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Suspension feeding by the Atlantic slipper limpet (*Crepidula fornicata*) and the northern quahog (*Mercenaria mercenaria*) in the presence of cultured and wild populations of the harmful brown tide alga, *Aureococcus anophagefferens*

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ABSTRACT

Within estuaries of New York, USA, recurrent harmful brown tides (*Aureococcus anophagefferens*) have contributed toward the collapse of two major bivalve fisheries (bay scallop, *Argopecten irradians* and northern quahog or hard clam, *Mercenaria mercenaria*), while populations of the Atlantic slipper limpet *Crepidula fornicata* have persisted in the presence of these blooms. Rates of suspension feeding by *C. fornicata* and *M. mercenaria* in the presence of different strains of *A. anophagefferens* and wild brown tide blooms were quantified to assess the potential impact of brown tides on slipper limpet and hard clam populations. 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 when fed *I. galbana* or non-toxic clones of *A. anophagefferens* ($p < 0.01$). 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* when fed bloom water were an order of magnitude greater than those of *M. mercenaria* ($p < 0.001$). Finally, during mesocosm experiments, *C. fornicata* reduced bloom densities of *A. anophagefferens* (10^6 cells mL^{-1}) 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 *A. anophagefferens* and suggest that this species could serve as a top-down control of blooms in shallow, poorly flushed estuaries.

1. Introduction

The Atlantic slipper limpet (*Crepidula fornicata*) is a suspension feeding gastropod native to the North American east coast. The species 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 stacks (Orton, 1952). Slipper limpets are considered invasive in Washington State and along Western European coasts, including France where they have dramatically increased in abundance since their introduction at the end of WWII (Blanchard, 1995). The Peconic Estuary, located on the eastern end of Long Island (NY, USA), supports large populations of *C. fornicata*. Surveys of the Peconic Estuary conducted in the mid-1990s reported maximal abundances of *C. fornicata* of 600 individuals m^{-2} and sizable populations throughout the system (Lewis et al., 1997). Population densities of this species in other Long Island estuaries have not been reported.

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 apparent 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 the gill and captures 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, some of which have been caused by persistent brown tide blooms of the picoplanktonic (~2 μm) pelagophyte, *Aureococcus anophagefferens* (as reviewed by Bricelj and Lonsdale, 1997; 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

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et al., 2001; Gastrich et al., 2004; Trice et al., 2004). In Long Island waters, blooms have occurred consistently within South Shore Estuaries since 1985, but occurred in the Peconic Estuary on eastern Long Island from 1985 to 1995 only (Bricelj and Lonsdale, 1997; Gobler et al., 2005). Cell concentrations as high as 3×10^6 cells mL^{-1} have been documented during blooms (Nuzzi and Waters, 1989) and the detrimental effects of these brown tides on shellfish and eelgrass beds have 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 (Cosper et al., 1987; Dennison, 1988). Brown tide caused recruitment failure and starvation in bay scallop populations (Bricelj et al., 1989) and high rates of mortality in bivalves during blooms have generally been attributed to cessation of feeding and starvation (Bricelj et al., 2001; Greenfield and Lonsdale, 2002). At *A. anophagefferens* concentrations exceeding 5×10^4 cells mL^{-1}, filter feeding in *Mercenaria mercenaria* is significantly reduced (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).

Preliminary experiments performed with *C. fornicata* have demonstrated this species can filter a wide range of particles $\geq$1 μm at very high concentrations ($>10^6$ particles mL^{-1}); and that the slipper limpet can feed on *A. anophagefferens* strain CCMP1784 over a wide range of densities (10^4–10^6 particles mL^{-1}; S.E. Shumway, unpubl.). Preliminary field experiments with *C. fornicata* during *A. anophagefferens* blooms have indicated that *C. fornicata* feeds during brown tides (S.E. Shumway, unpubl.); however, the ability of *C. fornicata* to feed in the presence of multiple strains of *A. anophagefferens* has not been reported and clearance rates of *C. fornicata* during brown tides have not been quantified.

This study compares 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*; Bricelj et al., 2001), as well as water from NY estuaries with varying concentrations of *A. anophagefferens*. Finally, the ability of the co-occurring molluscs to feed during brown tides was examined within large volume mesocosm experiments.

2. Methods

2.1. 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 (used in preliminary experiments) and has been reported as being not toxic to *M. mercenaria* (Bricelj et al., 2001, 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 *I. galbana* (3–5 μm), Tahitian strain (T-Iso), was cultured as an idealized food source for shellfish (Bricelj et al., 2001) under the same conditions described for *A. anophagefferens* (2–3 μm). Lastly, both *Synechococcus* sp. (0.8–1.5 μm) and *Nannochloropsis* sp. (2 μm) cultures were used in clearance rate experiments to assess the ability of *C. fornicata* to suspension feed in the presence of different picoplankton. The similar sizes of these algae permitted a direct comparison of shellfish clearance rates (Bricelj et al., 2001).

