Coincident patterns of waste water suspended solids reduction, water transparency increase and chlorophyll decline in Narragansett Bay

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A R T I C L E   I N F O

A B S T R A C T

Dramatic changes occurred in Narragansett Bay during the 1980s: water clarity increased, while phytoplankton abundance and chlorophyll concentration decreased. We examine how changes in total suspended solids (TSS) loading from wastewater treatment plants may have influenced this decline in phytoplankton chlorophyll. TSS loading, light and phytoplankton observations were compiled and a light- and temperature-dependent *Skeletonema*-based phytoplankton growth model was applied to evaluate chlorophyll supported by TSS nitrogen during 1983–1995. TSS loading declined 75% from ~0.60×10^6 kg month^{-1} to ~0.15×10^6 kg month^{-1} during 1983–1995. Model results indicate that nitrogen reduction related to TSS reduction was minor and explained a small fraction (~15%) of the long-term chlorophyll decline. The decline in NBay TSS loading appears to have increased water clarity and *in situ* irradiance and contributed to the long-term chlorophyll decline by inducing a physiological response of a ~20% reduction in chlorophyll per cell.

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1. Introduction

A long-term decrease in phytoplankton (as chlorophyll) has occurred in lower Narragansett Bay (NBay), declining from ~6 μg L^{-1} (1983) to ~3 μg L^{-1} in 1995 (Li and Smayda, 1998), continuing at the reduced level through the 2000s (Fulweiler et al., 2007). The long-term decline in chlorophyll in NBay has been attributed to various processes: increased water temperature (Cook et al., 1998; Oviatt, 2004; Nixon et al., 2009), changes in light availability related to increased cloudiness (Borkman, 2002; Nixon et al., 2009), changes in ctenophore (Sullivan et al., 2001) and copepod (Keller et al., 1999; Oviatt, 2004) grazing, and long-term variations in coupled ocean–atmosphere forcing such as the NAO (North Atlantic Oscillation; Hawk, 1998; Oviatt, 2004; Borkman and Smayda, 2009a) and the Gulf Stream (Borkman and Smayda, 2009b). During the early portion of the chlorophyll decline in the 1980s, improved wastewater treatment led to a dramatic decline in suspended solid loading (TSS) into NBay from wastewater treatment plants (WWTP). From 1983 to 1995, TSS loading decreased *ca.* 75%, from *ca.* 9×10^6 kg year^{-1} (1983–84) to $<3 \times 10^6$ kg year^{-1} (1992 to 1995) (Save the Bay, 1996; Borkman and Smayda, 1998). These solids, through their release of nitrogen and other nutrients, are a potential nutrient

source no longer available to phytoplankton. Although particulate N is a relatively small portion of N loading to NBay (~5%; Hamburg et al., 2008; Nixon et al., 2008), the potential role of the 6×10^6 kg year^{-1} reduction in WWTP particulate loading on the 13-year decline (1983–1995) in mean annual chlorophyll has not been evaluated. The question we examine is how much of the decrease in lower NBay chlorophyll may be attributed to the decrease in TSS loading *via* two potential mechanisms, 1) nitrogen reduction and 2) increased *in situ* light. A large body of field and experimental evidence indicates nitrogen limits phytoplankton growth in NBay (Smayda, 1974; Furnas et al.,1986; Furnas, 1983; Oviatt et al., 1995; Nixon, 1997; among others). Applying dose-yield kinetics leads to the expectation that the reduction in TSS loading would decrease biomass. However, if the decline in chlorophyll is related to N availability, the relationship is paradoxical because the early phase of chlorophyll reduction (1983–1995) occurred during a period of no apparent change in nitrogen loading (Hamburg et al., 2008; Nixon et al., 2008).

We apply a proximate, mass balance approach to quantify the linkages between the long-term (n = 13 years during 1983 to 1995) decline in wastewater TSS loading and chlorophyll concentration in lower NBay in an effort to explain the 1980s to 1990s decline in chlorophyll concentration. The model integrates the light and temperature-dependent growth rate of the dominant diatom (*Skeletonema costatum* s.l.) in NBay (Karentz and Smayda, 1984; Borkman and Smayda, 2009a) and

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the time series data available for WWTP TSS loading, incident irradiance, water clarity, temperature, chlorophyll, and *Skeletonema* abundance during 1983–1995.

2. Methods

2.1. Geographic setting and data sources

Narragansett Bay (*ca.* 327 km^2) is a well-mixed, relatively shallow (mean depth 9 m), estuary located southwest of Cape Cod along the eastern U.S. coast (*ca.* 41°30′N, 71°20′W), and is contiguous with Rhode Island Sound and Long Island Sound. Nutrient-enriched freshwater flowing into the upper NBay produces a pronounced salinity - nutrient gradient over the length of its 30 km axis, progressing from an upper region of low salinity (*ca.* 20) and elevated nutrients to a region of high salinity (*ca.* 33), and decreased nutrient at its entrance (Smayda and Borkman, 2008). The mean residence time of NBay water is 26 days, varying from 10 to 40 days dependent on the volume of freshwater input and wind conditions (Pilson, 1985). A detailed description of the geographic setting and the biological, physical and chemical oceanography of NBay is available in Desbonnet and Costa-Pierce (2008).

Water temperature, water clarity, incident and *in situ* irradiance, chlorophyll concentration and numerical abundance of *S. costatum* s.l. were measured weekly at a long-term monitoring station in unpolluted lower NBay (41°32′N × 71°23′W) from 1983 to 1995. Methodological details for measurement of water temperature, irradiance and water clarity are described in Smayda (1984, 1998) and Borkman and Smayda (1998); chlorophyll methods are available in Li and Smayda (1998), and *Skeletonema* numerical abundance methods are in Borkman and Smayda (2009a, 2009b). The 1983 to 1995 data used in our study are a subset from the long-term (1959 to present) Narragansett Bay Plankton Time Series. We analyze only the 1983 to 1995 portion of the data set because it is the only portion of the time series for which synchronous measurements of phytoplankton, chlorophyll concentration, irradiance, water clarity and TSS loading data are available. Incident solar irradiance during the time series initially was measured in the non-SI units of Langley day^{-1} (Pratt, 1965; Hitchcock and Smayda, 1977). We converted those data into Watts using the conversion 1 Langley day^1 = 0.485 W m^{-2} day^{-1} (National Institute for Standards and Technology, 2008). Incident irradiance was recorded using an Eppley pyrheliometer installed at the URI-GSO campus in Narragansett, RI (~10 km south of the long-term sampling site) during 1983 until 1987. From 1988 until 1995 incident irradiance was recorded using an Eppley pyrheliometer installed at Eppley Laboratories in Newport, RI (~11 km southeast of the long-term sampling site). The mean weekly *in situ* irradiance ('I bar') at the monitoring station was calculated from the daily *in situ* irradiance during the 1983 to 1995 period using the equation of Riley (1957) as modified by Hitchcock and Smayda (1977):

$$I\ bar = \frac{Io}{kz(1-e^{-kz})} \tag{1}$$

where Io is incident irradiance, k is the extinction coefficient (calculated from Secchi disk depth (D) after the formula of Holmes (1970): k = 1.44/D) and z is the mixed layer depth equivalent to the depth (8 m) of the long-term sampling station.

The collective monthly and annual WWTP TSS loading levels during 1983 to 1995 from 17 waste water treatment plants that discharge into NBay were compiled from reports issued by Save the Bay (1996). Locations of the main WWTP and the long-term loading history of metals, nitrogen and other pollutants to Narragansett Bay are shown in detail by Nixon and Fulweiler (2012). Some plants provided only total annual discharge data. For those, the total annual TSS discharge was seasonally adjusted based on the mean monthly pattern of TSS discharge at the three largest treatment plants during 1994 and 1995, *i.e.*, Fields Point,

Fall River and Blackstone (Worcester) Facilities. The nitrogen content of sludge from a representative RI treatment plant (located in Cranston, RI) was 2.5% of dry sludge weight (Oviatt et al., 1987). Monthly TSS loading was multiplied by this nitrogen content to approximate monthly nitrogen loading into NBay from sewage plant TSS.

