Journal of Sea Research 61 (2009) 84–94

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Multidecadal (1959–1997) changes in *Skeletonema* abundance and seasonal bloom patterns in Narragansett Bay, Rhode Island, USA

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ARTICLE INFO

Article history:
Received 30 September 2008
Accepted 6 October 2008
Available online 17 October 2008

Keywords:
Narragansett Bay
Skeletonema
Phytoplankton Time Series
Climate Change
North Atlantic Oscillation
Long-term Change
Northwest Atlantic
Phytoplankton Trends

ABSTRACT

A 38-year time series (January 1959 to May 1997) of weekly observations of abundance of the marine diatom *Skeletonema* spp. and related plankton habitat parameters in lower Narragansett Bay, Rhode Island was compiled and analyzed. A statistical change point test identified two different abundance regimes characterized by a *ca.* 45% decline in *Skeletonema* abundance. In the first 260 months of the time series (January 1959 to August 1980), the mean deseasonalized *Skeletonema* abundance was 2137 cells ml^{-1}, which declined to 1128 cells ml^{-1} in the final 201 months (August 1980 to May 1997) of the time series. The decline was greatest during the winter–spring bloom period; *Skeletonema* abundance in March declined from a mean of *ca.* 3300 cells ml^{-1} prior to the change-point to *ca.* 700 cells ml^{-1} after the change point.
Skeletonema exhibited three types of annual abundance patterns: winter–spring, summer and autumn bloom peaks. A decline in winter–spring *Skeletonema* abundance was part of a shift away from winter–spring bloom dominated annual cycles in the 1960s to summer bloom dominated annual cycles in the 1990s. Of 25 years suitable for analyses, *Skeletonema* winter–spring bloom dominated in 12 years, summer blooms dominated in ten years and autumn blooms dominated three years. Winter–spring *Skeletonema* bloom years tended to be bright, windy, cold, and have lower copepod (*Acartia hudsonica*) abundance in the first quarter, and were cool and had high *A. hudsonica* abundance in the fourth quarter. In contrast, during summer and fall *Skeletonema* bloom years the first quarters were darker, warmer, less windy and accompanied by higher first quarter *A. hudsonica* abundance. In summer and fall bloom years the fourth quarters were warm and had above-mean river flow and low *A. hudsonica* abundance. The observed first quarter environmental differences between winter–spring and summer–fall bloom years (*i.e.*, water temperature, wind, light) may be partially regulated by changes in weather induced by large-scale atmospheric circulation patterns. Years in which the North Atlantic Oscillation (NAO) index was relatively low (mean = −1.4) tended to have colder winters, and winter–spring bloom dominated *Skeletonema* annual cycles; years with high NAO index (>+1.1) featured warmer winters and summer or autumn *Skeletonema* blooms.

1. Introduction

Habitat variability is an inherent part of the phytoplanktonic life mode, affecting both growth and loss processes at the cellular, population and phytoplankton community levels. In temperate coastal waters, strong seasonal variation in physical habitat parameters (light, day-length, temperature, water column mixing) and concomitant changes in chemical (nutrients) and biological (growth and grazing rates) parameters lead to seasonally varying envelopes, *i.e.* ranges, in phytoplankton abundance patterns (Smayda, 1980; Reynolds, 1997; Longhurst, 1998). However, phytoplankton patterns in a given coastal (Smayda, 1998) or offshore region (Yoder et al., 1993) are not predictably constant over multiple years (Hulburt, 1983), and may even display chaotic behavior (Sugihara and May, 1990; Scheffer, 1991; Beninca et al., 2008). As a result, in those locations having long-term (>10 years) taxon-specific phytoplankton monitoring, long-term patterns of phytoplankton species abundance are often characterized by trends (Smayda, 1998; Smayda et al., 2004) and/or sudden shifts (Cloern et al., 2007) rather than perennially consistent levels. Such phytoplankton shifts are often accompanied by changes in 'marine climate' (Dayton et al., 1999) or local changes, for example, in nutrient loading (Cloern, 2001; Anderson et al., 2002) or grazing pressure (Deason and Smayda, 1982a,b; Cloern, 1996), which presumably alter the balance between phytoplankton growth and loss processes, with resultant changes in phytoplankton abundance. The combination of long-term changes in both local (watershed-scale) and distant (regional- to hemispherical-scale) climate influences on coastal waters may obscure understanding of processes driving long-term phytoplankton changes (Smetacek and Cloern, 2008).

