



## Interannual variability of *Aureococcus anophagefferens* in Quantuck Bay, Long Island: natural test of the DON hypothesis

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### Abstract

This study examined benthic and pelagic rate processes from the perspective of benthic dissolved organic matter (DOM) and its possible role in *Aureococcus anophagefferens* population dynamics. Sampling was conducted in Quantuck Bay, Long Island, New York, at three times in the summer of 2000 and two times in the summer of 2001. *A. anophagefferens* exhibited a large bloom between the May and July 2000 sample periods, but a smaller bloom was captured in the September 2000 sampling. Densities throughout 2001 were significantly lower than during 2000. There were few differences in most parameters measured between years, but the largest difference was the seasonal increase in both particulate (POM) and dissolved organic matter (DOM) during 2000 that was not observed during 2001. In particular, DOP accumulated the most, followed by DON and DOC, which resulted in significant seasonal decreases in the C:N:P ratios of the DOM pools. On the contrary, changes in elemental ratios of POM were not observed. The seasonal accumulation of DON appeared to be driven largely (~50%) by the flux of DON from the benthos in 2000, but during 2001, all measured DON fluxes were into the sediment from the water column. This is consistent with the lack of accumulation during this year. There was little evidence for changes in microzooplankton grazing pressure between 2000 and 2001, and therefore the accumulation of DON and DOP during 2000 could have provided a competitive advantage to *A. anophagefferens* over other picoalgal species (e.g., *Synechococcus*) resulting in the significant blooms observed in 2000.

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### 1. Introduction

Since 1985, the intercoastal bays of Long Island, New York, as well as a number of other estuaries along the US east coast, have been sporadically

plagued by blooms of the nuisance microalgae *Aureococcus anophagefferens* (Bricelj and Lonsdale, 1997). *A. anophagefferens* can reach cell densities in the field  $>10^9$  cells L<sup>-1</sup> giving the water a coffee-brown color, hence the ‘common name’ of the brown tide (Casper et al., 1989). Although evidence suggests that *A. anophagefferens* may produce a dopamine-like toxin (cf., Gainey and Shumway, 1989), the principle deleterious effects of the brow tide are related to ecosystem damage through the loss of seagrass beds

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(Dennison et al., 1989) and the near complete collapse of the Long Island Bay scallop fishery (Bricelj and Kuenstner, 1989).

High levels of temporal and spatial variability have thwarted efforts to reach a scientific consensus on causes of bloom initiation, maintenance, and demise of *A. anophagefferens* blooms. Consequently, hypotheses abound for both bloom initiation ‘nutrient triggers’ (Casper et al., 1987, 1990; Dzurica et al., 1989; Keller and Rice, 1989; Smayda, 1989; Nixon et al., 1994; Berg et al., 1997, 2002; LaRoche et al., 1997; Milligan and Casper, 1997; Breuer et al., 1999; Gobler and Sanudo-Wilhelmy, 2001a; Lomas et al., 2001; Gobler et al., 2002), and decreased microzooplankton grazing pressure (Lonsdale et al., 1996; Bricelj et al., 2001; Gobler et al., 2002). However, microzooplankton grazing mortality rates on *A. anophagefferens* are quite high (~0.2–0.5 per day; Gobler et al., 2002) even at densities in excess of  $4 \times 10^8$  cells L<sup>-1</sup> and a number of protozoan populations are efficient at grazing *A. anophagefferens* (Caron et al., 1989; Mehran, 1996).

Clearly the balance of bottom-up (nutrient) and top-down (grazing) controls directly impacts *A. anophagefferens* blooms (e.g., Gobler et al., 2002), but it is likely that this balance also has an indirect effect on bloom dynamics (e.g., Glibert, 1998). There is little doubt that microzooplankton grazing in aquatic systems is an important process in the release of labile marine dissolved organic matter (DOM; Nagata, 2000; Carlson, 2002). Whether it be from direct excretion of DOM (e.g., Miller and Glibert, 1998) or through ‘sloppy feeding’ (e.g., Lampert, 1978; Nagata and Kirchman, 1991, 1992), the production of labile DOM through grazing activity could enhance the growth rate of *A. anophagefferens* (e.g., Dzurica et al., 1989; Berg et al., 1997; Gobler and Sanudo-Wilhelmy, 2001a) at the same time that any selective grazing pressure might decrease inter-species competition. In fact given the general lack of data on the interannual variability of microzooplankton grazing and/or biomass in Long Island Bays to support long term changes in these processes and pools, one might conclude that despite the potential for significant grazing pressure, interannual variability in blooms of *A. anophagefferens* is more likely related to alleviation of a bottom-up control.

Bottom-up stimulation by nutrient enrichment does not immediately imply an *A. anophagefferens* bloom,

as inter-specific competition for the picoalgal niche is likely to occur (Sieracki, 2001). It has been hypothesized that under conditions of elevated DON concentrations (or more broadly DOM; Lomas et al., 2001), *A. anophagefferens* would become competitively dominant over other picoalgae, whether this DOM enrichment is related to interannual variability in groundwater inputs (LaRoche et al., 1997), the demise of prior phytoplankton blooms supported by inorganic nitrogen (Gobler and Sanudo-Wilhelmy, 2001b), or a direct DOM input from the sediment. This DOM hypothesis has received significant support from both controlled culture studies (Berg et al., 2002; Lomas, 2003) and experimentally manipulated field samples (Berg et al., 1997; Gobler and Sanudo-Wilhelmy, 2001b).

As part of a two-year study (2000–2001), we tested the hypothesis that brown tide events were related to accumulation of DOM in the water column through the efflux of DOM from the sediments, and that DOM flux was mediated by (a) the magnitude of prior bloom events, (b) sediment stability in relation to physical forcing, and (c) the ability of benthic autotrophs to sequester nutrients in the ecosystem. MacIntyre et al. (this volume) address the later two points. We sampled Quantuck Bay, a bay that commonly exhibits large brown tide blooms, and in 2000 two significant brown tide blooms occurred while in 2001 no brown tide blooms were observed. Our sampling effort provides a natural experiment to explore differences in the Quantuck Bay ecosystem between years and evaluate the role of benthic–pelagic coupling on *A. anophagefferens* population dynamics.

