850 (Fig. 2 - 4) where an increase of *A. anophagefferens* cell density resulted in a decreased clearance rate by *C. fornicata*. While these results suggests that high densities of *A. anophagefferens* (10^6 cells mL^{-1}) can reduce *C. fornicata* suspension-feeding, there was no cessation in feeding at high cell densities as seen in other bivalve species (Gainey and Shumway 1991; Shumway et al., unpubl.); in mesocosms, *C. fornicata* was able to clear 10^6 *A. anophagefferens* cells mL^{-1} down to 10^5 cells mL^{-1} in four days (Fig. 7).

At sufficient densities, grazing by suspension-feeding bivalves can play a pivotal role in controlling phytoplankton biomass in shallow estuaries (Officer et al. 1982). Furthermore, suspension-feeders are embedded within an overarching grazing cascade which can regulate both eutrophication and harmful algal blooms (Smayda 2008). In the case of brown tides, blooms have been shown to initiate when the dominant nitrogen source is dissolved organic matter (DOM) (Berg et al. 1997; Berg et al. 2003; Mulholland et al. 2004; Gobler et al. 2005) and when grazing pressure from zooplankton and bivalve

suspension-feeders has failed (Smayda 2008; and references therein). With the loss of the northern quahog population in Great South Bay and the absence of any other macrofaunal suspension-feeders, the grazing community has shifted to one dominated by zooplankton which often cannot control blooms (Bricelj 2009). A reduced rate of grazing by both pelagic and benthic grazers is believed to contribute to the persistence of *A. anophagefferens* blooms (Bricelj and Lonsdale 1997; Gobler et al. 2002; Caron et al. 2004; Gobler et al. 2004).

Benthic macrofauna not only contribute to the reduction in phytoplankton biomass, but are important contributors to the flux of nutrients to and from the sediment. A decrease in grazing lowers the grazer-mediated nutrient recycling which can further encourage ecosystem disruptive algal blooms such as *A. anophagefferens* (Sunda et al. 2006). Studies in the Bay of Brest, France have shown that *C. fornicata* (the now dominant benthic suspension-feeder in this eutrophied bay) may be preventing the occurrence of toxic alga blooms by acting as an effective silicate pump allowing diatoms to dominate throughout summer months (Ragueneau et al. 2002). Slipper limpets may play a similar role in NY estuaries where they are the dominant benthic suspension-feeder. While hard clams and bay scallops were the dominant resource bivalves in New York estuaries during the late twentieth century, landings of both species have declined by more than 99% (NYSDEC 2008) due in part to harmful brown tides blooms caused by *A. anophagefferens* (Gainey and Shumway 1991; Bricelj et al. 2001; Cerrato et al. 2004; Wazniak and Glibert 2004). In the Peconic Estuary, populations of the American slipper limpet (*C. fornicata*) were found at densities exceeding 600 individuals m^{-2} in the mid-1990s (Lewis et al. 1997). Populations of *C. fornicata* at levels similar to those present in

the Peconic Estuary were found in surveys of eastern Shinnecock Bay during this study, with densities up to 1,500 individ. m^{-2} and mean densities of 246 individuals m^{-2} (Table 2). Given the high densities of *C. fornicata* in these systems since the onset of brown tides, it seems this species may be filling a niche once dominated by bay scallops and other bivalves, maintaining high rates of filtration in shallow waters regardless of ambient *A. anophagefferens* densities.

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APPENDIX

Table 1 Physical parameters of sampling locations for the south shore of Long Island, NY, USA.

