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Shift of algal community structure in dead end lagoons of the Delaware Inland Bays during seasonal anoxia

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ABSTRACT: Development of seasonal anoxia and algal blooms was studied in Torquay Canal and Bald Eagle Creek, 2 dead end canals in the northern Rehoboth Bay, one of the 3 Delaware Inland Bays. Mean low water depth is ca. 2 m, but dredging has produced over a dozen holes with a water depth of 5.5 m. From May to September 2002, *in situ* temperature, salinity, pH, dissolved O_2 and H_2S were measured in the water column. Nutrients (NO_3^-, NO_2^-, NH_4^+ and PO_4^{3-}) were analyzed and the dominant members of the phytoplankton community were identified and numerated from samples collected in conjunction with *in situ* depth profiles. In early May, a significant potential harmful *Prorocentrum minimum* bloom (275 µg l^{-1} chl *a*) was present in Torquay Canal. Dissolved O_2 was supersaturated in the surface water, but H_2S developed below 2 m as the water column stratified. Diatom blooms were observed in late May and mid-July, the only times that O_2 penetrated deeper, but their biomass was not significant. In early September, a storm over 3 d partially mixed the water column, and a large *Heterosigma akashiwo* bloom (231 µg l^{-1} chl *a*) was observed. Our data indicate that nutrients accumulated in the water column from runoff, organic matter decomposition, and from Fe(III) (oxy)hydroxide reduction in sediments. High concentrations of H_2S, NH_4^+ and PO_4^{3-} were present in the bottom waters during summer. PO_4^{3-} and NH_4^+ from the bottom water entered shallower waters as the oxic–anoxic interface moved up to the surface. The supply of nutrients from bottom to surface waters supported harmful algal blooms during seasonal anoxic conditions as dinoflagellates and flagellates dominated over diatoms in surface waters. Seasonal anoxia development is not only a potential threat to fish and shellfish but also causes shifts of algal species to potentially harmful taxa.

KEY WORDS: Algal blooms · Anoxia · Harmful algal blooms · Hydrogen sulfide · Nutrient cycling · Stratification

INTRODUCTION

Although algal blooms are natural phenomena, their extent and frequency have increased globally over recent decades (Anderson et al. 2002) as human activities have input large amounts of nutrients into coastal waters. Eutrophication has been linked with the increased number of algal blooms, followed by anoxia, fish and shellfish kills, and effects on human health (Mallin et al. 1993, Anderson et al. 2002, Luther et al. 2004).

Nutrient dynamics affect algal community structure in complex ways. High primary production can be an indicator of high nutrient inputs; however, this is not always clear (Cloern 2001, Sharp 2001). Eutrophication also changes the ecosystem structure from dominance of perennial macro-algae and seagrass species towards ephemeral macro-algae and pelagic microalgae (Borum 1996). Nutrient overloading with changing N/P ratios may play an important role in shifting phytoplankton community compositions by promoting frequent harmful algal blooms. The shift of a biological

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community from benthic to pelagic also has effects on nutrient cycling because seagrass detritus consists of structural polysaccharides and has a lower mineralization rate, whereas phytoplankton contain more labile nitrogenous material (Herbert 1999). The quantity and quality of the organic matter supplied to the sediment control benthic nutrient regeneration and metabolism. As a result, nutrient enrichment can regulate biological diversities at all trophic levels within the coastal food web (Cloern 2001).

When large amounts of organic matter sink down to the bottom, nutrient recycling is accelerated and results in a rapid depletion of O_2. Other oxidants such as NO_3^-, Mn(III, IV), Fe(III), SO_4^{2-}, and CO_2 are used as electron acceptors, and anoxic environments eventually result (Froelich et al. 1979, Luther et al. 1997, Herbert 1999). As metabolism shifts from aerobic to anaerobic, sulfate reduction is stimulated (Jørgensen & Richardson 1996). Ammonium and phosphate are regenerated from organic matter decomposition through anaerobic metabolic processes when sulfate and Fe(III) (oxy)hydroxides are used as electron acceptors (Froelich et al. 1979, Luther et al. 1997). In addition, as sediments become anoxic, PO_4^{3-} is released from reduction of Fe(III) (oxy)hydroxides to the water column and stimulates secondary algal blooms (Rozan et al. 2002). Part of the NH_4^+ will also be oxidized to NO_3^- when NH_4^+ diffuses from anoxic into oxic water. This NO_3^- may be reduced to N_2 or N_2O gas (Froelich et al. 1979, Howarth et al. 1988, Luther et al. 1997, Boesch et al. 2001). In estuaries, half of the terrestrial nitrogen input may be lost via denitrification; however, in Chesapeake Bay, only 25% of the terrestrial nitrogen is lost through denitrification (Seitzinger 1988, Nixon et al. 1996). If hypoxia/anoxia develops, nitrification is inhibited, and less NO_3^- and NO_2^- are available for denitrification and 'annamox' reactions (Kuypers et al. 2003). More nitrogen exists as NH_4^+ and is assimilated by phytoplankton to support further primary production. The residence time of nitrogen increases, and eutrophication is aggravated (Kemp et al. 1990). Consequently, the time scale of the coupling of the pelagic and benthic systems can be shortened (Buchsbaum et al. 1991, Enriquez et al. 1993).

The spatial distribution and temporal dynamics of nutrients are of great significance in understanding the effects of eutrophication on outbreaks of harmful algal blooms so as to develop effective management programs to rehabilitate coastal regions (Cloern 1996, Anderson et al. 2002). This study examined the relationship of seasonal anoxia and harmful algal blooms in Rehoboth Bay by determination of the seasonal changes of temperature, salinity, pH, dissolved O_2, H_2S, nutrients (NO_3^-, NO_2^-, NH_4^+ and PO_4^{3-}) and phytoplankton community structure from May to September 2002. The Delaware Inland Bays are small, shallow and poorly flushed estuaries. These shallow waters are typical along mid-Atlantic and Gulf coasts (Maxted et al. 1997, Church et al. 2002). Eutrophication has resulted in adverse ecological effects as seasonal anoxia and fish kills occur in this ecosystem (Luther et al. 2004). A comprehensive understanding of how this coastal ecosystem responds to eutrophication is key for developing restoration strategies, which can be applied to other coastal ecosystems.

