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The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay

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ABSTRACT

The timing and magnitude of phytoplankton blooms have changed markedly in Narragansett Bay, RI (USA) over the last half century. The traditional winter–spring bloom has decreased or, in many years, disappeared. Relatively short, often intense, diatom blooms have become common in spring, summer, and fall replacing the summer flagellate blooms of the past. The annual and summer mean abundance (cell counts) and biomass (chl *a*) of phytoplankton appear to have decreased based on almost 50 years of biweekly monitoring by others at a mid bay station. These changes have been related to warming of the water, especially during winter, and to increased cloudiness. A significant decline in the winter wind speed may also have played a role. The changes in the phenology of the phytoplankton and the oligotrophication of the bay appear to have decreased greatly the quantity and (perhaps) quality of the organic matter being deposited on the bottom of the bay. This decline has resulted in a very much reduced benthic metabolism as reflected in oxygen uptake, nutrient regeneration, and the magnitude and direction of the net flux of N_2 gas. Based on many decades of standard weekly trawls carried out by the Graduate School of Oceanography, the winter biomass of bottom feeding epibenthic animals has also declined sharply at the mid bay station. After decades of relatively constant anthropogenic nitrogen loading (and declining phosphorus loading), the fertilization of the bay will soon be reduced during May–October due to implementation of advanced wastewater treatment. This is intended to produce an oligotrophication of the urban Providence River estuary and the Upper Bay. The anticipated decline in the productivity of the upper bay region will probably decrease summer hypoxia in that area. However, it may have unanticipated consequences for secondary production in the mid and lower bay where climate-induced oligotrophication has already much weakened the historically strong benthic–pelagic coupling.

1. Introduction

Phenology is the study of relationships between climate and the regular seasonal progression of biological events, such as the migration of animals and the flowering of plants. Marine ecologists have long attended to the arrivals and departures of fish and the blooming of phytoplankton, but a growing awareness of climate change has stimulated considerable recent interest in how the calendar of events in marine ecosystems may be shifting and in what the ecological consequences of these shifts might be (e.g. Jossi et al., 2003; Edwards and Richardson, 2004; Stenseth et al., 2004; Greve et al., 2005; Bering Sea Interagency Working Group, 2006; Kirby et al., 2007; Pilling et al., 2007; Beaugrand et al., 2008).

It is now clear that the coastal waters off southern New England have warmed since 1970 by about 1.2 °C in their annual mean and by about 1.7 °C in the winter and 1.0 °C in the summer (Nixon et al., 2003, 2004; Oviatt, 2004). In mid Narragansett Bay (RI, USA), the surface water during winter (D,J,F) has warmed on average by about 2.2 °C since 1960, though there is considerable interannual variability (Fig. 1). Such warming may have a particularly large impact on Narragansett Bay and other waters in this region because nearby Cape Cod forms an important barrier between boreal species to the north and warm water species to the south (Fig. 2) (Fish, 1925).

While most studies of phenology focus on the responses of individual species or groups of species to climate change (some Narragansett Bay examples include Oviatt, 2004; Costello et al., 2006; Collie et al., 2008), our purpose in this paper is to present and synthesize some of the evidence that suggests that warming and associated increased cloudiness and, perhaps, declining wind speed have had a major impact on productivity, benthic–pelagic coupling,

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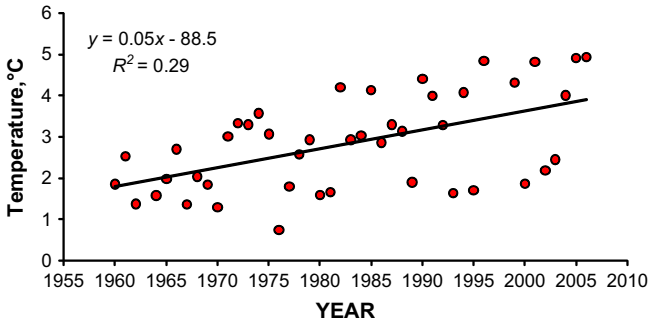

Fig. 1. Mean surface water temperatures during D,J,F in the middle of the West Passage of Narragansett Bay near Fox Is. (Fig. 2) as recorded by the sampling of D. Pratt, T.J. Smayda, and the GSO plankton monitoring program (data at http://www.narrbay.org/d_projects/plankton-tsv/plankton-tsv.htm) and (http://www.gso.uri.edu/phytoplankton/). Both slope and intercept of the regression are highly significant ($F = 17.212$, $p = 0.0002$).

and biogeochemical cycling in Narragansett Bay. We are fortunate in this effort that Narragansett Bay has been the site of extensive quantitative phytoplankton studies extending back to the early 1950s (Ferrara, 1953; Smayda, 1957). Narragansett Bay was also one of the first and most intensively studied coastal systems in which benthic oxygen uptake, benthic nutrient regeneration, and benthic denitrification were measured over annual cycles in the 1970s and 1980s (e.g. Hale, 1974; Nixon et al., 1976, 1980; Seitzinger et al., 1984). These early studies provide a strong historical base for comparison with recent conditions (e.g. Fulweiler and Nixon, in press; Fulweiler et al., 2007).

1.1. A note on Narragansett Bay

Various features of Narragansett Bay have been described frequently in the literature as part of specialized papers dealing with particular species or types of organisms or phenomena, but a detailed scientific overview has not been published for almost 30 years (Kremer and Nixon, 1978). The same is true for a popular description of the bay's ecology (Olsen et al., 1980). A set of detailed reviews of Narragansett Bay phytoplankton, zooplankton, icthyoplankton, benthos, demersal fish, organic pollutants, and heavy metals was prepared in 1989 by Hinga et al., Durbin and Durbin, Frithsen, Jeffries et al., Quinn, Bender, and Nixon, respectively, but these are not easily available to readers outside of the area. A new book devoted to the bay has just appeared, but it is focused on the history, consequences, and management of nutrient enrichment (Desbonnet and Costa-Pierce, 2008). For our purposes here, it may be useful to provide some brief background description of the ecosystem before discussing changing phenology, productivity, and benthic–pelagic coupling. Our description is restricted to basic physical features, phytoplankton, nutrients, and the benthos because these form the basis of most of the discussion that follows.

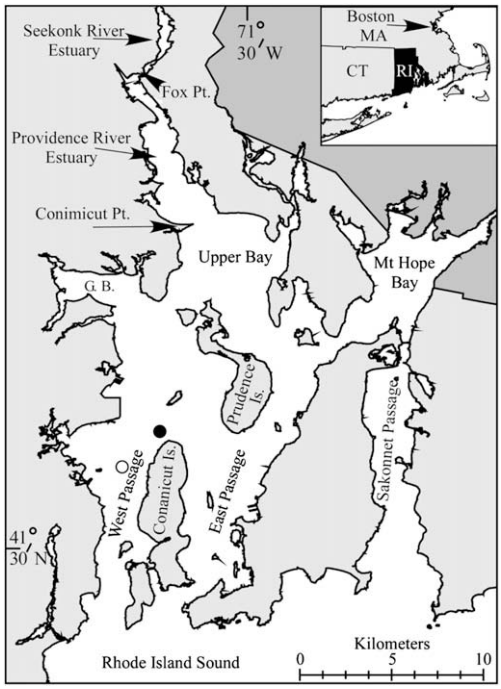

Fig. 2. Map of Narragansett Bay showing its location between Cape Cod, MA and Long Island, NY. Various placed mentioned in text are noted. G. B. is Greenwich Bay. The solid circle is the site of many historic and recent benthic flux measurements and the open circle is the long-term demersal fish trawl and phytoplankton monitoring station.

1.1.1. Size and shape

The bay as a whole is geographically complex and includes the Seekonk and Providence River estuaries in the north, a small shallow side embayment to the west (Greenwich Bay), a much larger appendage on the east (Mt. Hope Bay), and three longer passages, the West Passage, the East Passage, and the Sakonnet Passage (Fig. 2). As a practical matter, Mt. Hope Bay and the Sakonnet Passage are often not considered as part of Narragansett Bay proper, a practice we follow here. The Seekonk and Providence River estuaries are highly urbanized areas that receive most of the fresh water and sewage that enters the bay. In contrast with most of Narragansett Bay proper, they are frequently density stratified with hypoxic bottom waters in the shipping channel. Greenwich Bay and the Upper Bay also experience episodic hypoxia during summer (e.g. Deacutis et al., 2006; Melrose et al., 2007). The mouth of the Providence River estuary is marked by Conimicut Pt. (Fig. 2) below which the bay proper begins.

So defined, Narragansett Bay proper is 234 km^2 with a mean depth of 8.7 m at MLW. Mean tidal range is about 1.2 m. The Providence River estuary is 21.3 km^2 with a mean depth of 5.2 m. Distance from Fox Pt. at the head of the Providence River estuary to the mouth of the bay is about 40 km. A detailed hypsographic analysis (Chinman and Nixon, 1985) shows that the volume of the system increases slowly with distance below Fox Pt. until the divergence of the East and West Passages about 16 km south of Conimicut Pt., at the top of Prudence Island (Fig. 2). After another 15 km, the depth of the lower East Passage (about 19 m) becomes much greater than the lower West Passage (about 9 m) and its volume increases much more rapidly.

1.1.2. Salinity and temperature

Surface fresh water input to the bay averages only about 100 $m^3 s^{-1}$ (Pilson, 1985) with little additional contribution from ground water (Nowicki and Gold, 2008; Pilson, 2008). As a result, salinities are high (32 to about 25 in the bottom water throughout the system; 32 to about 20 in the surface water, Kremer and Nixon, 1978). The average water residence time in the bay is 26 days (Pilson, 1985). Water temperatures range from about 1 °C to 23 °C, with little difference most of the time between surface and bottom in the mid and lower bay (Hicks, 1959; Kremer and Nixon, 1978).

1.1.3. Phytoplankton

Narragansett Bay is now a phytoplankton-based system in which intertidal wetlands and macrophytes contribute little to the supply of organic matter. In the late 1800s and early 1900s eelgrass (*Zostera marina*) was widely distributed in the upper bay and Providence River estuary (Nixon et al., 2008), but at present only

some 150 ha are thought to remain, with none above Prudence Island (Fig. 2) (Bradley et al., 2007). The contribution of benthic microalgae has not been assessed, but deserves attention in the shallower parts of the bay. The phytoplankton has been described by Pratt (1959) and Karentz and Smayda (1998) among others. The weekly abundance and species composition in the mid West Passage during recent years can be found online at http://www.gso.uri.edu/phytoplankton/. There is a strong gradient in surface chlorophyll concentration and primary production from very high values during summer in the Providence River estuary and Upper Bay to low at the mouth (Kremer and Nixon, 1978; Oviatt et al., 2002) (Fig. 3). The up bay–down bay gradients in phytoplankton dynamics as they relate to nutrient inputs and water clarity have been analyzed extensively by Smayda and Borkman (2008).

1.1.4. Nutrients

The bay has been intensively fertilized with domestic wastewater since the introduction of public water supply and sewer systems beginning in the late 1800s. Detailed reconstruction of historical and recent nutrient inputs has shown that, until the last few years, inputs of nitrogen (N) to the bay have remained essentially constant since the early 1970s, and that phosphorus (P) inputs have declined significantly since the 1970s (Nixon et al., 2008). Implementation of advanced wastewater treatment has reduced the direct discharge of dissolved inorganic N (DIN) to the bay from sewage treatment plants during May–October by about 30% since 2000 (Pryor et al., 2007), but this represents less than a 10% drop in the annual total N load to the bay. When completely implemented throughout the watershed and along the shoreline of the bay, advanced wastewater treatment may ultimately reduce summer N inputs by 30–40% (Nixon et al., 2008).

Annual mass balances for organic carbon (C), N, and P with full secondary sewage treatment but prior to the recent move to advanced wastewater treatment showed that while anthropogenic sources dominated the inputs of N and P, phytoplankton production was by far the larger source of C (Nixon et al., 1995). The size of the historical winter–spring diatom bloom was regulated by the availability of DIN and dissolved silica (DSi) (Pratt, 1965; Smayda, 1973; Kremer and Nixon, 1978). During summer primary production and phytoplankton standing crops are strongly limited by the supply of DIN (Oviatt et al., 1995). Concentrations of DIN are very low ($<$1–2 μM) in the surface water of the mid and lower West and East Passages during summer (see nutrient data for a mid bay station in recent years at the url given above for phytoplankton). Based on intensive sampling between the mid West Passage and the head of the Providence River estuary in the mid 1980s, Smayda and Borkman (2008) concluded that Narragansett Bay could be divided into three zones, a light limited and Si sensitive "Enrichment Zone" in the Providence River estuary, a "Depuration Zone" in the Upper Bay basin, and a "Nutrient – Limited, N – Sensitive Zone" beginning in the upper West Passage. More recent data seem consistent with this picture (e.g. Fig. 3).

1.1.5. Benthos

Over 70% of the bay is deeper than 5 m at MLW (Chinman and Nixon, 1985), and most of the bottom is believed to be heterotrophic, with fine grained silt-clay sediments covering about 65% of the bottom (Nixon et al., 1995). Almost all of the rest is fine sand. We say "believed to be heterotrophic" on the basis of vertical light attenuation and water depth over most of the bay and the relationships between light and photosynthetic carbon fixation by microphytobenthos reported by MacIntyre et al. (1996).

Recent biweekly surveys at 16 stations around the bay showed that the annual mean vertical light attenuation coefficient ($-k$, m^{-1}) declined approximately linearly with distance from the head of the Providence River estuary to the mouth of the bay (Oviatt et al., 2002) (Fig. 4). Combining these data with the mean depth of various regions of the bay suggests that on average 1–2% of surface light reaches the average depth in the Providence River estuary, Upper Bay, and upper West Passage, 1% reaches the bottom of the lower West Passage and the upper East Passage, and 0.1% or less reaches the sediments of the Middle and lower East Passage. Incident light on the water surface ranges from about 5 to 65 E m^{-2} d^{-1} over the annual cycle so that sediments at the mean depth of the various portions of the bay may receive between 0.2 and 40 μmol m^{-2} s^{-1}. Measurements of carbon fixation by microphytobenthos over an annual cycle in Delaware Bay showed very low rates of photosynthesis at light levels less than about 50 μmol m^{-2} s^{-1} (MacIntyre et al., 1996). We go into this level of detail because virtually all of the benthic flux measurements made in the bay have been done in the dark. While microphytobenthos may clearly be an important factor influencing benthic fluxes in the shallow parts of the bay, for the system as a whole their contribution appears to be minimal.

There is a long history of studies describing the benthic communities in the bay, including Stickney and Stringer (1957), Phelps (1958), Hale (1974), Frithsen (1984), Rudnick et al. (1985), Grassle et al. (1985), Levin (1986) and Calabretta and Oviatt (2008). Frithsen (1989) struggled to synthesize all of the work to that point to generalize about spatial and temporal trends, but was frustrated by the range of sieve sizes and collection techniques used, the common focus on numbers rather than biomass, and the great seasonal variability in numbers. At least through the 1980s, the numbers of meiofauna and macrofauna were high in May and June

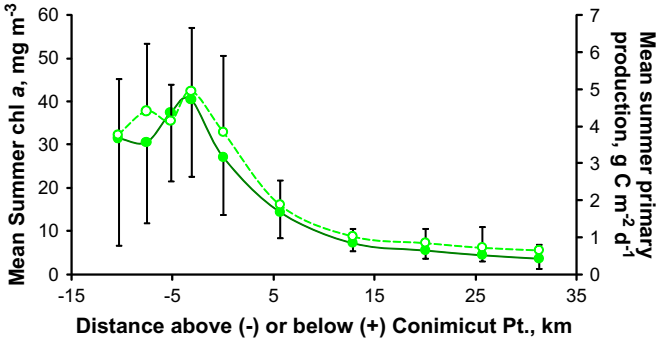

Fig. 3. Mean ± SD summer (J,J,A) near surface chlorophyll (solid points and line) and depth integrated ^{14}C particulate primary production with distance above (−) and below (+) Conimicut Pt. at the mouth of the Providence River estuary in 1997 (data from Oviatt et al., 2002, personal communication).