The phytoplankton of Narragansett Bay (Rhode Island, USA; Fig. 1) has been monitored on a regular basis since the late 1950s (Smayda,

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doi:10.1016/j.seares.2008.10.004

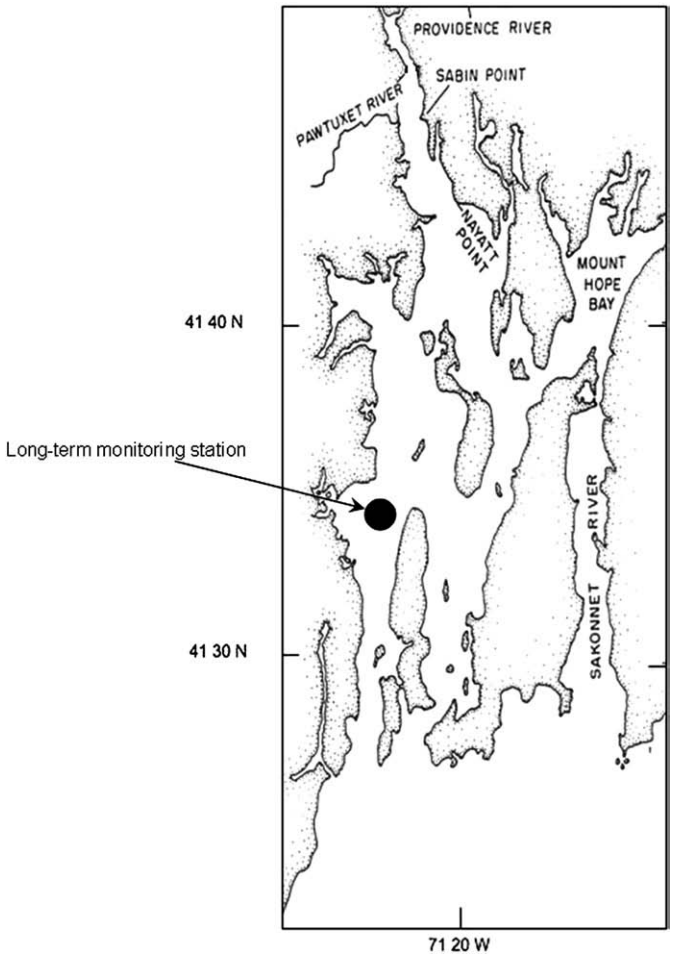

Fig. 1. Narragansett Bay, Rhode Island, USA showing location (41° 34′ 07″ N, 71° 23′ 31″ W) of long-term monitoring site in the lower West Passage of the bay.