2.2. 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) were recorded at each site using an YSI 556 MPS probe and GPS locations were recorded at each site. In July 2008, bay water was collected from six locations across south shore bays of Long Island (Great South Bay and Quantuck Bay) whereas in 2009 water was collected from Quantuck Bay on multiple dates in June and July (Fig. 1).

2.3. 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" (Riisgård, 2001) as outlined by Shumway et al. (1985). Since *M. mercenaria* was formerly the most abundant shellfish in Great South Bay, NY (NYSDEC 1970–2008), which hosts persistent brown tides (Gobler et al., 2005), 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 (Gobler et al., 2005). 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). Individual *C. fornicata* (40 ± 2.9 mm shell length) were separated from the stack according to the method described by Newell and Kofoed (1977) with each individual snail adhered to the top of an empty shell or stone. After

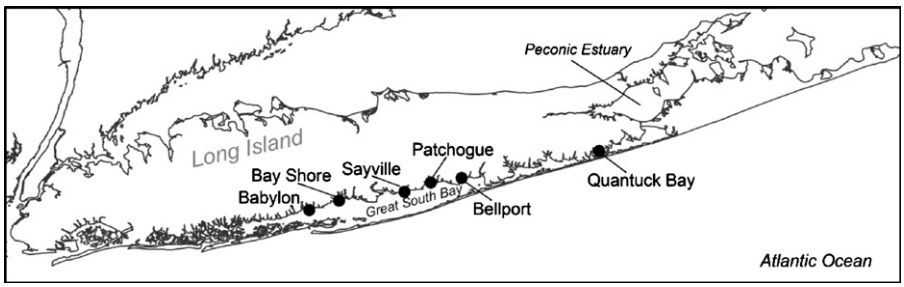

Fig. 1. Brown tide bloom water collection sites across the south shore of Long Island, NY, USA (Circles).

collection, animals were held at experimental temperatures (~21 °C) at the Stony Brook – Southampton Marine Station wet lab facility in a re-circulating 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.

On the day of the experiment, both *C. fornicata* and *M. mercenaria* were placed in 0.2 μm FSW under gentle aeration for at least 1 h (Shumway et al., 1985; Riisgård, 2001; Barillé et al., 2006). Thirteen numbered beakers (volume = 1 L) 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 initial 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 collected, 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 h from the time they were placed in the beaker, whereas *M. mercenaria* were allowed to feed for 1 h from the time the animals were observed to open and extend their siphon. Samples were collected every 15 min 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 Coughlan (1969). Cell counts from control beakers (three for each experiment) were averaged for clearance rate calculations. Once the experiment was concluded, animals were removed and frozen for 24 h. 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 $L\,h^{-1}\,g^{-1}$, 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. Experiments which build on prior work (S.E. Shumway, unpubl.) were conducted to quantify *C. fornicata* clearance rates of different size phytoplankton at multiple cell abundances. Treatments for these experiments included three algal species (*A. anophagefferens* CCMP1784, *Nanochloropsis* sp., and *Synechococcus* sp.) at three concentrations (10^4, 10^5, 10^6 cells mL^{-1}). For clearance rate experiments involving different strains of *A. anophagefferens* (CCMP1984, 1850, and 1794), cultures were fed to both shellfish species at concentrations of 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; 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 (10^5 and 10^6 *A. anophagefferens* cells $mL^{-1} = 1.25 \times 10^4$ and 1.25×10^5 *I. galbana* cells mL^{-1}, respectively). 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 × 2 algal species × 2 food concentrations). Cultures were counted prior to experiments using a hemacytometer and appropriate dilutions were made with 0.2 μm FSW. All clearance rates generated for field and culture experiments involving *A. anophagefferens* were expressed as clearance rates of *A. anophagefferens* or *I. galbana* in $L^{-1}\,h^{-1}$ g dry dry wt^{-1}.

2.4. Quantification of A. 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 $95.5 \pm 15.9\%$ recovery of samples spiked with known amounts of *A. anophagefferens*, a methodological relative standard deviation of $8.1 \pm 6.6\%$, and a mean detection limit of $3.6 \pm 2.1 \times 10^3$ 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 50 μm aperture which allowed for distinct peaks in cell densities to be resolved for both species (Bricelj et al., 2001). This counting method yielded a relative standard deviation of 6% for both species. Stock cultures of both species were verified microscopically with a hemacytometer and clearance rates determined on randomly selected samples with a hemacytometer were statistically identical to those obtained with the Coulter Counter.

2.5. Mesocosm experiments

Two mesocosm experiments were conducted during June 2008 to assess the ability of *C. fornicata* and *M. mercenaria* to 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. Densities of hard clams 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 individuals m^{-2}, Kraeuter et al., 2008), but lower than patch densities in NY during the 1970s (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 1400 individuals m^{-2} have been observed along the eastern shore of Shinnecock Bay (this study) which is similar to numbers

documented in the Bay of Brest, France (Chauvaud et al., 2000). 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 6–8 individuals, matching median stack sizes observed during field surveys. At the end of the experiment, *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). Temperature, salinity, dissolved oxygen, chlorophyll *a* and *A. anophagefferens* cell abundance were measured 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 (as chlorophyll *a*) and *A. anophagefferens* in the control mesocosms were determined as described above.

