Responses of benthic–pelagic coupling to climate change in a temperate estuary

Robinson W. Fulweiler · Scott W. Nixon

Abstract   This article reports the first demonstration of the impact of climate change on benthic–pelagic coupling and the biogeochemical cycles of a coastal marine system. Over the last 30 years Narragansett Bay, a 328-km^2 temperate estuary on the east coast of the United States, has undergone a variety of ecological changes. Building on a robust data set that spans three decades, we present a link between warming ($+1.7$°C in annual mean water temperature) in the bay and a marked decrease in sediment oxygen consumption, in the fluxes of ammonium and phosphate from sediments to the overlying water, and in sediment denitrification. We attribute this reduction in biogeochemical exchange to a dramatic drop in the standing crop of water-column chlorophyll as the system has shifted from one characterized by a dominant winter–spring bloom to one supported by more ephemeral and less intense summer–autumn blooms. The recent climate-induced oligotrophication of the bay will be further exacerbated by forthcoming nitrogen reductions due to tertiary sewage treatment.

Keywords   Climate change · Benthic–pelagic coupling · Oligotrophication · Denitrification · Nutrient regeneration · Phenology

R. W. Fulweiler (✉)
Department of Earth Sciences, Boston University, Boston, MA 02215, USA
e-mail: rwf@bu.edu

S. W. Nixon
Graduate School of Oceanography, University of Rhode Island, Narragansett, RI 02882, USA
e-mail: swn@gso.uri.edu

Introduction

> Even if the climate change—eutrophication linkage is well established for the pelagic system…it remains poorly defined for benthic–pelagic coupling and the benthos.
>
> Grall & Chauvaud (2002)

Coastal ecosystems around the world have been subjected to a variety of locally driven anthropogenic changes (e.g., nutrient enrichment: Valiela et al., 1992; Kinney & Roman, 1998; eutrophication: de Jonge et al., 1994; overfishing: Jackson et al., 2001; toxic pollutant loading: Kot-Wasik et al., 2004). Further complicating these local issues are regional and global forces, most notably climate change. Obvious possible effects of climate change on coastal systems include sea level rise, changes in precipitation patterns, and the associated pulsing of freshwater, nutrients, and sediment (Scavia et al., 2002), and perhaps increased

intensity of storms (Emanuel, 2005). Climate change may also affect coastal systems in more subtle ways by altering the phenology or sequencing of events (Farnsworth et al., 1995; Inouye et al., 2000; Walther et al., 2002; Edwards & Richardson, 2004). To date, the interactions between climate change, sediment biogeochemical cycling, and benthic–pelagic coupling have largely been ignored.

Over the last decade, various ecological changes in Narragansett Bay (Rhode Island, USA) have been reported, including a decrease in mean annual water column chlorophyll concentrations (Li & Smayda, 1998), replacement of boreal demersal fish with demersal decapods (Oviatt, 2004), and earlier development and larger populations of the major predator zooplankton, *Mnemiopsis leidyi* (Sullivan et al., 2001). These changes are thought to be mainly the result of climate variability (North Atlantic Oscillation) and a long-term warming trend (Nixon et al., 2003, 2004; Oviatt, 2004). There is a long history of work documenting the strong linkages between the benthos and the water column in Narragansett Bay, including benthic oxygen uptake and nutrient regeneration (Nixon et al., 1976, 1980), denitrification (Seitzinger et al., 1984; Nowicki & Oviatt, 1990), benthic responses to organic additions of ^{15}N-labeled (Garber, 1982) and ^{14}C-labeled (O'Reilly, 1984; Rudnick & Oviatt, 1986) and unlabeled (Kelly & Nixon, 1984; Grassle et al., 1985) organic matter, and predation pressure by the benthos on the water column (Doering et al., 1986; Doering, 1989; Oviatt, 2004). Building upon this study, we recently revisited the most well-studied site in the bay to measure benthic oxygen uptake, nutrient regeneration, and sediment denitrification over an annual cycle. Our main motivation for this study was to see whether it would be possible to document any changes in the biogeochemical cycling of Narragansett Bay benthos over the last 30 years. Also, the major wastewater treatment plants discharging to the bay are moving to tertiary treatment. This research will provide baseline data for future studies of denitrification and benthic fluxes after tertiary wastewater treatment is implemented. While this management intervention may improve the water quality in the upper bay, the consequences for the much larger mid- and lower bay are unknown.

The purpose of this article is twofold. The main goal is to report, we believe for the first time, a link between climate-induced changes in benthic–pelagic coupling and sediment biogeochemical cycles. Second, to highlight the possible interactions between climate change and management mitigation of nutrient enrichment.

Materials and methods

Site description

Narragansett Bay, including Mount Hope Bay, is a 328-km^2 phytoplankton-based temperate ecosystem (latitude 41°N) with a mean depth of 8.6 m and a mean flushing rate of 26 days (Pilson, 1985; Nixon et al., 1995). Freshwater input is relatively low (100 m^3 s^{-1}), with the result that the mid-bay is generally well mixed and there is only occasional weak vertical stratification (Nixon et al., 2005). Salinity follows a down-bay gradient from ∼20 psu at the head to ∼32 psu at the mouth of Narragansett Bay. The annual temperature varies from about 0 to 24°C.