2.2. Model development

We used the diatom *Skeletonema* as the representative phytoplankton taxon to model whether the recorded decline in mean annual chlorophyll in NBay was related to the decline in TSS discharge. *S. costatum* s.l. is numerically the most abundant diatom in NBay year-round; it accounts for a mean of 42% of total phytoplankton numerically (annual mean contribution range of 11% to 69%; Karentz and Smayda, 1984; Borkman and Smayda, 2009a). There is a wealth of experimental data for *Skeletonema* strains and populations from NBay, both *in situ* and in culture, including cellular N and chlorophyll quotas, the effect of irradiance, nutrients and temperature on cellular nutrient composition and growth rate (Smayda, 1973; Yoder, 1979; Falkowski et al., 1981; Sakshaug and Andresen, 1986; Langdon, 1987; Anning et al., 2000). We used the experimentally derived linear, positive relation between growth irradiance and nitrogen content of *S. costatum* s.l. reported by Langdon (1987) for the NBay strain SK 6C:

$$pg\ N\ cell-1 = 0.028\ I + 2.97 \tag{2}$$

where I is irradiance as W m^{-2}.

Accepting that nitrogen is the nutrient that primarily limits phytoplankton growth in NBay (Smayda, 1974; Furnas, 1983; Furnas et al., 1986; Kremer and Nixon, 1978; Oviatt et al., 1995), we applied the following schematic. TSS discharge was converted to the nitrogen concentration potentially available for phytoplankton assimilation. The estimated number of *Skeletonema* cells and their chlorophyll content produced by this nitrogen accretion from TSS was calculated using the relationships reported between light, temperature and cellular nitrogen content of *Skeletonema* and between light and chlorophyll (Langdon, 1987). The lower NBay station is well-mixed over its 8 m depth through most of the year (Hitchcock and Smayda, 1977), validating the use of depth-averaged irradiance (I bar) in the model. Using I bar as input (Eq. (1)), the nitrogen content of the *in situ* concentration (cells ml^{-1}) of *Skeletonema* was estimated for each month during 1983–1995 using the weekly population densities recorded at the monitoring site (Borkman, 2002; Borkman and Smayda, 2009a). Dividing the monthly TSS nitrogen load by the light-dependent, mean monthly cellular nitrogen content yielded an estimate of the number of *Skeletonema* cells potentially supported by the monthly TSS nitrogen load. Note that this is a maximum potential estimate and that given the relatively high ambient DIN levels, the actual phytoplankton growth response stimulated by TSS-derived DIN will be less than the predicted potential response.

The model monthly nitrogen load only accounts for DIN; we have ignored the potential role of dissolved organic nitrogen (DON) in the model. DON was excluded because it was not regularly monitored during the 1983–1995 period (Nixon et al., 2005). For reference, available data indicates the percentage of total N as DON discharged into NBay by WWTP is of the order of 14% to 19% of total N discharged (Nixon et al., 2008).

The *Skeletonema* cell number estimates were converted to chlorophyll applying Langdon's (1987) equation (Eq. 3) relating chlorophyll content of *S. costatum* cells to light intensity:

$$\begin{aligned} &\text{Irradiance}{<}24\ W\ m^{-2};\text{Chlorophyll} = 0.72\ pg\ cell^{-1} \\ &\text{Irradiance}{>}24\ W\ m^{-2};\text{Chlorophyll} = 0.41\ pg\ cell^{-1} \end{aligned} \tag{3}$$

The estimated chlorophyll biomass supported by WWTP TSS was divided by the volume (2724 × 10^6 m^3) of Narragansett Bay (Pilson, 1985) to get a coarse monthly estimate of the potential concentration of

chlorophyll supported by sewage plant TSS. The TSS nitrogen – *Skeletonema* model was run in Excel spreadsheets using a one month time step. The one month time-step is appropriate for a coarse estimate of the potential contribution of TSS nitrogen chlorophyll concentration as it approximates the average residence time of water in Narragansett Bay (Pilson, 1985).

2.3. Data analysis

Linear regression and was used to assess the hypothesis that changes in model output and field data occurred during 1983–1995. Monthly time step series of model output and field data were decomposed into seasonal cycle and long-term (1983–1995) trend components using time series analyses. We used Broekhuizen and McKenzie's (1995) time series analysis method, which is optimized to detect trends in time series that have strong seasonal variation, to decompose the time series into seasonal and trend components. This method has been used successfully to detect trends in North Sea zooplankton (Broekhuizen and McKenzie, 1995) and plankton abundance in Massachusetts Bay (Hunt et al., 2010) and NBay (Borkman and Smayda, 2009a). Linear regression was used to fit a straight line to trends, with the statistical fit (p value < 0.05) of the linear regression used as an indicator of the long-term linear trend. Time series analysis and data manipulation were done using Excel spreadsheets, and statistical analyses were completed using SAS JMP (SAS, 2012) and Prism (GraphPad, 1999) statistical software.

3. Results

Wastewater suspended solids (TSS) loading into Narragansett Bay during the 1983 to 1995 period displayed two dominant features: a strong seasonal signal and a long-term decline (Fig. 1). TSS loading varied seasonally; it was *ca.* 1.5 to 2-fold above annual mean levels during winter and spring (January–May) each year, decreased during June–October, and returned to above-mean levels during November–December. Removal of this strong seasonal cycle yielded a long-term, progressive decline in TSS loading during the 13 years from 1983 to 1995 (Fig. 1). Deseasonalized TSS loading declined 4-fold, from 0.6×10^6 kg month^{-1} in 1983–1984 to approximately 0.15×10^6 kg month^{-1} in 1994–1995, *i.e.*, a 75% reduction (Fig. 1). This trend was linear judged by the fit of a linear regression model

($r^2 = 0.97$, n = 144 month, p = <0.0001). Converted to annual loading, this reduction is equivalent to a TSS decline at a linearized rate of 0.46×10^6 kg per year.

We estimated the monthly nitrogen delivered into the bay from sewage plant TSS (Fig. 2) by multiplying the monthly TSS loading levels by the sludge nitrogen conversion factor of 2.5% of dry sludge weight derived by Oviatt et al. (1987). Monthly TSS nitrogen decreased from about 15×10^3 kg month^{-1} in 1983–1984 to *ca.* $2.5–5.0 \times 10^3$ kg month^{-1} in 1994–1995. Deseasonalized TSS nitrogen loading also displayed a linear decrease during 1983–1995 (linear regression, $r^2 = 0.97$, n = 144 months, p = <0.001; Fig. 2). On an annual basis, TSS nitrogen declined at a rate of *ca.* 11,490 kg per year during 1983–1995.

3.1. Chlorophyll

The potential impact of TSS nitrogen discharge into NBay on chlorophyll concentration was estimated using a N-assimilation - *Skeletonema*- chlorophyll model. In this model, the light-dependent cellular N-content of a NBay strain of *Skeletonema* experimentally derived by Langdon, (1987; Eqs. (2) and (3)) was used to estimate the number of *Skeletonema* cells and *Skeletonema* chlorophyll that TSS nitrogen could support at monthly time steps during 1983–1995. The predicted chlorophyll concentration supported by TSS nitrogen declined ~70%, from 0.7–0.8 µg L^{-1}, during 1983–1984 to 0.2 µg L^{-1} during 1994–1995 (Fig. 3). The decline was linear during 1983–1995 (linear regression, $r^2 = 0.88$, n = 13 years p = <0.0001). Following the linear regression, chlorophyll supported by TSS nitrogen fell from approximately 0.70 µg L^{-1} during the early 1980s to 0.24 µg L^{-1} during the mid-1990s. The progressive decrease in TSS nitrogen discharge over the 13 year period is predicted to have led to a *ca.* 0.50 µg L^{-1} decrease in mean annual chlorophyll.