## 2. Material and methods

### 2.1. Study site and sampling

Quantuck Bay is a small (~5 km<sup>2</sup>), shallow (1–2 m average depth) Long Island bay situated between Moriches Bay to the west and Shinnecock Bay to the east. Quantuck Bay has two creeks at the northern edge of the bay, and is flushed by tidal activity through the canals connecting it to Moriches and Shinnecock Bays. Historical data on selected biological and chemical parameters have been collected at a single station in the main channel (Suffolk County Department of Health Services (SCDHS) Station

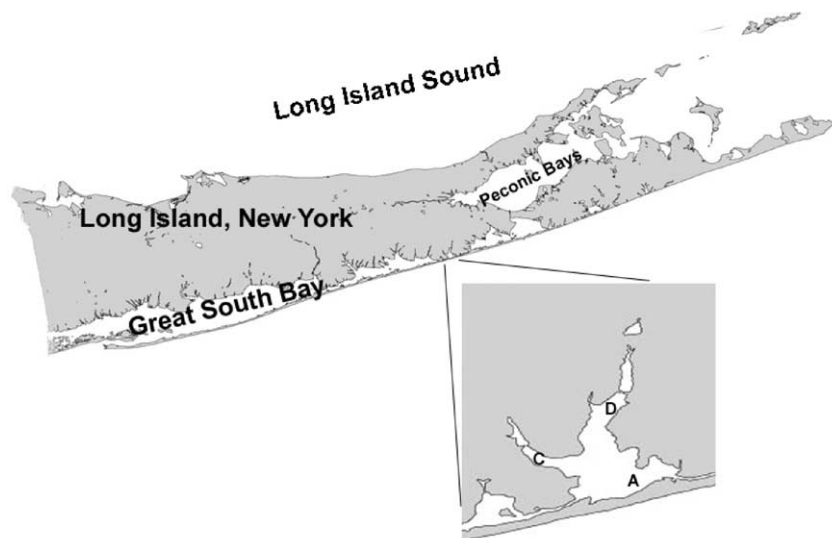


Fig. 1. Map of Suffolk County, Long Island, showing an expanded view of the Quantuck Bay sampling area and the three stations that were sampled during this project. Note that station A is Moriches Bay Station 200 sampled by SCDHS.

200; our station A, Fig. 1) since 1977. Between 1985 and the early 1990's, Quantuck Bay frequently had *A. anophagefferens* blooms  $>5 \times 10^8$  cells  $L^{-1}$ , but recently blooms have been more modest at  $2-4 \times 10^8$  cells  $L^{-1}$ .

For this study, three sites were sampled within the Quantuck Bay system; the site routinely monitored by SCDHS, and two others, one in each creek (Fig. 1). During 2000 and 2001, these three sites were sampled on five different occasions, May, July and September of 2000, and June and August of 2001, and sites were sampled for all parameters (described below) at least twice during each occasion, with the exception of benthic core fluxes, which were sampled once.

For benthic flux measurements, undisturbed sediment cores were collected using a pole coring device with 6.35 cm inner diameter acrylic liners; the 30 cm cores were filled with sediment to a depth of  $\sim 15$  cm. Cores were collected in duplicate from two locations bracketing each of the three main study sites for a total of four replicates at each site. Bottom water was collected from each site to serve as replacement water for the incubations and to fill the incubator (described below).

Surface water samples for pelagic nutrient concentrations, biomass stocks, and rate process measure-

ments were collected from each site early in the morning into 20 L cubitainers and kept dark in an ambient temperature cooler (to prevent light stress and warming during transit) until returning to the Southampton College Marine station ( $<2$  h transit time) where sub-samples were removed for the various measurements (described below). Estuaries along the south shore of Long Island are shallow and well-mixed (Wilson et al., 1991) ensuring that surface sample waters were representative of the entire water column. Coincident with these pelagic samples, separate sediment core samples were also taken to quantify benthic chlorophyll stocks (described below).

## 2.2. Biological and chemical analyses

Water column and benthic chlorophyll *a* samples were analyzed fluorometrically (Welschmeyer, 1994), with samples for water column chlorophyll *a* filtered on Whatman GF/F filters and benthic chlorophyll collected from the top 5 mm of triplicate sediment cores. Samples for suspended particulate organic carbon (POC), nitrogen (PON) and phosphorus (POP) were filtered onto pre-combusted ( $450^\circ C$ , 5 h) Whatman GF/F filters, dried at  $60^\circ C$  overnight and analyzed on a Control Equipment 240 Elemental Analyzer (POC,

PON; Sharp, 1974) or by dry combustion and acid hydrolysis (POP; Solorzano and Sharp, 1980). POC and PON concentrations were calculated from known masses of acetanilide that were analyzed with each run, and POP concentrations were calculated from known volumes of a standardized  $\text{KH}_2\text{PO}_4$  solution added to filters and processed with the field samples. Samples for dissolved inorganic and organic nutrients were collected from particulate sample filtrates and immediately frozen in pre-combusted ( $450^\circ\text{C}$ , 5 h) glass scintillation vials (dissolved free amino acids and dissolved monosaccharides) or acid-cleaned HDPE bottles (all others). Dissolved inorganic nitrogen,  $\text{NO}_2^-/\text{NO}_3^-$  and  $\text{NH}_4^+$ ,  $\text{PO}_4^{-3}$ , and urea were analyzed using standard colorimetric methods (Parsons et al., 1984). Dissolved organic carbon (DOC) was analyzed by high temperature catalytic oxidation on a Shimadzu TOC-5000 total organic carbon analyzer and calibrated against a glucose standard (Hansell, 1993). Dissolved organic nitrogen (DON) and phosphorus (DOP) were analyzed by high temperature persulfate oxidization (Valderrama, 1981) and then measured as  $\text{NO}_3^-$  and  $\text{PO}_4^{-3}$ , respectively. Dissolved free amino acids were analyzed fluorometrically using the methods of Parsons et al. (1984), calibrated against a mixed amino acid standard (Amino acid Standard H; Pierce Biotechnology, 20088), and corrected for cross-reaction of the *o*-phthalaldehyde with  $\text{NH}_4^+$  and urea as in Keil and Kirchman (1991). Dissolved monosaccharides were analyzed using the protocol of Johnson and Sieburth (1977) and calibrated against a known glucose solution.

*A. anophagefferens* densities from each site were determined on samples fixed in 1% glutaraldehyde (final concentration) using the immunofluorescent probe technique (Anderson et al., 1993), and were counted on a Nikon Optiphot epifluorescent microscope. Bacterial densities were enumerated following staining with SYTO 13 by flow cytometry (delGiorgio et al., 1996). Based upon size and nucleic acid staining, bacteria and detrital particles were discriminated from each other.