The first mesocosm experiment was carried out from 6 June 2008 to 9 June 2008. Nine mesocosms were each filled with 60 L 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 4.7×10^5 *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 to account for changes in *A. anophagefferens* densities not attributed to shellfish grazing, three mesocosms which contained four *M. mercenaria* (equivalent of 29 individuals m^{-2}, 11.5 g AFDW), and three mesocosms with four stacks each (26 individuals) of *C. fornicata* (equivalent of 188 individuals m^{-2}, 5.3 g 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′2166″N, Lon: 72°37′13.74″W) with 9.5×10^5 *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 (equivalent of 22 individuals m^{-2}, 7.0 g AFDW), and three mesocosms with four stacks each (34 individuals) of *C. fornicata* (equivalent of 245 individuals m^{-2}, 6.7 g AFDW).

2.6. 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 natural phytoplankton populations, 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).

3. Results

3.1. Clearance rates of phytoplankton cultures

The Atlantic slipper shell, *C. fornicata*, actively fed on the phytoplankton *A. anophagefferens*, *Nannochloropsis* sp., and *Synechococcus* sp. (diameters 0.8–3.0 μm) at equal rates (Fig. 2). Clearance rates were significantly greater at 10^5 cells mL^{-1} than 10^4 and 10^6 cells mL^{-1} for all species ($p < 0.001$; Two-way ANOVA; Fig. 2). This trend was most pronounced for clearance rates of *A. anophagefferens* ($p < 0.05$; Student-Newman–Keuls; Fig. 2).

Clearance rates of hard clams, *M. mercenaria*, were reduced in the presence of brown tide *A. anophagefferens* clone CCMP1794, while *C. fornicata* actively fed on this clone (Fig. 3A). When fed *I. galbana*, clearance rates of both species were similar, averaging 0.76 ± 0.24 L h^{-1} g^{-1} (Fig. 3). Clearance rates of *M. mercenaria* fed clone CCMP1794, however, were significantly lower than rates of individuals fed *I. galbana* at both 10^5 and 10^6 cells mL^{-1} biovolume level ($p < 0.05$; Student-Newman–Keuls; Fig. 3A). In contrast, clearance rates of *C. fornicata* fed *A. anophagefferens* and *I. galbana* at the 10^5 cells mL^{-1} biovolume level were nearly equal (Fig. 3A). At 10^6 cells mL^{-1}, clearance rates of *C. fornicata* fed *A. anophagefferens* CCMP1794 (0.59 ± 0.09 L h^{-1} g^{-1}) were greater than those of *M. mercenaria* but were significantly lower than those obtained when fed *I. galbana* at the equivalent biovolume (1.12 ± 0.11 L h^{-1} g^{-1}; $p < 0.05$; Student-Newman–Keuls; Fig. 3A). Finally, clearance rates of *M. mercenaria* fed *I. galbana* at the 10^6 biovolume level (1.06 ± 0.14 L h^{-1} g^{-1}) were significantly greater than at the 10^5 biovolume level (0.69 ± 0.14 L h^{-1} g^{-1}; $p < 0.05$; Student-Newman–Keuls) while the opposite was true of *C. fornicata* ($p < 0.05$; Student-Newman–Keuls; Fig. 3A).

Consistent with the findings for *A. anophagefferens* clone CCMP1794, clearance rates of *M. mercenaria* were greatly reduced in the presence clone CCMP1850, while rates of *C. fornicata* were not (Fig. 3B). Mean clearance rates of *M. mercenaria* fed clone

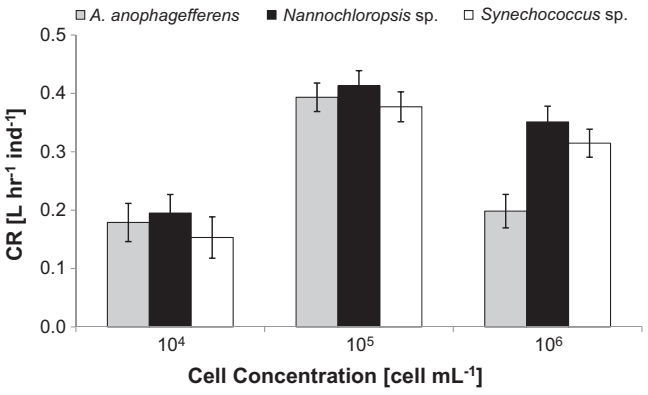

Fig. 2. Clearance rates (CR) of *A. anophagefferens* (2–3 μm), *Synechococcus* sp. (0.8–1.5 μm) and *Nannochloropsis* sp. (2 μm) at 10^4, 10^5, 10^6 cells mL^{-1} illustrating the ability of *C. fornicata* to clear small particles at equal rates. Error bars indicate standard error.