	Site	Lat	Lon	Temp. (°C)	Sal.	Total chlorophyll *a* [µg L^{-1}]	Chlorophyll *a* > 5 µm [µg L^{-1}]	*A. anophagefferens* Cell Density [cell mL^{-1}]
July 2008	Sayville	40° 43' 12"	-73° 05' 38"	24.7	27.1	23.25 ± 1.93	2.20 ± 0.23	8.1 ± 0.5 x10^5
	Bay Shore	40° 42' 39"	-73° 14' 22"	24.8	28.5	21.85 ± 2.05	2.95 ± 0.56	4.0 ± 0.4 x10^5
	Babylon	40° 40' 50"	-73° 18' 56"	24.6	28.0	16.41 ± 0.79	3.17 ± 0.72	1.8 ± 0.08 x 10^5
	Bellport	40° 45' 07"	-72° 55' 58"	25.0	24.5	7.65 ± 0.53	1.05 ± 0.03	3.0 ± 0.7 x 10^4
	Patchogue	40° 44' 50"	-73° 00' 34"	25.3	24.9	9.54 ± 0.98	1.87 ± 0.11	2.9 ± 0.2 x 10^4
Quantuck Bay	11-July-08	40° 48' 08"	-72° 37' 12"	25.0	27.2	30.36 ± 3.97	1.34 ± 0.09	1.1 ± 0.06 x 10^6
	25-June-09	40° 48' 08"	-72° 37' 12"	20.4	24.4	19.97 ± 6.12	7.31 ± 0.32	7.6 ± 0.3 x 10^5
	13-July-09	40° 48' 08"	-72° 37' 12"	24.3	25.3	43.28 ± 2.50	6.24 ± 0.66	1.3 ± 0.03 x 10^6
	23-July-09	40° 48' 08"	-72° 37' 12"	25.4	24.7	21.12 ± 1.77	4.11 ± 0.44	7.2 ± 0.4 x 10^5

Table 2 Results of *C. fornicata* survey in Shinnecock Bay [Ind. m^{-2} ± SE].

Site	Transect	*C. fornicata* count [Ind. m^{-2}]	Site Average [Ind. m^{-2}]	Shinnecock Average [Ind. m^{-2}]
North	1	243 ± 48	182 ± 63	272 ± 172
	2	56 ± 25		
	3	246 ± 51		
South	4	1,496 ± 216	776 ± 420	
	5	42 ± 17		
	6	790 ± 316		
East	7	239 ± 22	124 ± 63	
	8	112 ± 26		
	9	22 ± 6		
West	10	2 ± 1	6 ± 2	
	11	8 ± 4		
	12	10 ± 10		

Figure 1 Brown tide bloom water collection sites across the south shore of Long Island, NY, USA (diamonds). Triangles in Shinnecock Bay indicate *Crepidula* survey locations.