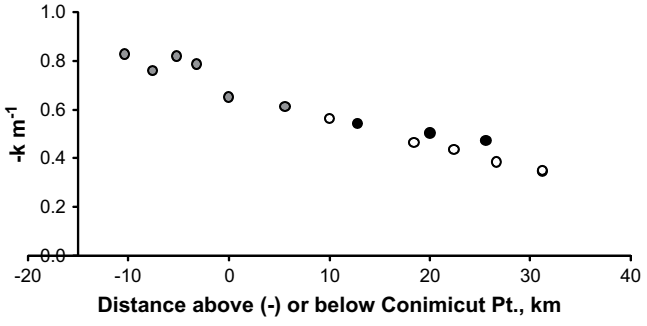

Fig. 4. Mean annual vertical light attenuation coefficient with distance above (−) and below (+) Conimicut Pt. at the mouth of the Providence River estuary in 1997/1998 (data from Oviatt et al., 2002 and personal communication). The gray points are at stations north of the point where the East and West Passage transects diverge (see Fig. 2).

followed by lowest abundance in late summer and fall, suggesting food limitation in late summer.

Since much of our discussion of changes in benthic–pelagic coupling in the bay will focus on the mid bay region just north of Jamestown or Conanicut Island (Fig. 2), it is worth adding some detail on the bottom in that area. This is the most intensively and frequently sampled part of the bay (Frithsen, 1989) and it served as the source of the sediments used in virtually all of the large mesocosm experiments carried out in the Marine Ecosystems Research Laboratory (MERL) (e.g. Rudnick et al., 1985; Rudnick and Oviatt, 1986; Doering and Oviatt, 1986). The site is 7–8 m deep with salinity of about 30 that varies little with season. The sediments are predominantly silt-clay (over 70%) with the remainder largely clay (almost 20%). Organic content of the surface sediment was about 4% with a C/N by weight of 7.6 in the 1970s (Hale, 1974). More recent analyses suggest that the C/N at the site has increased (mean of 10.9, range 9.5–13.9, Fulweiler, 2007). Light reaching the bottom may vary between about 4 and 80 $\mu mol\, m^{-2}\, s^{-1}$. The mid bay macro benthos is dominated by *Mediomastus* (a small sub-surface deposit feeding polychaete) and *Nucula* (a small bivalve). The results of recent sampling by C.A. Oviatt and her students can be seen at: www.gso.uri.edu/merl/data.htm and in Calabretta and Ovaitt (2008) where they provide complete taxonomic and abundance data. Because of its central location and use in the MERL experiments, this site has been included in almost all of the benthic flux measurements made in the bay. Fortunately, it is only about 7 km from the site of the long-term plankton and nutrient monitoring site off Fox Island (Fig. 2) studied by Pratt (1959, 1965), Smayda (1998) and the on-going plankton monitoring cited earlier. The mid bay region is similar to the average depth of Narragansett Bay as a whole (8.6 m) and contains the most common sediment type of the bay. Since it lies about 15–20 km below Conimicut Pt. (Fig. 2), water column chlorophyll is much lower than in the Providence River estuary but similar to that of the lower bay (Fig. 3).

2. Changing phenology and the winter–spring bloom

> It has long been known that on both the European and American coasts the most luxuriant diatom growth does not take place in the warmest months … throughout the shallow waters south of Cape Cod a rich winter diatom plankton starts usually in November and continues until March, reaching a maximum in December (Fish, 1925).

Since the basis for the biogeochemical linkage or coupling of the benthos and the overlying water begins with the primary production of organic matter in the water, we begin our analysis there.

The first reported quantitative study of the phytoplankton in Narragansett Bay was carried out in the upper West Passage (Fig. 2) between July 1952 and March 1953 (Ferrara, 1953). The results showed a strong winter bloom with two lesser blooms during summer, consistent with the semi-quantitative description reported over twenty-five years earlier by Fish (1925). The diatom *Skeletonema costatum* was the most abundant and persistent species, and comprised 80% of the total population. From this beginning, the ecology of Narragansett Bay has been tightly linked with the biology and ecology of what has universally been called *S. costatum* (Grev.) Cleve. While it is possible that the species was correctly identified, recent detailed studies of the genus have shown that *S. costatum* has, in fact, been frequently and incorrectly applied to a number of previously known and new species of *Skeletonema* (e.g. Sarno et al., 2005). The taxonomic confusion is understandable – the new distinctions are only apparent to experts using scanning and transmission electron microscopy and molecular techniques that have only recently become available. Specimens from Narragansett Bay have been examined using such techniques, and it appears that at least two species are now common in the bay, *S. japonicum* Zingone et Sarno in the winter and *S. grethae* Zingone et Sarno in the summer (Sarno et al., 2005, P. Hargraves, GSO, URI, personal communication, A. Zingone, Stazione Zoologica "Anton Dohrn", Naples, personal communication, Kooistra et al., 2008).

Ferrara's analysis (as well as early studies in the lower bay by Smayda, 1955, 1957) was part of a larger and longer sampling study by David Pratt (1959) that covered 15 stations in the Upper Bay, Greenwich Bay, and the lengths of the West and East Passages. Pratt noted the strong winter–spring bloom of diatoms as well as late summer diatom blooms, "principally *Skeletonema costatum*." He also reported that average standing crops were approximately the same in the West and East Passages and that, "the Upper Bay is more than three times as rich as the lower in both diatoms and flagellates." The latter observation still seems to hold, at least in terms of total chlorophyll (Fig. 3).

The best known description of the winter–spring bloom was provided in a later paper by Pratt (1965, p. 173) based on weekly samples collected in the upper, mid, and lower West Passage between January 1959 and June 1963:

> "The outstanding feature of the annual cycle is the winter–spring diatom flowering, which is extraordinary in its time of inception, intensity, and duration. Logarithmic growth begins usually in December, and after about a month terminates in a maximum sometimes exceeding 50,000 cells/ml; this is followed by a series of secondary peaks of diminishing amplitude, and the flowering period ends in late May or June."

Unfortunately, the Pratt (1965) paper did not include total cell counts or data for the mid bay. Fortunately, Pratt did pass on the total cell count data from the mid bay station to his colleague and former graduate student, T.J. Smayda, who made them available to us. Since the mid West Passage station became the location of long-term plankton studies by Smayda and his graduate students (e.g. Smayda, 1973; Karentz and Smayda, 1984, 1998; Li and Smayda, 1998; Smayda, 1998; Borkman, 2002; Borkman and Smayda, 2009) is the site of the ongoing monitoring program by the Graduate School of Oceanography (GSO) (http://www.gso.uri.edu/phytoplankton/), it is possible to make some direct comparisons of total cell counts at this station during recent years with the counts obtained by Pratt and his students a half century ago (Fig. 5).

While the long and intense winter–spring bloom was a dramatic component of the annual cycle in the early 1960s, it is clear that there were also episodic and intense summer and, in some years, fall blooms as well. The picture appears very different now, with no winter–spring bloom in many years, though shorter summer and fall blooms remain, and these can be quite intense (Fig. 5). The winters of the three recent years shown in Fig. 5 were all warm (Fig. 1). The delay and increasingly frequent loss of the winter–spring diatom bloom appears to have taken place gradually and erratically over the past 50 years, especially after the mid 1970s (Fig. 6). This represents a major change in the seasonal cycle of phytoplankton abundance that had prevailed for at least the previous 75 years (Fish, 1925).

There appear to have been other important changes as well as the shift in phenology of blooms. In contrast to the earlier situation, diatoms now appear to dominate most of the larger blooms throughout the summer. The major diatom in these summer blooms is *Skeletonema*, though *Chaetocerous*, *Leptocylindrus*, and *Thalassiosira* can also be briefly important (see web site above). Borkman (2002) reviewed all of the cell count data from the mid bay station from 1959 to 1996 and found *Skeletonema* much more abundant during the summer in recent decades than it was during

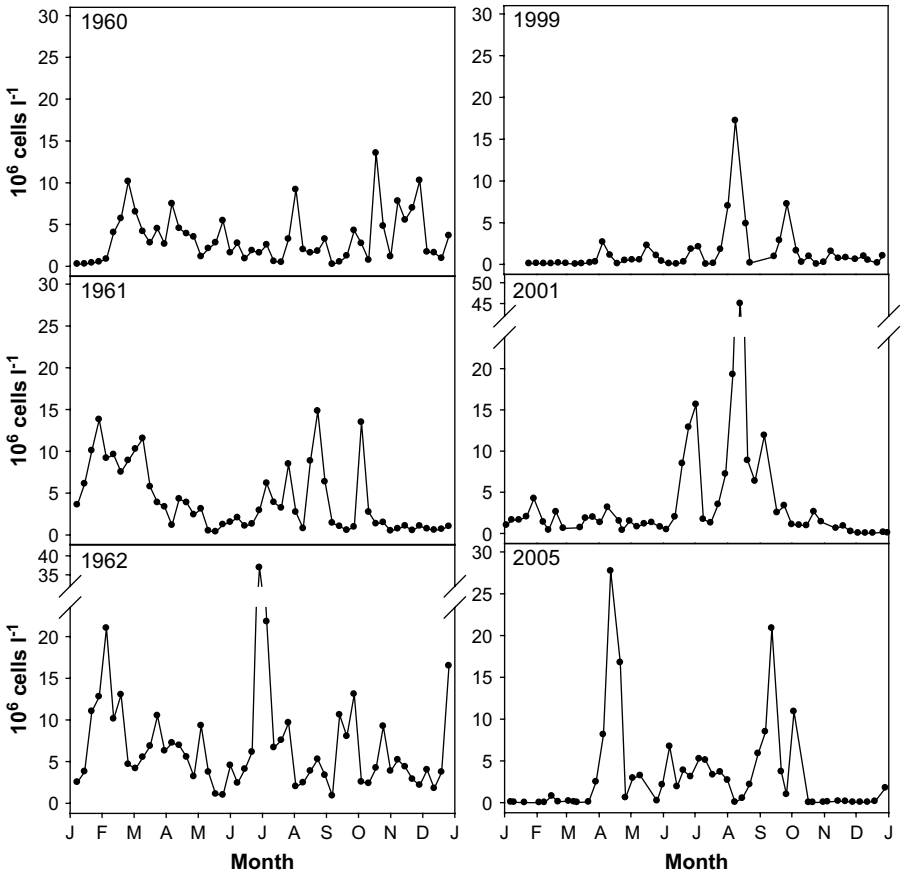

Fig. 5. Comparison of total phytoplankton cell counts at the long-term phytoplankton monitoring station in the middle West Passage (Fig. 2) during the early 1960s and early 2000s. Historic data of Pratt (1965) provided courtesy of T.J. Smayda (see Dwyer, 1980); recent data from the GSO plankton monitoring url given in text (courtesy of P. Hargraves). Earlier data pooled surface, mid depth, and near bottom; recent data mean of near surface and near bottom.

the 1960s. This appears to represent a change from Pratt's (1959) finding that microflagellates were much more abundant than *Skeletonema* in spring and early summer during the 1950s (Table 1). A detailed study of the abundance of different size fractions of the phytoplankton at this station in 1972–73 by Durbin et al. (1975) also found flagellates more abundant than diatoms during the summer. Such a change in the summer phytoplankton community may have important consequences for secondary production and biogeochemical cycling. For example, the quahog or hard clam, *Mercenaria mercenaria*, appears to feed preferentially on diatoms in the bay (Gearing et al., 1984) but does not filter at low temperatures (Loosanoff, 1939). Adult quahogs in the bay are now growing more rapidly than they did in the 1960s, perhaps in response to more abundant diatoms in the warmer months when they are feeding (Henry and Nixon, 2008). The ecological consequences of a decline in the winter species of *Skeletonema* (*S. japonicum*) and an increase in the summer species (*S. grethae*) are a rich topic for future research.

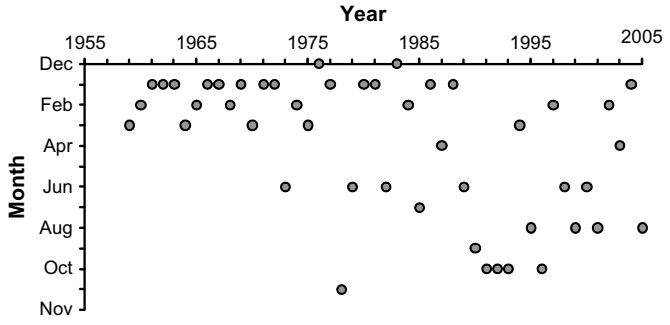

Fig. 6. Time of maximum bloom development in the West Passage of Narragansett Bay based on various sources, including Pratt (1965), Smayda (1998), Li and Smayda (1998), MERL monitoring (C. Oviatt, personal communication), and the GSO plankton monitoring url.

2.1. Declining standing crop

A casual inspection of even the small sample of years in Fig. 5 suggests that the mean abundance of the phytoplankton has also declined, and a time series plot of the annual mean total cell numbers over many years is consistent with this impression for both the annual mean and the winter mean (Fig. 7). A decline in the abundance of phytoplankton in the mid bay was first reported by Smayda (1998) based on diatom counts between 1959 and 1980 and by Li and Smayda (1998) based on weekly chlorophyll samples collected between 1973 and 1990. They noted a decline of 2.25 mg m^{-3} over the 18-year period. If additional chlorophyll data

Table 1
Seasonal mean concentrations (10^3 cells per liter) of phytoplankton sampled weekly in the surface water at station W8 off Fox Island in the mid West Passage during 1955–1956 (from Pratt, 1959).

	Winter–Early Spring	Late Spring–Early Summer	Late Summer	Fall
Diatoms	7200	135	1500	140
Flagellates	280	1075	560	600
Total	7480	1210	2060	740

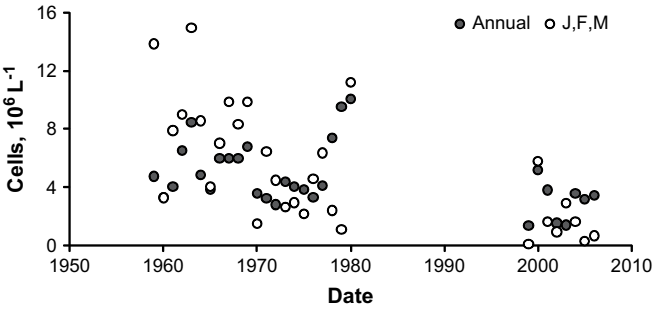

Fig. 7. Mean annual and winter total phytoplankton cell counts at the long-term monitoring site in the middle West Passage of Narragansett Bay (Fig. 2). Data sources as in Fig. 6 plus T.J. Smayda (personal communication). Both the slope ($p < 0.05$) and intercept ($p < 0.05$) for the annual mean vs. year are significant. The slope ($p < 0.0002$) and the intercept ($p < 0.0002$) are also significant for the winter mean.

collected by Smayda between 1991 and 1996 (personal communication) are added to the earlier Li and Smayda (1998) time series along with the measurements made more recently by the GSO plankton monitoring program (see web site above), it appears that the decline continued through 2006 (Fig. 8). While the frequent decline or loss of the winter–spring bloom is particularly conspicuous (as noted by Li and Smayda, 1998; Smayda, 1998), there has also been a marked decline in the mean summer chlorophyll (historical data provided by T.J. Smayda, more recent data from the GSO phytoplankton monitoring) (Fig. 8). And there has been a marked decline in the overall abundance of *Skeletonema*. Borkman's detailed study (2002) concluded that, "Winter–spring *Skeletonema* bloom duration declined from ca. six weeks in 1959–1963 to three weeks in 1978–1982 while first quarter abundance declined from 6000 cells ml^{-1} (1959–1963) to ca. 1200 cells ml^{-1} (1991–1996)."