Clayey silt and sand-silt-clay sediments comprise the majority of Narragansett Bay sediments (McMaster, 1960). For this study, sediment cores were collected from a station ∼7 m deep near the middle of Narragansett Bay (Fig. 1). With an annual mean vertical light attenuation coefficient of −0.55 m^{-1} (Oviatt et al., 2002), only about 2% of surface light reaches the heterotrophic bottom. This mid-bay station has been the site of many studies ranging from in situ experiments on sediment oxygen demand and nutrient regeneration (Nixon et al., 1976) to denitrification measurements using extracted cores (Seitzinger et al., 1984) and larger mesocosms (Nowicki, 1994). Sediment from this site has also been used for various experiments (i.e., assessments of the benthic community (Rudnick et al., 1985; Frithsen, 1989; Ellis, 2002); effects of organic enrichment on the benthos (Garber, 1982; Grassle et al., 1985); benthic predation on the water column (Doering et al., 1986; Oviatt, 2004) in the large mesocosms of the marine ecosystems research laboratory (MERL). Previous study has shown that sediments at this station are predominantly silt-clay (73%) with an organic content of 4.5% (Hale, 1974). At this mid-bay station, the dominant macrofauna include *Mediomastus ambiseta*, *Nephtys incisa*, *Amplisca*, and *Nucula annulata* (Seitzinger et al., 1984;
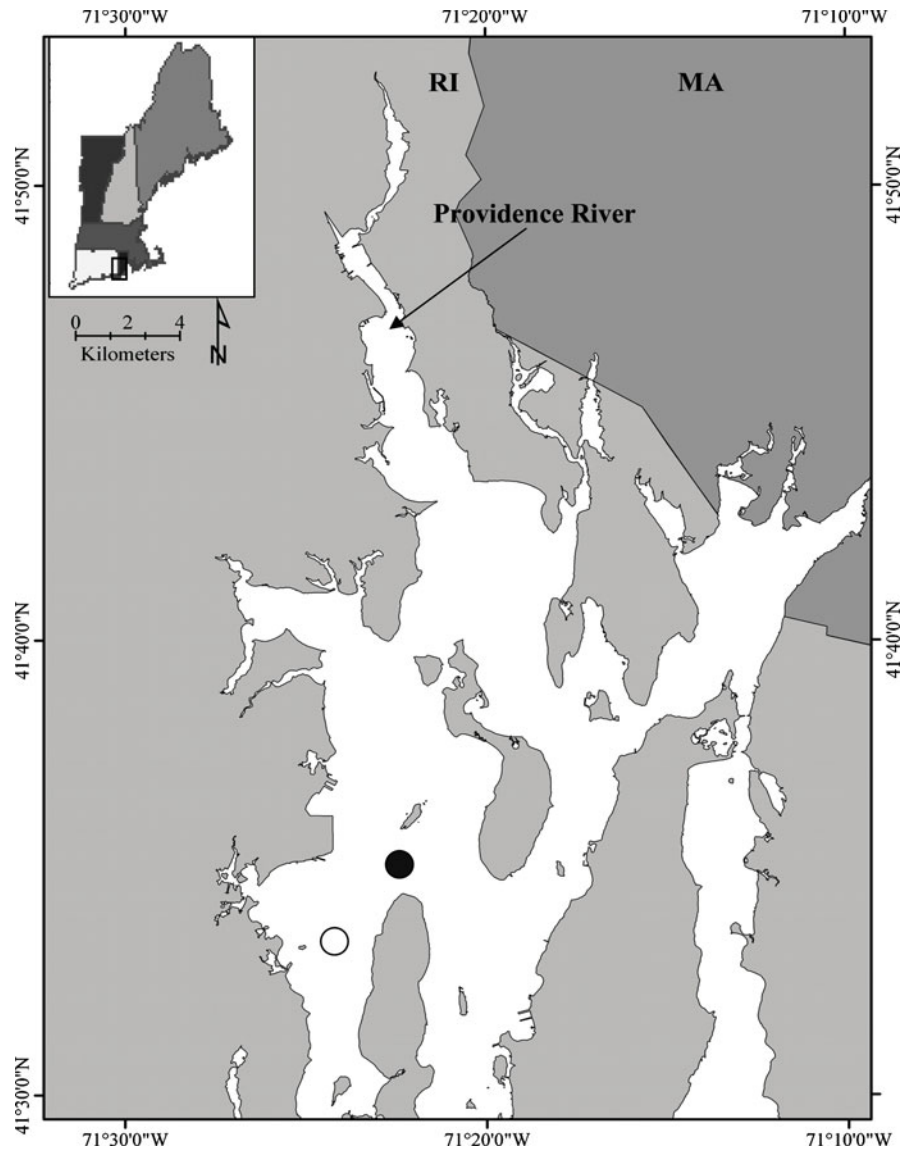
Rudnick et al., 1985). This site has been and is currently being monitored for benthic macro infauna and meiofauna species composition and abundance as part of the Environmental Protection Agency northeast coastal assessment program (C.A. Oviatt pers. comm., see http://www.gso.uri.edu/merl/data.htm).

Sediment collection and incubation

Over the annual cycle in 2005 and 2006, triplicate cores (78.5 cm^2 and $\sim$15 cm deep) were collected by SCUBA divers using a round PVC corer. Cores were maintained in the field at in situ temperatures and transported to an environmental chamber at the Graduate School of Oceanography where they were held in the dark in a water bath at field temperature. The cores were then left uncapped with oxygen bubbling gently through the overlying water overnight (8–12 h).

Throughout this study, the benthic flux measurements were conducted in the dark and separated into two incubations. During the first incubation, water samples were collected for dissolved gas analysis to measure denitrification using the N$_2$/Ar technique

(Kana et al., 1994; Giblin et al., 1995; Eyre et al., 2002). Then, after a 24-h period of no measurements, the second incubation for nutrient fluxes (NH_4^+, PO_4^-) was initiated. Sediment oxygen consumption was measured during both incubations. Before each set of flux measurements, the overlying water in the cores was carefully replaced with filtered (1 μm) Narragansett Bay water. Cores were then sealed with gas-tight lids containing magnetic stirrers and the overlying water was continuously stirred (40 rpm). Initial and final samples for Winkler analysis were collected from each core and oxygen was monitored over the course of the incubation using a Hach HQ10 LDO probe. N_2/Ar samples were collected in duplicate at five times during the incubation and preserved with $HgCl_2$. Dissolved inorganic nitrogen and phosphorus samples were collected at three points during the second incubation and filtered through glass fiber filters (Whatman GF/F 0.70 μm) using a 60-ml acid-washed polypropylene syringe. The filtrate was collected and stored in 60-ml acid-washed and deionized water-leached polyethylene bottles and stored at −15°C until analysis. An additional core container with no sediments was incubated as a control. When necessary, corrections were made for any changes that occurred, but the water column respiration was usually negligible.