During the 1983–1995 period, both TSS loading and mean annual chlorophyll concentration in lower NBay were in long-term decline. During the three decades from 1972 to 1997, mean annual chlorophyll concentrations progressively decreased *ca.* 50%, from 6 to 8 µg L^{-1} in the early 1970s to *ca.* 3–4 µg L^{-1} in 1990 (Li and Smayda, 1998), and remained at 3–4 µg L^{-1} during the 1999–2006 period (Fulweiler et al., 2007). During this period, 1995 – a year when the winter was unusually cold and chlorophyll elevated to levels typical of the 1970s - deviated from this long-term decline in chlorophyll. Excluding 1995, mean
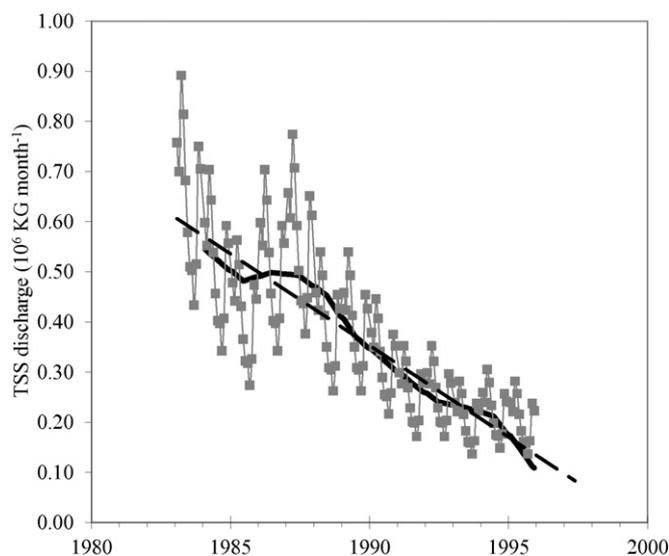

Fig. 1. Time series of Narragansett Bay waste water treatment plant total suspended solids (TSS) discharge 1983–1995. Monthly mean values (gray squares), trend (solid line) derived from time series analysis and linear regression (dashed line) fitted to trend are shown.
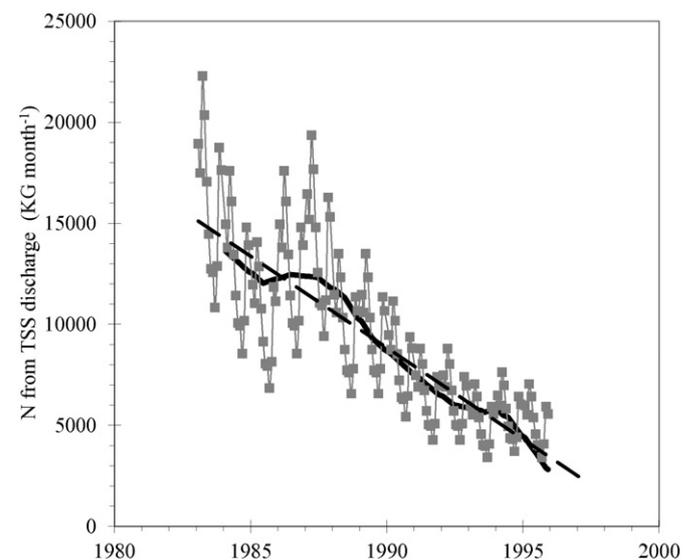

Fig. 2. Time series of estimated nitrogen derived from Narragansett Bay waste water treatment plant total suspended solids (TSS) discharge 1983–1995. Monthly mean values (gray squares), trend (solid line) derived from time series analysis and linear regression (dashed line) fitted to trend are shown.

Fig. 3. Time series of modeled chlorophyll concentration derived from Narragansett Bay waste water treatment plant total suspended solids (TSS) discharge 1983–1995. Monthly mean values (gray squares), trend (solid line) derived from time series analysis and linear regression (dashed line) fitted to trend are shown.
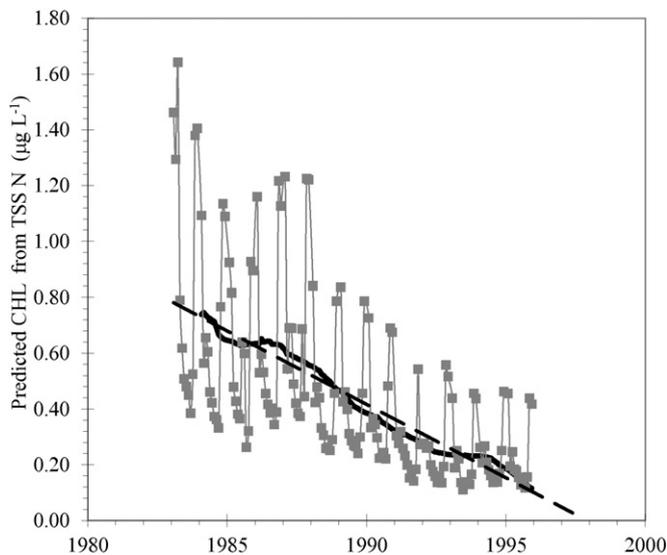
annual chlorophyll concentrations declined at a linear rate of 0.28 µg L^{-1} year^{-1} during 1983–1994, ($r^2 = 0.36$, n = 12 years, p = 0.0394). Relative to *in situ* chlorophyll measurements in NBay, the potential annual contribution of TSS nitrogen to chlorophyll synthesis to the *in situ* standing stock declined linearly from *ca.* 15% in 1983 to 6% in 1995 (linear regression, r^2–0.57, n = 13 years, p = 0.0028).

3.2. Water clarity and Chlorophyll

During 1972 to 1996, water clarity increased *ca.* 25%, with Secchi depth recordings increasing from *ca.* 2.4 m to 3.2 m (Borkman and Smayda, 1998). The water clarity trend during 1983–1995 was consistent with this long-term trend as Secchi depth increased from 2.7 m to 3.3 m in a linear fashion (linear regression, $r^2 = 0.40$, p = <0.0001; Fig. 4A) during 1983–1995. More recent measurements (http://www.gso.uri.edu/phytoplankton/Sample.xls) indicate water clarity has remained at the increased level that developed in the early 1990s; mean Secchi disk depth during 1990 to 2013 (mean = 3.1 m) was significantly greater than the pre-1990 mean of 2.6 m (Mann–Whitney test; p < 0.0001). The increase in water clarity led to an increasing trend in *in situ* light (I bar) during 1983–1995 (linear regression, r2 = 0.67, p = 0.0007; Fig. 4B). The *in situ* mean irradiance during the mid-1990s (~40 W m^{-2}) was ~25% higher than that observed during the mid-1980s (~32 W m^{-2}). There was no change in incoming irradiance during that period, *i.e.* the change in *in situ* light was entirely attributable to increased water clarity. The increased mean *in situ* irradiance that occurred during the 1983–1995 period corresponds to a *ca.* 25% increase over the mean annual *in situ* irradiance level of *ca.* 32 W m^{-2} observed during the 1960–1980 period reported by Smayda (1984). The number of weeks annually in which *in situ* light (I bar) exceeded the physiological threshold of 25 W m^{-2}, the intensity at which the cellular chlorophyll of the NBay strain of *Skeletonema* used in our model shifts from high to low cellular chlorophyll quotas (Langdon, 1987), increased decadally from 29.5 weeks (1970s) to 34.3 weeks (1980s) to 36.7 weeks (1990s) (ANOVA, F ratio = 4.002, df = 2, 24, p = 0.0329). This increase in water mass transparency added two additional months each year in the 1990s having a mean *in situ* light greater than 25 W m^{-2}. Model results, based on Langdon's (1987) chlorophyll - irradiance experiments on *Skeletonema*, showed a decrease in its mean cellular chlorophyll during 1983–1995 (linear regression, $r^2 = 0.82$, n = 13 years, p = <0.0001); *i.e.*, predicted cellular mean annual chlorophyll, which varies
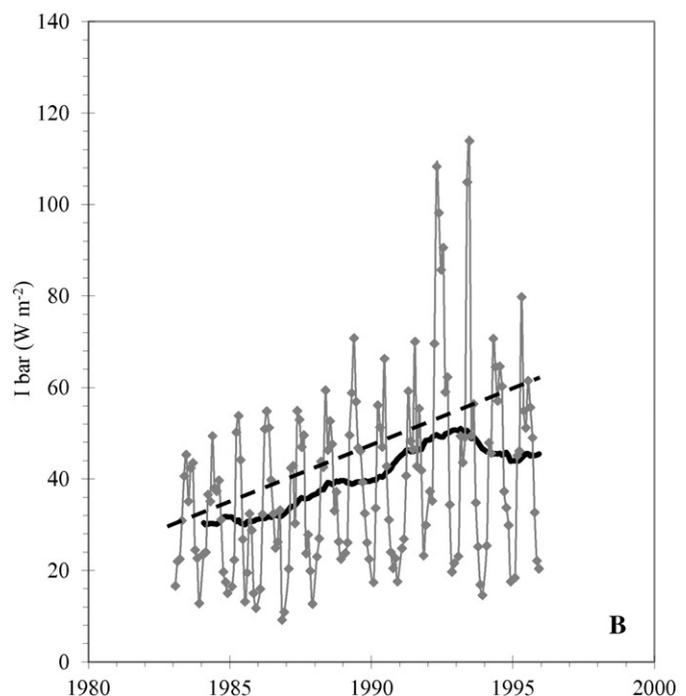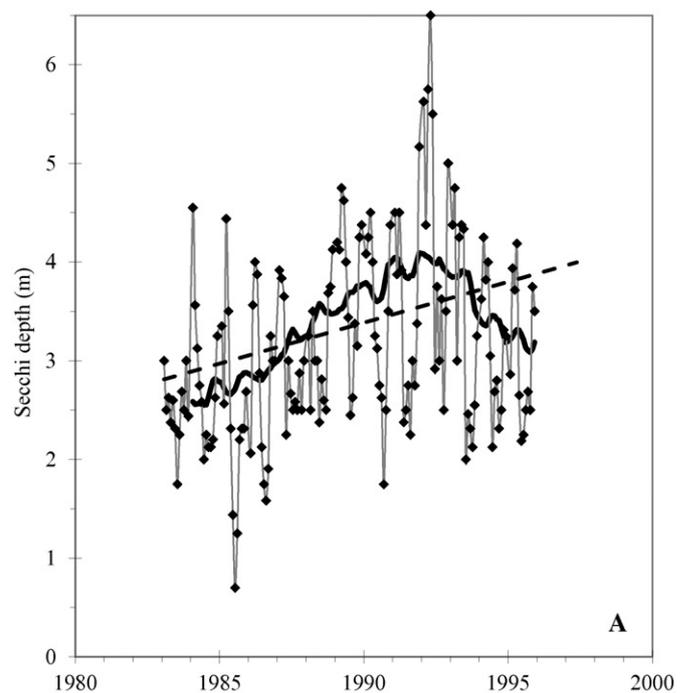