2.2. Declining primary production

Such changes in the abundance and standing crop of the phytoplankton raise the question of changes in the primary production of the bay. Unfortunately, the question is impossible to answer firmly with direct measurements because there have been only a few studies of primary production and they have used quite different techniques (e.g. Vargo, 1979; Oviatt et al., 1981 used oxygen changes; Furnas et al., 1976; Oviatt et al., 2002 used ^{14}C uptake; and Durbin and Durbin, 1981 used laboratory derived assimilation numbers with field chlorophyll). Different studies have also reported their results in different ways (e.g. depth integrated or per unit volume) and only the Oviatt et al. (1981, 2002) studies attempted to cover the entire bay. Perhaps the most direct comparison is between the ^{14}C based estimates of Furnas et al. (1976) and Oviatt et al. (2002) near the mid West Passage station. The former made measurements during 1974 (310 g C m^{-2} y^{-1}) and the latter during 1997–1998, a year with no winter–spring bloom (160 g C m^{-2} y^{-1}). Extensive studies by Keller (1988) have shown that ^{14}C uptake by the phytoplankton in Narragansett Bay (as in many other coastal systems reviewed by Brush et al., 2002) can be calculated very closely using a simple BZI approach (biomass as chl *a*, photic depth, incident light). Using this approach, the decline in chlorophyll in the mid bay (Fig. 8) suggests that primary production there may have declined from about 370 g C m^{-2} y^{-1} in the mid 1970s to about 210 g C m^{-2} y^{-1} in 2005 (Fulweiler et al., 2007). Both comparisons suggest a reduction in primary production at mid bay of about 40–50% over 25 years. As we argue in a later section on benthic fluxes, even this large decline may be an underestimate.

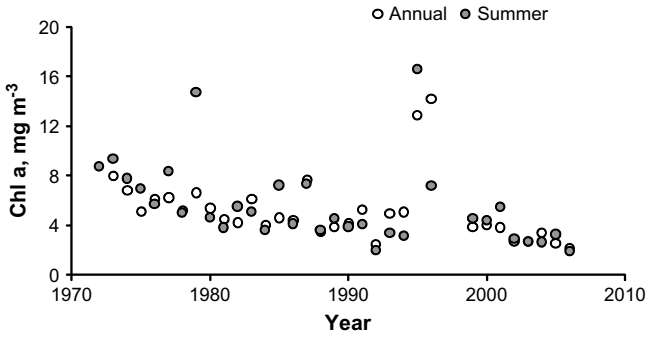

Fig. 8. Mean annual and summer chlorophyll at the long-term monitoring site in the middle West Passage of Narragansett Bay (Fig. 2). Annual data from Li and Smayda (1998) through 1990. Historical summer data and annual data from 1991 to 97 from T.J. Smayda (personal communication). All data from 1999 to 2006 from the GSO plankton monitoring url given in text. The high annual mean of 1995 was associated with a very cold winter (mean D,J,F = 1.7 °C, see Fig. 1). The mean annual chlorophyll decline is significant if two outliers (1995 and 1996) are removed ($p < 0.0001$). The summer chlorophyll decline is significant ($p < 0.05$). Expanded from Fulweiler and Nixon (in press).

A decline in the supply of organic matter to an ecosystem is called *oligotrophication* (Nixon, in press), the opposite of the well-known eutrophication that has been occurring due to increasing nutrient enrichment in many other coastal systems around the world (e.g. Nixon, 1995; Rabalais and Nixon, 2002; Valiela, 2006). While some of the ecological consequences of oligotrophication have become clear in lakes (e.g. Nay, 1996; Anderson et al., 2005), the phenomenon is only just beginning to be recognized in marine systems (Ozaki et al., 2004; Carstensen et al., 2006; Greening and Janicli, 2006; Philippart et al., 2007; Nixon, in press). While management interventions have been responsible for the few cases cited, we hypothesize that the oligotrophication of Narragansett Bay (at least to this point) has been induced by climate change. The only other case of climate-induced oligotrophication of a marine ecosystem that we are aware of is the remarkable indication of declining carrying capacity in the Bering Sea based on stable isotopic analysis of carbon in whale baleen (Schell, 2000) as well as declines in benthic macro-infauna biomass and benthic oxygen uptake in the northern Bering Sea (Grebmeier et al., 2006).

In spite of the impressive cell counts and chlorophyll of the winter–spring bloom, most of the primary production by the phytoplankton occurred during summer and early fall in the early 1970s (Vargo, 1979). Furnas et al. (1976) estimated that almost 75% of the total annual ^{14}C fixation during 1974 took place between May and September, inclusive, and over 40% occurred in July and August alone. Summer production exceeded winter in the more recent measurements as well (Oviatt et al., 2002). As shown by Furnas et al. (1976), most of this summer production was supported by DIN recycled within the water column, though benthic fluxes of NH_4^+ could have provided 20–50% of the net mid bay phytoplankton N demand in July and August of 1974. As we show later, that benthic contribution is now very much reduced, as is the summer standing crop of phytoplankton (Fig. 8).

2.3. Declining zooplankton?

While the focus of this paper is on the impact of changes in the phytoplankton on benthic–pelagic coupling, a question naturally arises about the responses of the zooplankton. Answering this question is complicated by at least two factors. First, the long history of zooplankton studies in Narragansett Bay was reviewed by Durbin and Durbin (1988), who concluded that it was virtually impossible to document trends in abundance up to that point because of the wide variety of sampling techniques that had been used in the different studies. Second, the warming winters (Fig. 1) have also

changed the phenology of the comb jelly, *Mnemiopsis leidyi*, a major predator on the summer zooplankton. As a result the *Mnemiopsis* now overwinter in greater numbers, proliferate much more quickly in the spring, and reach greater abundances in the summer than they did in previous decades (Sullivan et al., 2001). Costello et al. (2006) have shown a dramatic decrease in the maximum abundance of *Acartia tonsa*, the dominant summer copepod in the bay, when comparing the mean values obtained in various studies between 1951 and 1983 with their own study in 2000–2003. But that comparison must also suffer to some degree from sampling differences and, in any case, cannot distinguish between top down and bottom up influences. Even in the 1970s, when chlorophyll levels were considerably higher, both food limitation and predation appeared to be important in limiting *A. tonsa* abundance and production in this system (Durbin and Durbin, 1981). In analyzing samples collected during two years in the mid 1980s, Smayda and Borkman (2008) found positive spatial correlations between mean annual chlorophyll and mean annual zooplankton dry weight biomass that would suggest there has probably been a significant decline associated with the reduction in phytoplankton.

2.4. Declining organic deposition

It is difficult to quantify how the changes in the timing and magnitude of phytoplankton abundance and production have altered the deposition of organic matter on the bottom, including its quality as well as its quantity. Sediment trap measurements are not useful for this purpose because of resuspended sediments (Oviatt and Nixon, 1975). At least two attempts have been made to get around this problem by using the large (13 m^3, 5 m deep) MERL mesocosm tanks in which both ^{14}C labeling of phytoplankton and sediment traps can be used (Rudnick and Oviatt, 1986; Riebesell, 1989, respectively). Unfortunately, the results vary widely. In any case, extrapolation of these results to the bay is questionable. The tanks used in both studies were run in "batch mode" without any exchange of water with the adjacent Narragansett Bay as was the more common mode of operation of the facility. As noted by Riebesell (1989), this meant that the size and duration of the bloom were limited by the initial stock of nutrients in the mesocosm.

We can make an indirect assessment of maximum potential deposition during the traditional winter–spring bloom using a bay-wide survey of nutrient concentrations and chlorophyll made during an annual cycle in 1972–1973 (Kremer and Nixon, 1978). The bloom took up virtually all of the DIN in the bay as it developed from late January to early March and DIN concentrations below Conimicut Pt. remained near zero from March through June. With an initial DIN concentration of about 15 μM (and mean depth of 8.6 m) and assuming Redfield organic matter, this uptake would have been associated with new primary production of about 10 g C m^{-2}. To hold the concentration of DIN near zero, the phytoplankton would also have to have taken up virtually all of the DIN entering the system. Our measurements of DIN in the rivers and sewage treatment plants entering the bay during the 1970s (Nixon et al., 2005, 2008) amount to approximately 625 mmol m^{-2} in February through June, inclusive. This requires additional new production of about 50 g C m^{-2} for a total of 60 g C m^{-2}. This is still an underestimate of the total new production because it does not include the carbon fixed using the DIN in Rhode Island Sound water brought into the bay by the tides and entrained in the gravitational circulation. The sub pycnocline water in the sound has higher DIN concentrations than the mid and lower bay surface water. This input of DIN is much more uncertain, but various estimates have arrived at about 1.1 mmol m^{-2} d^{-1} (Nixon and Pilson, 1984; Nixon et al., 1995; Chaves, 2004). Over the five months this suggests new production of some 13 g C m^{-2}, giving a total of 73 g C m^{-2}. Of course, not all of this production was deposited on the bottom – some was respired in the water column and some must have been flushed from the system. But it does point to an upper constraint for the traditional winter–spring bloom deposition.

Studies in the MERL mesocosms and in natural systems in which sediment traps can be used effectively have shown that the deposition of organic matter from blooms is greatly reduced when the water is warmer (e.g. Smetacek, 1984; Rudnick and Oviatt, 1986; Keller et al., 1999). While grazing by zooplankton consumed little of the traditional winter–spring bloom in Narragansett Bay (Vargo, 1976; Deason, 1980) or in MERL mesocosms with a winter–spring bloom (Keller and Riebesell, 1989), the current situation with almost all of the blooms coming during spring, summer, and fall must be associated with greatly reduced deposition of organic matter on the bottom of the bay. Moreover, the cold water bloom deposition was almost completely made up of sinking phytoplankton (Keller and Riebesell, 1989) with a low C/N, while the material deposited during warmer conditions is of lower nutritional value with a higher C/N (Smetacek, 1984). Studies of the chemical composition of *Skeletonema* by Yoder (1979) also showed higher N/chl *a* and C/chl *a* in cells grown at 0 °C than in cells grown at higher temperatures (5, 10, 16, 22 °C). As concluded by Smetacek (1984, p. 533), "…the seasonal cycle in new and regenerated production in the pelagic system is of vital importance to the benthos both in terms of quantity and quality of the food supply."

3. Consequences for the benthos

> Numerous studies have documented that during a relatively brief period the spring phytoplankton bloom in temperate…regions can deliver as much as half of the total annual input of organic carbon to the benthos…Earlier blooms may occur in colder water, which would reduce consumption by pelagic heterotrophs and result in the input of a greater proportion of planktonic production to the bottom sediments…
>
> Townsend and Cammen (1988)

The dramatic shift of the Narragansett Bay winter–spring diatom bloom to spring, summer, and/or fall (Figs. 5 and 6) is an extreme example of the up to 20 day shifts in spring bloom initiation that Townsend and Cammen estimated using a decade of incident light data for Sheepscot Bay, Maine. The thesis of their now classic paper was that there might be a significant decline in food available for juvenile demersal fish in years when the spring bloom was delayed by a greater frequency of cloudy days. Later blooms would occur in warmer water where more of the primary production would be consumed by zooplankton. As a result, less of the organic matter would sink and support secondary production by benthic infauna, the important food for demersal fish.

While Narragansett Bay might seem a perfect setting to test this hypothesis, the data on benthic infauna are still confounded by all of the factors that frustrated Frithsen (1989). The major problem with the more recent sampling (which uses 300 μm mesh screens) and most of the historical studies is that only numbers of organisms have been reported, and these vary dramatically with time of sampling – even a week or two can make a big difference (Grassle et al., 1985; Frithsen, 1989). Efforts are underway by C.A. Oviatt and her students to estimate benthic biomass, but even with such estimates in hand there are few (if any) comparable data from the past for documenting long-term changes.

3.1. Declining epibenthic biomass in winter

There are consistent records of demersal fish and other epibenthic animal abundances at the mid bay long-term plankton

monitoring station (Fig. 2) that extend back to 1959. This standard weekly trawl sampling was begun by C.J. Fish (whose observations on the winter diatom bloom we quoted earlier). It was maintained for decades by H.P. Jeffries (e.g. Jeffries and Terceiro, 1985) and is now part of the GSO bay monitoring program overseen by J.S. Collie (www.gso.uri.edu/fishtrawl/). The RI Department of Environmental Management (DEM) has also monitored demersal fish during spring and fall at about 26 stations in the bay since 1979. Based on these data sets, there is no question that the abundance of demersal finfish in the bay has declined dramatically (at least during winter) and that the mean size of fish has declined significantly (e.g. Oviatt et al., 2003; Oviatt, 2004; Collie et al., 2008). However, it is difficult to know if, and to what degree, the change in timing and magnitude of the phytoplankton production has contributed to the decline in the fish. The decline is common in non-commercial as well as commercial benthic species (Oviatt et al., 2003), but it is particularly evident in winter flounder (*Pseudopleuronectes americanus*), a heavily exploited species. Using the DEM data, Oviatt et al. (2003) estimated that the biomass of demersal fish (including northern sea robin, red hake, skate, dogfish, tautog, windowpane flounder, and winter flounder) declined by about 75% between 1980–1985 and 1995–2000. As those authors point out, the warming of the bay itself may have contributed to the decline of boreal species such as the winter flounder. It is also possible that the warming may have had an indirect negative influence specifically on winter flounder by advancing the time when the sand shrimp, *Crangon septemspinosa*, a major predator on post-settlement winter flounder, becomes active (Jeffries, 2001; Taylor, 2003). But it is also possible that food limitation has played a role. A recent study of juvenile winter flounder in Narragansett Bay noted that there has been little recovery of stocks here despite a closure of the bay fishery and suggested that "…reduced size at age could be one factor responsible for the increased mortality of winter flounder juveniles." (Buckley et al., 2008).

The interpretation of the decline in demersal finfish is also complicated by large increases in the numbers of decapods in the bay, especially cancer crabs (*Cancer irroratus* and *C. borealis*) and lobster (*Homarus americanus*). After making an admittedly rough conversion from numbers to fresh weight for the decapods, Oviatt et al. (2003) and Oviatt (2004) estimated that their increase in total biomass (including shell) was about half the decline in finfish biomass. Since shell accounts for about 50–75% of the fresh weight of crabs and lobsters while skeletal material is usually less than 5% of the fresh weight of fish (Vinogradov, 1953), the meat biomass of the decapods may only amount to some 12–25% of the 75% loss in demersal finfish biomass.

We have estimated the average total fresh meat biomass of organisms captured during winter (J,F,M) and summer (J,A,S) in the standard 30 min GSO weekly trawl sampling at mid bay between 1960 and 2005 (Fig. 9). Since finfish biomass data have only been collected since 1994, we applied the average weight per individual of each species during each month of the last eleven years to the count data prior to 1994. Because the size of the individual fish has been declining (Collie et al., 2008) the decline in biomass is almost certainly greater than that shown in Fig. 9. For the decapods, we assumed that live meat biomass was 37% of the fresh weight of crabs and lobsters and 50% of the fresh weight of starfish and conchs (which are occasionally caught in large numbers in the trawls; C. Oviatt, personal communication and Sisson, 1973, respectively). While there is a great deal of interannual variability, winter biomass is now down by 80% while there is no significant trend in the summer biomass. The summer fish, however, are largely composed of pelagic feeders such as butterfish, scup, and squid while the winter contains many more benthic feeders. Collie et al. (2008) have noted a pronounced switch from benthic to

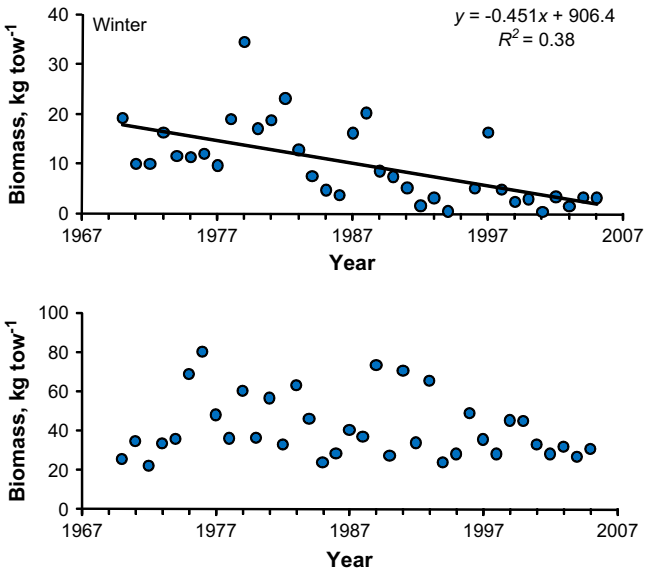

Fig. 9. Estimated mean live biomass (excluding shell) of demersal epibenthic animals collected by the GSO long-term fish trawl (approximately weekly sampling) off Fox Is. in the middle West Passage of Narragansett Bay during winter (J,F,M) and summer (J,J,A) (see Fig. 2). Seasons defined by taxonomic composition of the fish. See text for assumptions. Counts provided by J. Collie (personal communication) from the GSO demersal fish monitoring program. Sampling details are given in Collie et al. (2008). There is no significant trend in the summer fish but the overall decline in the winter is highly significant ($F = 20.02$; $p < 0.0001$). The decline since 1983 is also significant ($p = 0.021$) while there was not a significant slope between 1970 and 1983.

pelagic fish in the bay since 1980. The food required to support the demersal finfish in the past may also have been even greater than a simple comparison of the total epibenthic standing crop suggests since the production (and ingestion) per unit biomass of finfish is generally higher than for the invertebrates (Valiela, 1995, p. 238) that are now more abundant.