### 2.3. Rate process measurements

Oxygen productivity was determined using irradiance relationships of oxygen flux. Oxygen flux was determined by incubating (2–3 h) triplicate unfiltered

water samples in glass stoppered 20 mL test tubes in either flowing seawater trays or in tanks holding thermostatically controlled water, followed by immediate measurement of oxygen concentration. Illumination was from fluorescent lamps and irradiance gradients were produced by varying the distance between tubes and lamps and by covering with one or more layers of window screening or aluminum foil (in the case of the dark treatment). Oxygen was measured using membrane inlet mass spectrometry (Kana et al., 1994). This analyzer consisted of a quadrupole mass spectrometer with a silicone membrane inlet that exchanged the gases between the water and the instrument's vacuum system. Changes in the  $\text{O}_2/\text{Ar}$  ratio gave greatest precision and all changes in oxygen were calculated assuming a constant Ar concentration at 100% saturation throughout each incubation.

Water column nitrogen uptake rates were determined as described below.  $^{15}\text{NO}_3^-$ ,  $^{15}\text{NH}_4^+$ ,  $^{15}\text{N}$ -urea, and  $^{15}\text{N}$ -glutamic acid (all >98% enriched) were added to 100 mL samples in polycarbonate bottles to a final concentration of  $10\ \mu\text{M-N}$  and incubated for ~1 h at 60% of surface irradiance. Saturating additions of substrate were used because half-saturation concentrations for Long Island plankton populations are very low,  $<0.15\ \mu\text{M-N}$  for several nitrogen species examined (Lomas et al., 1996), and there was a concern for depletion of tracer substrate levels and/or isotopic substrate dilution even during short incubations (Glibert et al., 1982). Additional sampling of Quantuck and other south shore bays during the absence of brown tides has found nearly identical nitrogen uptake half-saturation concentrations, although maximum uptake rates were higher for some nitrogen substrates in the presence of brown tides (Lomas, in press). Because there was no difference in half-saturation concentrations for nitrogen uptake between populations with and without the brown tide organism, conversion of saturated rates to in situ rates will not be biased by inherently different nutrient affinities between brown tide and non-brown tide populations. Thus, the saturated rates of nitrogen uptake that were experimentally determined were corrected to in situ rates based upon Michaelis–Menten kinetic equations, ambient nutrient concentrations, and the grand mean (including all data regardless of the extent of the brown tide population) half-saturation concentrations for nitrogen uptake (Lomas et al., 1996). These in situ

rates are presented in this manuscript. Ambient concentrations of glutamic acid were not measured and therefore an assumed concentration of  $0.02 \mu\text{M-N}$  was used in the calculations (see Berg et al., 1997).

Bacterial production measurements were determined by following  $^3\text{H}$ -Leucine (Kirchman et al., 1985) incorporation during a 1–2 h incubation, in the dark at ambient temperature. Rates of Leucine incorporation were converted to C units using a carbon conversion factor of  $0.0031 \mu\text{g C pmol Leu}^{-1}$  (Kirchman and Ducklow, 1993).

Sediment flux core incubations were carried out in a circular incubator kept at ambient water temperature by the continuous pumping of surface water at the Southampton College Marine station dock, which was within  $2^\circ\text{C}$  of ambient temperatures within Quantuck Bay. The incubation cores were immediately placed in the chamber upon returning to the laboratory and were gently bubbled overnight. Such overnight submersion of the cores minimized artifacts of gas exchange between water and the acrylic incubation core. Stirring of the headspace above each core was carried out by a suspended magnet that was turned by a central magnetic turntable. At sunrise on the day after core collection, cores were sealed without any gas space and a dark incubation was initiated. Sampling intervals were 1.5–2 h and water samples were collected at four time points. After the fourth time point, the cores were illuminated with sunlight by removal of an opaque blanket and three more time points were collected at 1 h intervals. The sample water that was removed was replaced by inflow from a carboy containing ambient water such that the absence of gas space was maintained. Samples for gas analysis were collected in 7 mL ground glass stoppered tubes, forced by gravity flow from the ambient water. Mercuric chloride was added as a preservative and the sample tubes were stored underwater at ambient or subambient temperatures. Nutrient samples were collected in 20 mL syringes, filtered ( $0.2 \mu\text{m}$ ), and frozen for subsequent analysis. Analytes included  $\text{PO}_4^{-3}$ ,  $\text{NH}_4^+$ ,  $\text{NO}_3^-$ , DON and DOC (see above). Concentrations of  $\text{N}_2$ , as for  $\text{O}_2$  (see above) were estimated from  $\text{N}_2$ :Ar gas ratios in saturated water standards. The benthic core fluxes, as they are based upon the change in nutrient concentration in the headspace, are by definition net fluxes into or out of the sediment. For the purposes of this study, it is assumed that the flux rate determined during the dark incubation is

solely related to heterotrophic processes in the sediment while during the light incubation, it is assumed that the measured rate is the balance of heterotrophic and autotrophic processes. Therefore, the ‘daily’ benthic flux data should account for both the light and the dark responses and in this study are calculated as the sum of the rates in the light and dark portions of the incubation.

At the end of the incubation, samples for chlorophyll *a* were collected using a cutoff syringe. Duplicate samples were collected to a depth of 0.6 cm and frozen in a 15 mL centrifuge tube until analysis. Chlorophyll *a* was determined on acetone extracts of previously frozen sediment (Sun et al., 1993) using HPLC (Van Heukelem et al., 1994).

#### 2.4. Ancillary data

Additional data that was used in the interpretation and discussion of benthic–pelagic coupling and brown tide population dynamics were taken from SCDHS Water Quality Monitoring Data. Daily meteorological records used in the interpretation and discussion were from the National Weather Service automated monitoring station at Westhampton Beach Airport (<http://www.erh.noaa.gov/box/dailystns.shtml>). These data are based upon hourly observations used in operational forecasting, and are collected and immediately transferred to the internet without official NOAA QA/QC practices employed. Therefore, these data are not the official climatological record, but in most cases are highly accurate and many of the daily climate observations presented here are not available elsewhere.