Fig. 4. Trend in lower Narragansett Bay *in situ* light (I bar) at the long-term monitoring station during 1983 to 1995. Time series of 1983 to 1995 monthly mean observations (filled diamonds) with trend derived from time series analysis (solid line) and linear regression fitted to the 1983–1995 trend (dashed line) are shown.

seasonally, decreased from ~0.5 pg cell^{-1} (mid 1980s) to ~0.4 pg cell^{-1} during the mid-1990s. This change is equivalent to a 20% decline in cellular chlorophyll content between the mid-1980s and mid-1990s. The potential effects of TSS reduction on lower NBay water column chlorophyll concentration included both a direct reduction due to minor N reduction and an indirect effect due to the physiological reduction of chlorophyll per cell in response to clearer water and greater ambient irradiance. The maximum possible reduction in chlorophyll attributed to TSS nitrogen is an approximately 0.6 µg L^{-1} reduction in mean
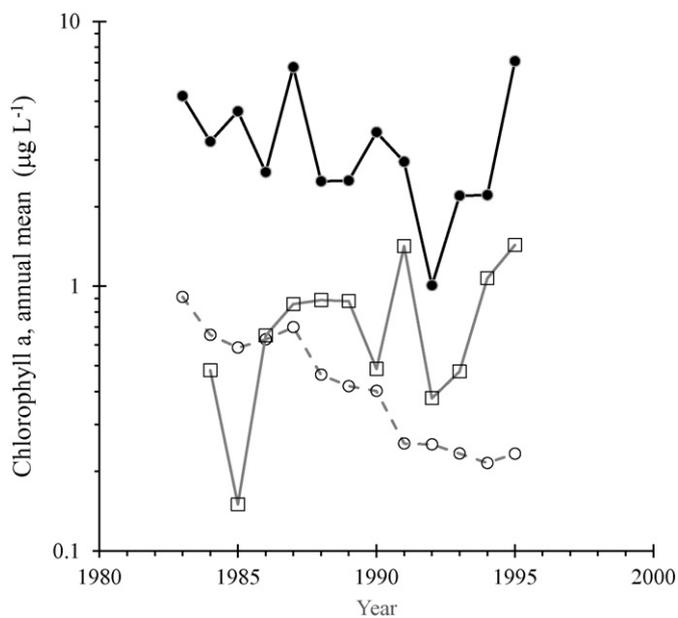
Fig. 5. Mean annual chlorophyll concentration (µg L^{-1}, filled circles) at lower Narragansett Bay monitoring station during 1983 to 1995; model estimates of mean annual chlorophyll concentration derived from TSS nitrogen (µg L^{-1}, open circles), model estimates of the reduction in chlorophyll concentration (µg L^{-1}, open squares) due to reduced chlorophyll per cell induced by increased water clarity relative to 1983 water clarity.

chlorophyll during 1983–1995 (Fig. 5). The reduction in cellular chlorophyll in response to clearer water has been greater - up to a 1.4 µg L^{-1} reduction in mean chlorophyll in some years (such as during 1991, 1995, Fig. 5). This reduction was solely a physiological response to increase *in situ* irradiance accompanying clearer water. The 1985 deviation in chlorophyll reduction (Fig. 5) was related to the drastic reduction in water clarity that occurred during the prolonged 1985 'brown tide' bloom of *Aureococcus anophagefferens* (Smayda and Borkman, 2008).

4. Discussion

4.1. Chlorophyll decline

An unresolved question is what explains the long-term decline in lower NBay chlorophyll? Enrichment experiments, bioassays, dialysis chamber experiments, *in situ* N-15 experiments and N budget analyses collectively suggest NBay is an N-sensitive ecosystem, although it has not been established whether this reflects physiological limitation or a yield-dose relationship (Smayda, 1974; Kremer and Nixon, 1978, Furnas et al., 1986; Furnas, 1983; Oviatt et al., 1995; Nixon, 1997). There are multiple sources of dissolved inorganic nitrogen (DIN) into NBay – river discharge, sewage waste water, advection of bottom water, and *in situ* recycling (Nixon et al., 2008). Hence, our interest in the influence of the progressive decline in TSS loading during 1983–1995 on the decline in chlorophyll during that 13-year period - when mean annual chlorophyll concentration declined by 44% from near 5.5 µg L^{-1} during the mid-1980s to 3.2 µg L^{-1} during the mid-1990s. Our proximate, mass balance analysis and *Skeletonema* light-nitrogen-chlorophyll growth model suggest the chlorophyll concentration supported by TSS nitrogen declined from 0.7 µg L^{-1} during the mid-1980s - equivalent to 12% of *in situ* chlorophyll - to 0.2 µg L^{-1} during the mid-1990s; a reduction equivalent to 6% of *in situ* chlorophyll. Our growth model predicts a relatively small change in TSS nitrogen loading - equivalent to <2% of total N-loading occurred and accounted for approximately 0.5 µg chl L^{-1} of the decline in *in situ* chlorophyll concentration during 1983–1995.

Wastewater treatment plants have been estimated to contribute approximately 65% of total N-loading into NBay (Nixon et al., 2008). More efficient N removal measures implemented post-2010 have further reduced wastewater treatment plant N-loading by an additional 20% (Krumholz, 2012) and upper Bay *in situ* DIN concentration has declined 50% post-2013 (Narragansett Bay Commission, 2014). Prior to these N-reduction measures, improvements in removal of sewage solids (TSS) during the late 1980s (Save the Bay, 1996) decreased TSS loading into NBay by 67% such that by the late 1990s TSS loading was one-third (*ca.* 0.2 × 10^6 kg month^{-1}) the level observed during the early 1980s (*ca.* 0.6 × 10^6 kg month^{-1}; Fig. 1). Particulate N loading is a relatively minor component of the total NBay N budget, contributing approximately 30 × 10^6 mol N y^{-1}, *i.e.*, about 5% of the total N loading of 576 × 10^6 mol N y^{-1} (Nixon et al., 2008). During 1983–1995, the contribution of TSS nitrogen to total N-loading declined. Using the N-budget of Nixon et al. (2008), sewage treatment plant particulate N loading declined from 2.4% of the total N loading in 1983 to 0.8% in 1995.