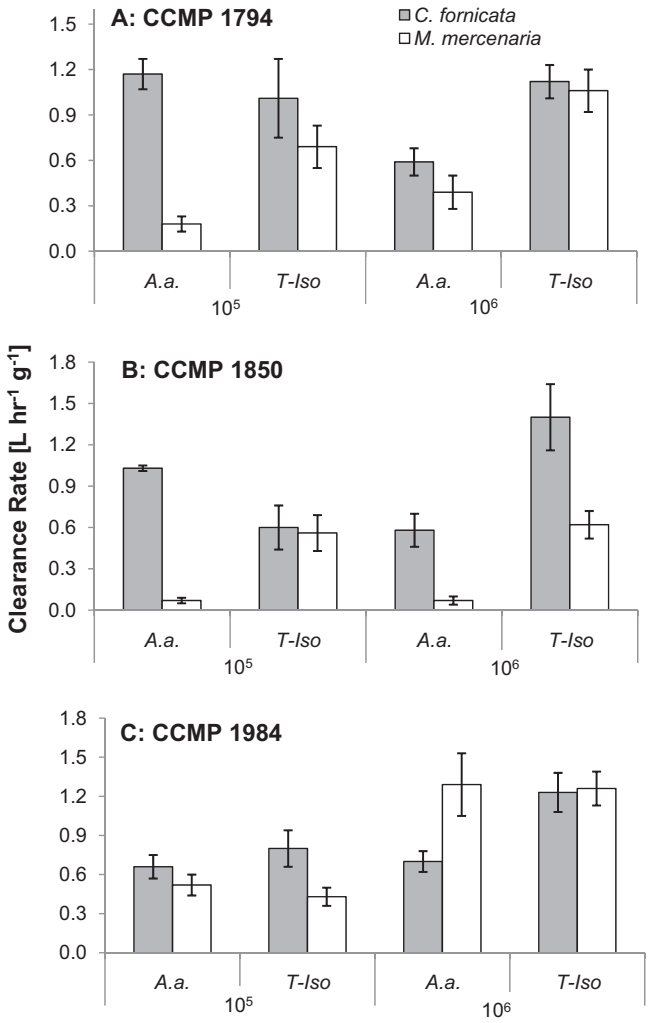

Fig. 3. Clearance rates of *C. fornicata* and *M. mercenaria* when fed three *A. anophagefferens* clones at 10^5 and 10^6 cells mL^{-1} (*A.a.*) and biovolume equivalents of *I. galbana* (*T-Iso*). Error bars in each figure represent standard error.

CCMP1850 at both food concentrations (0.07 ± 0.03 L h^{-1} g^{-1}) were nearly an order of magnitude lower than those obtained when fed *I. galbana* (0.64 ± 0.05 L h^{-1} g^{-1}; $p < 0.01$; Student-Newman–Keuls; Fig. 3B). In contrast, clearance rates of *C. fornicata* fed *A. anophagefferens* at 10^5 cells mL^{-1} were higher than those on *I. galbana* at the equivalent biovolume level (Fig. 3B). Clearance rates of *C. fornicata* fed clone CCMP1850 at 10^6 cells mL^{-1} were six-fold higher than those of *M. mercenaria*, but were lower than those when fed *I. galbana* at the equivalent biovolume ($p < 0.05$; Student-Newman–Keuls; Fig. 3B). Finally, clearance rates by both molluscs were higher when fed *I. galbana* at the 10^6 biovolume level than at the 10^5 biovolume level ($p < 0.05$; Student-Newman–Keuls; Fig. 3B).

In contrast to clones CCMP 1794 and CCMP 1850, clearance rates of *M. mercenaria* fed the non-toxic *A. anophagefferens* clone CCMP 1984 were not reduced (Fig. 3C). Clearance rates of *M. mercenaria* were, however, significantly higher in the presence of 10^6 cells mL^{-1} biovolume level than the 10^5 cells mL^{-1} for both food sources ($p < 0.05$; Student-Newman–Keuls; Fig. 3C). While clearance rates of *C. fornicata* were nearly equal for the two food sources at the 10^5 cells mL^{-1} biovolume level, rates were significantly higher in the presence of *I. galbana* (1.23 ± 0.15 L h^{-1} g^{-1}) compared to CCMP1984 at the 10^6 biovolume level (0.70 ± 0.08 L h^{-1} g^{-1}; $p < 0.05$; Student-Newman–Keuls).