In the present study, our data indicate that seasonal anoxia developed from early May through September in Rehoboth Bay in 2002. Phytoplankton communities changed dramatically during the sampling season: diatoms dominated when O_2 penetrated down to bottom sediments; dinoflagellates and flagellates were present in the surface, oxic–anoxic interface and bottom waters during seasonal anoxia in spite of high H_2S concentrations in the bottom waters. These results demonstrate that seasonal anoxia is not only a potential threat to fish and shellfish but also causes shifts of algal species to potentially harmful taxa.

MATERIALS AND METHODS

Sampling sites. Field sampling was conducted at Torquay Canal and Bald Eagle Creek, 2 dead end lagoons in the northern Rehoboth Bay, one of the 3 Delaware Inland Bays (Fig. 1). The mean low water depth of this area is about 2 m and a 1.4 m sill connects Torquay Canal with Bald Eagle Creek. Benthic sediments from these sites were used as fill for wetlands and housing developments in the 1960s (Maxted et al. 1997), creating over a dozen holes at the bottom of Torquay Canal and Bald Eagle Creek with a maximum water depth of 5.5 m. Sampling took place at Torquay Canal Sites 1 and 5, the control sites (2 m); Torquay Canal Sites 2, 3 and 4 (5.5 m); and Bald Eagle Creek Sites 6 and 9 with holes (5.5 m).

***In situ* measurements.** A 3-electrode voltammetric system was deployed *in situ* to measure real time dissolved O_2 and H_2S concentrations with high vertical resolution and low detection limits (Brendel & Luther 1995, Luther et al. 1998, 2001, Taillefert et al. 2000). This 3-electrode voltammetric system consisted of a solid state Au/Hg PEEK^{TM} microelectrode coupling with a solid-state Ag/AgCl reference electrode and a Pt counter electrode. With this voltammetric system, the seasonal anoxia development in the water column of the Delaware Inland Bays was followed without disturbing the environment, which was important for simultaneous chemical analysis.

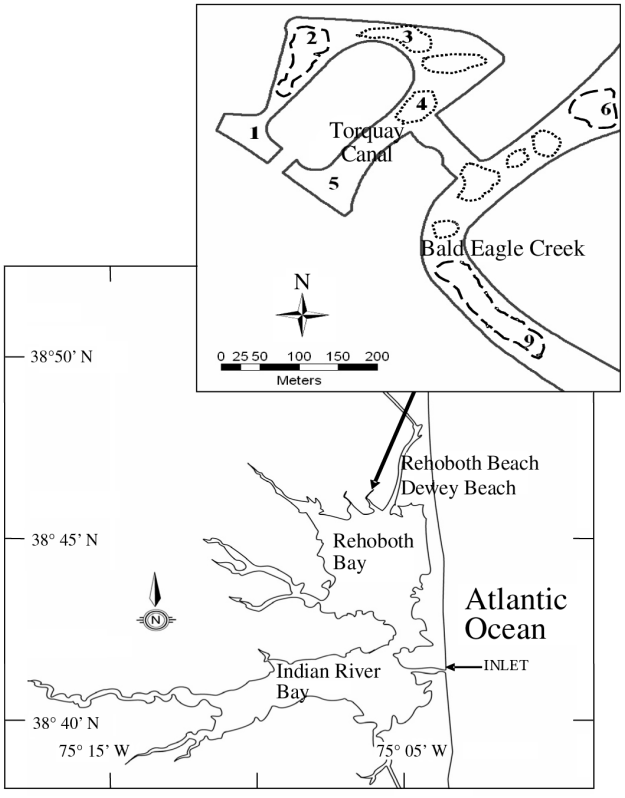

Fig. 1. Map of the 3 Delaware Inland Bays with an insert of the 2 dead end lagoons Bald Eagle Creek and Torquay Canal, in Rehoboth Bay. Numbers indicate the sites studied; dotted and dashed lines indicate water depths between 2 and 4 m and 4 and 5.5 m, respectively

The 3-electrode system was mated with an Analytical Instrument Systems, model DLK-100A, and was controlled by a laptop computer. The voltage scan ranged from –0.1 to –1.8 V and the scan rate was 1000 mV s^{-1}. Linear sweep voltammetry was used to determine O_2, and cyclic voltammetry was used to determine H_2S. A potential of –0.9 V was used as the conditioning step to remove any deposited sulfide when H_2S existed. Prior to fieldwork, standardizations for dissolved O_2 and H_2S were done in the laboratory (Brendel & Luther 1995, Luther et al. 1999, Rozan et al. 2002). Precision is typically better than 2% at the 95% confidence limit (Brendel & Luther 1995, Luther et al. 2002).

Temperature, salinity, pH, dissolved O_2 and H_2S data were collected every 2 wk with *in situ* analyzers at 7 sites. In addition to O_2 and H_2S measurements described above, temperature and salinity were obtained with a YSI-30 T-S meter with a 16 m cable. pH was measured with a portable Digi-Sense pH meter using a Sensorex pH electrode with a 6 m cable. The waterproof wires for the T-S sensor, pH sensor, and the PEEK™ working electrode were tied together, and to a lead weight encased in plastic. Data were obtained in real time from the surface (0.2 m) of the water column to the bottom (5.5 m).

Discrete sampling. Samples (750 ml) for nutrients, chlorophyll *a* (chl *a*) and phytoplankton community analysis were collected in 250 ml acid-washed polyethylene bottles using a plastic hand pump at Sites 2 and 9 (Fig. 1). Sampling depths were at the surface (0.2 m), interface, and bottom (5.5 m) as determined by *in situ* voltammetry. If O_2 was present throughout the water column, a mid-water column sample was also taken.

For nutrient analyses, samples were kept in a cooler at 4°C and were filtered through 0.2 µm Nuclepore polycarbonate filters on return to the laboratory and kept at –20°C until analysis. NO_3^- and NO_2^- were determined by anion chromatography with ultraviolet detection (Rozan & Luther 2002). NH_4^+ was determined using a flow injection analysis method (Hall & Aller 1992). PO_4^{3-} was determined using the molybdate blue complex method (Rozan et al. 2002).