The trend in ambient concentration of dissolved inorganic nitrogen (DIN) in lower NBay did not coincide with the 1982–1995 decline in TSS N loading (Li and Smayda, 1998; Smayda, unpublished). Mean annual DIN concentration at the long-term monitoring station varied between 4 and 9 µM and mean DIN concentration increased 37% between 1983 and 87 and 1991–1995 (Smayda, unpublished). Similarly, mean DIN concentration at the Graduate School of Oceanography dock, located approximately 10 km south of the long-term monitoring station, remained between approximately 4–6 µMol during 1983–1995, with no discernible trend (Krumholz, 2012) The dramatic reduction in chlorophyll (44% decline) during the 1980 to early 1990s period of no apparent change in N-loading and no apparent change (or even a modest increase) in *in situ* N-concentration, suggest factors other than nitrogen - separately or collectively - were driving the observed decline in chlorophyll concentration in lower NBay.

4.2. Model limitations

Our model is a simplification of the TSS loading-nitrogen-light-phytoplankton chlorophyll aspects of a complex, coupled human-natural system: Narragansett Bay. The model used physiological data derived from laboratory and field studies of *S. costatum* s.l. (*i.e.*, Langdon, 1987) and applied those measurements to a modeled NBay in which all phytoplankton cells are assumed to behave as *Skeletonema* cells. While *Skeletonema* spp. are important, and even the dominant diatom in NBay, present in 87% of samples examined during 1959 to the 1980s and 1990s (Karentz and Smayda, 1984, 1998; Borkman and Smayda, 2009a), incorporation of other dominant phytoplankton species into the model would be useful in further identification of long-term changes in nutrient-light control of phytoplankton. Similarly, we have used numerical abundance as a metric of *Skeletonema* dominance of phytoplankton abundance. This masks the million-fold range in phytoplankton size expressed as cell volume (Maranon, 2014) and may over-emphasize the importance of *Skeletonema* spp. Conversion of cell counts to their biovolume equivalents has not been completed for the long-term NBay time series, preventing a volume or carbon-based assessment of *Skeletonema* dominance of the phytoplankton community.

Another potential limitation of the model is the focus on dissolved inorganic nitrogen (DIN) as the only available N source for *Skeletonema* cell growth. Clearly, dissolved organic nitrogen (DON) is an important component of the global ocean N-budget (Zehr and Ward, 2002) and coastal N-budgets (Sharp, 1983). However, DON was not routinely monitored during the 1983–1995 period of interest (Nixon et al., 2005) and we have no quantitative DON data to evaluate. Available data indicated that while DON was a major component of WWTP N discharge prior to 1980, the DON fraction has fallen following treatment upgrades beginning in 1980 such that DON was on the order of 14% to 19% of total N discharged for samples collected during 1983, 2002 and 2003 (Nixon et al., 2008). The above caveats suggest areas for model

refinement and also suggest the estimates of *Skeletonema* may be underestimated by 15–20% depending on the fraction of DON that was available for *Skeletonema* growth.

One may also question the geographic extent of TSS particle loading changes in NBay. Most of the TSS loading was from large WWTP in the upper bay (Providence area and northward), approximately 24 km north of the long-term sampling station. There are limited Bay-wide TSS data available to evaluate the spatial distribution of suspended particles in the bay. However, model studies have shown a preferential transfer of suspended material from the upper bay to the West Passage of the Bay where the long-term sampling station is located (Corps of Engineers, 1959; Morton, 1972; Schenck and Davis, 1973; Oviatt and Nixon, 1975), with the amount of suspended particles decreasing exponentially with distance down-bay from Providence (Morton, 1972). Sediment accumulation rates reflect the gradient in particle loading, with slower rates in the lower bay (7–10 mg cm^{-2} year^{-1}) than in the upper bay (135–200 mg cm^{-2} year^{-1}; Santschi et al., 1984). However, there is a differential transfer of relatively small (~8 μm diameter) particles to the lower bay (Collins, 1976). These smaller particles have a greater weight-specific effect on light attenuation than larger particles (Postma, 1961) predominant in the upper bay. Given this preferential transport of small, light-attenuating particles, the dramatic reductions in TSS particle loading in the northern region of NBay are expected to increase water clarity at the long-term monitoring station and the lower NBay region.

The model estimated the standing crop of phytoplankton cells and phytoplankton chlorophyll in response to changing water clarity associated with reduction of TSS particle loading. A remaining question is whether the changes in standing crop have been accompanied by changes in photosynthetic rate that may have been driven by changing *in situ* irradiance. Unlike phytoplankton abundance and chlorophyll concentration, there is no continuous, long-term phytoplankton production time series data available for NBay. Interpretation of several primary production estimates completed during the 1970s (Furnas et al., 1976) through the 2000s (Oviatt et al., 2002) led Nixon et al. (2009) to the conclusion that primary production in lower NBay has declined from ~370 g C m^{-2} y^{-1} during the 1970s to ~210 g C m^{-2} y^{-1} during the 2000s. That is, increases in water clarity and *in situ* irradiance were not associated with a stimulation of primary production. This is not surprising given that experimental (Yoder, 1979) and model (Borkman, 2002) studies indicate that light limitation of phytoplankton growth in lower NBay is only expected for 12–16 weeks of the year (generally from late November through early February) and that phytoplankton growth rates during that period are ~70% of the temperature-limited maximum growth rate (Borkman, 2002). Also, this winter light limitation is largely due to reduction in day length rather than water clarity. Any potential stimulation of primary production rate associated with the trend towards clearer water has been offset by the reduction in standing crop and resulted in an apparent long-term decline in production in lower NBay (Nixon et al., 2009).

4.3. Plankton habitat changes

The 1980s were a period of rapid meteorological changes in the western North Atlantic, with distinct shifts in air and sea surface water temperature during 1982–1983 (Rodionov and Krovnin, 1992). NBay habitat changes coincident with the decline in chlorophyll include an increase in water temperature (Smayda, 1984; Cook et al., 1998; Nixon et al. 2009), decline in wind speed (Smayda 1984; Pilson 2008), a decline in incident irradiance (Smayda 1984; Nixon et al. 2009), and increase in water clarity (Borkman and Smayda 1998). Collectively, these changes in environmental variables during 1983–1995 present mixed signals regarding the potential mechanisms driving the long-term decline in chlorophyll concentration. Bottom-up control *via* nutrient limitation was not suggested since the concentrations of most (Si, PO_4, NH_4) nutrients at the lower Bay station increased and there was

no change in NO_3 during 1983–1995. The increase in ambient concentration of some nutrients, such as silica, may reflect reduced phytoplankton uptake rates coincident with the decline in diatom abundance during the 1980s (Borkman and Smayda, 2009a). Top-down control was not supported as zooplankton dry weight (a proxy of zooplankton abundance declined 83% during the period of chlorophyll decline (Smayda, unpublished). A long-term decline in mean annual incident irradiance (Io) has occurred in the Narragansett Bay region, having declined 10% (from 170 to 155 W m^{-2}) during the 1959 to 1980 period (Smayda, 1984). Similarly, Nixon et al. (2009) found winter irradiance (January–April) during the 37-year period from 1959 to 1996 declined *ca.* 15% - from *ca.* 140 to 120 W m^{-2} for the winter–spring bloom period (when the long-term seasonal decline in chlorophyll was greatest; Li and Smayda, 1998). The winter decline in irradiance was temperature related (Nixon et al., 2009). Irradiance during cold winters (typical of the 1960s) was *ca.* 15–20% greater than in warm, cloudy winters typical of the 1990s (Borkman, 2002), a pattern linked to variations in the North Atlantic Oscillation Index (Borkman and Smayda, 2009a). The apparent long-term decline in incident irradiance (Io) is contrary to the trend of increasing *in situ* irradiance (I bar) that occurred between 1983 to 1995 (Fig. 4). *In situ* irradiance is determined by the combined effects of incident irradiance (Io) and attenuation coefficient. During the 1983 to 1995 period of rapid TSS decline, there was no statistically significant difference in incident irradiance. We attribute the 28% increase in *in situ* irradiance to decreased light attenuation due to clearer water. The mean annual *in situ* light experienced by the phytoplankton in lower NBay, which is well-mixed throughout the year (Hitchcock and Smayda, 1977), increased ~28%, from 32 to 40 W m^{-2}, in response to the 22% increase (2.7 to 3.3 m) in mean Secchi depth observed during 1983–1995. This indicates the long-term (1960s to present) decline in NBay *in situ* irradiance, on the order of 10%, has been more than offset by the increase in lower Bay water clarity that occurred during 1983–1995. This resulted in a net increase in *in situ* light experienced by the phytoplankton during that period.