It would be surprising if the oligotrophication of Narragansett Bay had not played some role in the decline of demersal fish. Cross system comparisons have shown strong correlations between primary production and fisheries yield (Nixon, 1988), primary production and fish production (Iverson, 1990), and fish yield and chlorophyll concentrations (Ware and Thomson, 2005) in marine ecosystems. Moreover, the link between declining primary production and declining fish abundance and production has frequently been demonstrated in lakes (e.g. Nay, 1996). Nevertheless, we must admit that the situation with regard to the demersal fish may be too convoluted to offer definitive evidence of a benthic response (at least in part) to the changing phenology of the phytoplankton blooms. For that we must go to something simpler – the changing fluxes of oxygen and nutrients and nitrogen gas across the sediment–water interface.

3.2. Changes in benthic–pelagic fluxes

3.2.1. Historical background

The first of what became a great many measurements of the uptake of dissolved oxygen and the net flux of ammonium, nitrate plus nitrite, phosphate, and silicate between the bottom of Narragansett Bay and the overlying water were made in July, 1973 (Hale, 1975). That work grew into the first measurements of these fluxes over a complete annual cycle in a marine system and focused on three stations along the West Passage, including a mid bay station off the north end of Conanicut Island, not far from the long-term plankton monitoring station (Fig. 2) (Nixon et al., 1976; Kremer and

Nixon, 1978; Nixon et al., 1980). While the first study used large (2400 cm^2, 27 l) in situ chambers, subsequent work employed a variety of smaller and differently shaped cores collected by divers and incubated in the laboratory (e.g. McCaffrey et al., 1980; Kelly, 1983; O'Reilly, 1984; Nowicki and Nixon, 1985). As noted earlier, the number of flux measurements involving mid bay sediments increased dramatically because the area became the collection site for sediments used in virtually all the MERL experiments during the 1970s and 1980s (e.g. Pilson et al., 1980; Kelly and Nixon, 1984; Nixon et al., 1984; Oviatt et al., 1984; Kelly et al., 1985; Doering et al., 1986; Rudnick and Oviatt, 1986; Keller et al., 1987). Benthic metabolism measurements at MERL normally used a large incubation chamber that covered the entire 2.5 m^2 sediment tray in each mesocosm (Oviatt, 1981). Comparisons of fluxes measured in various ways did not show consistent differences, but there was a surprising lack of a gradient in fluxes measured from the Upper Bay to the mouth (Hale, 1975; Nixon et al., 1976).

3.2.2. Oxygen uptake and nutrient regeneration

The benthic oxygen uptake measurements of the mid 1970s showed that about 140 g C m^{-2} y^{-1} was being respired by the benthos or some 45% of the primary production reported by Furnas et al. (1976) for the mid bay in 1974. This seems a large fraction relative to a number of other productive coastal systems reviewed by Nixon (1981) and by Hopkinson and Smith (2005) in which correlations were found between the autochthonous and allocthonous carbon supply and benthic respiration. Such correlations suggest that primary production may have been on the order of 450–500 g C m^{-2} y^{-1} in the 1970s (Table 2). Phytoplankton production estimates for the mid bay using weekly chlorophyll measurements and laboratory determined assimilation ratios (Durbin et al., 1975; Durbin and Durbin, 1981; Table 2) also suggest that Furnas et al. (1976) may have underestimated carbon fixation, perhaps because they used 24 h long incubations. When DIN was virtually depleted during the highly productive summer months (e.g. Kremer and Nixon, 1978), their samples may have been strongly nutrient limited. If so, then the decline in primary production in the mid bay has been even greater than we calculated earlier.

Benthic metabolism was also strongly influenced by water temperature, though there was a marked seasonal effect such that rates of oxygen uptake and nutrient regeneration were significantly higher in the spring than they were at equivalent temperatures in the fall. This was interpreted as a sign of food limitation of the benthos during late summer and fall – as the water warmed in the spring, the benthos had an abundant supply of organic matter from the deposition of the winter–spring bloom, while little of the high summer production reached the bottom (Nixon et al., 1976, 1980; Kelly and Nixon, 1984). The coupling of the water column and the benthos through organic matter deposition and subsequent nutrient regeneration was clearly a major feature of the metabolism and biogeochemical cycling of the bay in the 1970s and early 1980s (Nixon et al., 1976; Kremer and Nixon, 1978; Kelly and Nixon, 1984).

Table 2
Various estimates of primary production in mid Narragansett Bay during the 1970s.

Study	Method	g C m^{-2} y^{-1}
Furnas et al. (1976)	24 h ^{14}C incubations	310
Nixon (1981)	Regession of benthic O_2 uptake against water column primary production + organic C input in many marine systems[a]	450
This study	As above using regression of Hopkinson and Smith (2005)	510
Durbin et al. (1975)	Using mean annual assimilation ratio and field	500
Durbin and Durbin (1981)	As above, but for March –September only	420

[a] Measured annual O_2 uptake = 140 g C m^{-2} y^{-1} assuming RQ of 1 (Nixon et al., 1976); allocthonous C input = 75 g C m^{-2} y^{-1} (Nixon et al., 1995).

3.2.3. Net N_2 fluxes

Narragansett Bay was also the site of the first direct measurements of the net flux of N_2 gas across the sediment–water interface using intact, unamended cores collected over an annual cycle (Seitzinger et al., 1980, 1984; Seitzinger, 1982). Stations were sampled in 1978–1979 and included the lower Providence River estuary, the mid bay where all the benthic fluxes of dissolved oxygen and nutrients were made by others, and just outside the bay in Rhode Island Sound. The results showed that, "Denitrification represents a major sink for fixed N in the bay; annually the N_2 production is equal to about 50% of the fixed N loading to the bay from rivers, land, and sewage" (Seitzinger et al., 1984, p. 73). Nowicki (1994) modified the water-replacement, gas chromatography technique used in the early work and returned to the mid bay site in 1986. Her results showed a lower average rate of denitrification (385 mmol m^{-2} y^{-1} compared with 520 mmol m^{-2} y^{-1}), but it was not clear if this apparent decline was real or an artifact of the use of different methods. In either case, denitrification in the sediments was still an important process in the bay.

3.2.4. The new situation-dramatic reductions in benthic respiration and nutrient regeneration; the appearance of N fixation

The gas chromatograph analyses used by Seitzinger and Nowicki have now been replaced by much more precise measurements of changes in the N_2/Ar ratio in water incubated over the sediments using membrane inlet mass spectrometry, MIMS (Kana et al., 1994, 1998; Eyre et al., 2002; Gardner et al., 2006). It was the development of this new technique that motivated us to begin making benthic flux measurements again, including N_2, in the summer of 2005, after a gap of almost twenty years.

Oxygen uptake rates calculated from the first cores collected in 2005 at the mid bay site were remarkably low compared with the measurements of the 1970s and 1980s. So were the rates of ammonium release and phosphate release. These low rates persisted and were significantly ($p < 0.01$) different from the earlier measurements (Fulweiler and Nixon, in press) (Fig. 10). Additional measurements in 2006 continued to show much lower benthic metabolism (Fig. 10). The exchange of nitrate (not shown) remained low and erratic with both uptake and release as observed in the past (Nixon et al., 1976; Fulweiler, 2007). An interesting exception to the marked decline in benthic fluxes was the release of dissolved silica, which remained at historic rates (Fig. 10).

Because of the strong link between primary production in the overlying water and the metabolism of the sediments below (Nixon, 1981; Kelly and Nixon, 1984; Seitzinger and Giblin, 1996; Boynton and Kemp, 2000; Hopkinson and Smith, 2005) it is compelling to attribute these major changes to the decline of phytoplankton biomass and production. But the change in the timing of blooms may be equally (or perhaps even more) important. As Smetacek (1984), Townsend and Cammen (1988), and others pointed out decades ago, the shift from cold water to warm water blooms as the major source of new organic matter in the bay almost certainly means that less of the new production now reaches the benthos. Moreover, as discussed earlier, the nutritional quality of the material deposited during summer and fall, when dissolved inorganic nitrogen is virtually depleted and much of the production is supported by recycled nutrients, is probably much lower (high C/N) than material deposited from a winter bloom. We must say "probably" because for reasons discussed earlier, it is difficult, if not impossible, to make direct measurements on the freshly sedimenting material in this system. As Smetacek (1984, p.

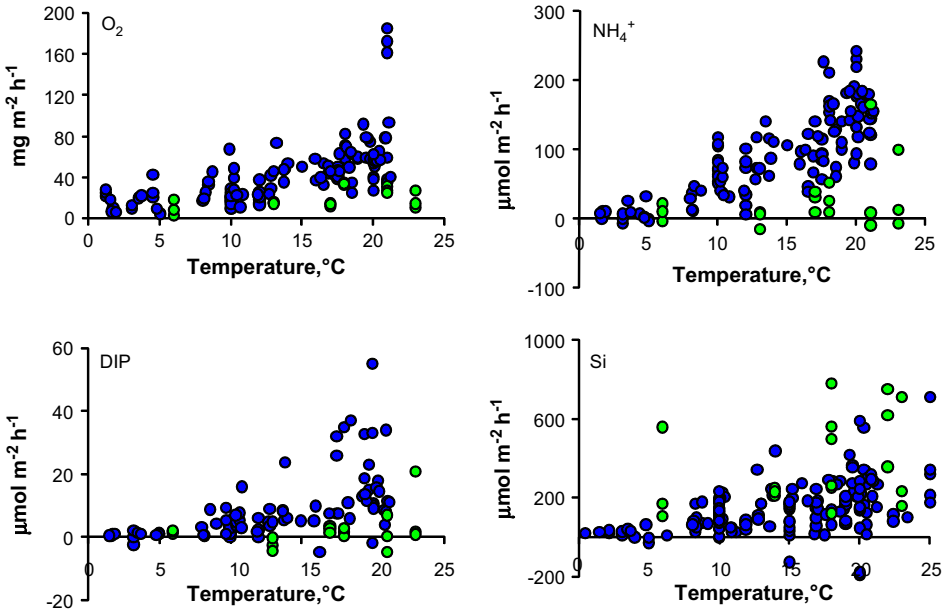

Fig. 10. Net fluxes of dissolved oxygen, ammonium, phosphate, and dissolved silicate across the sediment–water interface in mid Narragansett Bay (see Fig. 2) during the 1970s and 1980s (gray circles) and in 2005 and 2006. Historical data from various sources cited in text and author's unpublished measurements. Oxygen, ammonium, and phosphate fluxes modified and expanded from Fulweiler and Nixon (in press).

533) put it, "The particles sinking out of such [regenerating] systems are truly wastes, i.e. they are composed of refractory material with low essential element content." We noted earlier that the C/N content of the surface (0–2 cm) sediments at the mid bay site appears to have increased since the 1970s. The lack of change in the benthic silica flux is consistent with this interpretation. The warm water pelagic grazers and decomposers have no nutritional need for silica, which falls to the bottom in fecal pellets and/or diatom debris. The return of dissolved silica from the sediments thus remains high. Carbon, nitrogen, and phosphorus, however, are assimilated, respired, mineralized, and recycled in the water column with only a small fraction reaching the benthos.

The N_2 flux measurements that motivated our return to benthic flux work were even more surprising. In 2005, the mean annual rate of denitrification at the mid bay site was significantly ($p < 0.01$) lower than the measurements a quarter of a century earlier (40 $\mu mol\, m^{-2}\, h^{-1}$ compared to 75 $\mu mol\, m^{-2}\, h^{-1}$) (Fulweiler and Nixon, in press). Of course, the methods were quite different so it was hard to know if this apparent change was real. That became clear in the summer of 2006, when we found that bacteria in the sediments were actually fixing large amounts of nitrogen (Fulweiler et al., 2007). This was completely unexpected since deep heterotrophic marine sediments had never been shown to fix N at any significant rate. In fact, a ^{15}N tracer study using mid Narragansett Bay sediments in the mid 1980s showed virtually no or only very low N fixation (Seitzinger and Garber, 1987). With the exception of sea grass rhizospheres, mangroves, and salt marshes, even shallow marine sediments have shown no or very low rates of N fixation (see reviews by Capone, 1983; Howarth et al., 1988). A recent exception, however, is work in Texas estuaries by Gardner et al. (2006) and McCarthy et al. (2008) using MIMS that found high rates of net N fixation at some locations. Since virtually all of the earlier work on N fixation used the acetylene reduction technique (seldom, if ever, calibrated with ^{15}N), it is possible that more direct measurements of net N_2 flux using MIMS will discover that N fixation in heterotrophic marine sediments is more common and important than previously believed.

The switch from net denitrification to net N fixation in the sediments appears to be another consequence of the long decline in the quantity and/or quality of organic input to the bottom of Narragansett Bay. Experimental enrichment of N fixing sediments with spray dried phytoplankton to mimic historical boom depositions quickly reversed the net N_2 flux and returned the sediments to net denitrification (Fulweiler et al., 2007, 2008). While the evidence from measurements made in the summer and fall of 2006 suggests that net N_2 fixation may be confined to warmer temperatures, the summer rates of fixation were sufficiently high (about 200 $\mu mol\, m^{-2}\, h^{-1}$ at the mid bay site) that they made the sediments a net source of N to the bay over the annual cycle amounting to 20–60% of the direct discharge of N to the bay from sewage treatment plants (Fulweiler et al., 2007). The contrast with the situation described by Seitzinger et al. (1984) that we quoted earlier is dramatic. It remains to be seen if net N fixation will come to characterize the sediments of the bay or if the net N_2 flux varies from year-to-year or on shorter time scales with bloom dynamics in the overlying water. January and February of 2008 were marked by a dramatic winter phytoplankton bloom of historic proportions and summer 2008 benthic flux measurements are eagerly anticipated.

3.2.5. *A weaker coupling*

With hindsight, we should have anticipated that the major changes in the water column would have produced large changes in the metabolism of the benthos (as speculated by Keller et al., 1999; Oviatt et al., 2002 for the benthic macro-infauna). But the truth is that until we saw the changes in benthic fluxes we did not look hard at the water column. And when we did, two pieces of evidence came together for the first time. The decline in phytoplankton first reported for cell counts by Smayda (1998) and for chlorophyll by Li and Smayda (1998) covered the periods 1959–1980 and 1973–1990, respectively. While Smayda had continued his weekly monitoring through 1996, the results were not yet generally available. The GSO weekly plankton monitoring program did not begin until 1999. While these data were available on the web site, they had not been put together with the earlier published values. Once we put the

GSO data together with the Li and Smayda (1998) paper, the full extent of the decline became clear (Fulweiler and Nixon, in press; Fulweiler et al., 2007). Now, through the courtesy of T.J. Smayda, we have also been able to include his results for 1991–1996 as well as a breakout of his summer data to be married with the GSO summer data (Fig. 8). We have also been able to assemble the trend in cell counts (Figs. 5 and 7). While there are some procedural differences between the way chlorophyll samples were handled in the Smayda laboratory and in the GSO monitoring program (use of a 1 atm. manifold pump to filter samples vs 50 ml syringes; 5–10 ml sample vs 25 ml sample; goal of 1 month maximum storage of frozen (−20°C) filters vs up to 3 or 4 months on some occasions), it seems unlikely that these would have produced the continuation of the decline (D. Borkman, Smayda Laboratory, GSO, personal communication). And the cell counts should be free of such concerns.