1957; Pratt, 1959) with the patterns of phytoplankton bloom timing and abundance levels of dominant species generally established (Karentz and Smayda, 1984, 1998). Recent observations suggest that phytoplankton abundance in lower Narragansett Bay has declined (Li and Smayda, 1998; Fulweiler et al., 2007), especially during winter–spring months, a change speculated to have been in response to recent warming of winter water temperature and subsequent increases in temperature-dependent zooplankton grazing rate during winter (Keller et al., 1999). Winter water temperatures in Narragansett Bay and nearby regions have increased by 1.5–2.5 °C since the 1960s (Cook et al., 1998; Keller et al., 1999; Nixon et al., 2004; Smayda, unpublished). This warming appears to be partially related to changes in winter atmospheric circulation patterns of North Atlantic Oscillation (NAO) (Hawk, 1998; Keller et al., 1999). Consistent with increased temperature and the hypothesized increases in winter grazing, declines in winter–spring diatom abundance have occurred. An example of this is the dramatic decline in the abundance of the Arctic–Boreal diatom *Detonula confervacea* from mean winter (January–March) abundance of >2000 cells ml^{-1} during the 1960s to <500 cells ml^{-1} during the 1990s (Smayda et al., 2004). The decline in this Arctic–Boreal diatom might be expected given that Narragansett Bay is located (*ca.* 41° N latitude) at the biogeographic boundary between temperate and boreal coastal waters (Smayda et al., 2004). However, the decline in phytoplankton biomass has not been limited to the winter–spring. Mean annual biomass (using chlorophyll *a* as a proxy) decreased at a rate of *ca.* 1 mg m^{-2} per year in lower Narragansett Bay between 1973 and 1990, declining from *ca.* 50 mg chlorophyll m^{-2} in the early 1970s to *ca.* 30 mg chlorophyll m^{-2} in 1990 (Li and Smayda, 1998). Biomass (as chlorophyll) remained low (*ca.* 20–30 mg chlorophyll m^{-2}) in the late 1990s and early 2000s, and may have impacted the magnitude of benthic nitrogen flux (Fulweiler et al., 2007).

Diatoms of the genus *Skeletonema* comprise a large portion of the phytoplankton community in lower Narragansett Bay (Karentz and Smayda, 1984, 1998; Borkman, 2002) and in coastal temperate marine phytoplankton communities globally (Smayda, 1958; Braarud, 1962). In this paper, we analyze a 1959–1997 time series of weekly *Skeletonema* spp. abundance, and related planktonic habitat observations in lower Narragansett Bay. A high level of genetic (Gallagher, 1980) and physiological (Gallagher, 1982) variability has been identified for Narragansett Bay *Skeletonema*. The genus *Skeletonema* has been recently revised based on new ultrastructural (Zingone et al., 2005) and genetic (Sarno et al., 2005; Godhe et al., 2006; Kooistra et al., 2008) analyses. Based on this revision, there are at least two *Skeletonema* species in lower Narragansett Bay (Sarno et al., 2005; Kooistra et al., 2008) within the putative morpho-species *Skeletonema costatum* identified via light microscopy during the 1959–1997 time series. Here we analyze a 1959–1997 time series of weekly *Skeletonema* spp. (hereafter referred to as "*Skeletonema*") observations in lower Narragansett Bay to assess any long-term changes in its abundance level and seasonal pattern, and to evaluate the potential drivers and impacts of these changes.

2. Methods

2.1. Study site and sampling program

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 contiguous with Rhode Island and Long Island Sounds (Fig. 1). It lies within the coastal region extending from Maine to Virginia characterized by "extensive geographic continuity" in meteorology, climatic trends, and anomalies in air temperature, precipitation, wind stress and irradiance (Ingham, 1982). Nutrient-enriched freshwater flows into the upper bay via the Providence River estuary to produce a salinity - nutrient gradient with low salinity (*ca.* 20) and elevated nutrient at the head of the bay and higher salinity (*ca.* 33), and decreased nutrient at its entrance (Kremer and Nixon, 1978; Smayda and Borkman, 2008). The mean residence time of Narragansett Bay water is 26 days, varying from 10 to 40 days dependent on the volume of freshwater input and wind conditions (Pilson, 1985). Tidal currents dominate the circulation in which higher salinity water flows into Narragansett Bay from Rhode Island Sound through East Passage, and lower salinity water flows southward exiting through West Passage (Hicks, 1959) although more recent studies reveal a more complex physical oceanography than reported by these previous investigations (see Kincaid et al., 2003, 2008).