In situ light availability is an important regulator of temporal and spatial variation in phytoplankton production and blooms, and strongly linked to variations in water column turbidity (Hitchcock and Smayda, 1977; Cloern, 1987; Pennock and Sharp, 1994; Lancelot and Muylaert, 2011). For example, reduced *in situ* light levels limit the spatial distribution of *Skeletonema* blooms in Delaware Bay (Pennock and Sharp, 1994), and variations in turbidity partially determined spatial and annual variations in phytoplankton biomass in Chesapeake Bay (Harding, 1994). Initiation of winter–spring diatom blooms in NBay has been linked to attainment of an *in situ* mean irradiance threshold of 21 W m^{-2} threshold (Hitchcock and Smayda, 1977). In addition to influencing population processes like bloom distribution, turbidity through a reduction of *in situ* light may also alter the cellular chlorophyll content of phytoplankton. A reduction in cellular chlorophyll in response to increased irradiance is a widespread trait across all functional groups of marine phytoplankton (Prezelin and Alberte, 1978; Falkowski and Owens, 1980; Falkowski et al., 1981; Post et al., 1985; Geider et al., 1997). *S. costatum* s.l., the diatom used in our TSS nitrogen-chlorophyll model, exhibited a 2.5- to 18-fold decline in cellular chlorophyll, from ca. 8–9 pg cell^{-1} to ca. 0.5–1.0 pg cell^{-1} in response to an irradiance increase from ca 0.5 Einstein m^{-2} day^{-1} to ca 10 Einstein m^{-2} day^{-1} (Langdon, 1987; Goericke and Montoya, 1998). Similarly, a decline in chlorophyll content from 0.76 pg cell^{-1} at low light (0.15 mol photon m^{-2} h^{-1}, 14:10 L:D cycle) to 0.39 pg cell^{-1} at high light (2.2 mol photon m^{-2} h^{-1}, 14:10 L:D cycle) was observed in *Skeletonema* spp. by Sakshaug and Andresen (1986). Anning et al. (2000) observed a 50% reduction in *Skeletonema* cellular chlorophyll, from 1 pg chl per cell to 0.5 pg chl per cell, in response to an increase in irradiance from 50 to 1200 μmol photons m^{-2} s^{-1}. The diatom *Leptocylindrus danicus*, abundant in NBay, displayed a ca. 4-fold decline in chlorophyll (normalized to cell volume) in response to an irradiance

increase from 6 to 41 W m^{-2} (Verity, 1981). Cellular chlorophyll quotas vary at hourly to daily time scales (Post et al., 1985; Falkowski and Raven, 1997), with both 'shift-up' responses (decrease in cell chlorophyll with increasing irradiance) and 'shift-down' responses (increase in cell chlorophyll with decreasing irradiance). The physiological 'shift-up' response of decreased phytoplankton chlorophyll in response to increased water clarity due to reductions in anthropogenic turbidity is not usually considered in models of long-term chlorophyll change. Our TSS-light-chlorophyll model suggests cellular chlorophyll (pg chlorophyll cell^{-1}) declined 17% in response to the increase in *in situ* irradiance during 1983–1995, during a period in which field data showed a *ca.* 67% decline in chlorophyll concentration at the monitoring station. Thus, the physiological response of a 17% decline in cell chlorophyll in response to increased *in situ* light may explain approximately 1.5 to 2.0 μg L^{-1} of the long-term chlorophyll decline (Fig. 5). While the model results are simplified by being based solely on *Skeletonema* physiology, the field results most likely are complicated by changes in the relative abundance of phytoplankton species (Karentz and Smayda, 1984, 1998) not captured by the model.

Estuarine plankton populations are influenced by a combination of long-term variation in climatic forcing and local forcing (Smayda, 1998). In Narragansett Bay, long-term patterns in phytoplankton biomass (Li and Smayda, 1998), variations in winter–spring bloom intensity (Keller et al. 1999) and the bloom patterns of dominant phytoplankton (*Skeletonema* spp.; Borkman and Smayda 2009a) have been related to variations in coupled atmosphere–ocean forcing in the form of the NAO. However, the influence of regional climate variations and climate change may be enhanced or dampened by local, often anthropogenic, changes in the planktonic habitat (Cottingham et al., 2000; Cloern, 2001; Hallegraeff, 2010; Moss et al., 2011; Cloern and Jassby, 2012). The decline in NBay TSS loading appears to have strengthened the long-term chlorophyll decline by increasing both water clarity and *in situ* irradiance and inducing a physiological response resulting in reduced chlorophyll per cell. The shift in model-estimated chlorophyll per cell suggests that a transition from high (~0.52 pg chlorophyll cell^{-1}) to lower (~0.43 pg chlorophyll cell^{-1}) occurred in about 1987 coincident with a drop in TSS loading (Fig. 1) and the ongoing long-term warming trend (Cook et al., 1998; Oviatt, 2004; Nixon et al., 2009). In freshwater systems, transitions from eutrophic, turbid water with abundant phytoplankton to oligotrophic, clear water with reduced phytoplankton abundance have been linked to temperature-modulated top-down (grazer) control (Scheffer et al., 2001). In NBay the coincident warming trend, increased grazing (Keller et al., 1999; Sullivan et al., 2001) and increasing water clarity may have combined to cause a transition to a reduced chlorophyll concentration state in lower NBay.

4.4. Relevance to Narragansett Bay nitrogen reduction and oligotrophication

Based on a linear regression of DIN input versus primary production, Nixon (1997) concluded that a progressive anthropogenic increase in nitrogen input to NBay has led to its eutrophication, and that a doubling of phytoplankton primary production and a 3.5 fold increase in chlorophyll concentration (to 5.0 μg L^{-1}) have occurred since the first European contact. Since Nixon's (1997) analysis, chlorophyll levels in lower NBay have declined *ca.* 3.5 μg L^{-1} in 1999–2006 (Li and Smayda, 1998, Fulweiler et al., 2007). There was no apparent reduction in N-loading during this period (Li and Smayda, 1998; Hamburg et al., 2008; Krumholz, 2012). Anthropogenic alteration of marine systems likely occurs through an accumulation of both large and small impacts (Dayton et al., 1998). The focus in NBay, and many estuarine systems, has been on managing the loading, and therefore the impact of anthropogenic N addition (Conley et al., 2009). Ongoing improvements in NBay wastewater N-reduction have resulted in an un-replicated, uncontrolled 'grand experiment' in which ~100 years of high N loading have been reduced by ~50% (Nixon et al., 2008). We examined an early phase of this experiment in which N-loading was relatively unchanged,

but the discharge of WWTP suspended sediment particles was reduced by ~67% during 1983–1995. Patterns of declining TSS loading and declining chlorophyll concentration were associated. The indirect effect of increased *in situ* light and concomitant reduction in cellular chlorophyll content was an unexpected result of the TSS-reduction phase of the ongoing oligotrophication (Borkman, 2002; Borkman and Smayda, 2009a, Nixon et al., 2009) of NBay.

Our analyses suggest that a reduction in waste water treatment plant suspended sediment loading to the Bay had two effects on chlorophyll concentration. The first was a maximum of ~0.5 μg L^{-1} reduction of chlorophyll concentration due to the reduction in phytoplankton growth from reduced nitrogen in wastewater treatment plant TSS. The second effect is indirect, yet much larger. The 3.6 million tons per year reduction in TSS particle loading into NBay that occurred between 1983 and 1995, and the concomitant increase in water clarity induced a fundamental, physiologically-driven decline in phytoplankton cellular chlorophyll content. This physiological change in response to increased *in situ* irradiance explains ~1.5 μg L^{-1} of the long-term decline in lower Bay chlorophyll. A notable finding is that the indirect, physiological effect of reduced cellular chlorophyll in response to increased water clarity, a ~1.0–1.5 μg L^{-1} decline in chlorophyll, was approximately 3-fold greater than the maximum estimated direct effect (a ~0.5 μg L^{-1} d) of reduced N from TSS. Our model and analyses suggest that the reduction in TSS loading to NBay increased *in situ* light availability and resulted in a physiological response of decreased cellular chlorophyll content that has enhanced the climate-driven, long-term chlorophyll decline. The TSS-reduction during the 1980s set the stage for later water quality improvements such as N-reduction, by reducing chlorophyll concentration. This response, combined with temperature-sensitive climate-mediated changes, such as increased grazing (Keller et al., 1999; Oviatt, 2004), appear to have resulted in an oligotrophication of lower NBay during 1983–1995 characterized by reduction in chlorophyll without an apparent decline in N loading or *in situ* N concentration.