Taken together, the shift in the phenology of phytoplankton blooms, the declining phytoplankton chlorophyll and cell counts at the mid bay station, the marked decline in benthic metabolism, and the switch of net N_2 gas flux across the sediment–water interface that is reversible with organic enrichment provide compelling evidence that benthic–pelagic coupling has changed dramatically in Narragansett Bay. The decline in epibenthic animal biomass during winter is also consistent with this evidence. It seems a great irony that the bay in which so much of the early work was done documenting the strong coupling between the benthos and the water column should now be the place where we see some of the first signs that such coupling may be fundamentally altered.

4. What caused the changes?

The discussion and speculation that follow should be tempered with the perspective that we do not yet have a complete and convincing mechanistic explanation for the timing of the traditional winter–spring bloom, despite decades of research. Smayda (1973, p. 219) made a detailed study of the 1971–1972 bloom and concluded that, "Temperature, light, nutrients, grazing, possibly species interactions, and hydrographic disturbances regulated the seasonal dynamics of *Skeletonema costatum*." A quarter of a century later, and now established as one of the most experienced and respected marine phytoplankton ecologists, he would write (Smayda, 1998, p. 563), "Phytoplankton variability is commonplace and easily detectable, but the limited data on its properties of scale, multiple varieties, different periods, amplitudes and response times, and biological interactions make quantification of cause and effect and predictions problematic." All the complexities that made understanding the historical bloom such a challenge remain to make us humble about our ability to understand its passing. Perhaps it is as Smetacek and Pollehne (1986, p. 425) concluded long ago, "Rather than repeating the same cycle rigidly each year, Nature improvises as she goes along."

4.1. The MERL experiment and the Narragansett Bay model

There are at least two prevailing and related theories, and both may be at least partially correct. The first is that the warming we described in the introduction, especially the winter warming, has increased grazing pressure such that the winter–spring bloom cannot develop, at least during particularly warm years. Oviatt et al. (2002) have shown a weak ($R^2 = 0.32$) inverse correlation between mean weekly chlorophyll over the month of the winter–spring bloom and the mean water temperature during January–March, inclusive. More direct evidence for the importance of grazing comes from a mesocosm experiment using the MERL tanks (Keller et al., 1999). In that study, triplicate tanks were warmed or cooled a few degrees above or below the 1977–1989 Narragansett Bay mean winter temperature such that the average temperature during the December through January experiment was 5.3 or 1.3 °C in the warm and cool tanks, respectively. There were some complications caused by the settlement of large numbers of blue mussels, *Mytilus edulis*, in two of the warm and one of the cool tanks, but the two other cool tanks developed winter phytoplankton blooms while the warm tanks did not and zooplankton biomass was greater in the warmed systems. They also found (p. 351) that, "… warm systems… supplied little freshly sedimented material to the benthos" while cool systems showed "…sedimentation of large amounts of fresh phytodetritus to the benthos."

While the MERL results seem clear, there are two points that are relevant to these results as a complete explanation for events in the bay. First, the 4 °C temperature difference between cool and warm treatments may seem small, but all but one of the 26 winters in the Oviatt et al. (2002) regression fall within this range. In other words, the treatments represented close to the extreme range in winter temperature conditions in the bay over recent decades (Fig. 1). Second, the competing (or perhaps complementary) theory is that lower light in warmer winters (due to increased cloudiness) is an important contributing factor to delays or losses of the winter–spring bloom (Borkman, 2002) (Fig. 11). In this context it may be important that the apparent vertical light attenuation coefficient ($-k$, m^{-1}) of the water in the MERL mesocosms is much higher than in the bay. This is a consequence of the water being contained in an opaque cylinder. The mean k value did not differ between treatments in the warming experiment, but it averaged 1.22 m^{-1} (Keller et al., 1999), far greater than average k values anywhere in the bay (Fig. 4). A reasonable question is whether or not the phytoplankton that could not keep up with the grazing pressure in the warmed MERL tanks might have been able to keep up and even bloom if they had been exposed to more light. The importance of light in initiating the traditional winter–spring bloom in Narragansett Bay has been well established by incubation experiments (Smayda, 1973), analyses of time series field data at the mid bay station (Hitchcock and Smayda, 1977; Nixon et al., 1979) and by microcosm experiments and numerical modeling (Kremer and Nixon, 1978; Nixon et al., 1979).

The belief that grazing may play an important role in limiting the winter–spring bloom in Narragansett Bay is commonly traced to Martin (1966, 1970). But what Martin (1966, p. 67) concluded was,

> "Grazing severely limited the standing crop of this diatom [*Skeletonema*] when primary production was stopped or slowed by inadequate light intensities …"

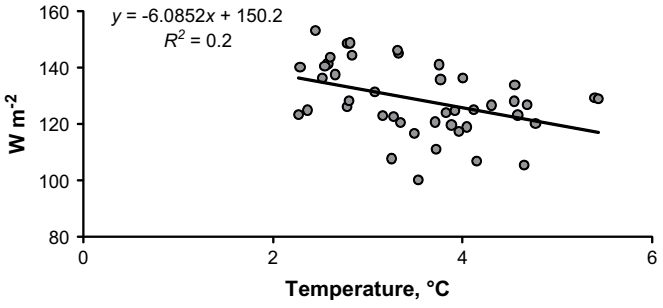

Fig. 11. Irradiance measured by the Eppley Laboratory in Newport, RI and surface water temperature at the long-term plankton monitoring station in the middle West Passage of Narragansett bay (see Fig. 2). Data from 1959 to 1996 from http://www.narrbay.org/d_projects/plankton-tsv/plankton-tsv.htm. Data for 1999 through 2005 from http://www.gso.uri.edu/phytoplankton/ and the Eppley Laboratory. Values are the mean of weekly temperature measurements and hourly light measurements during January through April. Both the intercept ($p < 0.0001$) and the slope ($p = 0.0057$) are significant ($F = 8.51$, $p < 0.0057$).

In other words, zooplankton grazing might be important in terminating the bloom, but not in preventing its initiation if light and nutrients were adequate. In fact, an experimental study of *Skeletonema* growth at low temperatures showed that maximum growth (i.e. with optimum light and nutrients) increased exponentially with temperature between 0 and 10 °C at 12.6% per °C, equivalent to a Q_{10} in this temperature range of 3.5 (Yoder, 1979). This contrasts with the Q_{10} of 1.9 between 4 and 16 °C for instantaneous gut clearance by the dominant winter zooplankton, *Acartia hudsonica* (Wlodarczyk et al., 1992). Since the copepods cannot feed any faster than they can clear their guts, this comparison suggests that if light and nutrients are abundant, *Skeletonema* (presumably *S. japonicum*) will respond to winter warming more positively than the copepods. Based on additional field and laboratory studies, Vargo (1976, p. 118) reached essentially the same conclusion as Martin, "The impact of grazing in regulating the diatom, and specifically the *Skeletonema* population in Narragansett Bay was minimal."

An extreme example of the temperature vs light question with regard to the winter–spring bloom was also explored numerically in the Narragansett Bay ecosystem model (Kremer and Nixon, 1978). Perhaps the strongest features of the model were the elaborate and detailed treatments of the influence of light on phytoplankton growth and the influence of temperature on zooplankton feeding, egg hatching, and the growth rate and development time of juveniles (followed as daily cohorts). One numerical experiment was to eliminate the annual water temperature cycle and run the model as it was normally done (the standard run), but with temperature set at the annual mean of 11.5 °C throughout the year. When this was done, the winter–spring bloom still developed, though a bit earlier than in the standard run. Overall, however, the winter–spring bloom was little altered even by a major winter warming when light was adequate. The reciprocal experiment in which the standard seasonal temperature cycle was used but light was held constant at various levels showed clearly that the timing and magnitude of the winter phytoplankton biomass was very sensitive to light.

4.1.1. Changes in the wind?

While Borkman's (2002) observation that warmer winters tend to be cloudier fits nicely with the field and model analyses documenting the importance of light in initiating the traditional winter–spring bloom, the data shown in Fig. 11 are not completely convincing as a full explanation for the delay and/or elimination of the bloom. A recent analysis of mean wind speed adjacent to the bay during the three windiest months of the year (F,M,A) has shown a much more dramatic decline in recent decades, from about 19 km h^{-1} in the late 1960s and early 1970s to about 15.5 km h^{-1} in the early 2000s (Pilson, 2008). Since the work of the wind in vertical mixing varies roughly as the cube of the speed (Niiler and Kraus, 1977; Husby and Nelson, 1982), this represents about a 45% decline in mixing potential. While the mid and lower bay are usually described as well mixed, especially during winter, such description is based on the fact that there are no or only small differences in the concentrations of various substances (e.g. nutrients, salt, chlorophyll) between near surface and near bottom waters. But the daily history of light exposure experienced by the phytoplankton in such a "well mixed" water column might vary a great deal depending on the wind.

The earlier analyses of field data for the winters of 1972–1973 and 1975 (Hitchcock and Smayda, 1977; Nixon et al., 1979, respectively) found that delayed cloudy winter blooms began when the mean light in the water column exceeded 40 Ly d^{-1} (4.2 J m^{-2} d^{-1}), the same as found by Riley (1967) in his studies of the annual bloom in Long Island Sound. In a rapidly mixed water column, the mean light may be a good description of the light field seen by an average phytoplankton cell. But with slower mixing, perhaps a higher incident light may be required to produce a strong bloom. Thus, there may be an interaction between the decreasing surface light due to increasing cloud cover in warm winters and the decrease in vertical mixing due to declining winter wind speeds. The truth is that we do not really know. As noted by Steemann-Nielsen and Hansen (1959), "It must be made clear at once that in Nature the investigation of the dependence of plankton photosynthesis on light is an extremely intricate problem." More recent evidence that this is still the case is provided by a series of instructive numerical experiments carried out by Lucas et al. (1998) in which the complex interactions of light and mixing on phytoplankton blooms were simulated for south San Francisco Bay, an admittedly very different system in terms of stratification.

4.1.2. Benthic grazers

As the absence of a winter bloom in the cool MERL tank with a dense settlement of blue mussels showed, zooplankton are not the only potential winter grazers in the bay. And the impact of benthic filter feeders is not limited by the relatively long lag time of zooplankton population responses (e.g. Petersen, 2004). The activity of many benthic filter feeders declines or ceases at low temperatures (Gerritsen et al., 1994). For example, the amount of time that the most widespread bivalve in the bay, the quahog or hard clam, *Mercenaria mercenaria*, spends open and filtering declines sharply below 10 °C (Loosanoff, 1939; Kremer and Nixon, 1978). While the blue mussel and the soft clam (*Mya arenaria*, also present in parts of the bay) do continue filtering at rates that decline approximately linearly with declining temperature, at least down to 2 °C (Riisgård, 2004), there is no evidence that their abundance (or that of other suspension feeders) has been increasing regularly over recent decades. On the other hand, it must be recognized that there has been no regular monitoring of such populations in the bay during this time. The depth of the bay may also be sufficient that benthic grazers are unlikely to be responsible for the loss of the winter-spring bloom. This was the conclusion of a detailed modeling study of benthic grazing in (much warmer) Chesapeake Bay for parts of the system that averaged 9 m, essentially the same as the mean depth of Narragansett Bay (Gerritsen et al., 1994).

4.1.3. Light, temperature, and nutrient limitation

It is possible that light limitation, warmer temperatures, and enhanced grazing have worked in concert to produce the changes that have taken place. Both DIN and DSi reach their maximum concentrations in late fall-early winter (Fig. 12). The longer the bloom is delayed by inadequate light, the more DIN and DSi are flushed offshore where concentrations are lower. Until 2004, when advanced wastewater treatment began to be implemented at some treatment plants between May–October, inclusive, the input of DIN to the bay from sewage treatment plants was relatively constant throughout the year. The same is true of direct atmospheric deposition. But the input from rivers varies strongly with river flow (Nixon et al., 1995, 2008). For DSi, of course, river flow is the only significant source. A simple steady-state conservative mixing model using average flushing rates as a function of fresh water inflow (Pilson, 1985) suggests that in the absence of biological uptake, volume-weighted average DIN concentrations in the bay as a whole would range from about 15 μM in January and February to less than 10 μM in all remaining months. Thus the amount of new production supported by the nutrient draw down is reduced by a third for later blooms. In addition, the amount of DIN brought into the bay by rivers also declines from almost 6 mmol m^{-2} d^{-1} in January and February to about 4.6 mmol m^{-2} d^{-1} in March,

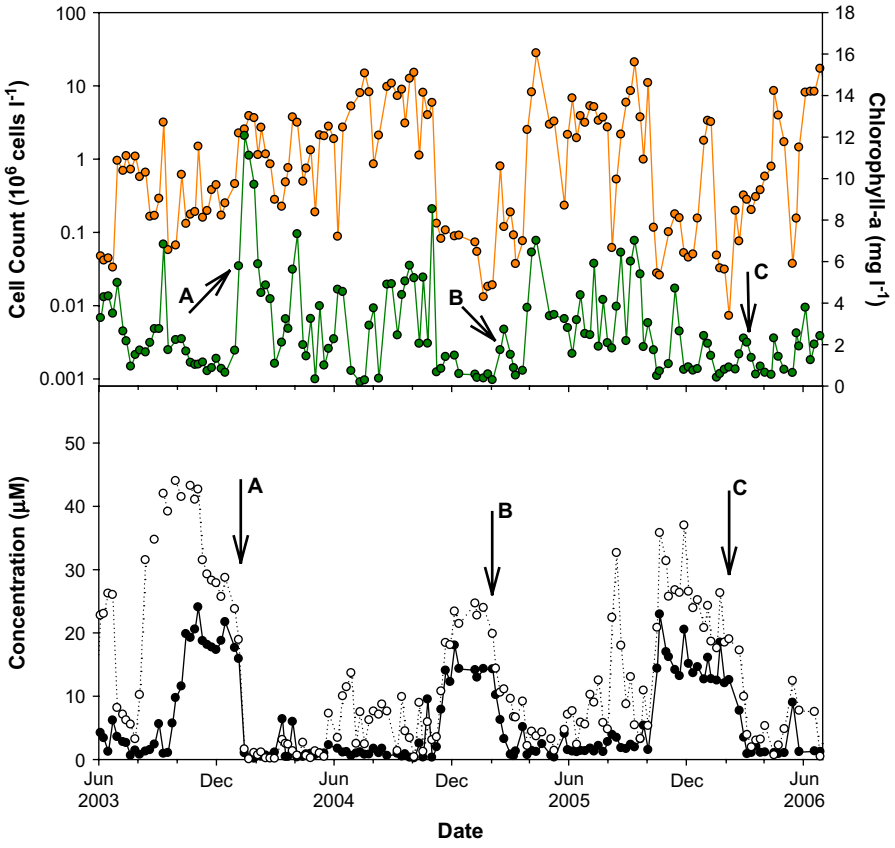

Fig. 12. Approximately biweekly measurements of mean near surface and near bottom chlorophyll *a*, total phytoplankton cell counts, dissolved inorganic nitrogen (DIN), and dissolved silicate (DSi) at the long-term plankton measuring station in the middle West Passage of Narragansett Bay from June 2003 through June 2006. Plankton data from http://www.gso.uri.edu/phytoplankton/. Nutrient data are from our laboratory and available at the same url.

3.7–3.9 mmol m^{-2} d^{-1} in April and May, and 2.7–2.9 mmol m^{-2} d^{-1} in June and July. The combined effect is that nutrient limitation will set in earlier for later blooms, thus exacerbating the impact of higher grazing rates at warmer temperatures.

The loss of the winter–spring bloom deposition appears to reduce the mean standing crop of summer phytoplankton as well (Fig. 8), perhaps because the nutrients formerly stored on the bottom are now flushed offshore. As a result, the flux of ammonium from the sediments is much reduced during summer (Fig. 10) and the summer primary production may have become even more dependent on rapid recycling within the water column than it was in the 1970s (Furnas et al., 1976). Interestingly, the mean concentrations of DIN and DSi in the mid bay during summer appear little changed from conditions during the early 1970s, while reductions in DIP in rivers and sewage treatment plant effluents (Nixon et al., 2008) are reflected in significantly lower DIP concentrations (Table 3). Production in the mid and lower bay during summer was, and remains, strongly nutrient limited. We don't know if the reduction in ammonium fluxes from the sediments is reflected directly in the reduced standing crop of phytoplankton or if the C/N of the phytoplankton has also changed.