### 3. Results

#### 3.1. Brown tide bloom dynamics in Quantuck Bay

Average *A. anophagefferens* counts collected as part of this sampling effort agreed reasonably well with the survey record of SCDHS. Differences between our data and the data of SCDHS can be attributed to the large inter-day variability ( $\text{CV} = 50\%$ ) that was twice as large as the intra-bay variability ( $\text{CV} = 25\%$ ). Therefore, the SCDHS cell count data can be used to provide the dynamics of the *A. anophagefferens*

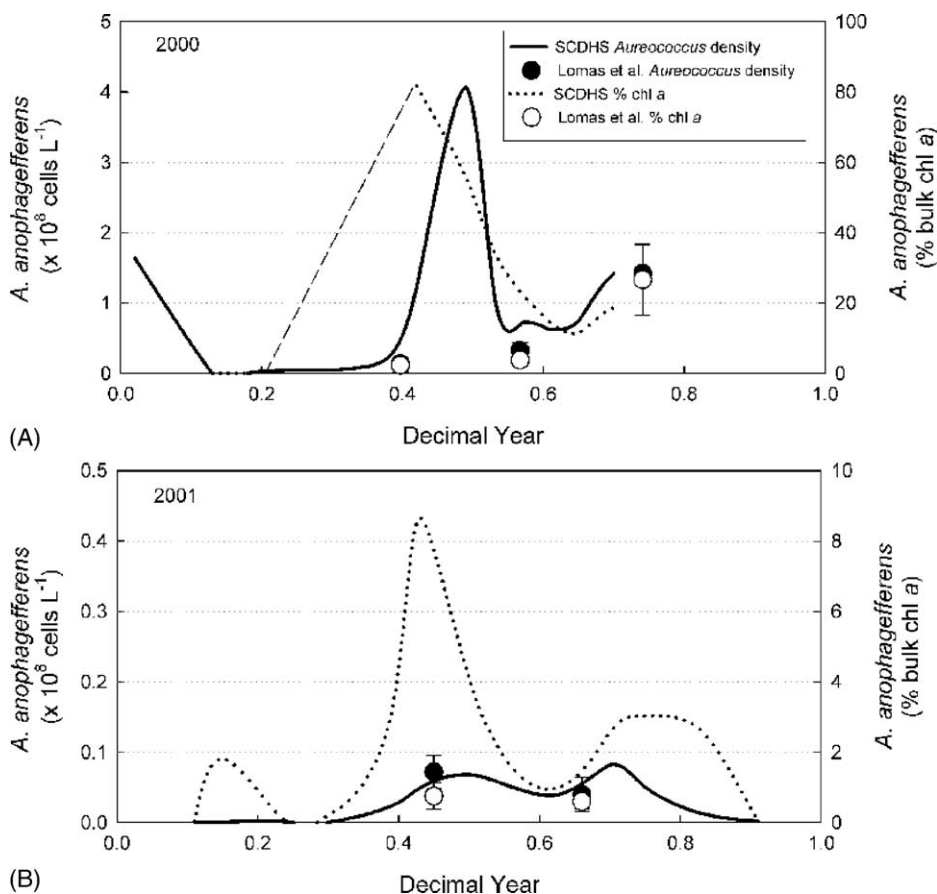


Fig. 2. Annual population dynamics of *A. anophagefferens* in Quantuck Bay during (A) 2000 and (B) 2001. Open and filled circles represent *A. anophagefferens* counts (cells  $L^{-1}$ ) and percentage of bulk chlorophyll *a*, respectively, collected as part of this project. Solid and broken lines represent *A. anophagefferens* counts (cells  $L^{-1}$ ) and percentage of bulk chlorophyll *a*, respectively, collected by SCDHS. Error bars on symbols represent the 95% confidence interval range for the data collected at all three study sites during each sampling period. Note the factor of 10 differences in both y-axis scales between 2000 and 2001.

population around the time of our study. The two years of this study, 2000 and 2001, differed markedly in terms of *A. anophagefferens* population dynamics and the contribution of *A. anophagefferens* to overall chlorophyll biomass (Fig. 2). Two peaks in *A. anophagefferens* density that reached  $4 \times 10^8$  and  $1.5 \times 10^8$  cells  $L^{-1}$  were observed in June and September, respectively, with a lower 'background' level of  $\sim 0.5\text{--}0.8 \times 10^8$  cells  $L^{-1}$  during the mid-summer. Cell densities during 2001 were 10-fold lower throughout the summer/fall (Fig. 2). During the height of the June 2000 bloom, *A. anophagefferens* exceeded 80% of the bulk chlorophyll (assuming

$0.035$  pg chlorophyll *a* per cell; (Lomas et al., 1996; Milligan and Cosper, 1997), while during the smaller bloom in September 2000, *A. anophagefferens* constituted  $\sim 25\%$  of the bulk chlorophyll. During July 2001, a peak in contribution of *A. anophagefferens* was observed, although it was  $<10\%$  of bulk chlorophyll, and less than 5% of chlorophyll during August.

### 3.2. Pelagic and benthic stocks and rate processes

There were few significant differences between 2000 and 2001 in the measured pelagic and benthic

Table 1

Mean ( $\pm 95\%$  confidence limit) physical, biological and chemical data for each sample interval in Quantuck Bay

Parameter/date	May 2000	July 2000	September 2000	June 2001	August 2001
Water temperature ( $^{\circ}\text{C}$ )	14.8 (1.5)	23.1 (1.5)	16.2 (0.3)	20.0 (0.5)	25.0 (0.6)
Bacterial density ( $\times 10^9$ cells $\text{L}^{-1}$ )	4.8 (1.0)	13.8 (3.3)	12.3 (6.7)	10.3 (0.2)	4.4 (0.1)
Pelagic Chl <i>a</i> ( $\text{mg m}^{-3}$ )	30.7 (17.3)	35.6 (3.8)	22.3 (17.2)	47.2 (15.3)	22.8 (10.0)
Benthic Chl <i>a</i> ( $\text{mg m}^{-2}$ )	72.7 (33.9)	53.6 (17.0)	35.0 (7.2)	57.7 (41.6)	N.A.
POC ( $\mu\text{mol L}^{-1}$ )	184.6 (50.4)	407.6 (73.6)	276.0 (103.5)	398.8 (175.2)	306.7 (146.9)
PON ( $\mu\text{mol L}^{-1}$ )	25.2 (6.8)	48.5 (5.2)	39.8 (11.7)	44.4 (42.4)	35.9 (19.8)
POP ( $\mu\text{mol L}^{-1}$ )	1.2 (0.2)	4.1 (0.8)	2.8 (0.7)	3.4 (1.2)	3.5 (0.7)
$\text{NO}_2/\text{NO}_3^-$ ( $\mu\text{mol L}^{-1}$ )	2.9 (5.0)	0.2 (0.3)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)
$\text{NH}_4^+$ ( $\mu\text{mol L}^{-1}$ )	0.4 (0.3)	0.2 (0.1)	0.1 (0.1)	0.1 (0.1)	0.1 (0.1)
$\text{PO}_4^{3-}$ ( $\mu\text{mol L}^{-1}$ )	1.0 (0.3)	1.1 (0.3)	0.4 (0.4)	0.4 (1.0)	0.9 (0.3)
Urea ( $\mu\text{mol-N L}^{-1}$ )	0.2 (0.3)	0.1 (0.1)	0.2 (0.4)	0.4 (0.1)	0.4 (0.8)
DFAA ( $\mu\text{mol L}^{-1}$ )	0.5 (0.2)	0.4 (0.1)	0.5 (0.2)	N.A.	N.A.
Total monosaccharides ( $\mu\text{mol L}^{-1}$ )	2.0 (0.3)	2.6 (0.3)	2.2 (1.4)	N.A.	N.A.