Analytical methods

N_2/Ar was measured using MIMS (Kana et al., 1994; Giblin et al., 1995) including a Pfeiffer Quadrupole Mass Spectrometer and a flow-through silicone capillary membrane inlet (Bay Instruments, Easton, Maryland). Dissolved inorganic nitrogen and phosphorus concentrations were analyzed using a Lachat Instrument QuikChem 8000 flow injection analyzer (Table 1). Oxygen concentrations were determined using the Winkler method with manual titration.

Data analysis

The N_2 flux for each core was determined by the rate of change in N_2 concentration (Groffman et al., 2006). For the N_2/Ar method, the change in N_2 concentration is determined from the change in N_2/Ar multiplied by the Ar concentration at air saturation (Colt, 1984). N_2 production was then determined from a five-point linear regression (Giblin et al., 1995). Sediment oxygen consumption was determined by subtracting the final concentration from the initial concentration and dividing by the total time of the incubation. Rates were then prorated for the volume and area of the core. Nutrient fluxes were initially calculated as above for oxygen. However, upon further examination, it was noticed that fluxes decreased over time, most likely because of a decrease in the concentration gradient between the sediments and the overlying water. To avoid underestimating the nutrient fluxes, the flux between the initial and middle time points of the incubation was calculated. Differences between the historical and most recently collected data and their relationship with temperature were examined using a two-way ANOVA and least-squared difference (LSD) multiple comparison test.

Results

Oxygen uptake and nutrient fluxes

Sediment oxygen consumption over the annual cycle ranged from a low of 3 mg m^{-2} h^{-1} at 6°C to a high of 27 mg m^{-2} h^{-1} at 23°C (Fig. 2). The low-temperature measurements (4 mg m^{-2} h^{-1} at 5°C) in this study were similar to the historical data, but the annual mean in the past (43 mg m^{-2} h^{-1}) was much higher than what was measured here (14 mg m^{-2} h^{-1}). Overall, the oxygen consumption measurements in this study showed no significant ($P < 0.01$) relationship with

Table 1 Analytical methods used in this study	Parameter	Method reference	Detection limit
	N_2/Ar ratio	Kana et al., 1994	0.03%
	Ammonium	US EPA, 1983a; Grasshoff, 1976	0.07 μM
	Nitrite + Nitrate	US EPA, 1997; Grasshoff, 1976	0.02 μM
	Orthophosphate	US EPA, 1983b; Grasshoff, 1976	0.01 μM
	Oxygen	Lambert & Oviatt, 1983; Carrit & Carpenter, 1966	0 mg O_2 l^{-1}

Fig. 2 Sediment oxygen uptake over the annual temperature cycle for mid-Narragansett Bay sediments. Historical data (*closed circles*) from Nixon et al. (1976, 1980) and unpublished data. Most recent 2005/2006 data (*open circles*) from this study
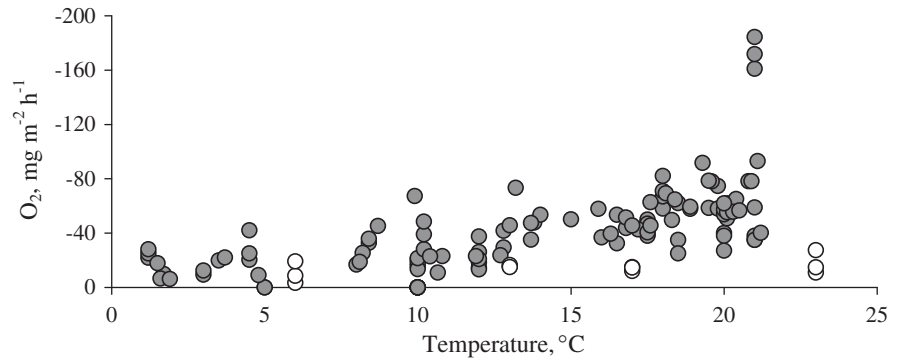
Fig. 3 Ammonia fluxes over the annual temperature cycle for mid-Narragansett Bay sediments. Historical data (*closed circles*) from Nixon et al. (1976, 1980) and unpublished data. Most recent 2005/2006 data (*open circles*) from this study
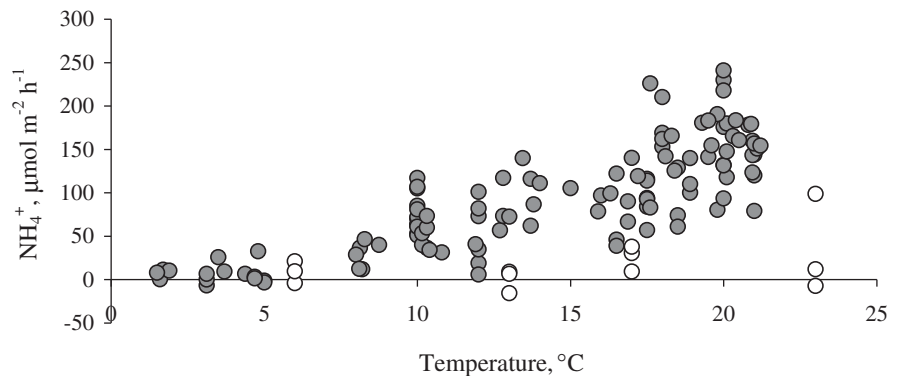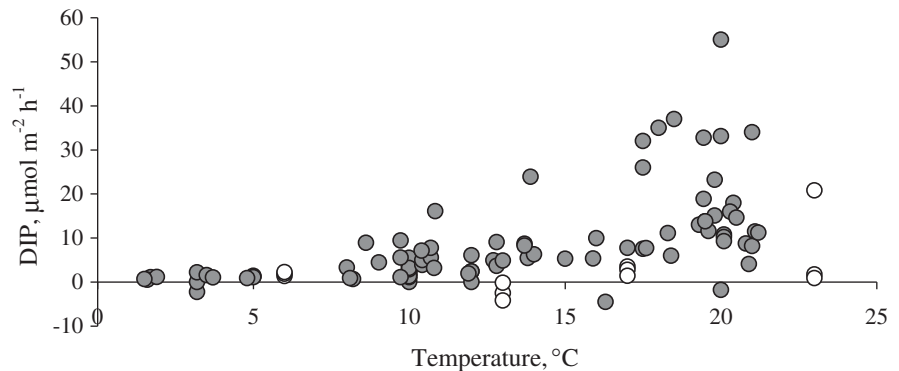
Fig. 4 Dissolved inorganic phosphate (DIP) fluxes over the annual temperature cycle for mid-Narragansett Bay sediments. Historical data (*closed circles*) from Nixon et al. (1976, 1980) and unpublished data. Most recent 2005/2006 data (*open circles*) from this study