Between January 1959 and May 1997, surface water samples were collected weekly at a long-term monitoring station (41° 34′ 07″ N, 71° 23′ 31″ W) in the West Passage of lower Narragansett Bay, Rhode Island, USA (Fig. 1; see also Pratt, 1959, 1965; Smayda, 1973), and analyzed for phytoplankton numerical abundance, species composition, and related chemical (nutrient: NH_4, NO_3, $Si(OH)_4$, PO_4), meteorological, and physical (salinity, temperature, Secchi depth) properties. Details of the methodology are available in Smayda (1973; phytoplankton abundance), Furnas (1982, 1983; nutrient concentration), Deason (1980) and Fofonoff (1994; zooplankton abundance). Live phytoplankton counts were made using a Sedgwick–Rafter chamber scanned at 250× magnification using either Olympus or Zeiss microscopes equipped with phase contrast optics. For each of the 1430 weekly samples counted during January 1959 to May 1997, the entire 1 ml chamber was examined, giving a nominal *Skeletonema* detection limit of 1 cell ml^{-1}. Records of local meteorological variables, including wind speed and precipitation (monitored at T.F. Green

Airport by NOAA, 1959–1997), and river flow (monitored at various gauging stations; USGS, 1959–1996) were also compiled (see Smayda, 1998). Environmental indices were also used, including the NAO index of Hurrell (1995; available at: www.met.rdg.ac.uk/cag/NAO/Data.html) and an index of the position of the north wall of the Gulf Stream as it turns eastward, away from the coast of North America (see Taylor 1995, 1996; available at: http://www.pml.ac.uk/pml/Gulfstream/inetdat.htm).

While samples were usually collected weekly, quantitative phytoplankton data are not available for 1987, 1992 and 1993, the second halves of 1963, 1982 and 1986 and the first halves of 1988 and 1994. Sampling was bi-weekly in 1990 and 1991. Other gaps in the weekly data collections were distributed randomly throughout the sampling period. For the 38-year time series (1995 weeks), data on phytoplankton abundance data are available for 1430 weeks (72%), with at least one sample collected in 381 of the 461 months. Linear interpolation was used to fill in single week gaps in the *Skeletonema* time series, resulting in 24 of the 38 years having all 52 weeks of data for analyses. The mean sampling frequency during 1959–1997 averaged one sample every ten days. While this paper analyzes the 1959–1997 data, regular sampling was resumed in January 1999 after an 18-month (June 1997–December 1998) sampling gap. The post-1999 Narragansett Bay plankton time series data (available at www.gso.uri.edu/phytoplankton) are not analyzed here; however some portions of the later data are discussed for comparison to the 1959–1997 observations and analyses.

2.2. Statistical analyses

Skeletonema abundance data were checked for normality with the Shapiro–Wilk test; the distribution of raw *Skeletonema* counts was not normal (W:normal of 0.567, $p=0.0001$), but skewed to the right, with a strong linear dependence of annual variance on mean annual abundance ($r^2=0.84$, $p=0.0001$, $n=35$ years). Therefore, raw cell abundance data were transformed before statistical analyses to stabilize the variance and to reduce the skew of the data. The natural logarithm (ln) transform (Karentz and Smayda, 1984) was used with the minimum cell detection level (1 cell ml^{-1}) added to all values prior to transformation. If zero values are common in a time series, the ln-transform may not be appropriate, since it may fail to normalize the error distribution (Broekhuizen and McKenzie, 1995). However, zero values (*i.e.*, *Skeletonema* not detected) were only found in about 4% of the *Skeletonema* observations. The natural log transform stabilized variance and removed the linear dependence of annual *Skeletonema* variance on annual mean abundance. Accordingly, ln transformed data were used to analyze *Skeletonema* trends and annual patterns, but back-transformed values in original units (*i.e.*, cells ml^{-1}) are reported in the text and figures.