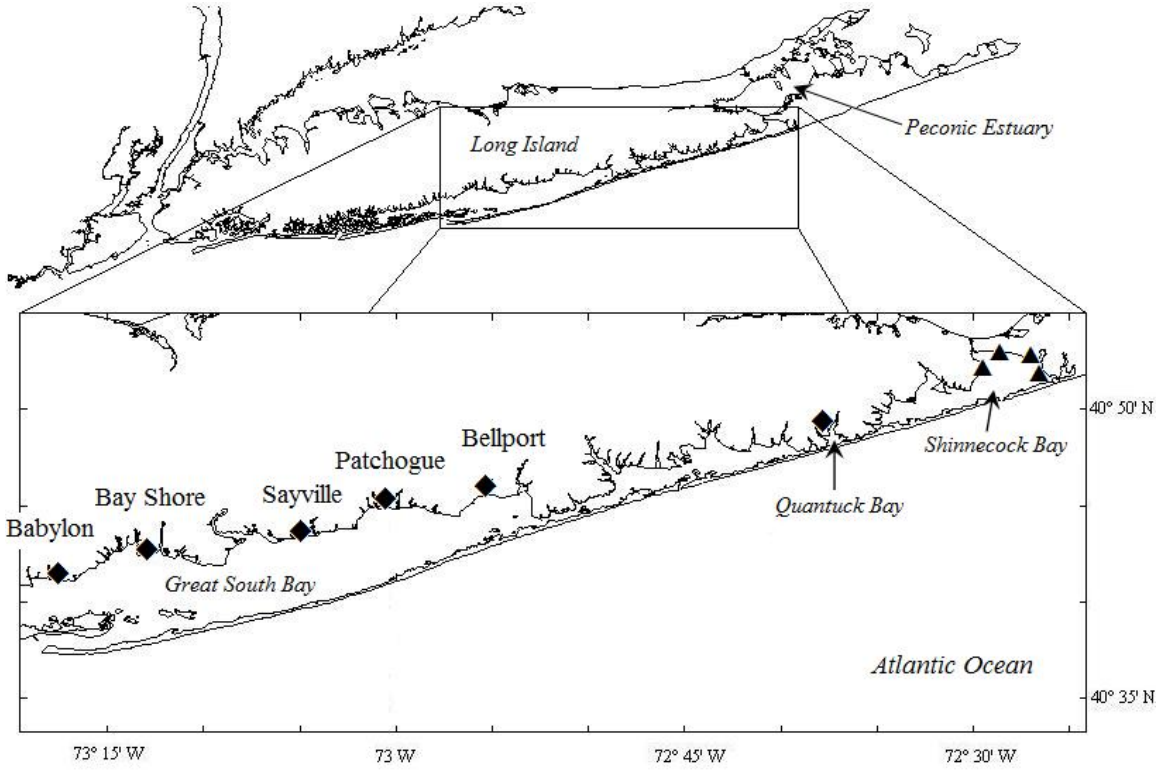


Figure 2 Clearance rates (CR) of *C. fornicata* and *M. mercenaria* when fed 10^5 and 10^6 *A. anophagefferens* clone CCMP1794 cells mL^{-1} (A.a.) and biovolume equivalents of *I. galbana* (T-iso). Error bars indicate standard error.

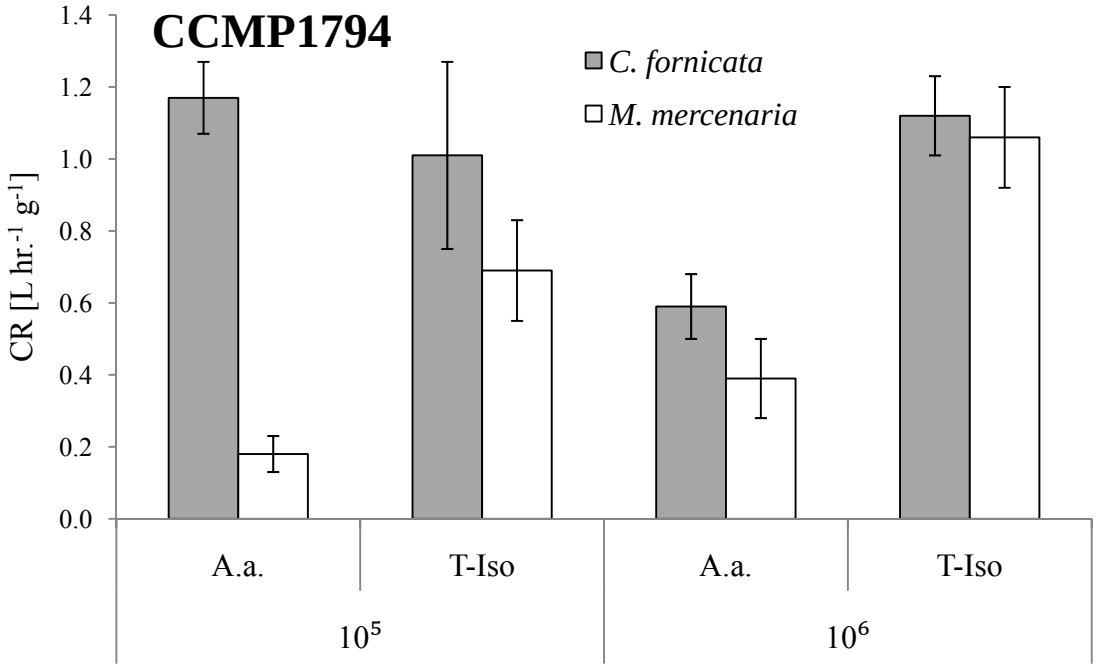


Figure 3 Clearance rates (CR) of *C. fornicata* and *M. mercenaria* when fed 10^5 and 10^6 *A. anophagefferens* clone CCMP1850 cells mL^{-1} (A.a.) and biovolume equivalents of *I. galbana* (T-iso). Error bars indicate standard error.