For chl *a* and phytoplankton community analysis, samples were kept in a cooler at ambient temperature. On returning to the laboratory, samples were filtered through 0.2 µm Nuclepore polycarbonate filters. The filters were kept at –20°C until chl *a* analysis was performed. Acetone was used to extract chl *a* for 24 h at –20°C and a fluorometer was used to determine the concentrations of chl *a* (Schmidt & Hutchins 1999).

Phytoplankton communities were analyzed using a method designed for the rapid identification and enumeration of harmful algal blooms in field samples with a standard compound microscope (Whereat et al. 2004). Live samples were used to facilitate the identification of marine flagellates, particularly raphidophytes (class Raphidophyceae), which lose distinctive features when preserved. Samples were held at ambient temperature until screening, which occurred within 6 h of collection. Two to three 40 µl drops, drawn from a well-mixed 250 ml sample, were examined on a conventional slide with cover slip. Phytoplankton were identified according to the taxonomy of Tomas (1997). Potentially toxic phytoplankton which had previously been found in the Delaware Inland Bays were identified to the species level, but many phytoplankton, particularly those smaller than 10 µm, were identified to higher taxonomic levels. Estimates of cell density below 1×10^6 cells l^{-1} were determined by averaging the number of cells seen in each 40 µl drop. Estimates of cell density above 1×10^6 cells l^{-1} were determined by averaging the number of cells seen per field of view at 100× magnification across at least 10 fields of view.

The relationships among environmental parameters were investigated by Pearson correlation coefficient analysis using SPSS statistical software with untransformed data (Kritzberg et al. 2005).

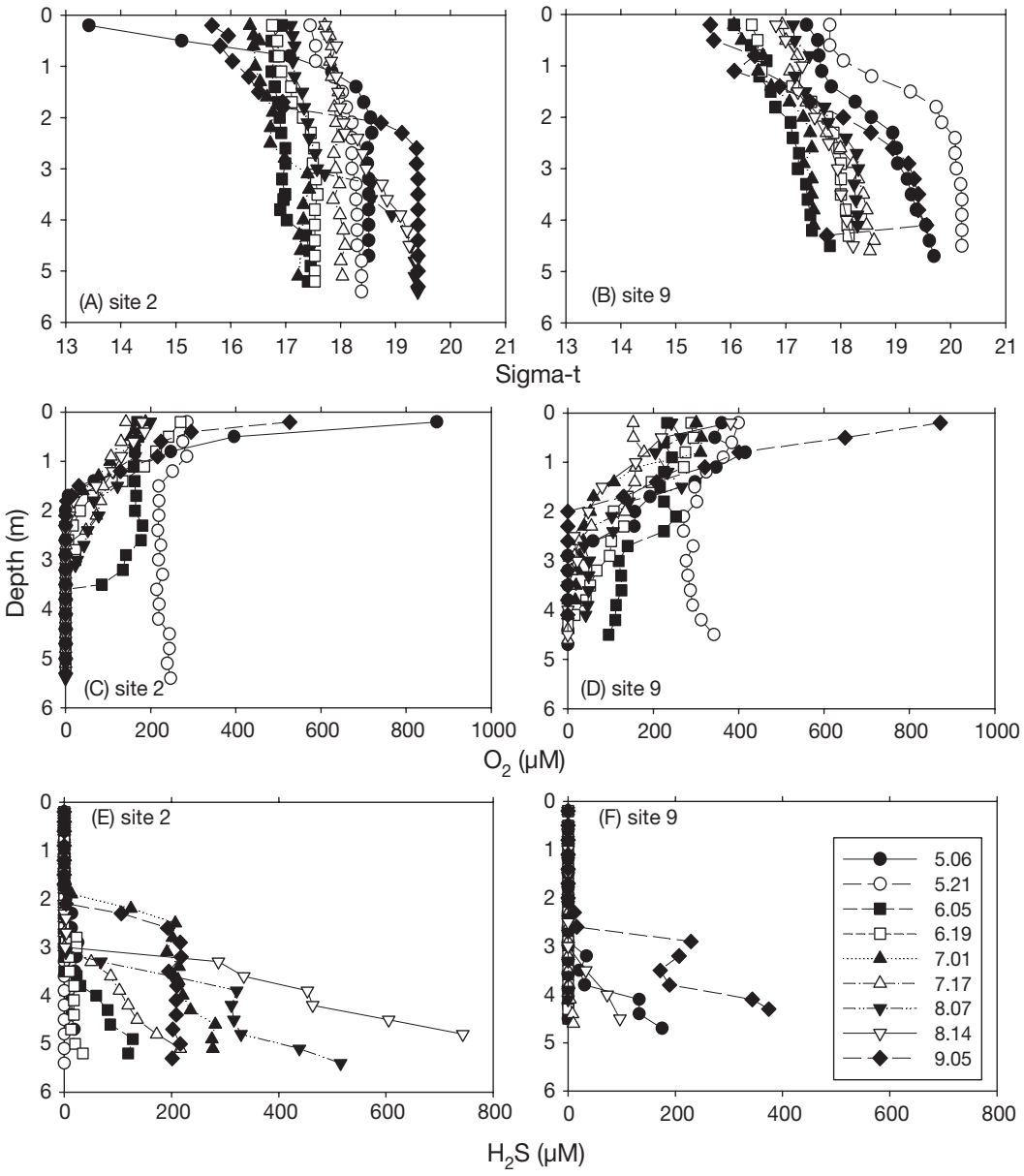

Fig. 2. (A,B) Density (as sigma-t), (C,D) dissolved O_2, and (E,F) H_2S vs. depth at Torquay Canal Site 2 and Bald Eagle Creek Site 9 for 2002

RESULTS

Physical–chemical parameters (density, O_2, H_2S, O_2 penetration depth)

The water column was stratified in early May at Torquay Canal Site 2 and Bald Eagle Creek Site 9 (Fig. 2A,B). At Site 2, surface water density given in sigma-t units was 13.4, but below 2 m the density increased to 18.5. Stratification was less pronounced from late May to mid-June but became greater in early July. Although stratification was lost on July 17 due to strong winds prior to sampling, it built up again thereafter in the water column and remained through August. In early September, after a 3 d rain storm, the water column was partially mixed, but on September 5 stratification was as great as that on May 6. Stratification in summer 2002 was not as substantial as in 2001 as evidenced by the O_2 penetration depth (Fig. 3) (Luther et al. 2004). Stratification at the main hole of Site 9 also developed from early May, but was not as substantial as in Torquay Canal and in 2001(Fig. 2B).