temperature. This is surprising since all of the historical data sets for mid-Narragansett Bay, including measurements made in situ, in extracted cores, and in the large (13 m^3) MERL mesocosms (Oviatt et al., 1993) showed an exponential relationship between oxygen uptake and temperature (Nixon et al., 1976). In the most recent measurements, the rates were also significantly ($P < 0.01$) lower than the historical rates.

The measurements of ammonium flux over the annual cycle in this study also showed small uptakes and releases (Fig. 3). With an influx of −15 μmol m^{-2} h^{-1} and an efflux of 98 μmol m^{-2} h^{-1}, the mean ammonium flux (14 μmol m^{-2} h^{-1}) was significantly ($P < 0.01$) lower than the historical mean (94 μmol m^{-2} h^{-1}) (Nixon et al., 1980). Previously, ammonium regeneration has exhibited a marked increase with higher temperatures, but this no longer appears to be true. Dissolved inorganic phosphate (DIP) flux ranged from −4 to 21 μmol m^{-2} h^{-1} with a mean of 2.5 μmol m^{-2} h^{-1} (Fig. 4). This range is significantly ($P < 0.01$) lower than the historical range (−5 to 55 μmol m^{-2} h^{-1}) and mean (8 μmol m^{-2} h^{-1}).

Fig. 5 Denitrification over the annual temperature cycle for mid-Narragansett Bay sediments. Historical data (*closed circles*) from Seitzinger et al. (1984) and Nowicki (1994). Most recent 2005/2006 data (*open circles*) from this study
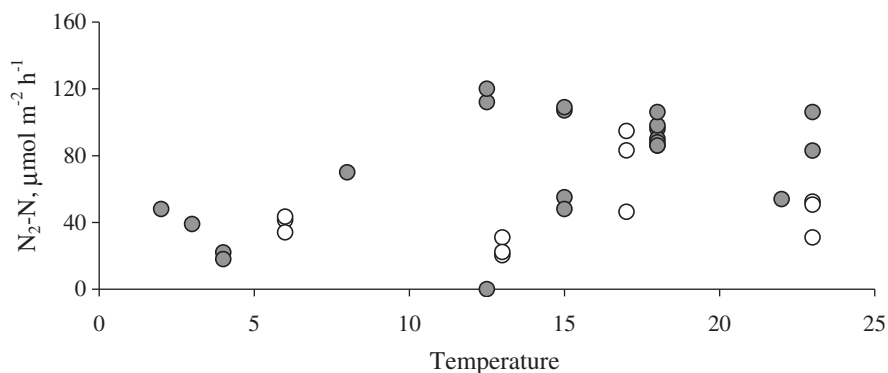
Remarkably, as seen with oxygen and ammonia, DIP fluxes also showed no increase with temperature as they had in the past.

Denitrification rates

Using the N_2/Ar technique, we found denitrification rates ranging from 22 to 100 μmol N_2-N m^{-2} h^{-1}. Seitzinger et al. (1984) reported seasonal denitrification rates measured for 1979 at the mid-bay station that ranged from 40 to 109 μmol N_2-N m^{-2} h^{-1}. Additional denitrification measurements made by Nowicki (1994) using sediment from this site and a slightly modified technique varied from 18 to 120 μmol N_2-N m^{-2} h^{-1}. While the rates in this study are similar to those measured previously, the mean annual rate has significantly ($P < 0.01$) declined from 74 μmol N_2-N m^{-2} h^{-1} in 1979 to 40 μmol N_2-N m^{-2} h^{-1} in 2005/2006. Neither the present nor the historic denitrification rates exhibit a positive relationship with increasing temperature (Fig. 5).

Discussion

The analytical techniques used to measure the concentrations of oxygen, ammonia, and phosphate have not changed substantially between the earlier work and the current study and therefore analytical changes do not confound these comparisons. Unfortunately, it is possible that the denitrification decline may be an artifact of changing methodology. No direct comparisons between the N_2 technique, used by Seitzinger et al. (1984) and Nowicki (1994), and the N_2/Ar technique have yet been reported. However, the oxygen and nutrient regeneration measurements

reported previously are not confounded by changing analytical techniques, and their large declines suggest that the decline in denitrification is also real.