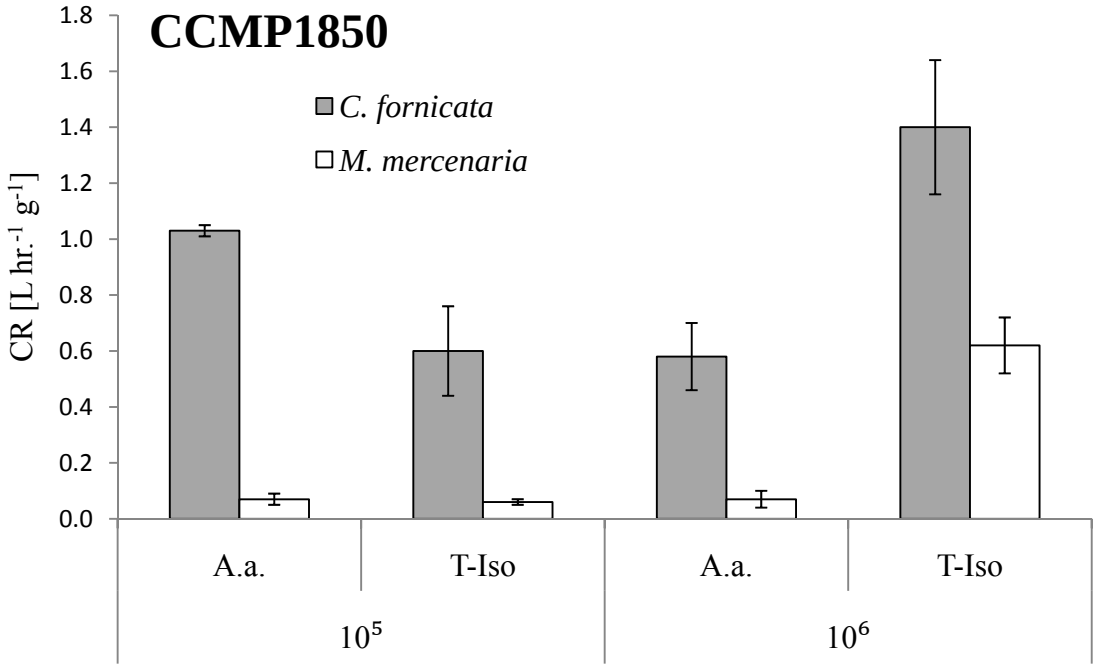


Figure 4 Clearance rates (CR) of *C. fornicata* and *M. mercenaria* when fed 10^5 and 10^6 *A. anophagefferens* clone CCMP1984 cells mL^{-1} (A.a.) and biovolume equivalents of *I. galbana* (T-iso). Error bars indicate standard error.

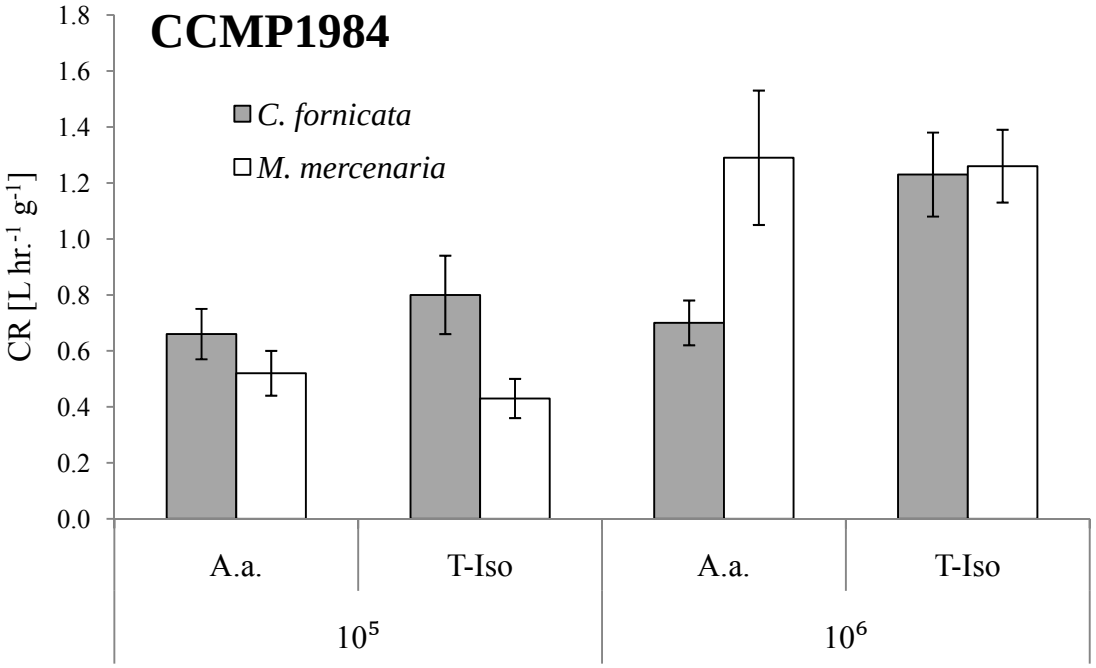


Figure 5 Clearance rate (CR) of molluscs (solid bars) on *A. anophagefferens* cells compared to *A. anophagefferens* cell concentration (striped bars) at each site during the 2008 and 2009 brown tide blooms in Long Island south shore bays and estuaries. Error bars indicate standard error.