Acknowledgments

References

Anning, T., MacIntyre, H.L., Pratt, S.M., Sammes, P.J., Gibb, S., Geider, R.J., 2000. Photoacclimation in the marine diatom *Skeletonema costatum*. Limnol. Oceanogr. 45, 1807–1817.

Borkman, D.G., 2002. Analysis and Simulation of *Skeletonema costatum* Grev. Cleve Annual Abundance Patterns in Lower Narragansett Bay 1959 to 1996 Ph.D. Thesis. University of Rhode Island. 395 pp.

Borkman, D.G., Smayda, T.J., 1998. Long-term trends in water clarity revealed by Secchi disk measurements in lower Narragansett Bay, Rhode Island, USA. ICES J. Mar. Sci. 55, 668–679.

Borkman, D.G., Smayda, T.J., 2009a. Multidecadal 1959–1997 changes in *Skeletonema* abundance and seasonal bloom patterns in Narragansett Bay, Rhode Island, USA. J. Sea Res. 61, 84–94.

Borkman, D.G., Smayda, T.J., 2009b. Gulf Stream position and winter NAO as drivers of long-term variations in the bloom phenology of the diatom *Skeletonema costatum* "species-complex" in Narragansett Bay, RI, USA. J. Plankton Res. 31, 1407–1425.

Broekhuizen, N., McKenzie, E., 1995. Patterns of abundance for *Calanus* and smaller copepods in the North Sea: time series decomposition of two CPR data sets. Mar. Ecol. Prog. Ser. 118, 103–120.

Cloern, J.E., 1987. Turbidity as a control on phytoplankton biomass and productivity in estuaries. Cont. Shelf Res. 7, 1367–1381.

Cloern, J.E., Jassby, A.D., 2012. Drivers of change in estuarine–coastal ecosystems: discoveries from four decades of study in San Francisco Bay. Rev. Geophys. 50, 1–33.

Cloern, J.E., 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Progr. Ser. 210, 223–253.

Collins, B.P., 1976. Suspended material transport: Narragansett Bay, Rhode Island. Estuar. Coast. Mar. Sci. 4, 33–44.

Conley, D.J., et al., 2009. Controlling eutrophication: nitrogen and phosphorus. Science 323, 1014–1015.

Cook, T., Folli, M., Klinck, J., Ford, S., Miller, J., 1998. The relationship between increasing sea-surface temperature and the northward spread of *Perkinsus marinus* Dermo. disease epizootics in oysters. Est. Coast. Shelf Sci. 46, 587–597.

Corps of Engineers (US), 1959. Contamination dispersion in estuaries: Narragansett Bay. Miscellaneous Paper No. 2–232. US Army Engineer Waterways Experiment Station, Vicksburg, Mississippi.

Cottingham, KL, J.A. Rusak & P.R. Leavitt. 2000. Increased ecosystem variability and reduced predictability following fertilisation: evidence from paleolimnology. Ecol. Lett. 3: 340–348.

Dayton, P.K., Tegner, M.J., Edwards, P.B., Riser, K.L., 1998. Sliding baselines, ghosts, and reduced expectations in kelp forest communities. Ecol. Appl. 8, 309–322.

Desbonnet, A., Costa-Pierce, B. (Eds.), 2008. Science for Ecosystem-Based Management: Narragansett Bay in the 21st Century. Springer, Berlin 570 pp.

Falkowski, P.G., Owens, T.G., 1980. Light-shade adaptation: two strategies in marine phytoplankton. Plant Physiol. 66, 632–635.

Falkowski, P.G., Raven, J., 1997. Aquatic Photosynthesis. Blackwell, Oxford 375 pp.

Falkowski, P.G., Owens, T.G., Ley, A.C., Mauzerall, D.C., 1981. Effects of growth irradiance levels on the ratio of reaction centers in two species of marine phytoplankton. Plant Physiol. 68, 969–973.

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

Furnas, M.J., 1983. Nitrogen dynamics in lower Narragansett Bay, Rhode Island. 1. Uptake by size-fractionated phytoplankton populations. J. Plankton Res. 5, 657–676.

Furnas, M.J., Hitchcock, G.L., Smayda, T.J., 1976. Nutrient-phytoplankton relationships in Narragansett Bay during the 1974 summer bloom, pp. 118–133. Estuarine Processes 1. Academic Press, N.Y.

Furnas, M.J., Smayda, T.J., Deason, E.E., 1986. Nitrogen dynamics in lower Narragansett Bay. II. Phytoplankton uptake, depletion rates of nitrogenous nutrient pools, and estimates of ecosystem remineralization. J. Plankton Res. 8, 755–769.

Geider, R.J., MacIntyre, H.L., Kana, T.M., 1997. Dynamic model of phytoplankton growth and acclimation: responses of the balanced growth rate and the chlorophyll a:carbon ratio to light, nutrient-limitation and temperature. Mar. Ecol. Progr. Ser. 148, 187–200.

Goericke, R., Montoya, J.P., 1998. Estimating the contribution of microalgal taxa to chlorophyll a in the field – variations of pigment ratios under nutrient- and light-limited growth. Mar. Ecol. Prog. Ser. 169, 97–112.

GraphPad, 1999. GraphPad Prism statistical software version 3.0. GraphPad Software, Inc.

Hallegraeff, H.G., 2010. Ocean climate change, phytoplankton community responses and harmful algal blooms: a formidable predictive challenge. J. Phycol. 46, 220–235.

Hamburg, S. P., Pryor, D. and Vadeboncoeur, M.A. 2008. Nitrogen inputs to Narragansett Bay: An historical perspective. In Desbonnet, A. and Costa-Pierce, B. eds., Science for Ecosystem-Based Management: Narragansett Bay in the 21st Century. Springer, Berlin. pp. 177–210.

Harding, L.W., 1994. Long-term trends in the distribution of phytoplankton in Chesapeake Bay: roles of light, nutrients and streamflow. Mar. Ecol. Progr. Ser. 104, 267–291.

Hawk, J.D., 1998. The Role of the NAO in Winter Climate Variability as it Relates to the Winter–Spring Bloom in Narragansett Bay University of Rhode Island M.S. Thesis. 148 pp.

Hitchcock, G.L., Smayda, T.J., 1977. The importance of light in the initiation of the 1972-1973 winter–spring bloom in Narragansett Bay. Limnol. Oceanogr. 22, 126–131.

Holmes, R.W., 1970. The Secchi disk in turbid coastal waters. Limnol. Oceanogr. 15, 688–694.

Hunt, C.D., Borkman, D.G., Libby, S., LaCouture, R., Turner, J., Mickelson, M., 2010. Phytoplankton patterns in Massachusetts Bay 1992-2007. Estuar. Coasts 33, 448–470.

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

Karentz, D., Smayda, T.J., 1984. Temperature and seasonal occurrence patterns of 30 dominant phytoplankton species in Narragansett Bay over a 22-year period 1959-1980. Mar. Ecol. Progr. Ser. 18, 277–293.

Keller, A.A., Oviatt, C.A., Walker, H.A., Hawke, J.D., 1999. Predicted impact of elevated temperature on the magnitude of the winter–spring bloom in temperate coastal water: a mesocosm study. Limnol. Oceanogr. 44, 344–356.

Kremer, J.N., Nixon, S.W. (Eds.), 1978. A Coastal Marine Ecosystem: Simulation and Analysis. Springer Verlag, NY 217 pp.

Krumholz, J.S., 2012. Spatial and temporal patterns in nutrient standing stock and mass balance in response to load reductions in a temperate estuary Ph.D. Thesis. University of Rhode Island. 380 pp.

Lancelot, C., Muylaert, K.U., 2011. Trends in estuarine phytoplankton ecology. In: Wolanski, E., et al. (Ed.), Treatise on Estuarine and Coastal Science: Functioning ecosystems at the land-ocean Interface. Elsevier, Amsterdam, pp. 5–15.

Langdon, C., 1987. On the causes of interspecific differences in the growth-irradiance relationship for phytoplankton. I. A comparative study of the growth-irradiance relationship of three marine phytoplankton species: *Skeletonema costatum*, *Olisthodiscus luteus* and *Gonyaulax tamarensis*. J. Plankton Res. 9, 459–482.