Ecological responses to climate change in narrangansett Bay

Narragansett Bay has traditionally been characterized by a strong winter–spring diatom bloom that usually begins in mid-November and reaches peaked concentrations at the end of December or early January (Pratt, 1959). However, over the last three decades the timing and magnitude of the phytoplankton bloom in Narragansett Bay have decreased dramatically. Long-term monitoring of the phytoplankton at a station near the middle of the bay (Fig. 1) shows that mean annual water-column chlorophyll concentrations have decreased by almost 70% since 1970 (Fig. 6). Most of the decline in the annual means is associated with changes in the traditional winter–spring bloom which has arrived later or not at all (Oviatt et al., 2002). The abundance of diatoms during the bloom has also declined (Karentz & Smayda, 1998; Li & Smayda, 1998). Since chlorophyll is tightly coupled with the rate of ^{14}C uptake in this system (Keller & Riebesell, 1989) as well as in many others (see recent review by Brush et al., 2002), this decline has almost certainly been associated with a marked decline in the rate of primary production.

The cause of the oligotrophication of Narragansett Bay is not well understood, but it cannot be attributed to a reduction in nitrogen inputs as they have remained essentially unchanged for at least 25 years (Nixon et al., 2008). There is some correlative evidence that climate variability (North Atlantic Oscillation) and long-term warming trends may be

Fig. 6 Mean annual water column chlorophyll *a* concentrations at the mid-bay station (see Fig. 1). Historical data (*closed circles*) from Li & Smayda (1998). Most recent data (*open circles*) from the Graduate School of Oceanography/URI (see http://www.gso.uri.edu/ phytoplankton)
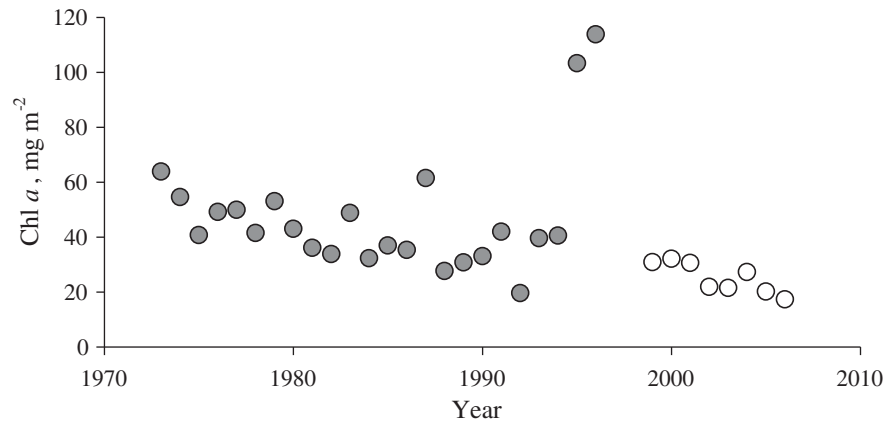
responsible (Hawk, 1998; Borkman, 2002; Oviatt et al., 2002; Oviatt, 2004). Winter warming in the bay is highly significant. Warming has amounted to an increase of about 1.7°C during the 1990s compared with the period between 1890 and 1970 at nearby Woods Hole, MA, where it is known that water temperature is closely correlated with that in Narragansett Bay (Nixon et al., 2003, 2004). Townsend & Cammen (1988) found that year-to-year variation in the spring bloom in the Gulf of Maine was controlled by light and not temperature. Working in Narragansett Bay, however, Borkman (2002) found that warmer winters tended to be cloudier, thus making it difficult to separate temperature and light effects. Experiments with the large MERL mesocosms have shown that slightly warmer temperatures reduce or eliminate winter–spring phytoplankton blooms in Narragansett Bay, presumably because of higher grazing pressure (Keller et al., 1999). Field evidence also confirms that warmer winters are associated with a delayed or complete elimination of the winter–spring bloom (Oviatt et al., 2002).

Regardless of the reason, the loss of the winter–spring bloom is particularly alarming for a benthic community that is already food-limited by the end of summer. Tracer and mass balance studies, also carried out in the MERL mesocosms, have shown that a smaller fraction of the summer blooms is deposited on the bottom compared with winter–spring blooms (Rudnick & Oviatt, 1986; Keller et al., 1999). From the field (Rudnick et al., 1985; Craig, 1989; Ellis, 2002), from mesocosm study (Grassle et al., 1985; Beatty, 1991), and from a numerical model (McKenna 1987), there is considerable evidence that certain groups of the meio- and macro-benthic infauna have

historically been food-limited during summer in Narragansett Bay.

Implications for management

There is a common impression among environmental groups, some managers, and some scientists that nuisance blooms of macroalgae (especially *Ulva* sp.) are increasing and, more importantly, that bottom waters in upper Narragansett Bay and the Providence River (actually an estuary at the head of the bay, Fig. 1) are developing more frequent, intense, and widespread hypoxia (e.g., Rhode Island Department of Environmental Management, 2003). Unfortunately, historical data are not really available to address the question of change in either of these conditions. Because of this, many of the major wastewater treatment plants that discharge directly to the bay are in the process of upgrading to tertiary treatment, thus reducing total nitrogen loading to the bay. Nixon et al. (2005) estimated that by 2010 summer nitrogen inputs to Narragansett Bay may decrease between 30% and 40%. Clearly, these reductions will have significant impacts on the new production of the bay because ^{14}C uptake and bloom formation are strongly limited by nitrogen availability during summer (Furnas et al., 1976; Oviatt et al., 1995), when concentrations of dissolved inorganic nitrogen are very low or undetectable in the surface water of the mid- and lower bay (Fig. 7). It is anticipated that with less phytoplankton production there will be less organic matter deposition to the sediments, less benthic respiration, and therefore fewer hypoxic/anoxic events. However, we have shown here that there have been large