3.2. Clearance rates in the presence of brown tide bloom water

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 (1.07×10^6 and 8.11×10^5 cells mL^{-1}, respectively), moderate in Bay Shore and Babylon (4.02×10^5 and 2.30×10^5 cells mL^{-1}, respectively), and lower in Bellport and Patchogue (2.98×10^4 and 2.85×10^4 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* cell abundance with time) displayed by each suspension feeder in 2008. *Crepidula fornicata* displayed a maximal rate of 2.53 ± 0.45 L h^{-1} g^{-1} in Babylon and a minimal rate of 0.25 ± 0.06 L h^{-1} g^{-1} in Sayville while *M. mercenaria* displayed a maximal rate of 0.18 ± 0.14 L h^{-1} g^{-1} in Babylon and a minimal rate of 0.04 ± 0.02 L h^{-1} g^{-1} in Sayville. *Crepidula fornicata* displayed *A. anophagefferens*-specific clearance rates (1.36 ± 0.46 L h^{-1} g^{-1}) which were an order of magnitude greater than those of *M. mercenaria* (0.13 ± 0.03 L h^{-1} g^{-1}; $p < 0.001$; Mann-Whitney Rank Sum Test) (Figs. 4 and 5). For experiments were conducted during the 2009 brown tide bloom in Quantuck Bay, stacks and individual *C. fornicata* displayed *A. anophagefferens*-specific clearance rates (0.13 ± 0.04 and 0.11 ± 0.04 L h^{-1} g^{-1} respectively) which were approximately twice as fast as those of hard clam rates (0.07 ± 0.03 L h^{-1} g^{-1}; Fig. 4).

Clearance rates by both shellfish co-varied with densities of *A. anophagefferens*. The highest clearance rates (2.53 ± 0.45 L h^{-1} g^{-1} for *C. fornicata* and 0.18 ± 0.06 L h^{-1} g^{-1} for *M. mercenaria*) were found using water from locations with low *A. anophagefferens* densities ($1.8 \pm 0.88 \times 10^4$ cells mL^{-1}, Babylon; Fig. 4). The lowest clearance rates (0.04 ± 0.01 L h^{-1} g^{-1} for *C. fornicata* and 0.04 ± 0.01 L h^{-1} g^{-1} for *M. mercenaria*) were found using water from

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 [cells mL^{-1}]
July 2008							
Sayville	40°43′12″	−73° 05′ 38″	24.7	27.1	23.25 ± 1.93	2.20 ± 0.23	$8.1 \pm 0.5 \times 10^5$
Bay Shore	40°42′39″	−73° 14′ 22″	24.8	28.5	21.85 ± 2.05	2.95 ± 0.56	$4.0 \pm 0.4 \times 10^5$
Babylon	40°40′ 50″	−73° 18′ 56″	24.6	28.0	16.41 ± 0.79	3.17 ± 0.72	$1.8 \pm 0.08 \times 10^5$
Bellport	40°45′ 07″	−72° 55′ 58″	25.0	24.5	7.65 ± 0.53	1.05 ± 0.03	$3.0 \pm 0.7 \times 10^4$
Patchogue	40°44′50″	−73° 00′ 34″	25.3	24.9	9.54 ± 0.98	1.87 ± 0.11	$2.9 \pm 0.2 \times 10^4$
Quantuck Bay							
11-July-08	40°48′08″	−72° 37′ 12″	25.0	27.2	30.36 ± 3.97	1.34 ± 0.09	$1.1 \pm 0.06 \times 10^6$
25-June-09	40°48′08″	−72° 37′ 12″	20.4	24.4	19.97 ± 6.12	7.31 ± 0.32	$7.6 \pm 0.3 \times 10^5$
13-July-09	40°48′08″	−72° 37′ 12″	24.3	25.3	43.28 ± 2.50	6.24 ± 0.66	$1.3 \pm 0.03 \times 10^6$
23-July-09	40°48′08″	−72° 37′ 12″	25.4	24.7	21.12 ± 1.77	4.11 ± 0.44	$7.2 \pm 0.4 \times 10^5$

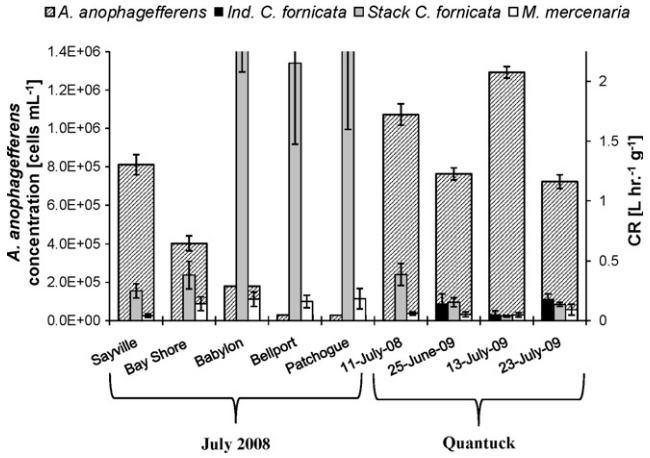

Fig. 4. Clearance rate (CR) of molluscs (solid bars) on *A. anophagefferens* cells compared to *A. anophagefferens* cell concentration (striped bars) at each site during the 2008 and 2009 brown tide blooms in Long Island south shore bays and estuaries. Error bars indicate standard error.