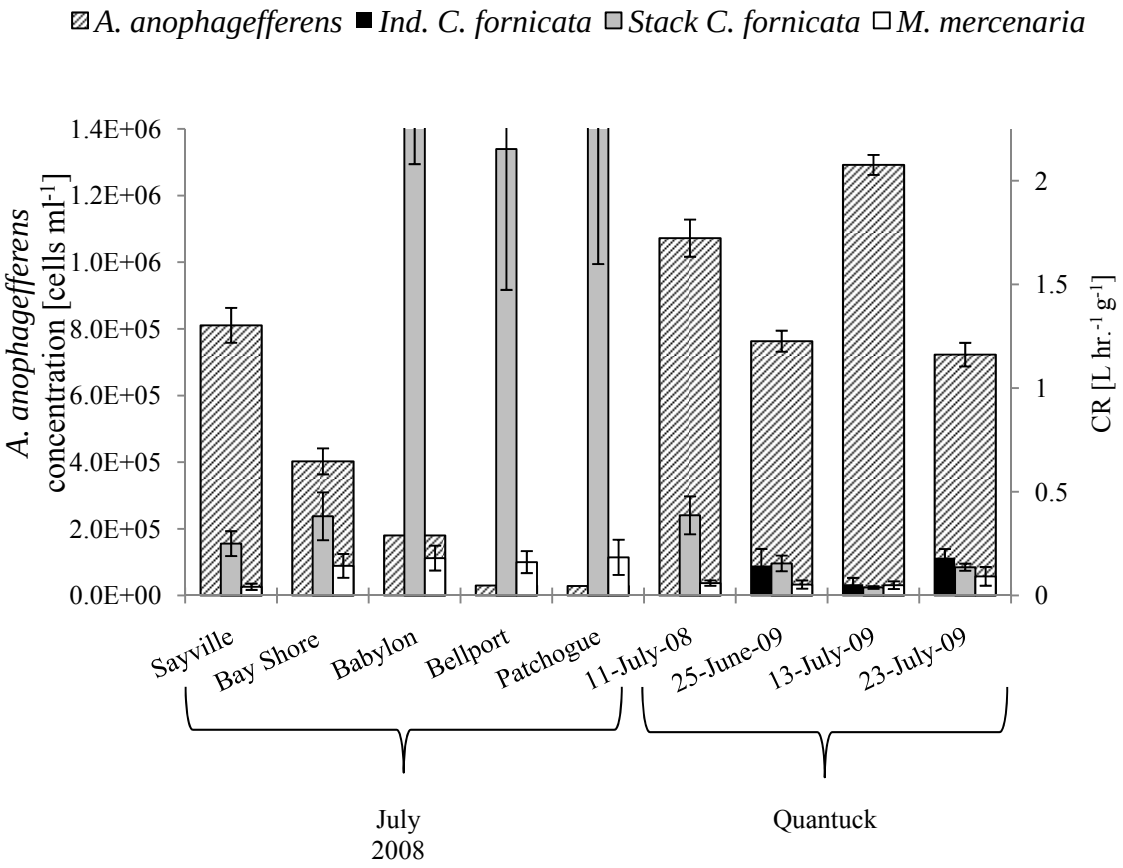
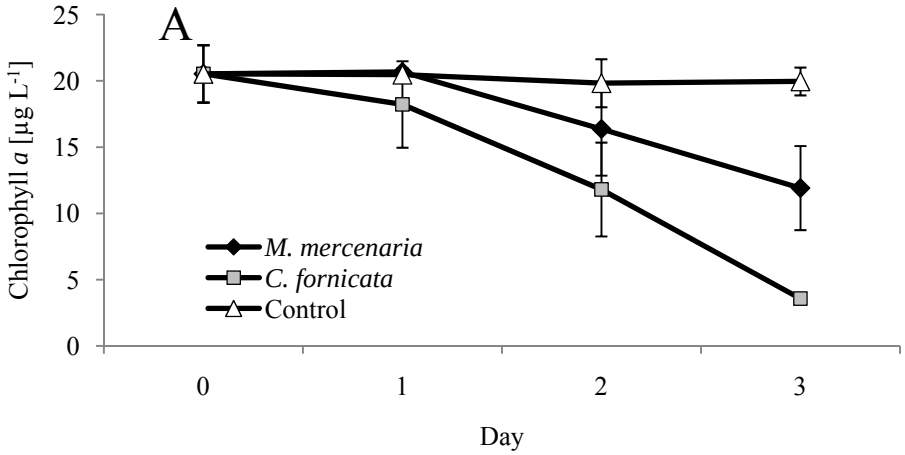
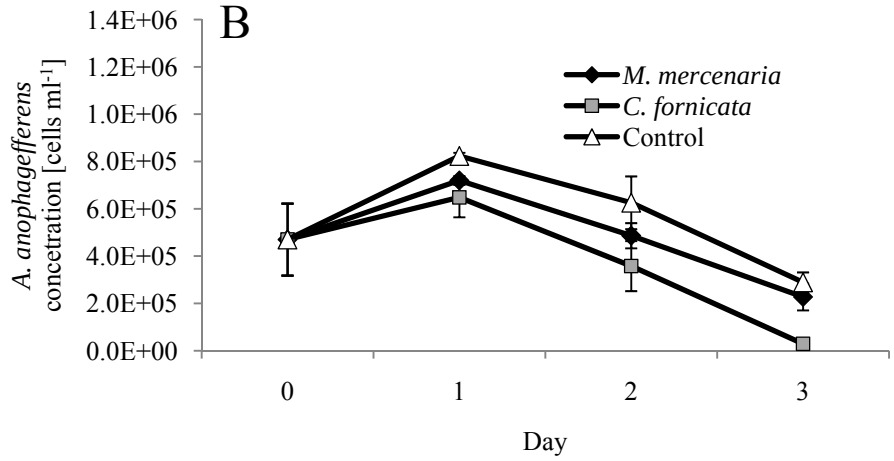