Li, Y., Smayda, T.J., 1998. Temporal variability of chlorophyll in Narragansett Bay during an eighteen year time-series. ICES J. Mar. Sci. 55, 661–667.

Maranon, E., 2014. Cell size as a key determinant of phytoplankton metabolism and community structure. Ann. Rev. Mar. Sci. 7, 241–264. http://dx.doi.org/10.1146/annurev-marine-010814-015955.

Morton, R.W., 1972. Spatial and temporal distribution of suspended sediment in Narragansett Bay and Rhode Island Sound. Geological Society of America Memoir. 133, pp. 131–141

Moss, B., Kosten, S., Meerhoff, M., Battarbee, R.W., Jeppesen, E., Mazzeo, N., Havens, K., Lacerot, G., Zhengwen, L., De Meester, L., Paerl, H., Scheffer, M., 2011. Allied attack: climate change and eutrophication. Inland Waters. 1, pp. 101–105.

Narragansett Bay Commission. 2014. Dissolved inorganic concentrations in upper Narragansett Bay. Monitoring summary published by the Narragansett Bay Commission, updated 12/1/2014. Available at: http://snapshot.narrabay.com/app/.

National Institute for Standards and Technology, 2008. Guide for the use of the international system of units SI. In: Thompson, A., Taylor, B.N. (Eds.), NIST Special Publication, 2008 ed. 811 90 pp.

Nixon, S.W., 1997. Prehistoric nutrient inputs and productivity in Narragansett Bay. Estuaries 20, 253–261.

Nixon, S.W., Buckley, B.A., Granger, S.L., Harris, L.A., Oczkowski, A.J., Fulweiler, R.W., Cole, L.W., 2008. Nitrogen and phosphorous 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, Berlin, pp. 101–175.

Nixon, S.W., Fulweiler, R.W., Buckley, B.A., Granger, S.L., Nowicki, B.L., Henry, K.M., 2009. The impact of changing climate on phenology, productivity, and benthic–pelagic coupling in Narragansett Bay. Est. Coast. Shelf Sci. 82, 1–18.

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. A report to the Narragansett Bay Commission and Rhode Island Sea Grant from the Graduate School of Oceanography, University of Rhode Island, Narragansett, RI.

Nixon, S.W., Fulweiler, R.W., 2012. Ecological footprints and shadows in an urban estuary, Narragansett Bay, RI, USA. Reg. Environ. Change 12, 381–394. http://dx.doi.org/10.1007/s10113-011-0221-1.

Oviatt, C.A., Keller, A., Reed, L., 2002. Annual primary production in Narragansett Bay with no bay-wide winter–spring bloom. Estuar. Coast Shelf Sci 54, 1013–1026.

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

Oviatt, C.A., Nixon, S.W., 1975. Sediment resuspension and deposition in Narragansett Bay. Estuar. Coast. Mar. Sci. 3, 201–217.

Oviatt, C.A., Doering, P., Nowicki, B., Reed, L., Cole, J., Frithsen, J., 1995. An ecosystem level experiment on nutrient limitation in temperate coastal marine environment. Mar. Ecol. Prog. Ser. 116, 171–179.

Oviatt, C.A., Quinn, J.G., Maughan, J.T., Ellis, J.T., Sullivan, B.K., Gearing, J.N., Gearing, P.J., Hunt, C.D., Sampou, P.A., Latimer, J.S., 1987. Fate and effects of sewage sludge in the coastal marine environment: a mesocosm experiment. Mar. Ecol. Prog. Ser. 41, 187–203.

Pennock, J.R., Sharp, J.H., 1994. Temporal alternation between light- and nutrient-limitation of phytoplankton production in a coastal plain estuary. Mar. Ecol. Prog. Ser. 111, 275–288.

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

Pilson, M.E.Q., 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, Berlin, pp. 35–46.

Post, A.F., Dubinsky, Z., Wyman, K., Falkowski, P.G., 1985. Physiological responses of a marine planktonic diatom to transitions in growth irradiance. Mar. Ecol. Prog. Ser. 25, 141–149.

Postma, H., 1961. Suspended matter and Secchi disc visibility in coastal waters. Neth. J. Sea Res. 1, 359–390.

Pratt, D.M., 1965. The winter–spring diatom flowering in Narragansett Bay. Limnol. Oceanogr. 10, 173–184.

Prezelin, B.B., Alberte, R.S., 1978. Photosynthetic characteristics and organization of chlorophyll in marine dinoflagellates. Proc. Natl. Acad. Sci. U. S. A. 75, 1801–1804.

Riley, G.A., 1957. Phytoplankton of the north central Sargasso Sea. Limnol. Oceanogr. 2, 252–270.

Rodionov, S.N., Krovnin, A.S., 1992. The 1980's in the context of climatic changes in the North Atlantic region. ICES Mar. Sci. Symp. 195, 93–102.

Sakshaug, E., Andresen, K., 1986. Effect of light regime upon growth rate and chemical composition of a clone of *Skeletonema costatum* from the Trondheimsfjord, Norway. J. Plankton Res. 8, 619–637.

Santschi, P.H., Nixon, S., Pilson, M., Hunt, C., 1984. Accumulation of sediments, trace metals (Pb, Cu) and total hydrocarbons in Narragansett Bay, Rhode Island. Estuar. Coast. Shelf Sci. 19, 427–449.

SAS 2012. SAS JMP Statistical Software, version 10.0. SAS Institute, Inc.

Save the Bay, 1996. Wastewater Treatment Plant Performance Survey, 1994 and 1995. Save the Bay, Inc. Providence, RI. 51 pp. and 83 p. Appendix.

Scheffer, M., Straile, D. van Nes, E.H, and Hosper, H. 2001. Climactic warming causes regime shifts in lake food webs. Limnol. Oceanogr., 46: 1780–1783.

Schenck, H., Davis, A., 1973. A turbidity survey of Narragansett Bay. Ocean Eng. 2, 169–181.

Sharp, J.H., 1983. The distribution of inorganic nitrogen and dissolved and particulate organic nitrogen in the sea. In: Carpenter, E.J., Capone, D.G. (Eds.), Nitrogen in the Marine Environment. Academic Press, New York, NY, pp. 1–36.

Smayda, T.J., 1973. The growth of *Skeletonema costatum* during a winter–spring bloom in Narragansett Bay, Rhode Island. Norw. J. Bot. 20, 219–247.

Smayda, T.J., 1974. Bioassay of the growth potential of the surface water of lower Narragansett Bay over an annual cycle using the diatom *Thalassiosira pseudonanna* oceanic clone 13-1. Limnol. Oceanogr. 19, 889–901.

Smayda, T.J., 1984. Variations and long-term changes in Narragansett Bay, a phytoplankton-based coastal marine ecosystem: relevance to field monitoring for pollution assessment. In: White, H. (Ed.), Concepts in Marine Pollution Measurements. Univ. Maryland, College Park, MD, pp. 663–679.

Smayda, T.J., 1998. Patterns of variability characterizing marine phytoplankton, with examples from Narragansett Bay. ICES J. Mar. Sci. 55, 562–573.

Smayda, T.J., Borkman, D.G., 2008. Nutrient and phytoplankton gradients in Narragansett Bay. In: Desbonnet, A., Costa-Pierce, B. (Eds.), Science for Ecosystem-Based Management: Narragansett Bay in the 21st Century. Springer, Berlin, pp. 423–476.

Sullivan, B.K., Van Keuren, D., Clancy, M., 2001. Timing and size of blooms of the ctenophore *Mnemiopsis leidyi* in relation to temperature in Narragansett Bay, RI. Hydrobiologia 451, 113–120.

Verity, P., 1981. Effects of temperature, irradiance, and day length on the marine diatom *Leptocylindrus danicus* Cleve. I. Photosynthesis and cellular composition. J. Exp. Mar. Biol. Ecol. 55, 79–91.

Yoder, J.A., 1979. Effect of temperature on light-limited growth and chemical composition of *Skeletonema costatum* Bacillariophyceae. J. Phycol. 15, 362–370.

Zehr, J.P., Ward, B.W., 2002. Minireview: nitrogen cycling in the ocean: New perspectives on processes and paradigms. Appl. Environ. Microbiol. 68, 1015–1024.