The overall impact of the changing phenology on seasonal nutrient cycles also remains unclear. Writing of the 1950s and 1960s, Pratt (1965, p. 181) noted that, "…silicate is usually undetectable during most of the winter and spring and reappears as flowering wanes, attains an annual maximum (often in July)…" The situation is often very different now, with DSi remaining high during much of the winter as in 2005 and 2006 and low during much of the summer (Fig. 12). Some other changes in nutrients probably have little or nothing to do with changes in the ecology of the bay. For example, Pratt (1965) reported that the fall nitrate maximum in the late 1950s and early 1960s seldom exceeded 5 µM while it reached 5–10 µM in mid West Passage by the early 1970s and remains at that level during the fall maximum today. This was almost certainly due to improvements in sewage treatment that raised oxygen levels in the rivers draining to the bay and thus stimulated nitrification of the formerly high ammonium levels in the rivers (Nixon et al., 2008). Phosphate has declined as a result of P removal from detergents and improved sewage treatment (Nixon et al., 2008).

Close comparison of the time course of phytoplankton cell counts, chlorophyll, DIN and DSi at the mid bay station reveals periods of match and mismatch. For example, the winter of 2003/2004 showed sharp declines in DIN and DSi in late December/early January that coincided with rapid increases in chlorophyll and cell counts – the historical pattern (Fig. 12, Arrow A). During the winter of 2005, however, the decline in DIN and DSi was slower, did not

Table 3
Comparison of mean surface water nutrient concentrations (µM ± SD) during summer (J,J,A) in Narragansett Bay near the middle of the West Passage (off Fox Island) in 1972–1973 and in 2003 through 2006. Early data from Kremer and Nixon (St.8) (1978), more recent data from our laboratory http://www.gso.uri.edu/phytoplankton/).

	NH_4^+	NO_{3+2}	DIN	Si	PO_4^{3+}
1972–1973, $N=7$	0.13 ± 0.13	0.30 ± 0.53	0.43	15.5 ± 10.9	1.69 ± 0.59
2003, $N=13$	1.16 ± 1.29	0.71 ± 0.86	1.87	17.5 ± 16.3	0.65 ± 0.54
2004, $N=12$	0.83 ± 0.40	0.12 ± 0.08	0.95	5.4 ± 3.5	0.76 ± 0.30
2005, $N=13$	0.70 ± 0.45	0.55 ± 0.24	1.25	10.1 ± 12.5	0.58 ± 0.32
2006, $N=10$	0.65 ± 0.55	0.28 ± 0.18	0.93	10.6 ± 14.0	0.60 ± 0.43

take place until late January and February, and was accompanied by only a modest increase in chlorophyll compared with cell counts (Fig. 12, Arrow B). This was repeated in winter 2006 when cell counts increased strongly with nutrient declines in late winter but chlorophyll showed little response (Fig. 12, Arrow C). The stoichiometry of the chlorophyll response is also of concern, though we recognize that N:C:Chl ratios are quite variable depending on species composition, nutritional status, etc. For example, a 15 μM drop in DIN due to phytoplankton uptake should support about 1200 μg of C fixation. Based on the extensive review by Cloern et al. (1995), over 80% of C:Chl ratios of light-limited phytoplankton fall between 20 and 60 (Brush et al., 2002), thus suggesting a chlorophyll increase of 20–60 mg m^{-3} compared with the observed increases of 2–6 mg m^{-3} in 2005 and 2006 (Fig. 12). Of course, some of the chlorophyll is lost to grazing, sinking, and flushing, but the discrepancy is still disconcerting. The magnitude of the cell count increases associated with the DIN uptake seems more in line with expectations. Assuming that the blooms were largely *Skeletonema*, fixation of 1200 μg of C might yield an increase of about 13 million cells per liter (Parsons and Takahashi, 1973, p. 39), a response roughly consistent with the observations (Fig. 12).

4.1.4. The speed of benthic responses

Regardless of what is ultimately shown to have been the cause(s) for the remarkable changes observed in Narragansett Bay, the response time of benthic–pelagic coupling has probably been rapid. While ^{14}C labeled organic additions in the MERL mesocosms have shown that there may be time lags of several months between deposition and remineralization of the winter–spring bloom (Rudnick and Oviatt, 1986), annual mass balance calculations have shown that only a small amount (perhaps 5–10%) of the primary production and allocthonous organic carbon accumulates in the sediments over an annual cycle (Nixon et al., 1995). Shorter term studies of the remineralization of ^{15}N labeled organic matter in sediment cores have suggested that the half life of detrital N landing on the sediment surface is on the order of 1–2 months in the spring (8 °C) and 2–3 weeks in the fall (16 °C) (Garber, 1982). Similar ^{14}C labeled deposition studies by O'Reilly (1984) also suggested that 95% of added organic matter would be remineralized within 4–8 months at 10 °C. Additional deposition experiments with cores at 15 °C showed that over 80% of organic matter deposited on the bottom was remineralized over an annual cycle and that benthic metabolism responded very rapidly (a few days) to organic additions at 15 °C (Kelly and Nixon, 1984). Taken together with the experiments showing that the net flux of N_2 gas across the sediment–water interface can switch from net denitrification in one summer to net fixation in the next, and that organic additions can reverse the net flux from fixation to denitrification in a matter of a few days (Fulweiler et al., 2007, 2008), this body of evidence suggests that the strength of benthic–pelagic coupling in the bay may vary markedly from year to year and, perhaps, from month to month.

4.1.5. A legacy effect?

The situation in Narragansett Bay may be particularly interesting with regard to the net N_2 flux between the water and the sediments because of the bay's long history of intensive fertilization with anthropogenic nitrogen. As an urban estuary, the bay has been a highly productive phytoplankton-based system for well over a century (Nixon et al., 2008). While the prehistoric bay may also have been highly productive, much of that production was probably provided by sea grasses, kelp beds, and epibenthic algae in the shallows (Nixon, 1997; Nixon et al., 2008). The distribution and accumulation of organic matter in the sediments from these sources would have been quite different from the pattern that emerged with the switch to dense phytoplankton blooms in the upper bay in the late 1800s (Nixon, 1989, Fig. 3). If the changing climate and changing phenology of blooms has meant that less good quality (lower C/N) organic matter has been reaching the sediments during the past few decades, the long legacy of relatively high C/N organic matter accumulated in the sediments may now provide a substrate in which N fixing bacteria are at an advantage over denitrifiers. If so, the bay may now be in a delicate balance – in cold, clear winters a rich winter–spring bloom results in a large amount of high quality organic matter reaching the bottom, thus stimulating benthic secondary production, sustaining higher summer nutrient regeneration, higher new production by the summer phytoplankton, and some nitrogen removal in the sediments. Perhaps this also happens following some intense blooms in the summer associated with episodic storm inputs of nitrogen. On the other hand, increasingly warm and cloudy winters may lead to reduced new production, less organic deposition, and, perhaps, net N fixation by the sediments in summer. It is too soon to know if the latter is a recurrent phenomenon.

5. What next?

The great question for scientists and managers alike is what will happen over the next few years as a large, politically mandated reduction in N inputs to Narragansett Bay from sewage treatment plants during warmer months is fully implemented. Since the city of Providence, the largest source of sewage N at the head of the bay, will also be treating its storm water runoff for N removal between May and October, even episodic DIN inputs will be reduced during the warm months. How will this management intervention interact with the changing phenology of the bay? The climate-induced oligotrophication of the mid bay may have gone as far as it can go, at least in terms of new production during years with warm, cloudy winters (Figs. 7 and 8). Most of the summer DIN input from land appears to have been taken up in the Providence River estuary and the Upper Bay even when anthropogenic inputs were high (Fig. 3, Kremer and Nixon, 1978; Oviatt et al., 2002; Smayda and Borkman, 2008). In the future virtually none of the DIN from land may reach the West and East Passages. If there is little or no winter–spring storage of N on the bottom of the mid and lower bay, summer new production there may be largely a function of DIN inputs from Rhode Island Sound. While this is an inexhaustible source, DIN concentrations in surface water there are also very low during summer, so the net input must be small. Total ^{14}C uptake will probably continue to be supported by rapid recycling in the water column, but food for the benthos may be in very short supply.

5.1. Linking upper bay primary production and lower bay secondary production

The reduction of N in sewage discharged to the rivers draining into the bay and directly to the upper bay will almost certainly have the intended effect of reducing primary production and algal biomass in the estuaries and Upper Bay and probably reduce summer hypoxia in those areas. But what will be the impact of that loss of primary production on the rest of the bay? How important has the anthropogenically stimulated primary production at the head of the bay become to secondary production, especially the production of benthic animals, in the rest of Narragansett Bay? Recent extensive measurements of the stable isotopes of N (^{15}N and ^{14}N) in hard clams throughout the bay showed that the animals all appear to be living in large part on phytoplankton who's growth has been supported by heavy anthropogenic N in the Providence River estuary and Upper Bay (Oczkowski et al., 2008). While N taken up in the estuary and Upper Bay might support the growth of the

phytoplankton as they are carried some way down the bay as shown by York et al. (2007) in Waquoit Bay on Cape Cod, it is also possible that phytoplankton sinking out of the surface waters in the upper bay might be delivered to the benthos of the mid and lower bay. For those used to thinking of classic estuarine circulation this might seem surprising. However, recent numerical modeling and observational ADCP data have shown that under different wind conditions there is a net flow of bottom water from the upper to the lower bay through either the West or the East Passage (Rogers, 2008). This may begin to explain why age specific growth rates of the hard clams have not uniformly changed throughout the bay from rates measured half a century ago despite the decline in mid bay phytoplankton (Henry and Nixon, 2008). While growth rates of juvenile clams (<2 years) have decreased, adults actually appear to have been able to take advantage of the warming temperatures and/or changing phenology (more diatoms in summer) to increase their growth rates (Henry and Nixon, 2008). If this food source is significantly reduced and the transport of DIN from the upper bay to the mid and lower bay is virtually eliminated, most of the secondary production in the bay will have to be supported by the already much reduced new production in the mid and lower bay.

An optimistic prediction might be that summer N_2 fixation will add enough N to the mid and lower bay that new production there will be enhanced while hypoxia will be improved in the much more stratified Upper Bay and Providence River estuary. Given the large storage of high C/N organic matter in the bay's sediments, high rates of net N_2 fixation might continue for a long time. It might become a future much like the distant past, with clearer waters in the shallower upper parts of the bay and estuary allowing some regrowth of eelgrass and more epibenthic algae. N_2 fixation in eelgrass beds and by photosynthetic bacteria in the shallower sediments might be complemented with heterotrophic N_2 fixation in the deeper carbon-rich sediments. The biologically fixed N might ultimately be excreted into the overlying water to support phytoplankton production in the mid and lower bay. We might create a bay without the steep gradients in phytoplankton primary production and chlorophyll that have probably characterized the past century or more, but with equal or higher overall secondary production. The best of both worlds. On the other hand, the marine N cycle in general, and in Narragansett Bay in particular, has proven to be more complicated and interesting than we thought it was only a decade ago. And the biogeochemical cycling of this critical limiting nutrient in this bay is embedded in an ecosystem that has been changing dramatically in response to changing climate and other anthropogenic pressures. We should expect further surprises and watch closely.

5.2. Scaling up

It is reasonable to ask if other estuaries and bays in this area are experiencing changes similar to those observed here. Summer primary productivity and phytoplankton blooms have declined in nearby Boston Harbor, but that is due to large-scale sewage diversion (Libby et al., 2007). Benthic metabolism has also declined in the harbor (Tucker et al., 2008). More intriguing are widespread declines in the abundance of diatoms (but not total phytoplankton) and copepods in Massachusetts Bay and Cape Cod Bay from 1992 through 2006 (Libby et al., 2007). However, there appears to have been no statistically significant change in primary production by the phytoplankton in Massachusetts Bay during that time (Oviatt et al., 2007), and benthic oxygen uptake and nutrient regeneration (with the exception of DSi) have not declined (Tucker et al., 2008). South of Cape Cod, water column chlorophyll declined significantly between 1987 and at least 1998 in Buzzards Bay, about 45 km east of Narragansett Bay (Turner et al. in press Phytoplankton chlorophyll has also declined markedly in Peconic Bay at the eastern end of Long Island, but this appears to be a response to a decline in nitrogen concentrations (Suffolk County Department of Health Services, 2007). Narragansett Bay is unique in this region in the long time series of phytoplankton data and benthic metabolism measurements and in its relative stability of nutrient inputs during recent decades (Nixon et al., 2008). These circumstances may have come together to allow us to observe a development that would not be apparent in many other coastal areas. After an extensive review of phytoplankton bloom dynamics in coastal marine systems around the world, Cloern and Jassby (2008) concluded, "…our synthesis shows that the timing and amplitude of phytoplankton variability usually do not follow recurrent and spatially synchronous seasonal patterns in nearshore coastal waters where variability tied to large-scale climate can be overwhelmed by local processes."

Those of us who study Narragansett Bay are not used to drawing parallels between our small, shallow, urban estuary and much larger continental shelf systems like the Bering Sea or the North Sea. But it is almost eerie to read the account of changes taking place in the northern Bering Sea given by Grebmeier et al. (2006). They, too, report warming waters, a reduced flux of carbon to the bottom, declining benthic oxygen uptake rates, declining benthic populations, an increase in pelagic compared to demersal fish, and an overall weakening of what was "tight pelagic–benthic coupling" in the late 1980s. In the North Sea, too, recent work has shown that climate-induced changes in the benthos can propagate through pelagic food chains from phytoplankton to fish and fundamentally alter benthic–pelagic coupling (Kirby et al., 2007). In fact, there is a renewed appreciation for the "tight trophic coupling" demonstrated in the pelagic ecosystems of the Northeast Atlantic that may make them particularly sensitive to climate changes (Richardson and Schoeman, 2004). A recent review of data from chlorophyll through copepods to cod in the North Atlantic found that the greatest susceptibility to warming appeared to be in areas where the mean annual temperature lay between 9 and 12 °C, with a maximum between 9 and 10 °C (Beaugrand et al., 2008). The coastal waters off southern New England south of Cape Cod averaged about 10.5 °C from the late 1800s until recent warming from the 1970s and reached 11.9 °C during the 1990s (Nixon et al., 2004).

Of course, there are important differences and complications in comparing these much larger systems with Narragansett Bay – for example, the loss of sea ice is probably not an important factor here and predation by diving sea ducks and marine mammals has not so far attracted much attention. But the atmospheric and hydrographic forcings which seem to be responsible for dramatic ecosystem changes in the northern Bering Sea and the north Atlantic may, like the smaller scale changes here, be ultimately linked to global warming and its associated climate changes. That such large changes in marine ecosystems of such a wide range of scale may be due to secular changes that appear small relative to interannual variation is a sobering observation and an important caution.

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References

Anderson, N., Jeppesen, E., Soendergaard, M., 2005. Ecological effects of reduced nutrient loading (oligotrophication) on lakes: an introduction. Freshwater Biology 50, 1589–1593.

Bering Sea Interagency Working Group, 2006. Climate Change and the Bering Sea Ecosystem. Alaska Fisheries Science Center Processed Report 2006-01, Seattle, WA, 30 pp. Available from: http://www.afsc.noaa.gov/Publications/ProcRpt06.htm.

Beaugrand, G., Edwards, M., Brander, K., Luczak, C., Ibanez, F., 2008. Causes and projections of abrupt climate-driven ecosystem shifts in the North Atlantic. Ecology Letters 11, 1157–1168.

Borkman, D., 2002. Analysis and Simulation of *Skeletonema costatum* (Grev.) Clev Annual Abundance Patterns in Lower Narragansett Bay 1959 to 1996. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 395 pp.

Borkman, D., Smayda, T., 2009. Multidecadal (1959–1997) changes in Skeletonema abundance and seasonal bloom patterns in Narragansett Bay, Rhode Island, USA. Journal of Sea Research 61, 84–94.