Dissolved O_2 was saturated or supersaturated in the surface water but undetectable in the holes during

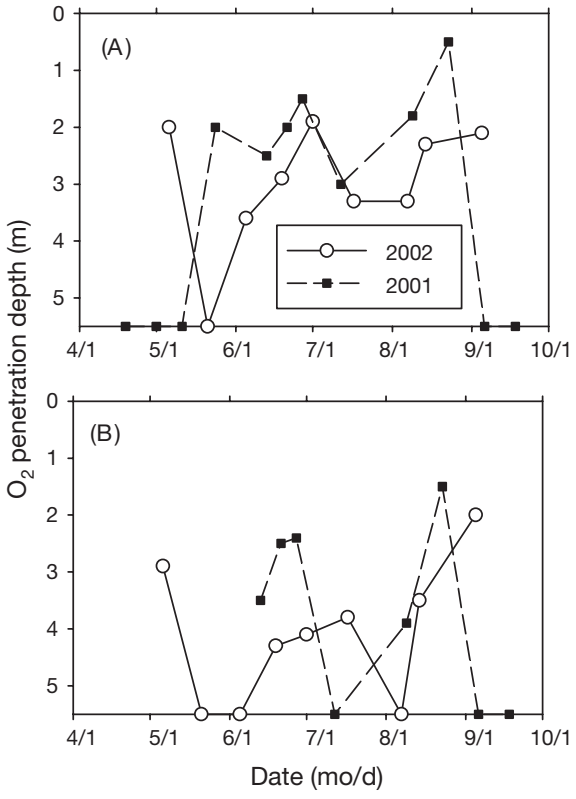

Fig. 3. Comparison of O_2 penetration depths at (A) Torquay Canal Site 2 and (B) Bald Eagle Creek Site 9 for 2001 and 2002

most samplings (Fig. 2C,D). At Site 2, O_2 was 872 µM in the surface water on May 6 because of a *Prorocentrum minimum* bloom (see 'Algal community structure'), but was not detected below 1.7 m. Due to windy weather in mid-May, the water column was mixed and O_2 penetrated into the bottom water on May 21. In the summer of 2002, precipitation was at its record low for the past 100 yr (Department of Natural Resources and Environmental Control, DNREC), but winds were stronger than in 2001 and some O_2 was mixed down into the holes (Fig. 3A). From June 5 to September 5, O_2 was detected in the surface water, but was undetectable in the bottom water. Winds were not strong enough to completely mix the water column in Torquay Canal. A high O_2 concentration of 530 µM was found again on September 5 because of a *Heterosigma akashiwo* bloom (see 'Algal community structure').

At Site 9 (Fig. 2D), O_2 was supersaturated in the surface water on May 6; however, no O_2 was detected in the bottom water (below 3 m). From May 21 to June 19, O_2 penetrated into the deep water but was less than surface O_2 levels. By mid-July, O_2 was not detected in the bottom water. On August 7, O_2 in the bottom water increased to 42 µM. A week later, O_2 was not detectable in the bottom water. On September 5, surface O_2 concentration reached 870 µM because of a *Heterosigma akashiwo* bloom (see 'Algal community structure'), with bottom water O_2 again undetectable. These O_2 data along with the density data show that stratification developed in these areas.

H_2S was produced in the holes of Torquay Canal and Bald Eagle Creek in 2002 (Fig. 2E,F). On May 6, 18.6 µM H_2S was detected in the bottom water of Site 2 although surface water O_2 was supersaturated. Stratification prevented O_2 from penetrating into deep water and H_2S from reaching the surface water. In July, H_2S at the bottom of Site 2 was over 200 µM and increased to 744 µM in mid-August. The 3-layer structure in H_2S concentration also indicates that surface waters did not mix with interface or bottom waters. On September 5, the concentration of H_2S decreased over 3-fold to 217 µM in the bottom water, indicating that the bottom water had mixed upwards to at least 2 m or higher in the water column although H_2S was not detected in the surface water.

H_2S was also found at Site 9 during the first sampling (Fig. 2F). The concentration of H_2S was 175 µM in bottom water, much higher than that found in Torquay Canal. The highest concentration of H_2S in Bald Eagle Creek was 374 µM in 2002, much lower than the highest in 2001 (1.4 mM on June 27, 2001; Luther et al. 2004). Three-layer structures in H_2S concentration were also detected at Site 9, but H_2S was not found throughout the summer as in Torquay Canal and in 2001 (Luther et al. 2004).

Wind can mix the water column and force O_2 to penetrate deeper. Fresh water run-off can decrease the surface water salinity and keep the water column stratified. In Torquay Canal, the O_2 penetration depths (Fig. 3A) were greater than 3 m from late May to mid-August in 2002 except for July 1 when the O_2 penetration depth was 1.9 m (the shallowest for the entire summer). However, in 2001, the O_2 penetration depths were only about 2 m or less from May 24 to August 23, which was shallowest at 0.5 m (Luther et al. 2004).

In Bald Eagle Creek, the O_2 penetration depths were also deeper than 3.5 m from late May to mid-August 2002 (Fig. 3B), and were generally greater than those in 2001. Winds mixed O_2 down below 4 m from June to early August, and sulfide was likely oxidized by abiotic and biotic oxidation processes.

Torquay Canal is completely surrounded by houses and trees, whereas Bald Eagle Creek has houses only on one side, the other side being undeveloped marsh. The housing pattern around Torquay Canal and Bald Eagle Creek affects how the winds force O_2 to penetrate deeper in these waters.