Fig. 7 Annual surface water-column dissolved inorganic nitrate (DIN) concentrations at the mid-bay station for 2005. Data available at http://www.gso.uri.edu/phytoplankton/
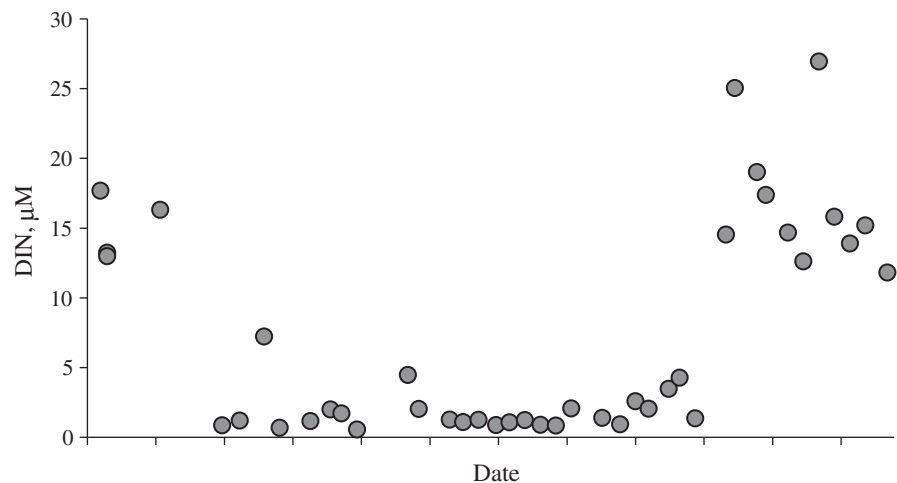
reductions in pelagic chlorophyll in the mid-bay and that respiration and nutrient regeneration by the benthos of mid-Narragansett Bay have declined greatly over the past three decades. Others have shown a positive effect of nitrogen loading on benthic biomass (Josefson & Rasmussen, 2000) and a positive relationship between primary and secondary production (Nixon et al., 1986). Since climate change has already begun the oligotrophication of a once highly productive bay, it is possible that reductions of nitrogen input during the growing season will have a significant negative impact on secondary production throughout the mid- and lower bay, a much larger area than the regions currently exposed to frequent hypoxia.

References

Beatty, L. L., 1991. The response of benthic suspension feeders and their grazing impact on phytoplankton in eutrophied coastal ecosystems. Ph.D. Thesis, University of Rhode Island, Graduate School of Oceanography, Narragansett, RI, 352 pp.

Borkman, D. G., 2002. Analysis and simulation of *Skeletonema costatum* (Grev.) Cleve annual abundance patterns in lower Narragansett Bay 1959–1996. Ph.D. Thesis, University of Rhode Island, Graduate School of Oceanography, Narragansett, RI, 395 pp.

Brush, M. J., J. W. Brawley, S. W. Nixon & J. N. Kremer, 2002. Modeling phytoplankton production: problems with the Eppley curve and an empirical alternative. Marine Ecological Progress Series 238: 31–45.

Carrit, D. E. & J. H. Carpenter, 1966. Recommendation procedure for Winkler analyses of sea water for dissolved oxygen. Journal of Marine Research 24: 313–318.

Colt, J., 1984. Computation of dissolved gas concentrations in water as functions of temperature, salinity, and pressure. American Fisheries Society Special Publication 14.

Craig, N. I., 1989. Age and growth history characteristics of *Nucula annulata* in undisturbed and nutrient enhanced environments. M.S. Thesis, University of Rhode Island, 93 pp.

de Jonge, V. N., W. Boynton, C. F. D'Elia, R. Elmgren & B. L. Welsh, 1994. Responses to developments in eutrophication in four different North Atlantic estuarine systems. In Dyer, K. R. & R. J. Orth (eds), Changes in Fluxes in Estuaries. Olsen & Olsen, Fredensberg: 179–196.

Doering, P. H., 1989. On the contribution of the benthos to pelagic production. Journal of Marine Research 47: 371–383.

Doering, P. H., C. A. Oviatt & J. R. Kelly, 1986. The effects of the filter-feeding clam *Mercenaria mercenaria* on carbon cycling in experimental marine mesocosms. Journal of Marine Research 44: 839–861.

Edwards, M. & A. J. Richardson, 2004. Impact of climate change in marine pelagic phenology and trophic mismatch. Nature 430: 881–884.

Ellis, G., 2002. An examination of the benthic macrofauna of Narragansett Bay and the possible implications of winter–spring bloom intensity on population size. M.S. Thesis, University of Rhode Island, Narragansett, RI.

Emanuel, K. A., 2005. Increasing destructiveness of tropical cyclones over the past 30 years. Nature 436: 686–688.

Eyre, B. D., S. Rysgaard, T. Dalsgaard & P. B. Christensen, 2002. Comparison of isotope pairing and N2:Ar methods for measuring sediment denitrification—assumptions, modifications, and implications. Estuaries 25: 1077–1087.

Farnsworth, E. J., J. Núñez-Farfán, S. A. Careaga & F. A. Bazzaz, 1995. Phenology and growth of three temperate forest life forms in response to artificial soil warming. Journal of Ecology 83: 967–977.

Frithsen, J. B., 1989. The benthic communities within Narragansett Bay: an assessment completed for the Narragansett Bay Project. Rhode Island Department of Environmental Management, Providence, RI, 28 pp.

Furnas, M. J., G. L. Hitchcock & T. J. Smayda, 1976. Nutrient-phytoplankton relationships in Narragansett Bay during the 1974 summer bloom. In Wiley, M. (ed.), Estuarine Processes: Uses, Stresses, and Adaptation to the Estuary, Vol. 1. Academic Press, New York: 118–133.

Garber, J. H., 1982. ^{15}N-tracer and other laboratory studies of nitrogen remineralization in sediments and waters from Narragansett Bay, Rhode Island. Ph.D. Thesis, University of Rhode Island, Graduate School of Oceanography, Narragansett, RI, 276 pp.