The weekly observations ($n=1\,430$) of *Skeletonema* abundance were pooled into monthly mean values, and the resultant 461 month time series (January, 1959 to May, 1997) was analyzed for trends and seasonal abundance patterns. Observations were available in 381 of the 461 months of the time series, *i.e.*, missing data (gaps) represented 17% of the time series. The bulk of the missing data is from the three years that lack observations (1987, 1992, and 1993). Adverse effects of data gaps in analyses of time series are influenced by the length of the gap relative to the entire time series length (Emery and Thomson, 1997). For the *Skeletonema* time series, the longest consecutive gap was 24 months (*ca.* 5% of 461 months). Monte Carlo simulations have indicated that data gaps of up to 30% of the time series length can be interpolated without significant loss of a signal if the gap is $<1/3$ of the period of the signal of interest (Sturges, 1983). Accordingly, given a maximum gap of two years, the *Skeletonema* time series should be able to identify trends with periods of > six years duration. Gaps in the data (notably 1987, 1992, and 1993) were filled by interpolation using a natural cubic spline (second derivatives of end points set to zero; Emery and Thomson, 1997). The fit of the interpolated data was tested by comparing interpolated values to known data segments and yielded a correlation of 0.83 ($n=361$, $p<0.001$).

To decompose the time series into long-term trend and seasonal components, methods similar to those used in analyzing a 34 year time series of North Sea zooplankton abundance (Broekhuizen and McKenzie, 1995) were utilized. Briefly, the long-term trend was first estimated by calculating a 12-month moving average smoother of the raw observations. At each monthly time-step, the 12-month moving average trend was subtracted from the monthly *Skeletonema* observations to yield residuals used as an initial estimate of the seasonal component of the time series. The seasonal component estimates (monthly residuals) were then subtracted from the original monthly time series to give a deseasonalized time series representing the long-term trend. This trend was smoothed by a moving average smoother with a window equivalent to 15% of the time series (69 months). Sixty-nine months was chosen as an averaging window because it corresponds to approximately three times the length of the largest data gap, and is the minimum period in which trends in this time series are expected to be detected (Sturges, 1983). The estimated long-term trend was well correlated with observed mean annual *Skeletonema* abundance (r^2 of mean annual observed *Skeletonema* and the estimated deseasonalized trend was 0.93, $n=27$ years, $p=0.0001$). Seasonal (monthly) *Skeletonema* patterns for each year of the time series were then estimated by subtracting the long-term trend from each monthly observation of the time series.

The presence of change points in the original (raw counts) *Skeletonema* time series was determined using a non-parametric (rank transform) change point test that allows estimation of significance levels associated with the change point (Page, 1955, 1957; Pettit, 1979). In a series of observations (x1, x2,…,xn) this change point statistic tests the null hypothesis that all the observations in the entire series come from the same population against the alternative hypothesis that part of the time series (x1,…,xm) has a different distribution function than the remainder of the time series (xm+1,…,xn). The change point, as identified by the test, is the observation in the time series at which the difference in distributions (in this example xm) is detected. This type of test has been used to identify change points driven by climate change in a 140 year record of date of ice break-up in Lake Baikal (Livingstone 1997, 1999).

Seasonal *Skeletonema* patterns, derived from the time series analysis above, for each year were analyzed by cluster analysis to identify different *Skeletonema* annual patterns. The average linkage method (unweighted pair-group method using arithmetic averages; or UPGMA) was used in cluster analysis. Once identified, the monthly *Skeletonema* abundance within each annual bloom pattern was calculated and plotted to identify types of *Skeletonema* annual cycles. Monthly means among cluster types were compared by the Kruskal–Wallis test with Dunn's multiple comparison post test. The quarterly and annual means of environmental variables (temperature, irradiance, nutrient concentration, zooplankton abundance, etc.) associated with each bloom pattern were also compared by Kruskal–Wallis test followed by Dunn's multiple comparison post test to compare mean ranks. Because the number of occurrences of one bloom pattern (group 3, autumn bloom) was small ($n=3$), distribution of the Kruskal–Wallis H statistic may not have approximated a Chi-square distribution. Accordingly, we used critical values of the H statistic distribution for small sample sizes (Zar, 1999; Table B13) and have provided the Kruskal–Wallis H statistic in tables comparing bloom patterns.