locations with extremely high *A. anophagefferens* densities ($1.3 \pm .03 \times 10^6$ cells mL^{-1} Quantuck Bay; Fig. 4). For all field-based experiments, clearance rates of *A. anophagefferens* by *C. fornicata* were significantly faster than those of *M. mercenaria* under both bloom ($>3.5 \times 10^4$ cells mL^{-1}) and non-bloom conditions ($<3.5 \times 10^4$ cells mL^{-1}; $p < 0.01$; Fig. 5). Both molluscan species displayed lower clearance rates when exposed to higher *A. anophagefferens* densities ($>3.5 \times 10^4$ cells mL^{-1}; $p < 0.01$; Fig. 5) and there were significant inverse correlations between clearance rates of each species and *A. anophagefferens* abundance (Fig. 4; Spearman Correlation, $p < 0.05$).

3.3. Mesocosm experiments with brown tide bloom water

The first mesocosm experiment, performed on 6 June 2008, using bloom water from Great South Bay (4.7×10^5 *A. anophagefferens* cells mL^{-1} and ambient chlorophyll *a* of 21 $\mu g\ L^{-1}$) and a *C. fornicata* treatment biomass level (5.3 g AFDW) which 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 $3.57 \pm 0.43\ \mu g\ L^{-1}$ chlorophyll *a* and $2.9 \pm 1.6 \times 10^4$ *A. anophagefferens* cells mL^{-1}. In contrast, the control and *M. mercenaria* treatments had chlorophyll *a* and *A. anophagefferens* abundances ($19.96 \pm 1.05\ \mu g\ L^{-1}$ and $2.9 \pm 0.4 \times 10^5$ cells mL^{-1}, and $11.91 \pm 3.17\ \mu g\ L^{-1}$ and $2.3 \pm 0.6 \times 10^5$ cells mL^{-1}, respectively) that were both significantly greater than the *C. fornicata* treatment ($p < 0.05$; One-Way ANOVA). At the end of the experiment, clearance rates by *M. mercenaria* (0.08 ± 0.03 L h^{-1} g^{-1}) were significantly lower than those by *C. fornicata* 0.61 ± 0.06 L h^{-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 (9.5×10^5 *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 ($9.5 \pm 2.2 \times 10^5$ cells mL^{-1} and $6.1 \pm 2.3 \times 10^5$ cells mL^{-1}, respectively, on day four) or chlorophyll *a* ($35.26 \pm 3.12\ \mu g\ L^{-1}$ and $31.08 \pm 2.27\ \mu g\ L^{-1}$, respectively). In stark contrast, in mesocosms containing 6.7 g AFDW of *C. fornicata*, *A. anophagefferens* cell densities ($1.1 \pm 0.3 \times 10^5$ cells mL^{-1}) and chlorophyll *a* levels ($19.38 \pm 6.91\ \mu g\ L^{-1}$) were reduced to levels significantly lower than levels found in the control and *M. mercenaria* treatments ($p < 0.05$; One-Way ANOVA; Fig. 7).

4. Discussion

At sufficient densities, grazing by suspension feeding bivalves can play a pivotal role in controlling phytoplankton biomass in shallow estuaries (Officer et al., 1982; Newell, 2004). Further, 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 caused by the harmful pelagophyte *A. anophagefferens*, blooms have been shown to initiate when the dominant nitrogen source is dissolved organic matter (DOM) (Berg et al., 1997; Mulholland et al., 2002; Gobler

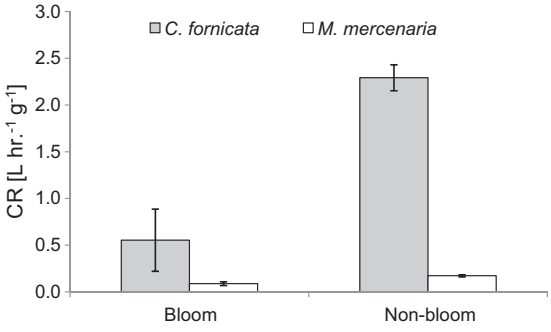

Fig. 5. Mean clearance rates (CR) of *C. fornicata* (grey bars) and *M. mercenaria* (white bars) during the 2008 and 2009 brown tide blooms in Long Island south shore bays. "Bloom" refers to *A. anophagefferens* densities >35,000 cells mL^{-1} and "Non-bloom" refers to *A. anophagefferens* densities <35,000 cells mL^{-1} since this cell abundance is known to inhibit feeding by *M. mercenaria* (Bricelj et al., 2001).