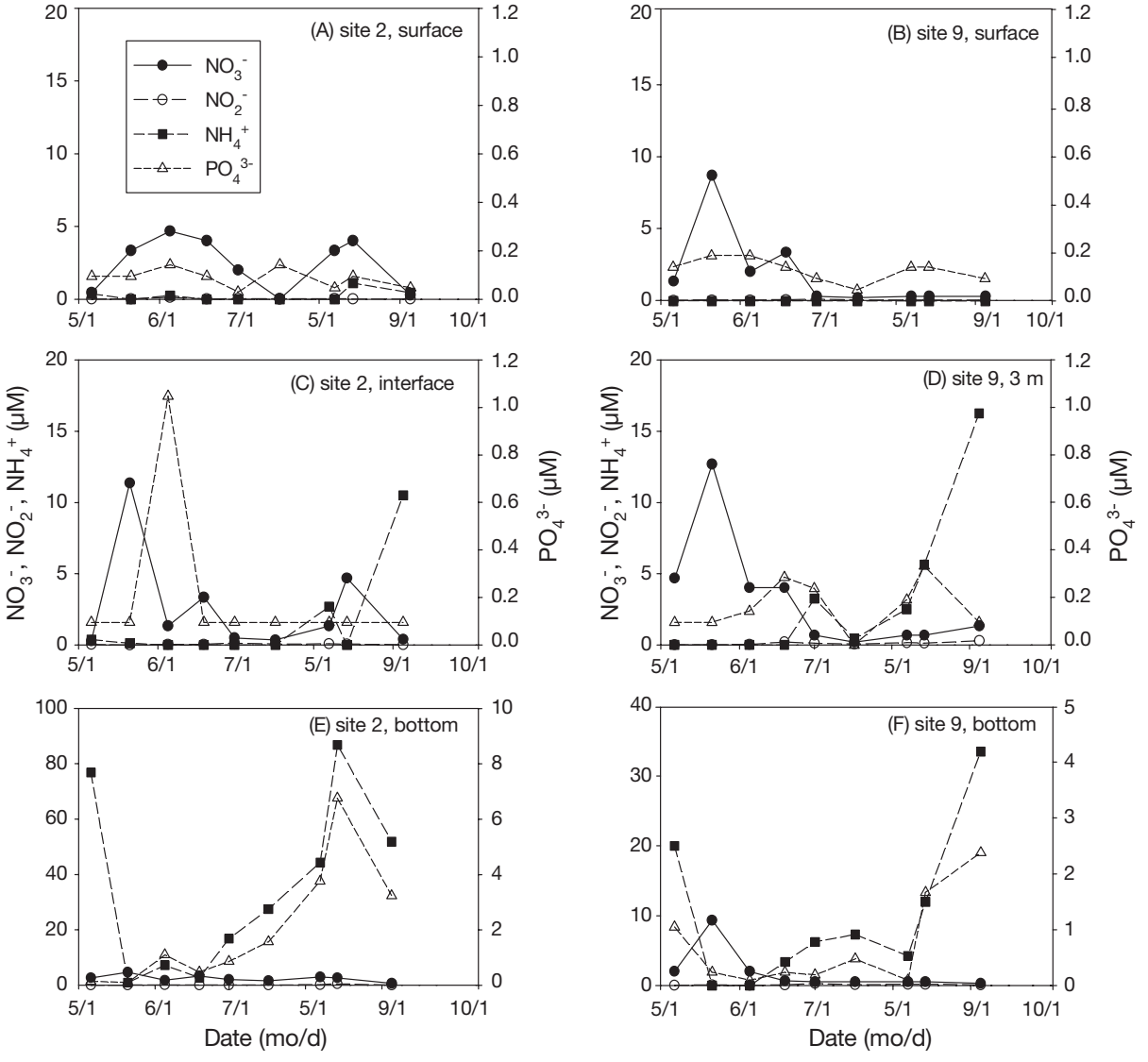

Fig. 4. Nutrient concentrations in the surface, interface and bottom waters of (A,C,E) Torquay Canal Site 2 and (B,D,F) Bald Eagle Creek Site 9

Nutrients

Surface waters

Nitrate was generally higher than NH_4^+ and PO_4^{3-} in the surface waters (Fig. 4A,B). At Site 2, NO_3^- was drawn down on May 6 (*Prorocentrum minimum* bloom), July 17 (*Leptocylindrus* sp. bloom) and September 5 (*Heterosigma akashiwo* bloom) (see 'Algal community structure'). At Site 9 (Fig. 4B), 8.7 µM NO_3^- was measured on May 21 when there was a diatom bloom; NO_3^- decreased in June and was low through September. Ammonium and phosphate were low in the surface water at both sites.

Interface waters

At both Sites 2 (Fig. 4C) and 9 (Fig. 4D), the highest NO_3^- concentration was measured on May 21 as the diatom bloom occurred. Ammonium was low from May to July but increased from August to September. Phosphate concentrations were similar to those in surface waters except for a high value of 1.1 µM on June 5 at Torquay Canal.

Bottom waters

Ammonium and phosphate were much higher in bottom waters. At Site 2 (Fig. 4E), NH_4^+ was 77 µM in