Boynton, W., Kemp, M., 2000. Influence of river flow and nutrient loads on selected ecosystem processes – a synthesis of Chesapeake Bay data. In: Hobbie, J. (Ed.), Estuarine Science-a Synthetic Approach to Research and Practice. Island Press, Washington, DC, pp. 269–298.

Bradley, M., Raposa, K., Tuxbury, S., 2007. Report on the Analysis of True Color Aerial Photography to Map and Inventory *Zostera marina* L. in Narragansett Bay and Block Island Sound. University of Rhode Island Environmental Data Center, Narragansett Bay National Estuarine Research Reserve, Save the Bay, 16 pp.

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

Buckley, L., Collie, J., Kaplan, A., Crivello, J., 2008. Winter flounder larval genetic population structure in Narragansett Bay, RI: recruitment to juvenile young-of-the-year. Estuaries and Coasts 31, 745–754.

Calabretta, C., Ovaitt, C., 2008. The response of benthic macrofauna to anthropogenic stress in Narragansett Bay, Rhode Island: a review of human stressors and assessment of community conditions. Marine Pollution Bulletin 56, 1680–1695.

Capone, D., 1983. Benthic nitrogen fixation. In: Carpenter, E., Capone, D. (Eds.), Nitrogen in the Marine Environment. Academic Press, New York, pp. 105–137.

Carstensen, J., Conley, D., Andersen, J., Ærtebjerg, G., 2006. Coastal eutrophication and trend reversal: a Danish case study. Limnology and Oceanography 51, 398–408.

Chaves, J., 2004. Potential Use of ^{15}N to Assess Nitrogen Sources and Fate in Narragansett Bay. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 113 pp.

Chinman, R., Nixon, S., 1985. Depth–Area–Volume Relationships in Narragansett Bay. RI Sea Grant Marine Technical Report 87. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 64 pp.

Cloern, J., Jassby, A., 2008. Complex seasonal patterns of primary producers at the land–sea interface. Available from: Ecology Letters http://www3.interscience.wiley.com/journal/119877643/issue.

Cloern, J., Grenz, C., Vidergar-Lucas, L., 1995. An empirical model of the Phytoplankton chlorophyll:carbon ratio – the conversion factor between productivity and growth rate. Limnology and Oceanography 40, 1313–1321.

Collie, J., Wood, A., Jeffries, H., 2008. Long-term data reveal climate forcing of coastal fish community structure. Canadian Journal of Fisheries and Aquatic Sciences 65, 1352–1365.

Costello, J., Sullivan, B., Gifford, D., 2006. A physical–biological interaction underlying variable phonological responses to climate change by coastal zooplankton. Journal of Plankton Research 28, 1099–1105.

Deacutis, C., Murray, D., Prell, W., Saarman, E., Korhun, L., 2006. Hypoxia in the upper half of Narragansett Bay, RI, during August 2001 and 2002. Northeastern Naturalist 13, 173–198.

Deason, E., 1980. Grazing of *Acartia hudsonica (A. clausi)* on *Skeletonema* in Narragansett Bay (USA): influence of food concentration and temperature. Marine Biology 60, 101–113.

Desbonnet, A., Costa-Pierce, B. (Eds.), 2008. Science for Ecosystem-based Management – Narragansett Bay in the 21st Century. Springer Verlag, New York, p. 570.

Doering, P., Oviatt, C., 1986. Application of filtration rate models to field populations of bivalves: an assessment using experimental mesocosms. Marine Ecology Progress Series 31, 265–275.

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

Durbin, A., Durbin, E., 1981. Standing stock and estimated production rates of phytoplankton and zooplankton in Narragansett Bay, Rhode Island. Estuaries 4, 24–41.

Durbin, A., Durbin, E., 1988. Zooplankton and Ichthyoplankton in Narragansett Bay: Status and Trends. Part 1: Zooplankton. Final Report to the New England Interstate Water Pollution Control Commission for the Narragansett Bay Project. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI.

Durbin, E., Krawiec, R., Smayda, T., 1975. Seasonal studies on the relative importance of different size fractions of phytoplankton in Narragansett Bay (USA). Marine Biology 32, 271–287.

Dwyer, R., 1980. Frequency Domain Studies of the Dynamics of an Estuarine Ecosystem. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 158 pp.

Edwards, M., Richardson, A., 2004. Impact of climate change on marine phenology and trophic mismatch. Nature 430, 881–884.

Eyre, B., Rysgaard, S., Dalsgaard, T., Christensen, P., 2002. Comparison of isotope pairing and N_2:Ar methods for measuring sediment denitrification – assumptions, modifications, implications. Estuaries 25, 1077–1087.

Ferrara, R., 1953. Phytoplankton Studies in Upper Narragansett Bay. MS thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 62 pp.

Fish, C., 1925. Seasonal distribution of the plankton of the Woods Hole region. Bulletin of the United States Bureau of Fisheries XLI, 91–175.

Frithsen, J., 1984. Metal incorporation by benthic fauna: relationships to sediment inventory. Estuarine, Coastal and Shelf Science 19, 523–539.

Frithsen, J., 1989. The Benthic Communities Within Narragansett Bay. Final Report to The Narragansett Bay Project, RI Dept. of Environmental Management, Providence, RI. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 92 pp.

Fulweiler, R., 2007. The Impact of Climate Change on Benthic–Pelagic Coupling and the Biogeochemical Cycling of Narragansett Bay, RI. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 250 pp.

Fulweiler, R., Nixon, S. Responses of benthic–pelagic coupling to climate change in a temperate estuary. Hydrobiologia, in press.

Fulweiler, R., Nixon, S., Buckley, B., Granger, S., 2007. Reversal of the net dinitrogen gas flux in coastal marine sediments. Nature 448, 180–182.

Fulweiler, R., Nixon, S., Buckley, B., Granger, S., 2008. Net sediment N_2 fluxes in a coastal marine system – experimental manipulations and a conceptual model. Ecosystems, 1168–1180.

Furnas, M., Hitchcock, G., Smayda, T., 1976. Nutrient-phytoplankton relationships in Narragansett Bay during the 1974 summer bloom. In: Wiley, M. (Ed.), Estuarine Processes, vol. 1. Academic Press, NY, pp. 118–133.

Garber, J., 1982. ^{15}N Tracer and Other Laboratory Studies of Nitrogen Mineralization in Sediments and Waters from Narragansett Bay, Rhode Island. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 276 pp.

Gardner, W., McCarthy, M., An, S., Sobolev, D., Sell, K., Brock, D., 2006. Nitrogen fixation and dissimilatory nitrate reduction to ammonium (DNRA) support nitrogen dynamics in Texas estuaries. Limnology and Oceanography 51, 558–568.

Gearing, J., Gearing, P., Rudnick, D., Requejo, A., Hutchins, M., 1984. The isotopic variability of organic carbon in a phytoplankton-based temperate estuary. Geochemica et Cosmochemica Acta 48, 1089–1098.

Gerritsen, J., Holland, A., Irvine, D., 1994. Suspension-feeding bivalves and the fate of primary production: an estuarine model applied to Chesapeake Bay. Estuaries 17, 403–416.

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

Grebmeier, J., Overland, J., Moore, S., Farley, E., Carmack, E., Cooper, L., Frey, K., Helle, J., McLaughlin, F., McNutt, S., 2006. A major ecosystem shift in the northern Bering Sea. Science 311, 1461–1464.

Greening, H., Janicli, A., 2006. Toward reversal of eutrophic conditions in a subtropical estuary: water quality and seagrass response to nitrogen loading reductions in Tampa Bay, Florida, USA. Environmental Management 38, 163–178.

Greve, W., Prinage, S., Zidowitz, H., Nast, J., Reiners, F., 2005. On the phenology of North Sea icthyoplankton. ICES Journal of Marine Science 62, 1216–1223.

Hale, S., 1974. The Role of Benthic Communities in the Nutrient Cycles of Narragansett Bay. MS thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 123 pp.

Hale, S., 1975. The role of benthic communities in the nitrogen and phosphorus cycles of an estuary. In: Howell, F., Gentry, J., Smith, M. (Eds.), Mineral Cycling in Southeastern Ecosystems. US Energy Research and Development Administration CONF-740513, pp. 291–308.

Henry, K., Nixon, S., 2008. A half century assessment of hard clam, *Mercenaria mercenaria*, growth in Narragansett Bay, Rhode Island. Estuaries and Coasts, 31, 755–766.

Hicks, S., 1959. The physical oceanography of Narragansett Bay. Limnology and Oceanography 4, 316–327.

Hitchcock, G., Smayda, T., 1977. The importance of light in the initiation of the 1972–1973 winter–spring bloom in Narragansett Bay. Limnology and Oceanography 22, 126–131.

Hopkinson, C., Smith, E., 2005. Estuarine respiration: an overview of benthic, pelagic, and whole system respiration. Oxford. In: del Giorgio, P., Williams, P. (Eds.), Respiration in Aquatic Ecosystems, pp. 122–146.
Howarth, R., Marino, R., Lane, J., Cole, J., 1988. Nitrogen fixation in freshwater, estuarine, and marine ecosystems. Limnology and Oceanography 33, 669–687.
Husby, D., Nelson, C., 1982. Turbulence and vertical stability in the California Current. CalCOFI Report 23, 113–129.
Iverson, R., 1990. Control of marine fish production. Limnology and Oceanography 35, 1593–1604.
Jeffries, H., 2001. Rhode Island's ever changing Narragansett Bay. Maritimes 41, 1–5.
Jeffries, H., Terceiro, M., 1985. Cycle of changing abundances in the fishes of the Narragansett Bay area. Marine Ecology Progress Series 25, 239–244.
Jeffries, P., Hale, S., Keller, A., 1989. Historical Data Assessment – Finfishes of the Narragansett Bay Area. Final Report to the Narragansett Bay Project, RI Dept. of Environmental Management, Providence, RI. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 407 pp.
Jossi, J., John, A., Sameoto, D., 2003. Continuous plankton recorder sampling off the east coast of North America: history and status. Progress in Oceanography 58, 313–325.
Kana, T., Darkangelo, C., Munt, M., Oldham, J., Bennett, E., Cornwell, J., 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.
Kana, T., Sullivan, M., Cornwell, J., Groskowski, K., 1998. Denitrification in estuarine sediments determined by membrane inlet mass spectrometry. Limnology and Oceanography 43, 334–339.
Karentz, D., Smayda, T., 1984. Temperature and the seasonal occurrence pattern of 30 dominant phytoplankton species in Narragansett bay over a 22-year period (1959–1980. Marine Ecology Progress Series 18, 277–293.
Karentz, D., Smayda, T., 1998. Temporal patterns and variations in phytoplankton community organization and abundance in Narragansett Bay during 1959–1980. Journal of Plankton Research 20, 145–168.
Keller, A., 1988. Estimating phytoplankton productivity from light availability and biomass in the MERL mesocosms and Narragansett Bay. Marine Ecology Progress Series 45, 159–168.
Keller, A., Riebesell, U., 1989. Phytoplankton carbon dynamics during a winter–spring bloom in an enclosed marine ecosystem: primary productivity, biomass and loss rates. Marine Biology 103, 131–142.
Keller, A., Frithsen, J., Oviatt, C., Maughan, J., Sullivan, B., Nixon, S., Pilson, M., 1987. Marine Ecosystem Responses to Sewage Sludge and Inorganic Nutrient Additions: a Mesocosm Experiment Data Report. MERL Series, Report No. 6. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 237 pp.
Keller, A., Oviatt, C., Walker, H., Hawk, J., 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., 1983. Benthic–Pelagic Coupling in Narragansett Bay. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 195 pp.
Kelly, J., Nixon, S., 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.
Kelly, J., Berounsky, V., Nixon, S., Oviatt, C., 1985. Benthic-pelagic coupling and nutrient cycling across an experimental eutrophication gradient. Marine Ecology Progress Series 26, 207–219.
Kirby, R., Beaugrand, G., Lindley, J., Richardson, A., Edwards, M., Reid, P., 2007. Climate effects and benthic–pelagic coupling in the North Sea. Marine Ecology Progress Series 330, 31–38.
Kooistra, W., Sarno, D., Balzano, S., Gu, H., Andersen, R., Zingone, A., 2008. Global diversity and biogeography of *Skeletonema* species (Bacillariophyta). Protist 159, 177–193.
Kremer, J., Nixon, S., 1978. A Coastal Marine Ecosystem-Simulation and Analysis. In: Ecological Studies 24. Springer Verlag, NY, 217 pp.
Levin, L., 1986. Effects of enrichment on reproduction in the opportunistic polychaete *Streblospio benedicti* (Webster): a mesocosm study. Biological Bulletin 171, 143–160.
Li, Y., Smayda, T., 1998. Temporal variability of chlorophyll in Narragansett Bay, 1973–1990. ICES Journal of Marine Science 55, 661–667.
Libby, S., Borkman, D., Geyer, R., Keller, A., Mansfield, A., Turner, J., Anderson, D., Oviatt, C., Hyde, K., 2007. Water Column Monitoring in Massachusetts Bay: 1992–2006. Massachusetts Water Resources Authority Report ENQUAD 2007 – 11. Boston, 228 pp.
Loosanoff, V., 1939. Effect of temperature upon shell movements of clams, *Venus mercenaria* (L). Biological Bulletin 76, 171–182.
Lucas, L., Cloern, J., Koseff, J., Monismith, S., Thompson, J., 1998. Does the Sverdurp critical depth model explain bloom dynamics in estuaries? Journal of Marine Research 56, 375–415.
MacIntyre, H., Geider, R., Miller, D., 1996. Microphytobenthos: the ecological role of the "secret garden" of unvegitated shallow – water habitats. I Distribution, abundance and primary production. Estuaries 19, 186–201.
Martin, J., 1966. Phytoplankton–Zooplankton Relationships in Narragansett Bay II: the Seasonal Importance of Zooplankton Grazing and Nutrient Excretion. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 99 pp.
Martin, J., 1970. Phytoplankton–zooplankton relationships in Narragansett Bay. IV. The seasonal importance of grazing. Limnology and Oceanography 15, 412–418.
McCaffrey, R., Myers, A., Morrison, G., Bender, M., Ludtke, N., Cullen, D., Froelich, P., Klinkhammer, G., 1980. The relation between pore water chemistry and benthic fluxes of nutrients and manganese in Narragansett Bay, Rhode Island. Limnology and Oceanography 25, 31–44.
McCarthy, M., McNeal, K., Morse, J., Gardner, W., 2008. Bottom-water hypoxia effects on sediment–water interface nitrogen transformations in a seasonally hypoxic shallow bay (Corpus Christi May, TX, USA). Estuaries and Coasts 31, 521–531.
Melrose, D., Oviatt, C., Berman, M., 2007. Hypoxic events in Narragansett Bay during the summer of 2001. Estuaries and Coasts 30, 47–53.
Nay, J., 1996. Oligotrophication and its discontents: effects of reduced nutrient loading on reservoir fisheries. American Fisheries Society Symposium 16, 285–295.
Niiler, P.P., Kraus, E., 1977. One-dimensional models of the upper ocean. In: Krauss, E. (Ed.), Modelling and Prediction of the Upper Layers of the Ocean. Pergamon Press, NY, pp. 1443–1472.
Nixon, S., 1981. Remineralization and nutrient cycling in coastal marine ecosystems. In: Neilson, B., Cronin, L. (Eds.), Estuaries and Nutrients. Humana Press, Clifton, NJ, pp. 111–138.
Nixon, S., 1988. Physical energy inputs and the ecology of lake and marine ecosystems. Limnology and Oceanography 33, 1005–1025.
Nixon, S., 1989. An extraordinary red tide and fish kill in Narragansett Bay. In: Cosper, E., Bricelj, E., Carpenter, E. (Eds.), Novel Phytoplankton Blooms. Springer, NY, pp. 429–447.
Nixon, S., 1995. Coastal marine eutrophication: a definition, social causes, and future concerns. Ophelia 41, 199–219.
Nixon, S., 1997. Prehistoric nutrient inputs and productivity in Narragansett Bay. Estuaries 20, 253–261.
Nixon, S. Eutrophication and the macroscope. Hydrobiologia, in press.
Nixon, S., Pilson, M., 1984. Estuarine total system metabolism and organic exchange calculated from nutrient ratios: an example from Narragansett Bay. In: Kennedy, V. (Ed.), The Estuary as a Filter. Academic Press, NY, pp. 261–290.
Nixon, S., Oviatt, C., Hale, S., 1976. Nitrogen regeneration and the metabolism of coastal marine bottom communities. In: Anderson, J., Macfadyen, A. (Eds.), The Role of Terrestrial and Aquatic Organisms in Decomposition Processes. Blackwell, London, pp. 269–283.
Nixon, S., Oviatt, C., Kremer, J., Perez, K., 1979. The use of numerical models and laboratory microcosms in estuarine ecosystem analysis- simulations of a winter phytoplankton bloom. In: Dame, R. (Ed.), Marsh-Estuarine Systems Simulation. University of South Carolina Press, Columbia, SC, pp. 165–188.
Nixon, S., Kelly, J., Furnas, B., Oviatt, C., Hale, S., 1980. Phosphorus regeneration and the metabolism of coastal marine bottom communities. In: Tenore, K., Coull, B. (Eds.), Marine Benthic Dynamics. University of South Carolina Press, Columbia, SC, pp. 219–242.
Nixon, S., Pilson, M., Oviatt, C., Donaghay, P., Sullivan, B., Seitzinger, S., Rudnick, D., Frithsen, J., 1984. Eutrophication of a coastal marine ecosystem – an experimental study using the MERL microcosms. In: Fasham, M. (Ed.), Flows of Energy and Materials in Marine Ecosystems: Theory and Practice. Plenum Press, NY, pp. 105–135.
Nixon, S., Granger, S., Nowicki, B., 1995. An assessment of the annual mass balance of carbon, nitrogen, and phosphorus in Narragansett Bay. Biogeochemistry 31, 15–61.
Nixon, S., Granger, S., Buckley, B., 2003. The warming of Narragansett Bay. University of Rhode Island. 41°N, The Magazine of the RI Sea Grant and Land Grant Programs 2, 18–20. http://seagrant.gso.uri.edu/41N/vol2No1/baywarming.html.
Nixon, S., Granger, S., Buckley, B., Lamont, M., Rowell, B., 2004. A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts. Estuaries 27, 397–404.
Nixon, S., Buckley, B., Granger, S., Harris, L., Oczkowski, A., Cole, L., Fulweiler, R., 2005. Anthropogenic Nutrient Inputs to Narragansett Bay – a Twenty-Five year perspective. Final Report to the Narragansett Bay Commission and RI Sea Grant. Granduate School of Oceanography, University of Rhode Island, Narragansett, RI, 50 pp.
Nixon, S., Buckley, B., Granger, S., Harris, L., Oczkowski, A., Fulweiler, R., Cole, L., 2008. Nitrogen and phosphorus inputs to Narragansett Bay: past, present, and future. In: Desbonnet, A., Costa-Pierce, B. (Eds.), Science for Ecosystem-based Management, Narragansett Bay in the 21st Century. Springer, NY, pp. 101–175.
Nowicki, B., 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., Gold, A., 2008. Groundwater nitrogen transport and input along the Narragansett bay coastal margin. In: Desbonnet, A., Costa-Pierce, B. (Eds.), Science for Ecosystem-based Management: Narragansett Bay in the 21st Century. Springer, NY, pp. 67–100.
Nowicki, B., Nixon, S., 1985. Benthic community metabolism in a coastal lagoon ecosystem. Marine Ecology Progress Series 22, 21–30.
Oczkowski, A., Nixon, S., Henry, K., DiMilla, P., Pilson, M., Granger, S., Buckley, B., Thornber, C., McKinney, R., Chaves, J., 2008. Distribution and trophic importance of anthropogenic nitrogen in Narragansett Bay: an assessment using stable isotopes. Estuaries and Coasts 31, 53–69.
Olsen, S., Robadue, D., Lee, V., 1980. An Interpretive Atlas of Narragansett Bay. In: University of Rhode Island Marine Bulletin 40. Coastal Resources Center, 82 pp.
O'Reilly, J., 1984. Carbon Flow in a Coastal Marine Bottom Community. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 199 pp.
Oviatt, C., 1981. Effects of different mixing schedules on phytoplankton, zooplankton and nutrients in marine microcosms. Marine Ecology Progress Series 4, 57–67.