Figure 6 The mesocom experiment conducted on 6-June-08 with water collected from Great South Bay in Long Island, NY (Lat: 40° 41' 34.98" N, Lon: 73° 9' 15.9" W). CR = Clearance Rate. Error bars indicate standard error, n = 3. A. Changes in chlorophyll *a*, B. Changes in *A. anophagefferens* densities, C. Community clearance rates (CR) of *A. anophagefferens* cells on day 3 by each mollusc population.





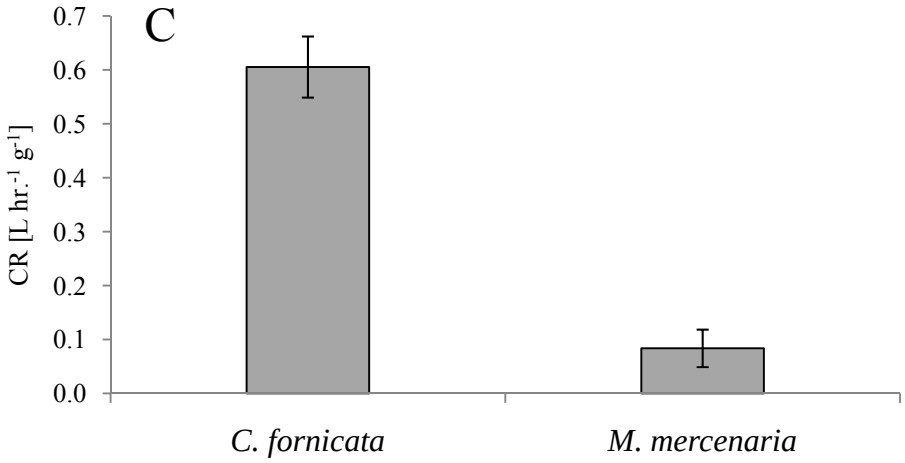


Figure 7 Mesocom experiment conducted on 12-June-08 with water collected from Quantuck Bay in Long Island, NY (Lat: 40° 48' 21.66" N, Lon: 72° 37' 13.74" W). CR = Clearance Rate. Error bars indicate standard error, n = 3. A. Changes in chlorophyll *a*, B. Changes in *A. anophagefferens* densities, C. Community clearance rates (CR) of *A. anophagefferens* cells on day 4 by each mollusc population.