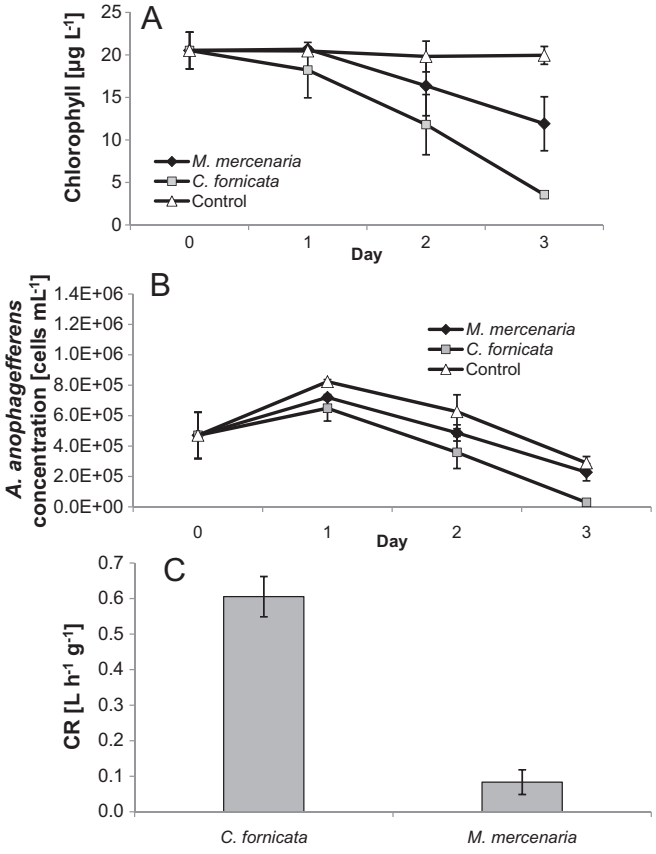

Fig. 6. The mesocom experiment conducted on 6-June-08 with water collected from Great South Bay in Long Island, NY (Lat: 40°41′34.98″ N, Lon: 73°9′15.9″W). CR = Clearance Rate. Error bars indicate standard error, $n = 3$. (A) Changes in chlorophyll *a*, (B) changes in *A. anophagefferens* densities,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

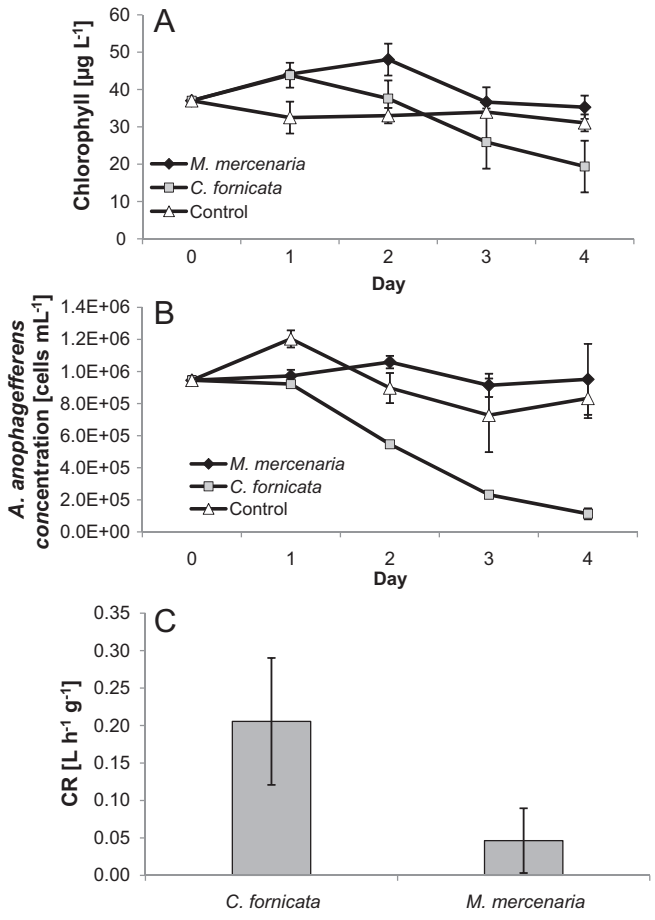

Fig. 7. Mesocom experiment conducted on 12-June-08 with water collected from Quantuck Bay in Long Island, NY (Lat: 40°48′21.66″N, Lon: 72°37′13.74″W). CR = clearance rate. Error bars indicate standard error, $n = 3$. (A) Changes in chlorophyll *a*, (B) changes in *A. anophagefferens* densities, (C) community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

et al., 2005) and when grazing pressure from zooplankton and bivalve suspension feeders has failed (Smayda, 2008; and references therein, Bricelj, 2009). 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 (*Argopecten irradians*) in the Peconic Estuary leading to the demise of this population (Bricelj and Lonsdale, 1997). Across the south shore of Long Island, brown tide blooms have occurred almost annually 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). Chronic annual blooms in Chinchoteague Bay (MD) have restricted the growth of hard clams in that estuary (Wazniak and Glibert, 2004). In contrast to these commercially important bivalves, we have demonstrated that the Atlantic slipper limpet (*C. fornicata*) can graze robustly in the presence of *A. anophagefferens* (both toxic and non-toxic cultured strains, as well as wild populations) and maintain moderate clearance rates even at concentrations exceeding 10^6 *A. anophagefferens* cells mL^{-1} (Figs. 2–7).