stock parameters, including particulate plankton biomass and dissolved inorganic or organic nutrients (Table 1). Temperature and salinity were similar between years with the exception of lowered salinity in June 2001 due to a significant rain event that occurred during the first few days of sampling. Bacterial densities during 2000 were significantly greater than 2001, likely associated with the significant *A. anophagefferens* bloom (Sieracki, 2001). Average benthic chlorophyll was 33–50% greater in the early

summer of 2000 than during early summer of 2001 which suggested there had been greater light penetration and increased growth of microphytobenthos (MacIntyre et al., this volume), increased sedimentation of phytoplankton and/or decreased rates of loss. There was also a 50% higher ( $P < 0.05$ ; Student's *t*-test) concentration of pelagic chlorophyll in early summer 2001 versus 2000. There was a clear seasonal accumulation of particulate organic matter during the summer in both years.

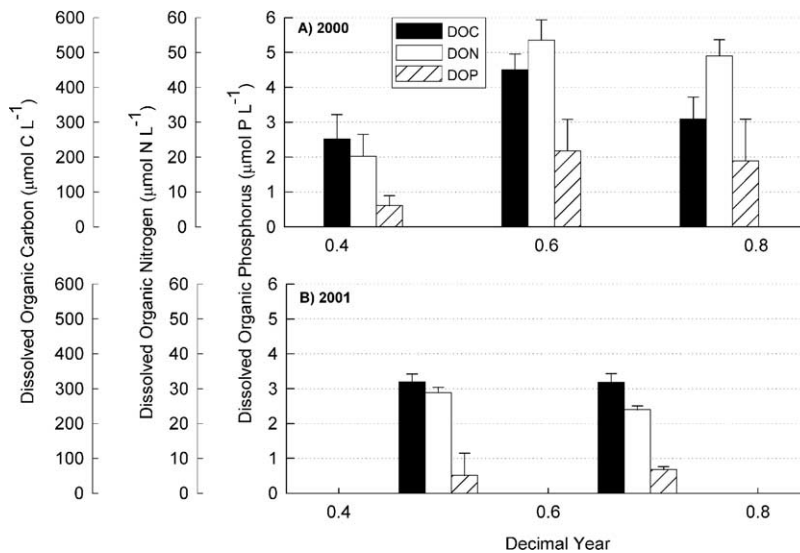


Fig. 3. Seasonal dynamics of dissolved organic carbon, nitrogen and phosphorus concentrations in Quantuck Bay during (A) 2000 and (B) 2001. All concentrations are given as  $\mu\text{mol L}^{-1}$ , but note the factor of 10 difference between scales for each nutrient. Error bars on symbols represent the 95% confidence interval range for the data collected at all three study sites during each sampling period.

There were marked seasonal (in 2000) and interannual differences in dissolved organic nutrient concentrations between 2000 and 2001 (Fig. 3). Seasonally during 2000, there was a significant ( $P$ -value  $<0.001$ ) increase in dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP) pools from May to July. DOC concentrations increased by  $\sim 80\%$ , while DON and DOP concentrations increased by 160 and 190%, respectively. This seasonal increase in dissolved organics was not observed in 2001, and in fact, DOC concentrations in June and August of 2001 were not significantly different than DOC concentrations in May and September of 2000, suggesting that the higher level of DOC in July 2000 was either very short-lived (i.e., produced and consumed on the order of 1–2 weeks) or not produced in 2001. DON concentrations in June 2001 were greater than concentrations in May 2000, but were not nearly as high as in July 2000, and in fact decreased throughout the summer. DOP concentrations were not different between May 2000 and June 2001, and did not accumulate during 2001 as they did during 2000 (Fig. 3).

As with the measured benthic and pelagic stock concentrations, there were few differences, either seasonally or interannually, in measured benthic and pelagic rate processes (Table 2). The microphytobenthic community was net heterotrophic (on a daily basis) in all months sampled. However, in 2001, light-enhanced community respiration resulted in microphytobenthic community production and respiration rates that were double the rates measured in 2000, suggesting a significantly greater consumption of organic matter by the benthos during 2001. The pelagic plankton community displayed comparable interannual patterns of  $\text{NH}_4^+$

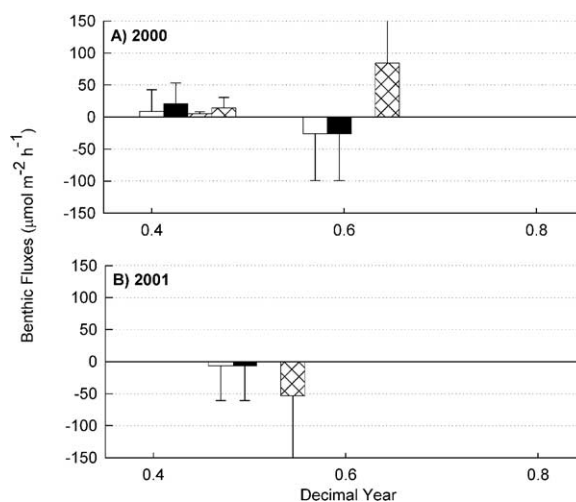


Fig. 4. Net benthic  $\text{NO}_3^-$  (open bars),  $\text{NH}_4^+$  (solid bars), urea (single hatched bars), and bulk DON (cross-hatched bars) fluxes. Error bars represent the 95% confidence interval range for the data collected at all three study sites during each sampling period. Note that a positive flux is a flux into the water column and a negative flux is into the sediment.

and  $\text{NO}_3^-$  uptake, however, rates of organic nitrogen utilization (urea and glutamic acid) were substantially ( $>$ three-fold) greater in 2001 than in 2000. Net benthic nitrogen fluxes ( $\text{NO}_3^-$ ,  $\text{NH}_4^+$ , urea and bulk DON) (Fig. 4) were relatively low ( $<30 \mu\text{mol m}^{-2} \text{h}^{-1}$ ) although there was a high variance. A notably high rate of DON flux out of the sediment was observed in July 2000. Low rates of denitrification reflect an advantage that the benthic autotrophic community has over nitrifying bacteria in the competition for sediment ammonium; nitrification is likely the limit to denitrification in this system.