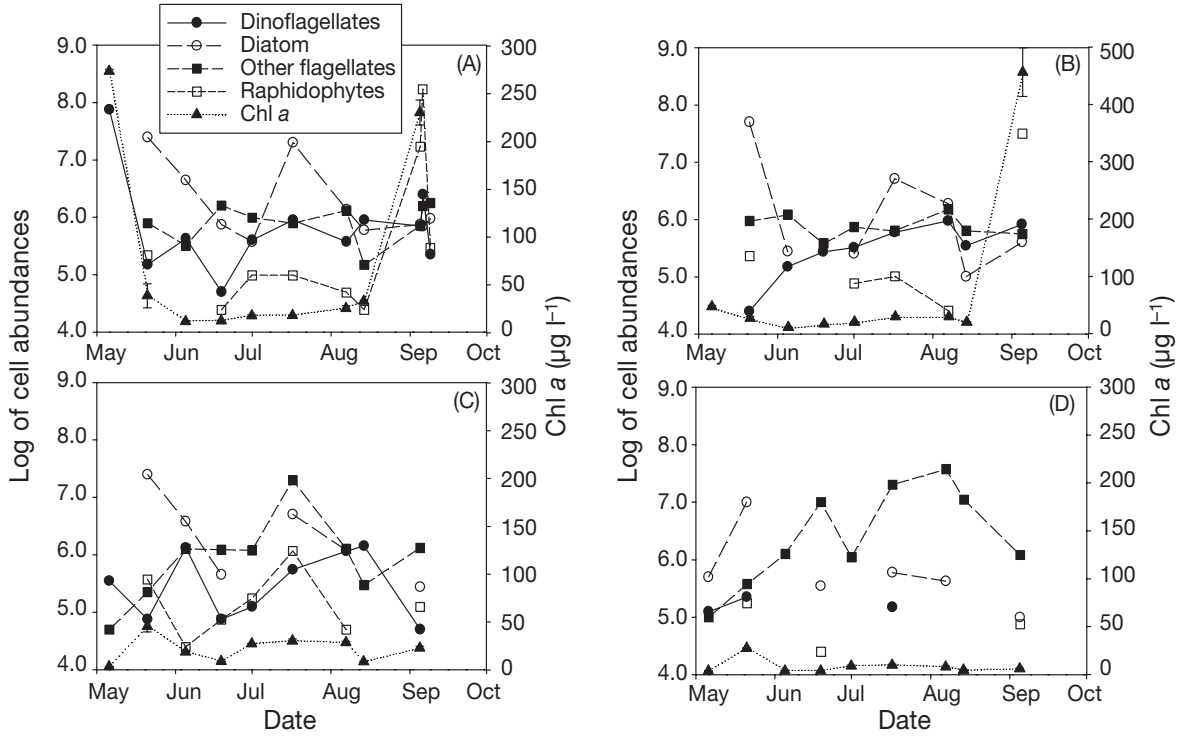

Fig. 5. Algal cell abundances and chl *a* in the (A) surface, (C) interface and (D) bottom waters of Torquay Canal Site 2 and (B) the surface waters of Bald Eagle Creek Site 9

early May. As O_2 was mixed down to the bottom on May 21, NH_4^+ decreased. From July 1, H_2S increased in the hole and NH_4^+ accumulated to 87 µM in mid-August. Water column mixing during the early September storm likely released NH_4^+ into the surface and interface waters, leading to the decrease of NH_4^+ in the bottom water and the increase in surface and interface waters. Phosphate increased with the same trend as for NH_4^+, with a 6.8 µM maximum observed in mid-August. The storm in early September also released PO_4^{3-} into the surface water, resulting in algal blooms (see 'Algal community structure'). Bottom water overturn can provide NH_4^+ and PO_4^{3-} to the surface water to support algal blooms.

At Site 9 (Fig. 4F), NH_4^+ and PO_4^{3-} also accumulated during the seasonal anoxia period. NH_4^+ was as high as 34 µM and PO_4^{3-} 2.4 µM in the bottom waters in early September. NO_2^- concentrations were between 0.02 and 0.5 µM in the water column at both sites.

Algal community structure

Algal blooms (defined as $>10^7$ cells l^{-1}) occurred in Torquay Canal and Bald Eagle Creek in 2002. Highest cell abundances were found in the surface waters; however, algal species were also present in interface and bottom waters even though Secchi depths were only about 0.6 m and H_2S was present in the holes. The algal community structure changed dramatically with seasonal anoxia development as shown below.

Surface waters—Torquay Canal

In surface waters, different algal species dominated at different times (Fig. 5A). On May 6, a significant bloom, dominated by the dinoflagellate *Prorocentrum minimum* (class Dinophyceae), was present in the surface water of Site 2. Cell abundance was 7.5×10^7 cells l^{-1} and total chl *a* was 275 µg l^{-1}. On May 21, O_2 penetrated into the bottom water (Fig. 2C) and H_2S was not detected throughout the water column (Fig. 2E). A mixed bloom of small centric and pennate diatoms (class Bacillariophyceae) occurred on May 21, with a cell abundance of 2.5×10^7 cells l^{-1} and chl *a* of 39.5 µg l^{-1}. Although a single species diatom bloom (*Leptocylindrus* sp.) of 2×10^7 cells l^{-1} was observed on July 17, chl *a* was only 18.9 µg l^{-1}, close to the average background level for the year (20.6 µg l^{-1}). On September 5, a flagellate bloom dominated by *Heterosigma akashiwo* (class Raphidophyceae) of 1.75×10^7 cells l^{-1} and total chl *a* of 231 µg l^{-1} occurred. From additional phytoplankton sampling at a nearby shallow water site

100 m away, it appeared that the cell density of *H. akashiwo* increased dramatically to 17.6×10^7 cells l^{-1} on September 6, but the bloom had declined by September 9. The tides moved H_2S (and nutrients) from Site 2 to this shallow water site as the interface moved upwards at Site 2 in Torquay Canal (Luther et al. 2004).

Besides the significant *Prorocentrum minimum* and *Heterosigma akashiwo* blooms on May 6 and September 5, respectively, flagellates and dinoflagellates were present in all the surface samples. Statistical analysis using Pearson correlation coefficients indicates that the cell abundances of flagellates and dinoflagellates have a modest inverse correlation ($r = -0.505$, $p = 0.136$).

Surface waters—Bald Eagle Creek

The phytoplankton community in the surface waters of Site 9 was similar to those in Torquay Canal (Fig. 5B). On May 6, total chl *a* was 44.7 µg l^{-1} in the surface water, about 5 times lower than that in Torquay Canal. As algal cells were not screened before May 21 at Site 9, we do not have cell abundance data for the early May samples. On May 21, a mixed bloom of small centric and pennate diatoms with a cell abundance of 5×10^7 cells l^{-1} and chl *a* of 24 µg l^{-1} was observed. Cell abundance was twice that found at Site 2. A *Heterosigma akashiwo* bloom was also observed on September 5 in the surface water at the main hole. The cell abundance was 3.08×10^7 cells l^{-1} and total chl *a* was 453 µg l^{-1}, much higher than those in Torquay Canal on September 5.

Interface waters—Torquay Canal

Algal community structure was different at the oxic–anoxic interface zone from those found in the surface waters (Fig. 5C). On May 21, mixed diatoms with a cell abundance of 2.5×10^7 cells l^{-1} were found in the interface water and decreased in early June. From mid-June, flagellates dominated in the interface waters, with a maximum of 2×10^7 cells l^{-1} measured on July 17. *Heterosigma akashiwo* was 1×10^6 cells l^{-1} on July 17. Dinoflagellate species were also present in the interface waters. These data demonstrate that harmful algae existed not only in the surface but also in the interface waters, where O_2 was not measurable and H_2S was measurable.