Giblin, A., C. Hopkinson, J. Tucker, B. Nowicki & J. Kelly, 1995. Metabolism, nutrient cycling and denitrification in Boston harbor and Massachusetts Bay sediments in 1994. MWRA Environmental Quality Report Series No. 95-13. MA Water Resources Authority, Boston, 56 pp.

Grall, J. & L. Chauvaud, 2002. Marine eutrophication and benthos: the need for new approaches and concepts. Global Change Biology 8: 813–830.

Grasshoff, K., 1976. Methods of Seawater Analysis, 2nd Edition. Verlag Chemie, Weinheim.

Grassle, J. F., J. P. Grassle, L. S. Brown-Leger, R. F. Petrecca, N. J. Copley, 1985. Subtidal macrobenthos of Narragansett Bay. Field and mesocosm studies of the effects of eutrophication and organic input on benthic populations. In Gray, J. S. & M. E. Christiansen (eds), Marine Biology of Polar Regions and Effects of Stress on Marine Organisms. John Wiley, New York: 421–434.

Groffman, P. M., M. Altabet, J. K. Bohlke, K. Butterbach-Bahl, M. B. David, M. K. Firestone, A. E. Giblin, T. M. Kana, L. P. Nielsen & M. A. Voytek, 2006. Methods for measuring denitrification: diverse approaches to a difficult problem. Ecological Applications 16: 2091–2122.

Hale, S., 1974. The role of benthic communities in the nutrient cycles of Narragansett Bay. Ph.D. Thesis, University of Rhode Island, Narragansett, RI.

Hawk, J. D., 1998. The role of the North Atlantic oscillation in winter climate variability as it relates to the winter–spring bloom in Narragansett Bay. M.S. Thesis, University of Rhode Island, Narragansett, RI.

Inouye, D. W., B. Barr, K. B. Armitage & B. D. Inouye, 2000. Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Sciences 97: 1630–1633.

Jackson, J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Cooke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S. Lenihan, J. M. Pandolfi, C. H. Peterson, R. S. Steneck, M. J. Tegner & R. R. Warner, 2001. Historical overfishing and the recent collapse of coastal ecosystems. Science 293: 629–637.

Josefson, A. B. & B. Rasmussen, 2000. Nutrient retention by benthic macrofaunal biomass of Danish estuaries: importance of nutrient load and residence time. Estuarine, Coastal and Shelf Science 50: 205–216.

Kana, T. M., C. Darkangelo, M. D. Hunt, J. B. Oldham, E. Bennett & J. C. Cornwell, 1994. Membrane inlet mass-spectrometer for rapid high-precision determination of N_2, O_2, and Ar in environmental water samples. Analytical Chemistry 66: 4166–4170.

Karentz, D. & T. J. Smayda, 1998. Temporal patterns of variations in phytoplankton community organization and abundance in Narragansett Bay during 1959–1980. Journal of Plankton Research 20: 145–168.

Keller, A. A. & U. Riebesell, 1989. Phytoplankton carbon dynamics during a winter–spring diatom bloom in an enclosed marine ecosystem: primary production, biomass, and loss rates. Marine Biology 103: 131–142.

Keller, A. A., C. A. Oviatt, H. A. Walker & J. D. Hawk, 1999. Predicted impacts of elevated temperature on the magnitude of the winter–spring phytoplankton bloom in temperate coastal waters: a mesocosm study. Limnology and Oceanography 44: 344–356.

Kelly, J. R. & S. W. Nixon, 1984. Experimental studies of the effect of organic deposition on the metabolism of a coastal marine bottom community. Marine Ecology Progress Series 17: 157–169.

Kinney, E. H. & C. T. Roman, 1998. Response of primary producers to nutrient enrichment in a shallow estuary. Marine Ecological Progress Series 163: 89–98.

Kot-Wasik, A., J. Dębska & J. Namieśnik, 2004. Monitoring or organic pollutants in coastal waters of the Gulf of Gdansk, Southern Baltic. Marine Pollution Bulletin 49: 264–276.

Lambert, C. E. & C. A. Oviatt, 1983. Manual of Biological and Geochemical Techniques in Coastal Areas. MERL Publication Series, Report No. 1, 281 pp.

Li, Y. & T. J. Smayda, 1998. Temporal variability of chlorophyll in Narragansett Bay 1973–1990. ICES Journal of Marine Science 55: 661–667.

McKenna, J. E., 1987. An analysis of food limitation in the benthic communities of Narragansett Bay using a numerical simulation model. Ph.D. Thesis, University of Rhode Island, Graduate School of Oceanography, Narragansett, RI, 293 pp.

McMaster, R. L., 1960. Sediments of Narragansett Bay system and Rhode Island Sound, Rhode Island. Journal of Sedimentary Petrology 30: 249–274.

Nixon, S. W., C. A. Oviatt & S. S. Hale, 1976. Nitrogen regeneration and the metabolism of coastal marine bottom communities. In Anderson, J. M. & A Macfayden (eds), The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. Blackwell, Oxford: 269–283.

Nixon, S. W., J. R. Kelly, B. N. Furnas, C. A. Oviatt & S. S. Hale, 1980. Phosphorus regeneration and the metabolism of coastal marine bottom communities. In Tenore, K. R. &

B. C. Coull (eds), Marine Benthic Dynamics. University of South Carolina Press, Columbia: 219–242.

Nixon, S. W., C. A. Oviatt, J. Frithsen & B. Sullivan, 1986. Nutrients and the productivity of estuarine and coastal marine ecosystems. Journal of the Limnological Society of Southern Africa 12: 43–71.

Nixon, S. W., S. L. Granger & B. L. Nowicki, 1995. An assessment of the annual mass balance of carbon, nitrogen, and phosphorus in Narragansett Bay. Biogeochemistry 31: 15–61.