Table 2

Mean ( $\pm 95\%$  confidence limit) pelagic and benthic rate process for each sample interval in Quantuck Bay

Parameter/date	May 2000	July 2000	September 2000	June 2001	August 2001
Pelagic gross production ( $\mu\text{mol O}_2 \text{L}^{-1} \text{h}^{-1}$ )	11.9 (4.0)	18.1 (3.9)	11.8 (5.4)	17.0 (10.2)	N.A.
Pelagic respiration ( $\mu\text{mol O}_2 \text{L}^{-1} \text{h}^{-1}$ )	1.4 (0.6)	4.4 (2.6)	1.1 (0.6)	3.3 (5.3)	N.A.
Bacterial production ( $\text{mg C m}^{-3} \text{h}^{-1}$ )	0.5 (0.9)	9.6 (1.8)	6.9 (2.8)	N.A.	14.4 (3.9)
Benthic gross production ( $\mu\text{mol O}_2 \text{m}^{-2} \text{h}^{-1}$ )	-818 (1671)	-757 (577)	-838 (764)	-2551 (1564)	N.A.
Benthic respiration ( $\mu\text{mol O}_2 \text{m}^{-2} \text{h}^{-1}$ )	-1342 (733)	-1039 (518)	-1088 (342)	-2076 (884)	N.A.
$\text{NO}_3^-$ uptake ( $\mu\text{mol L}^{-1} \text{h}^{-1}$ )	0.06 (0.07)	0.23 (0.19)	0.04 (0.06)	0.20 (0.27)	0.20 (0.11)
$\text{NH}_4^+$ uptake ( $\mu\text{mol L}^{-1} \text{h}^{-1}$ )	0.32 (0.16)	1.71 (0.79)	0.45 (0.47)	0.83 (0.28)	1.25 (0.28)
Glutamate uptake ( $\mu\text{mol L}^{-1} \text{h}^{-1}$ )	0.01 (0.01)	0.02 (0.01)	0.01 (0.01)	0.11 (0.11)	0.20 (0.09)
Urea uptake ( $\mu\text{mol L}^{-1} \text{h}^{-1}$ )	0.07 (0.05)	0.29 (0.13)	0.11 (0.06)	0.82 (0.30)	0.67 (1.10)

Note, negative fluxes are fluxes into the sediment.

Table 3

Mean ( $\pm 95\%$  confidence limit) ratios for system photosynthesis (gross P) and respiration (R), bacterial production (BP) and Gross P, and bulk particulate and dissolved organic nutrients for each sample interval in Quantuck Bay

Parameter/date	May 2000	July 2000	September 2000	June 2001	August 2001
Gross P:R (mol:mol)	7.9 (3.3)	5.9 (2.8)	8.2 (10.4)	5.8 (5.8)	N.A.
BP:gross P (mol:mol)	0.002 (0.002)	0.055 (0.013)	0.070 (0.041)	N.A.	N.A.
POC:PON (mol:mol)	7.3 (0.5)	8.3 (0.9)	6.9 (0.5)	9.0 (0.6)	8.6 (2.8)
POC:POP (mol:mol)	160.3 (35.7)	100.0 (13.8)	97.6 (29.7)	93.7 (27.8)	86.9 (70.1)
PON:POP (mol:mol)	21.8 (4.4)	12.1 (1.9)	14.1 (3.8)	10.5 (3.6)	10.2 (6.8)
DIN:DIP (mol:mol)	4.8 (5.7)	0.3 (0.2)	0.5 (1.2)	0.7 (1.1)	0.2 (0.1)
DOC:DON (mol:mol)	13.0 (3.8)	8.4 (1.8)	6.4 (2.4)	11.1 (1.7)	13.3 (2.6)
DOC:DOP (mol:mol)	453.5 (237.9)	244 (118)	230.7 (136)	478.3 (160.7)	469.4 (158.9)
DON:DOP (mol:mol)	38.4 (19.2)	28.2 (8.3)	35.4 (27.6)	43.1 (17.8)	35.2 (5.2)

Note, the gross P data were converted to carbon units for comparison with BP using an assumed PQ = 1.2.

### 3.3. Ecological stoichiometry

Both the bulk particulate and dissolved organic matter ratios became relatively enriched in phosphorus from spring to summer in 2000 (Table 3). The same was not the case for dissolved organic matter ratios in 2001, which were statistically identical to ratios in May 2000. Elemental ratios for particulate matter were low in 2001, suggesting that the particulate biomass was of similar quality between years.

### 3.4. Meteorological forcing

Meteorological records were organized into seasonal means representing winter (January to March), spring (April to June), and summer (July to September). A comparison of regional meteorological forcing suggested that there were no significant differences in seasonal air temperature, prevailing wind direction or sky cover (Table 4). There were significantly higher average winter wind speeds in 2000 than in 2001, but

Table 4

Mean ( $\pm 95\%$  confidence limit), cumulative (sum for each 3-month period) and median seasonal and interannual meteorological conditions as measured at Westhampton Airport