Bottom waters—Torquay Canal

Flagellates were the dominant class in the bottom waters (Fig. 5D). Mixed diatoms of 1×10^7 cells l^{-1} were found on May 21 when O_2 was present in the bottom water (Fig. 2C). Thereafter, flagellates dominated in bottom waters and cell abundances even increased as bottom water H_2S accumulated from July to August. On July 17, flagellate cell abundance was 2×10^7 cells l^{-1} and increased to 3.74×10^7 cells l^{-1} on August 7. Although there was a decrease in cell abundance on August 14, it was still significant at the 1.1×10^7 cells l^{-1} level. After the storm in early September, the cell abundance of flagellates sharply decreased to 1.2×10^6 cells l^{-1}. Flagellates survived in the holes in spite of high concentrations of H_2S in the bottom waters; however, dinoflagellates were always low in concentration.

Our algal data demonstrate that 2 large potentially harmful algal blooms occurred (~10^8 cells l^{-1}): the *Prorocentrum minimum* bloom in Torquay Canal in early May and the *Heterosigma akashiwo* blooms at both locations in early September. Besides these 2 blooms, dinoflagellates generally had higher cell abundances in the interface waters than in the bottom waters. However, flagellates had higher cell abundances than those of dinoflagellates in the interface and bottom waters. Total dinoflagellates and flagellates all had low cell abundance in surface waters except during blooms, whereas diatom cell abundances were low all the time except for the May 21 and July 17 samples.

DISCUSSION

The water column was stratified and seasonal anoxia developed in Torquay Canal and Bald Eagle Creek in 2002. High concentrations of H_2S were present in the holes and harmful algal blooms occurred in surface waters. *Prorocentrum minimum* and *Heterosigma akashiwo* blooms were found in the surface waters of Torquay Canal during May and September, respectively (Fig. 5A,B). Dinoflagellates and flagellates were present in the interface and bottom waters with high H_2S concentrations (Fig. 5C,D).

In coastal areas, flushing rate and water depth play a major role in regulating the duration of nutrient availability to algal assemblages. Estuaries with high flushing rates have less algal production than those with poor flushing because the former have less water residence time. Chesapeake Bay has a mean water residence time of about 35 d and a mean depth of 9 m (Magnien et al. 1992, Anderson et al. 2002). Its early spring biomass can produce chl *a* exceeding 50 µg l^{-1} (Glibert et al. 1995, Malone et al. 1996, Anderson et al. 2002). The Rehoboth Bay has a 3 mo water residence time (DNREC, Inland Bays/Atlantic Ocean Basin Assessment Report 2001) and exchanges water with Torquay Canal and Bald Eagle Creek, which have a mean low water depth of 2 m (Luther et al. 2004). Thus,

we are not surprised that the biomass produced here (e.g. 231, 275 and 453 µg l^{-1} chl *a*, Fig. 5A,B) is higher than in Chesapeake Bay.

Wind and precipitation can also affect blooms in shallow lagoons (Cloern 1996). The density data show pronounced stratification of the water column in May but mild stratification from June to August 2002. After July 2002, H_2S in the bottom water of the Torquay Canal main hole (Site 2) was over 200 µM and increased to 744 µM in mid-August (Table 1). Algal concentrations were at very low levels in the surface waters because of low surface nutrient inputs and no bottom water overturn. This season-long anoxia in the holes accelerated PO_4^{3-} and NH_4^+ recycling and accumulation from organic matter decomposition. PO_4^{3-} was also released into the pore water and diffused into the overlying bottom water when Fe(III) (oxy)hydroxides in the sediments were reduced to FeS because FeS minerals do not bind PO_4^{3-} (Rozan et al. 2002). In early September, a storm with a few days of rain partially mixed the water column based on density, O_2, and H_2S data (Fig. 2). The storm led to a release of PO_4^{3-} and NH_4^+ from bottom waters to the interface and surface waters to promote the bloom on September 5 (Fig. 4E,F). The concentration of *Heterosigma akashiwo* was 1.76×10^7 cells l^{-1} on September 5 and greatly increased 10-fold on September 6. This finding is similar to previous work of Kreiberg (1999) as *H. akashiwo* can grow quickly with division rates of 1 to 5 d^{-1} (Kreiberg 1999).

If we use the highest concentration of PO_4^{3-} at 6.8 µM in the bottom water at Site 2 to calculate the quantity of organic matter that could be produced by this phosphorus supply to the surface water, the average concentration of organic mater in the 2 m deep oxic surface waters would be 17 g m^{-3}, based on the surface area of 15 000 m^2 at Site 2 and an anoxic layer of 3 m depth. Thus, one hole can produce a huge amount of organic matter in this shallow ecosystem.

In contrast to Torquay Canal, O_2 and H_2S were lower in the bottom waters of Bald Eagle Creek from July to early August 2002. However, H_2S developed in the main hole from mid-August and reached a value of 374 µM on September 5 (Table 1). On that date, a large *Heterosigma akashiwo* bloom was observed in the surface water at this site, similar to in Torquay Canal.

N/P ratios can reflect the dynamics of algal blooms. At Site 2 (Table 1), only 3 sampling dates had N/P ratios below 16 in the surface water. These 3 sampling dates coincided with high cell abundances. It seems that lower N/P ratios favor dinoflagellate and flagellate blooms (the *Leptocylindrus* sp. bloom had low biomass on July 17). In the bottom water at Site 2, N/P ratios ranged from 8 to 22 from June to September and reflected decomposition of organic matter.