Oviatt, C., 2004. The changing ecology of temperate waters during a warming trend. Estuaries 27, 895–904.
Oviatt, C., Nixon, S., 1975. Sediment resuspension and deposition in Narragansett Bay. Estuarine and Coastal Marine Science 3, 201–217.
Oviatt, C., Buckley, B., Nixon, S., 1981. Annual phytoplankton metabolism in Narragansett Bay calculated from survey field measurements and microcosm observations. Estuaries 4, 167–175.
Oviatt, C., Pilson, M., Nixon, S., Frithsen, J., Rudnick, D., Kelly, J., Grassle, J., Grassle, J., 1984. Recovery of a polluted estuarine ecosystem: a mesocosm experiment. Marine Ecology Progress Series 16, 203–217.
Oviatt, C., Doering, P., Nowicki, B., Reed, L., Cole, J., Frithsen, J., 1995. An ecosystem level experiment on nutrient limitation in temperate coastal marine environments. Marine Ecology Progress Series 116, 171–179.
Oviatt, C., Keller, A., Reed, L., 2002. Annual primary production in Narragansett Bay with no bay-wide winter–spring bloom. Estuarine, Coastal and Shelf Science 54, 1013–1026.
Oviatt, C., Olsen, S., Andrews, M., Collie, J., Lynch, T., Raposa, K., 2003. A century of fishing and fish fluctuations in Narragansett Bay. Reviews in Fisheries Science 11, 221–242.
Oviatt, C., Hyde, K., Keller, A., Turner, J., 2007. Production patterns in Massachusetts Bay with outfall relocation. Estuaries and Coasts 30, 35–46.
Ozaki, K., Uye, S., Kusumoto, T., Hagino, T., 2004. Interannual variability of the ecosystem of the Kii Channel, the Inland Sea of Japan, as influenced by bottom intrusion of cold and nutrient-rich water from the Pacific Ocean, and a recent trend of warming and oligotrophication. Fisheries Oceanography 13, 65–79.
Parsons, T., Takahashi, M., 1973. Biological Oceanographic Processes. Pergamon Press, NY.
Petersen, J., 2004. Grazing on pelagic primary producers-the role of benthic suspension feeders in estuaries. In: Nielsen, S., Banta, G., Pedersen, M. (Eds.), Estuarine Nutrient Cycling: the Influence of Primary Producers. Kluwer, Boston, MA, pp. 129–152.
Phelps, D., 1958. A Quantitative Study of the Infauna of Narragansett Bay in Relation to Certain Physical and Chemical Aspects of their Environments. MS thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 56 pp.
Philippart, C., Beukema, J., Cadee, G., Dekker, R., Goedhart, P., vanlperen, J., Leopold, M., Herman, P., 2007. Impacts of nutrient reduction on coastal communities. Ecosystems 10, 95–118.
Pilling, G., Miller, R., Easey, M., Maxwell, D., Tidd, A., 2007. Phenology and North Sea cod *Gadus morhua* L.: has climate change affected otolith annulus formation and growth? Journal of Fish Biology 70, 584–599.
Pilson, M., 1985. On the residence time of water in Narragansett Bay. Estuaries 8, 2–14.
Pilson, M., 2008. Narragansett Bay amidst a globally changing climate. In: Desbonnet, A., Costa-Pierce, B. (Eds.), Science for Ecosystem-based Management: Narragansett Bay in the 21st Century. Springer, NY, pp. 35–46.
Pilson, M., Oviatt, C., Nixon, S., 1980. Annual nutrient cycles in a marine microcosm. In: Giesy, J. (Ed.), Microcosms in Ecological Research. US Department of Energy, Symposium Series 52 (CONF-781101), pp. 753–778.
Pratt, D., 1959. The phytoplankton of Narragansett Bay. Limnology and Oceanography 4, 425–440.
Pratt, D., 1965. The winter–spring diatom flowering in Narragansett Bay. Limnology and Oceanography 10, 173–184.
Pryor, D., Saarman, E., Murray, D., Prell, W., 2007. Nitrogen Loading from Wastewater Treatment Plants to Upper Narragansett Bay. Narragansett bay Estuary Program Report NBEP-2007-122, 36 pp.
Rabalais, N., Nixon, S., 2002. Nutrient over-enrichment in coastal waters: global patterns of cause and effect. Estuaries 25, 4B.
Richardson, A., Schoeman, D., 2004. Climate impact on plankton ecosystems in the Northeast Atlantic. Science 305, 1609–1612.
Riebesell, U., 1989. Comparison of sinking and sedimentation rate measurements in a diatom winter/spring bloom. Marine Ecology Progress Series 54, 109–119.
Riisgård, H., 2004. Zoobenthic consumers of the primary production in the marine environment. Recent Research Developments in Environmental Biology 1, 269–315.
Riley, G., 1967. The plankton of estuaries. In: Lauff, G. (Ed.), Estuaries. American Association for the Advancement of Science Publication, No. 83, pp. 316–328. Washington, DC.
Rogers, J., 2008. Circulation and transport in upper Narragansett Bay. MS thesis. Graduate School of Oceanography, University of Rhode Island, Kingston, RI, 95 pp.
Rudnick, D., Oviatt, C., 1986. Seasonal lags between organic carbon deposition and mineralization in marine sediments. Journal of Marine Research 44, 815–837.
Rudnick, D., Elmgren, R., Frithsen, J., 1985. Meiofaunal prominence and benthic seasonality in a coastal marine ecosystem. Oecologia 67, 157–168.
Sarno, D., Wiebe, Kooistra, W., Medlin, L., Percopo, I., Zingone, A., 2005. Diversity in the genus *Skeletonema* (Bacillariophyceae). II. An assessment of the taxonomy of *S. costatum*-like species with the description of four new species. Journal of Phycology 41, 151–176.
Schell, D., 2000. Declining carrying capacity in the Bering Sea: isotopic evidence from whale baleen. Limnology and Oceanography 45, 459–462.
Seitzinger, S., 1982. The Importance of Denitrification and Nitrous Oxide Production in the Nitrogen Dynamics and Ecology of Narragansett Bay, Rhode Island. Ph.D. thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 145 pp.
Seitzinger, S., Garber, J., 1987. Nitrogen fixation and $^{15}N_2$ calibration of the acetylene reduction assay in coastal marine sediments. Marine Ecology Progress Series 37, 65–76.
Seitzinger, S., Giblin, A., 1996. Estimating denitrification in North Atlantic continental shelf sediments. Biogeochemistry 35, 235–260.
Seitzinger, S., Nixon, S., Pilson, M., Burke, S., 1980. Denitrification and N_2O production in near-shore marine sediments. Geochimica et Cosmochimica Acta 44, 1853–1860.
Seitzinger, S., Nixon, S., Pilson, P., 1984. Denitrification and nitrous oxide production in a coastal marine ecosystem. Limnology and Oceanography 29, 73–83.
Sisson, R., 1973. Biological and Commercial Fisheries Related Research on the Channeled Welk *Busycon canaliculatum* (Linne) in Narragansett Bay, Rhode Island. MS thesis. University of Rhode Island, Kingston, RI, 62 pp.
Smayda, T., 1955. Phytoplankton Studies in Lower Narragansett Bay. MS thesis. Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 114 pp.
Smayda, T., 1957. Phytoplankton studies in lower Narragansett Bay. Limnology and Oceanography 11, 342–359.
Smayda, T., 1973. The growth of *Skeletonema costatum* during a winter–spring bloom in Narragansett Bay, Rhode Island. Norwegian Journal of Botany 20, 219–247.
Smayda, T., 1998. Patterns of variability characterizing marine phytoplankton, with examples from Narragansett Bay. ICES Journal of Marine Science 55, 562–573.
Smayda, T., Borkman, D., 2008. Nutrient and plankton dynamics in Narragansett Bay. In: Desbonnet, A., Costa-Pierce, B. (Eds.), Science for Ecosystem-based Management, Narragansett Bay in the 21st Century. Springer, NY, pp. 431–484.
Smetacek, V., 1984. The supply of food to the benthos. In: Fasham, M. (Ed.), Flows of Energy and Materials in Marine Ecosystems. NATO Conference Series. Plenum Press, NY, pp. 517–547.
Smetacek, V., Pollehne, F., 1986. Nutrient cycling in pelagic systems: a reappraisal of the conceptual framework. Ophelia 26, 401–428.
Stickney, A., Stringer, L., 1957. A study of the invertebrate bottom fauna of Greenwich Bay, R.I. Ecology 38, 111–122.
Steemann-Nielsen, E., Hansen, V., 1959. Light adaptation in marine phytoplankton populations and its interrelation with temperature. Physiologia Plantarum 12, 353–370.
Stenseth, N., Ottersen, G., Hurrell, J., Belgrano, A., 2004. Marine Ecosystems and Climate Variation – the North Atlantic Perspective. Oxford University Press.
Suffolk County Department of Health Services, 2007. Response to Public Comments on Total Maximum Daily Load for Nitrogen in the Peconic Estuary, 27 pp. Available from:. Prepared in Cooperation with the U.S. EPA, NY State Department of Environmental Conservation and the Peconic Estuary Program http://www.dec.ny.gov/docs/water_pdf/tmdlnitrpecnresp.pdf.
Sullivan, B., Van Keuren, D., Clancy, M., 2001. Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, Rhode Island. Hydrobiologia 451, 113–120.
Taylor, D., 2003. Size-dependent predation on post-settlement winter flounder, *Pseudopleuronectes americanus* by sand shrimp, *Crangon septemspinosa*. Marine Ecology Progress Series 263, 197–215.
Townsend, D., Cammen, L., 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.
Tucker, J., Kelsey, S., Giblin, A., Hopkinson, C., 2008. 2007 Annual Benthic Nutrient Flux Monitoring Report. Massachusetts Water Resources Authority. Report ENQUAD 2008–12. Boston, 59 pp.
Turner, J., Borkman, D., Lincoln, J., Gauthier, D. and Petitpas, C., Plankton studies in Buzzards Bay, Massachusetts, USA. VI. Phytoplankton and water quality, 1987 to 1998. Marine Ecology Progress Series, in press.
Valiela, I., 1995. Marine Ecological Processes, second ed. Springer, NY, 686 pp.
Valiela, I., 2006. Global Coastal Change. Blackwell Publishing, Malden, MA.
Vargo, G., 1976. The Influence of Grazing and Nutrient Excretion by Zooplankton on the Growth and Production of the Marine Diatom, *Skeletonema costatum* (Greville) Cleve, in Narragansett Bay. Ph.D. thesis. Oceanography, University of Rhode Island, Narragansett, RI, 118 pp.
Vargo, G., 1979. The contribution of ammonia excreted by zooplankton to phytoplankton production in Narragansett Bay. Journal of Plankton Research 1, 75–84.
Vinogradov, A., 1953. The Elementary Composition of Marine Organisms (J. Efron, J. Setlow, Trans.). Sears Foundation for Marine Research, Yale University, New Haven, CT, 647 pp.
Ware, D., Thomson, R., 21 April 2005. Bottom-up ecosystem trophic dynamics determine fish production in the northeast Pacific. Sciencexpress, 10. 10.1126/science.1109049. www.sciencexpress.org.
Wlodarczyk, E., Durbin, A., Durbin, E., 1992. Effect of temperature on lower feeding thresholds, gut evacuation rate, and diel feeding behavior in the copepod *Acartia hudsonica*. Marine Ecology Progress Series 85, 93–106.
Yoder, J., 1979. Modeling the Effect of Light Intensity and Temperature on the Growth Rate and Biomass of *Skeletonema costatum* (Bacillariophyceae) and other Diatoms. Ph.D., Graduate School of Oceanography, University of Rhode Island, Narragansett, RI, 145 pp.
York, J., Quay, P., Valiela, I., 2007. Stable isotopic detection of ammonium and nitrate assimilation by phytoplankton in the Waquoit Bay estuarine system. Limnology and Oceanography 52, 144–155.