The northern quahog, *M. mercenaria*, displayed clearance rates similar to those of *C. fornicata* when fed an ideal food source (*I. galbana*). These two shellfish diverged widely, however, in their feeding abilities in the presence of noxious strains of *A. anophagefferens* (CCMP 1794 and CCMP 1850; Smith et al., 2008). On average, clearance rates of *C. fornicata* fed these two *A. anophagefferens* strains were five-fold greater than clearance rates of *M. mercenaria* ($p < 0.01$; *t*-test; Fig. 5). The large reduction in feeding by *M. mercenaria* in the presence of *A. anophagefferens* has also been observed in *M. edulis* (Tracey, 1988; Bricelj et al., 1989, 2001; Gallager et al., 1989) and has been linked to the dopamine-like inhibitory compound found on the extracellular polysaccharide coating of *A. anophagefferens* (Gainey and Shumway, 1991). The toxicity of this coating has specifically been shown to cause a decrease in the activity of the lateral cilia of the gills of numerous bivalve species including *M. mercenaria*, the mussels *M. edulis* and *Modiolus modiolus*, and the oysters *Crassostrea virginica*, and *Ostrea edulis* (Gainey and Shumway, 1991). Unlike 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 (Fig. 2) and to feed under high particle loads (Jørgensen et al., 1984; Barillé et al., 2006). This difference in particle capture mechanism likely accounts for the ability of *C. fornicata* to filter high densities of small, noxious cells such as *A. anophagefferens* which inhibit feeding some in bivalves.

In the presence of bloom populations of *A. anophagefferens* (10^4–10^6 cells mL^{-1}), *C. fornicata* consistently displayed clearance rates more than an order of magnitude greater than those of *M. mercenaria* (Figs. 4 and 5). These low clearance rates for *M. mercenaria* are consistent with prior research since *A. anophagefferens* densities were frequently at or far above the threshold level known to inhibit *M. mercenaria* clearance rates (Bricelj et al., 2001). There was a similar effect of *A. anophagefferens* on *C. fornicata* during culture and field experiments as clearance rates at 10^6 cells mL^{-1} were lower than at 10^5 cells mL^{-1}. Unlike *M. mercenaria*, *C. fornicata* maintained moderate clearance rates even as brown tide cell densities approached and sometimes exceeded 10^6 cells mL^{-1}. This was most obvious during mesocosm experiments when *C. fornicata* significantly reduced chlorophyll *a* and *A. anophagefferens* cell densities in tanks with bloom concentrations of *A. anophagefferens* (10^5–10^6 cells mL^{-1}) while equal or greater biomass levels of *M. mercenaria* did not. 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* abundance. Collectively, these results 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.

Some harmful algae display a wide range of toxicity or noxious effects among culture strains and field populations (Burkholder and Glibert, 2009) and this study provided two observations consistent with this concept. Feeding by *M. mercenaria* was strongly inhibited by all field populations of *A. anophagefferens* and two of the three culture strains examined (clones CCMP1794 and CCMP1850). In contrast, clearance rates of *M. mercenaria* fed clone CCMP1984 were similar to those fed *I. galbana*. CCMP1984 is clone CCMP1784 without bacteria (Berg et al., 2002) and this strain has been previously identified as non-toxic to hard clams (Bricelj et al., 2001), perhaps because it has been in culture for twice as long as strains which inhibited *M. mercenaria* feeding, CCMP1794 and CCMP1850 (24 vs. 12 years. in culture). This finding also demonstrates, for the first time, that the palatability of clone CCMP1784 is not related to the bacterial assemblage present in this culture. Variability in the effects of *A. anophagefferens* on *C. fornicata* was also evident in four field experiments when brown tide densities were high (10^5–10^6 cells mL^{-1}) and clearance rates of slipper shells were lower than rates observed when feeding on cultures of *A. anophagefferens* or other 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, like monocultures. there are differences in *A. anophagefferens* field populations which affect clearance rates (Burkholder and Glibert, 2009). Regardless, even in these field experiments when *C. fornicata* feeding rates were lower, these rates were twice the rates displayed by *M. mercenaria*.

While hard clams and bay scallops were the two most commercially important bivalves in New York estuaries during the late twentieth century, landings of both species have declined by more than 99% in estuaries which experienced brown tide (Gobler et al., 2005; NYSDEC, 2008). In the Peconic Estuary, populations of the Atlantic slipper limpet (*C. fornicata*) were found at densities exceeding 600 individuals m^{-2} in the mid-1990s (Lewis et al., 1997) and populations of *C. fornicata* at similar levels were found in surveys of the eastern shore of Shinnecock Bay during this study, with densities up to 1500 individuals m^{-2} and mean densities of 246 individuals m^{-2}. Given the high densities of *C. fornicata* in these systems, 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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