Parameter	Year 2000			Year 2001		
	Mean	Cumulative	Median	Mean	Cumulative	Median
January to March—winter						
Temperature ( $^{\circ}\text{C}$ )	0.94 (1.6)	–	1.2	–0.3 (0.8)	–	0.0
Rainfall (inches per month)	0.09 (0.05)	8.2	–	0.16 (0.10)	14.9	–
Wind speed ( $\text{m s}^{-1}$ )	4.8 (0.4)	–	4.6	4.2 (0.4)	–	3.9
Prevailing wind direction ( $^{\circ}$ )	–	–	230	–	–	275
Sky cover	3.8 (0.7)	–	3.2	3.9 (0.7)	–	3.1
April to June—spring						
Temperature ( $^{\circ}\text{C}$ )	12.3 (1.4)	–	13.3	13.5 (1.2)	–	13.6
Rainfall (inches per month)	0.12 (0.07)	10.86	–	0.11 (0.08)	10.1	–
Wind speed ( $\text{m s}^{-1}$ )	4.1 (0.3)	–	4.0	3.6 (0.2)	–	3.4
Prevailing wind direction ( $^{\circ}$ )	–	–	210	–	–	210
Sky cover	3.8 (0.7)	–	2.9	3.5 (0.7)	–	1.9
July to September—summer						
Temperature ( $^{\circ}\text{C}$ )	18.6 (1.1)	–	19.4	19.8 (0.8)	–	19.4
Rainfall (inches per month)	0.12 (0.06)	10.9	–	0.11 (0.06)	9.7	–
Wind speed ( $\text{m s}^{-1}$ )	3.3 (0.2)	–	3.2	3.2 (0.3)	–	3.0
Prevailing wind direction ( $^{\circ}$ )	–	–	220	–	–	205
Sky cover	3.4 (0.7)	–	2.1	2.5 (0.5)	–	1.5

Note sky cover is a dimensionless estimate of the clear sky condition, with values of 1 being the minimum and 10 being the maximum.

not in any other season. This increased winter wind speed was not apparently related to increased storm events and rainfall as might be expected. In fact, daily rainfall levels were nearly twice as high in the winter of 2001 than in winter of 2000; rainfall during the spring and summer were statistically similar. This resulted in a nearly 20% higher winter to summer rainfall in 2001 than in 2000.

#### 4. Discussion

During the course of this two-year field study, significant differences in brown tide population dynamics occurred, thus providing a natural test of current DOM/Brown Tide Bloom models.

##### 4.1. Evaluation of brown tide 'organic nutrient' models and the role of benthic–pelagic coupling

There are currently two related 'bottom-up' models of *A. anophagefferens* population dynamics that are based upon field data (LaRoche et al., 1997; Gobler and Sanudo-Wilhelmy, 2001b). Both models are fundamentally similar; they hypothesize that increases in DON would favor blooms of *A. anophagefferens*, yet they differ in the mechanisms of action. LaRoche et al. (1997) hypothesized that decreases in groundwater inputs, averaged over the 12-month prior to a brown tide bloom, would lead to relatively lower  $\text{NO}_3^-$  inputs, and relative increases in the importance of DON, as a potential nitrogen source, that would favor *A. anophagefferens* blooms. Gobler and Sanudo-Wilhelmy (2001b) modified this model by suggesting that short-term variability, weeks to months, in groundwater flow would stimulate *A. anophagefferens* blooms by first stimulating blooms of non-*Aureococcus* species that fuel accumulation of DOM, that then supports brown tide blooms.

Seasonality of the precipitation/evaporation balance is the dominant influence on groundwater recharge for eastern Long Island (Steenhuis et al., 1985) and seasonal patterns of hydraulic gradients closely match seasonal patterns in groundwater flow and subsurface discharge into the coastal bays (Gobler and Sanudo-Wilhelmy, 2001b). Therefore, as already hypothesized, it is likely that interannual variability in

seasonal rainfall will have an impact on the brown tide population dynamics later in a year especially if winter rainfall is different. Winter rainfall during 2001 (Table 4) was significantly greater (~80%) than in 2000, while spring and summer rainfalls were nearly identical. However, the 12-month 1999–2000 (June 1999 to May 2000) average rainfall was no different ( $P > 0.05$ ) than the 12-month 2000–2001 (June 2000 to May 2001) average rainfall. Given this, one might expect, by either DOM model, that brown tide blooms would be more likely during the summer of 2001, compared to 2000. The caveat here may well be related to the lack of accumulation of DOM in 2001, when the models would have predicted significant accumulations. It would appear that the lack of accumulation of DOM, conditions correlated with brown tide blooms (Lomas et al., 2001), would suggest differences in the ecosystem that are not included in current DOM/Brown Tide Bloom models.

There are two possible modifications to the DOM/Brown Tide Bloom models that might be brought to bear on these differences in DOM accumulation. First, there was a significant shift away from phytoplankton light absorption to detrital matter light absorption (see MacIntyre et al., this volume) from the summer of 2000 to the summer of 2001, as well as an overall increase in total light attenuation. Although, greater rainfall may have led to increased nutrients (note the timing of both our data and the SCDHS data does not suggest this), it also appears to have led to significantly increased detrital particle loads that may have resulted in light limitation of phytoplankton communities during this time (see also Kana et al., this volume) and restricted the growth of the spring bloom. This restriction of the spring bloom would potentially limit both the recycling and accumulation of DOM in the water column, and the accumulation of organic matter in surface sediments leading to the observed reduced (indeed a change in the direction of fluxes) benthic fluxes.

Second, there was the aforementioned change in direction of benthic nutrient fluxes. Our data show that in 2000, there was a significant flux of DON into the water column (Fig. 4). If this efflux rate had been maintained over ~30 days (time frame between May sampling and June peak in *A. anophagefferens* maximum) and assuming an 8–10 day residence time for