Nixon, S. W., S. Granger & B. Buckley, 2003. The warming of Narragansett Bay. 41°N A Publication of Rhode Island Sea Grant and Land Grant Programs 2: 18–20. Available at: http://www.seagrant.gso.uri.edu/41N/Vol2 No1/baywarming.html.

Nixon, S. W., S. Granger, B. A. Buckley, M. Lamont & B. Rowell, 2004. A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts. Estuaries 27: 397–404.

Nixon, S. W., B. Buckley, S. Granger, L. Harris, A. Oczkowski, L. Cole & R. Fulweiler, 2005. Anthropogenic nutrients to Narragansett Bay: a twenty-five year perspective. A Report to the Narragansett Bay Commission and Rhode Island Sea Grant. Available at http://www.narrabay.com/Documents/PDFs/Bay_Commission_Report%20.pdf.

Nixon, S. W., B. Buckley, S. Granger, L. Harris, A. Oczkowski, R. Fulweiler & L. Cole, 2008. Nutrient inputs to Narragansett Bay: past, present, and future. In Desbonnet, A., A. B. Colt & B. A. Costa-Pierce (eds), Science of Ecosystem-Based Estuary Management: Narragansett Bay in the 21st Century. Springer, New York: 101–175.

Nowicki, B. L., 1994. The effect of temperature, oxygen, salinity, and nutrient enrichment on estuarine denitrification rates measured with a modified nitrogen gas flux technique. Estuarine, Coastal and Shelf Science 38: 137–156.

Nowicki, B. L. & C. A. Oviatt, 1990. Are estuaries traps for anthropogenic nutrients? Evidence from estuarine mesocosms. Marine Ecology Progress Series 66: 131–146.

O'Reilly, J. E., 1984. Carbon flow in a coastal marine bottom community. Ph.D. Thesis, University of Rhode Island, 199 pp.

Oviatt, C. A., 2004. The changing ecology of temperate coastal waters during a warming trend. Estuaries 27: 895–904.

Oviatt, C. A., P. Doering, B. L. Nowicki & A. Zoppini, 1993. Net system production in coastal waters as a function of eutrophication, seasonality, and benthic macrofaunal abundance. Estuaries 16: 247–254.

Oviatt, C. A., P. Doering, B. Nowicki, L. Reed, J. Cole & J. Frithsen, 1995. An ecosystem level experiment on nutrient limitation in temperate coastal marine environments. Marine Ecology Progress Series 116: 171–179.

Oviatt, C., A. Keller & L. Reed, 2002. Annual primary production in Narragansett Bay with no bay-wide winter–spring phytoplankton bloom. Estuarine, Coastal and Shelf Science 54: 1013–1026.

Pilson, M. E. Q., 1985. On the residence time of water in Narragansett Bay. Estuaries 8: 2–14.

Pratt, D. M., 1959. The phytoplankton of Narragansett Bay. Limnology and Oceanography 4: 425–440.

Rhode Island Department of Environmental Management, 2003. The Greenwich Bay Fish Kill—August 2003. Causes, Impacts and Responses Report. 32 pp.

Rudnick, D. T. & C. A. Oviatt, 1986. Seasonal lags between organic carbon deposition and mineralization in marine sediments. Journal of Marine Research 44: 815–837.

Rudnick, D. T., R. Elmgren & J. B. Frithsen, 1985. Meiofaunal prominence and benthic seasonality in a coastal marine ecosystem. Oecologia 67: 157–168.

Scavia, D., J. C. Field, D. F. Boesch, R. W. Buddemeier, V. Burkett, D. R. Cayan, M. Fogarty, M. A. Harwell, R. W. Howarth, C. Mason, D. J. Reed, T. C. Royer, A. H. Sallenger & J. G. Titus, 2002. Climate change impacts on U.S. Coastal and Marine Ecosystems. Estuaries 25: 149–164.

Seitzinger, S., S. W. Nixon & M. E. Q. Pilson, 1984. Denitrification and nitrous oxide production in a coastal marine ecosystem. Limnology and Oceanography 29: 73–83.

Sullivan, B. K., D. VanKeuren & M. Clancy, 2001. Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, Rhode Island. Hydrobiologia 451: 113–120.

Townsend, D. W. & L. M. Cammen, 1988. Potential importance of the timing of spring plankton blooms to benthic–pelagic coupling and recruitment of juvenile demersal fishes. Biological Oceanography 5: 215–229.

US EPA, 1983a. Methods for chemical analysis of water and wastes, EPA-600/4-79-020, Revised March 1983, Method 365.3. U.S. Environmental Protection Agency, Ohio.

US EPA, 1983b. Methods for chemical analysis of water and wastes. EPA-600/4-79-020, Revised March 1983, Method 365.5. U.S. Environmental Protection Agency, Ohio.

US EPA, 1997. Determination of nitrate and nitrite in estuarine and coastal waters by gas segmented continuous flow colorimetric analysis. In Ortner, P. B. & C. J. Fischer (eds), Methods for Chemical Analysis of Water and Wastes, Revision 2.0, Method 353.4. U.S. Environmental Protection Agency, Ohio.

Valiela, I., K. Foreman, M. LaMontagne, D. Hersh, J. Costa, P. Peckol, B. DeMeo-Anderson, C. D'Avanzo, M. Babione, C. Sham, J. Brawley & K. Lajtha, 1992. Couplings of watersheds and coastal waters: sources and consequences of nutrient enrichment in Waquoit Bay, Massachusetts. Estuaries 15: 443–457.

Walther, G., E. Post, P. Convey, A. Menzel, C. Parmesan, J. C. Beebee, J. Fromentin, O. Hoegh-Guldberg & F. Bairlein, 2002. Ecological response to recent climate change. Nature 416: 389–395.