Table 1. Data for bottom water (H_2S and N/P ratio) and surface water (chl *a*, N/P ratio, cell abundances of *Heterosigma akashiwo* and *Prorocentrum minimum*) at Torquay Canal Site 2 and Bald Eagle Creek Site 9. ND: not detectable; NA: not analyzed

Date (mo/d/yr)	H_2S (µM)	Chl *a* (µg l^{-1})	Cell abundances (×10^6)		N/P ratio	
			Heterosigma akashiwo	*Prorocentrum minimum*	Surface water	Bottom water
Site 2						
5/06/02	18.6	275	<0.01	75	8.9	557
5/21/02	247	39.5	0.23	0.3	35.4	59.3
6/05/02	119	12.5	<0.01	<0.01	35.4	8.3
6/19/02	34.6	13.2	0.3	<0.01	42.4	12.9
7/01/02	277	18.6	0.3	<0.01	68.6	22.1
7/17/02	216	18.9	0.1	<0.01	0.4	18.6
8/07/02	516	26.4	<0.01	<0.01	71.3	12.6
8/14/02	744	33.8	<0.01	<0.01	54.3	13.3
9/05/02	217	231	17.6	<0.01	15.9	16.3
9/06/02	NA	NA	176	<0.01	NA	NA
Site 9						
5/06/02	175	44.7	NA	NA	9.6	21.1
5/21/02	ND	24.3	0.23	<0.01	45.9	39.7
6/05/02	ND	8.58	<0.01	<0.01	10.8	21.6
6/19/02	ND	14.2	<0.01	<0.01	23.9	17.4
7/01/02	ND	17.8	<0.01	<0.01	4.3	37.3
7/17/02	10.2	27.2	<0.01	<0.01	5.1	16.7
8/07/02	ND	27.3	<0.01	<0.01	2.4	52.4
8/14/02	96.7	17.7	<0.01	<0.01	2.4	7.6
9/05/02	374	453	30.8	<0.01	3.6	14.2

At Site 9 (Table 1), N/P ratios were low from July in the surface water, whereas those in the bottom water reflected the dynamics of anoxia and organic matter decomposition. The surface water N/P ratios stayed below 10 as H_2S increased over the summer; thus, seasonal anoxia provided a rich source of PO_4^{3-} to the surface water after mixing events. N/P ratios in the bottom water of Bald Eagle Creek were typically higher than those in Torquay Canal. This may be due to lower H_2S concentrations in the bottom water of Bald Eagle Creek than in Torquay Canal so less PO_4^{3-} was released from Fe(III) (oxy)hydroxides reduction. The deeper O_2 penetration depths at Bald Eagle Creek, particularly in early August, also suggest this possibility.

Higher harmful algal cell density occurred when more H_2S developed in the bottom waters and the interface moved up to shallower depths (Table 2). Chl *a* and algal cell abundances in surface waters correlated with changes of the interface depth at both Sites 2 and 9. The chl *a* in surface waters decreased sharply as the interface depth moved deeper, with a significant negative correlation for the Bald Eagle Creek data ($r = -0.669$, $p = 0.049$). Dinoflagellate and raphidophyte cell abundances also decreased in surface waters at both Sites 2 and 9 when the oxic–anoxic interface moved deeper, especially at Site 9 ($r = -0.749$, $p = 0.032$). However, diatoms showed a reverse trend with dinoflagellates and raphidophytes. When the oxic–anoxic interface moved to deeper depth, diatom cell abundances increased in the surface water at both Sites 2 and 9, with a highly significant correlation for Site 2 ($r = 0.817$, $p = 0.004$). In Torquay Canal surface waters, 2 large blooms of *Prorocentrum minimum* (dinoflagellate) and *Heterosigma akashiwo* (raphidophyte) species were found when the interface depths were at 2 and 2.1 m, respectively (Fig. 3, Table 1). Diatoms were the dominant species when the interface depth was deeper than 3.5 m (Figs. 3 & 5A,B). Although the strength of the correlations at Sites 2 and 9 varied, the trends were similar at both sites.

Our data indicate that seasonal anoxia increased harmful algal biomass and caused shifts of algal community structure from diatoms to dinoflagellates and flagellates. In Torquay Canal and Bald Eagle Creek, diatoms dominated in late May when O_2 was present in the bottom waters. Although the *Leptocylindrus* sp. had high cell abundance on July 17, algal cells were only 5 to 10 µm in diameter. These 2 diatom blooms did not produce significant biomass because chl *a* did not exceed 50 µg l^{-1}, as has been observed in early spring in the Chesapeake Bay (Glibert et al. 1995, Malone et al. 1996). Eutrophication causes the decline of diatom species, as well as a shift in phytoplankton community structure that can lead to important changes at higher trophic levels (Starr et al. 1990, Anderson et al. 2002).

Table 2. Pearson correlation coefficients of interface depths vs. surface algal cell abundances at Sites 2 and 9. Data used for calculations are from Figs. 3 & 5. Significant relationships are shown in **bold**

	Chl *a*	p	Dinoflagellates+ raphidophytes	p	Diatoms	p
Site 2	−0.432	0.246	−0.389	0.267	**0.817**	**0.004**
Site 9	**−0.669**	**0.049**	**−0.749**	**0.032**	0.405	0.319

Marine flagellates also have a migration strategy to out-compete diatoms for nutrients. Flagellates can migrate down to 10–15 m across a stratified layer to assimilate nutrients at night and then go back to the surface water during the day to carry out photosynthesis by using the accumulated nutrient (Yamochi & Abe 1984, Watanabe et al. 1988). *Chattonella antique* can store orthophosphate from deep PO_4^{3-}- rich water, and *Heterosigma akashimo* can assimilate PO_4^{3-} to synthesize polyphosphate and store P in an intracellular phosphate pool. Intracellular polyphosphate is considered to control algal growth and development (Watanabe et al. 1988, Kimura et al. 1999).

Harmful algal blooms occur along all coastal regions of the United States with increasing frequency (Hoagland et al. 2002) and can affect the full spectrum of life, from the biochemical to the ecosystem level. Our results indicate that stable temperature and salinity stratification inhibited vertical mixing of the water column in Torquay Canal and Bald Eagle Creek. Thus, O_2 could not penetrate down to the bottom water, and H_2S, NH_4^+ and PO_4^{3-} were produced in the holes. As H_2S, NH_4^+ and PO_4^{3-} accumulated in the bottom waters, the interface moved up to shallower depths. Thus, bottom water nutrients from anoxic holes can lead to eutrophication and harmful algal blooms via 3 processes. First, flagellates only needed to migrate down about 2 m to the interface waters to uptake nutrients and then return to the surface water to conduct photosynthesis. Second, the supply of nutrients and some light penetration could support flagellates conducting photosynthesis at the interface. Third, storm events partially mixed the water column and released nutrients to the surface water. We conclude that seasonal anoxia development in the Delaware Inland Bays is not only a potential threat to fish and shellfish but also causes shifts of algal community structure from diatoms to dinoflagellates and flagellates.

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