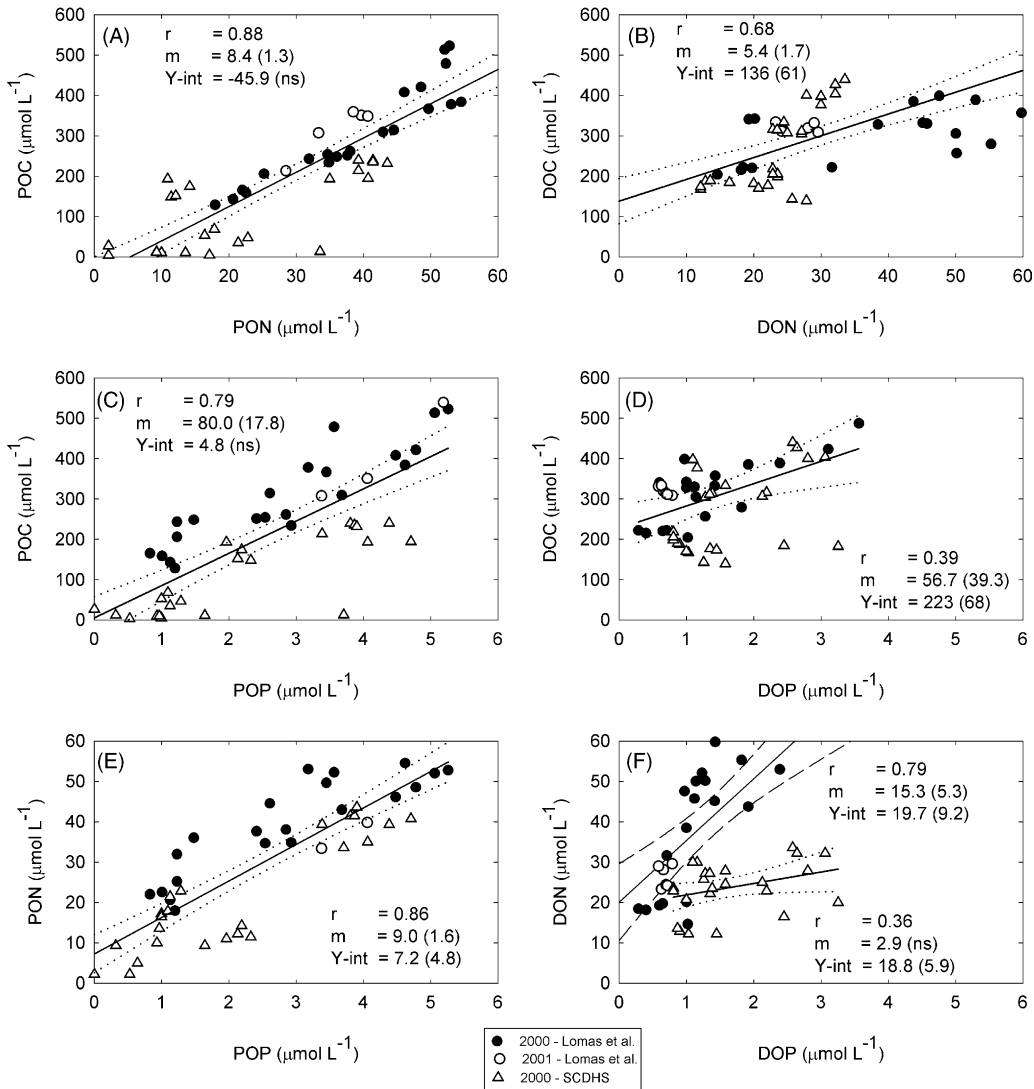


Fig. 5. Bi-variate plots of particulate and dissolved organic matter collected during our sampling in 2000 (solid circles) and 2001 (open circles), and the SCDHS in 2000 (open triangles). The solid lines represent the best fit to all data in a plot, with the exception of panel F, and the dotted or dashed (panel F) lines represent the 95% confidence intervals. The correlation coefficient ( $r$ ), slope ( $m$ ;  $\pm 95\%$  confidence limit), and  $Y\text{-int}$  ( $\pm 95\%$  confidence limit) for each set of data are provided in the corresponding panels. n.s. means that the parameter is not significantly different than zero.

this body of water (Gobler, personal communication), then this benthic flux would have accounted for  $\sim 50\%$  of the DON accumulation that was observed from May to July 2000. The flux of DON in 2001 was into the sediment and would clearly have a significant negative impact on seasonal DON accumulation in the water

column, and the DON loss also appears to have had an impact on *A. anophagefferens* population dynamics. Moreover, the rates of DON uptake are small relative to potential benthic fluxes and they would have a smaller impact on the dynamics of DON in Quantuck Bay. Changes in directionality of the flux could

be partially due to a decrease in organic matter inputs from pelagic or benthic algae, which are related to differences in nutrient inputs and submarine light fields.

#### 4.2. Ecological stoichiometry of Long Island coastal bays

Ecological stoichiometry is the study of the balance of energy and multiple chemical elements and their ecological interactions (Elser and Urabe, 1999). This includes, but is not limited to, environmental physiology, population dynamics and community organization, and provides a framework for the interpretation of ecological data. The current study, just as an earlier study by Lomas et al. (2001) suggests that brown tide blooms are associated with environments that are relatively enriched in DON and DOP, however, this is the first study to highlight the stoichiometric uncoupling of particulate and dissolved organic matter pools (Table 3, Fig. 5). These results suggest that any change in various planktonic groups (i.e., brown tide versus non-brown tide populations) do not have a demonstrable impact on the overall stoichiometry of particulate or dissolved organic material, but appear to have an impact on the differential cycling of organic material between the particulate and dissolved pools. These findings have been confirmed by elemental particulate ratios in cultures of *A. anophagefferens* are not different from particulate ratios in a variety of *Synechococcus* isolates (Alexander, Glibert, and Lomas, unpublished; Heldal et al., 2003), but no comparative data exist for DOM.

Bulk organic matter ratios, especially DOM, only tell part of the story as they can include material that was not produced during the current productive season but rather was carried over from previous production seasons or from allochthonous sources. Plots of measured concentrations of particulate and dissolved organic matter (Fig. 5) show that, in general, data from both years of our study and from the SCDHS database agree in the magnitude and ratio for particulate organic matter, but not for dissolved organic matter. The presence of the brown tide organism leads to higher DOC:DOP and DON:DOP ratios. More importantly, these data show that the ratio at which particulate organic matter is produced (Fig. 5a, c and e) is generally less than the bulk average (Table 3). This is

truly exaggerated in the dissolved organic matter pool where the ratio of organic matter produced is two- to seven-fold lower than the bulk ratio. Surprisingly, the ratio of DOC:DON produced is about one-half of the particulate organic matter ratio, while DOC:DOP and DON:DOP ratios are about five-fold lower than particulate ratios suggesting that Quantuck Bay microbial communities in general selectively retain DON and DOP. Further studies are warranted to examine the impacts of phytoplankton community composition on the coupling between particulate and dissolved organic nutrient cycles.

## 5. Conclusions

This study allows us to examine the potential for pelagic and benthic rate processes, not yet measured as part of the Brown Tide Research Initiative, to explain interannual variability in *A. anophagefferens* population dynamics. The lack of DOM (and most importantly DOP) accumulation in the non-brown tide year appears to be a strong correlate for understanding the growth dynamics of this species. Our benthic flux numbers for DON are sufficiently large as to not only explain 50% of the accumulation during 2000, but the lack of accumulation in 2001 as well. As this study focused on bottom up controls within a natural system, there was no selective inhibition of the grazing community (i.e., bottle effects), and no evidence for differences in microzooplankton community structure between years (Sieracki, 2001; Sieracki and O'Kelly, 2002), it is likely that the bloom observed in 2000 resulted from *A. anophagefferens* successfully out-competing other co-occurring phytoplankton species.

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