3. Results

3.1. Skeletonema abundance

Skeletonema spp. abundance ranged from 0 to 108,750 cells ml^{-1}; the overall mean *Skeletonema* abundance during January, 1959 to May,

1997 was 2087 cells ml^{-1}. Mean annual abundance varied by greater than 25-fold, from a maximum of 3525 cells ml^{-1} during 1984 to an annual minimum of 134 cells ml^{-1} in the following year (1985). Decadal mean *Skeletonema* abundance declined from >2000 cells ml^{-1} during the 1960s (2087 cells ml^{-1}) and 1970s (2327 cells ml^{-1}) to *ca.* 1500 cells ml^{-1} during the 1980s (1425 cells ml^{-1}) and 1990s (1533 cells ml^{-1}). *Skeletonema* comprised a mean of 42% of total diatom abundance; its contribution to mean annual total diatom abundance during 1959–1997 ranged from 11% (1985) to 69% (1971). The long-term pattern in *Skeletonema's* mean annual abundance explained *ca.* 70% of the long-term variation in total diatom abundance (Fig. 2). Embedded within this pattern was an apparent decline in the percentage of total diatoms comprised by *Skeletonema*, which declined from a decadal mean of 48–50% (1960s and 1970s) to 33% of total diatoms during the 1980s and the first seven years of the 1990s.

Decomposition of the 1959–1997 time series into a long-term trend and seasonal pattern revealed a trend of relatively constant mean deseasonalized *Skeletonema* abundance of *ca.* 2000 cells ml^{-1} from the 1960s to the early 1980s. This deseasonalized trend represents the base *Skeletonema* abundance level, about which the seasonal pattern fluctuated. During the 1980s, the *Skeletonema* trend fell progressively until a level of <1000 cells ml^{-1} was reached during the 1990s (Fig. 3). More recent observations (data available at www.gso.uri.edu/phytoplankton) indicate that *Skeletonema* abundance during 1999–2005 has remained near the lower abundance level observed in the mid-1990s, with a 1999–2005 mean abundance level of 1220 cells ml^{-1}.

The non-parametric change point test also indicated that the 1980s were a period of significant change in *Skeletonema* abundance in lower Narragansett Bay. This non-parametric change point test identified August, 1980 as the dominant change point in the January 1959–May 1997 time series. This change point represents a threshold in the time series that maximizes the difference in the mean abundance levels prior to and following the change point. For *Skeletonema* in lower Narragansett Bay, the change point in August, 1980 marked a significant shift (p=<0.0001; Wilcoxon 2-sample test), from a mean abundance level of 2137 cells ml^{-1} during January 1959–August 1980 to a level of 1128 cells ml^{-1} during the period from September 1980 to May 1997 (Fig. 3).

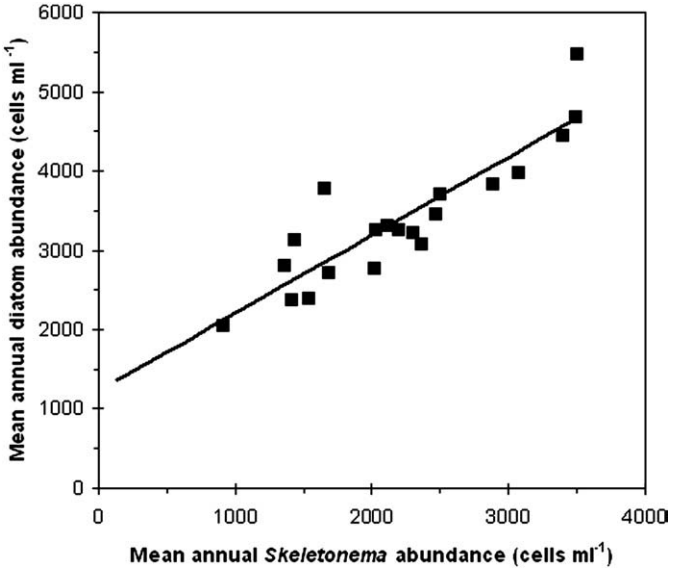

Fig. 2. Contribution of mean annual *Skeletonema* spp. abundance to mean annual diatom abundance. Variation in *Skeletonema* spp. annual abundance explained 69% of the variance in total diatom abundance during 1959–1996 (y=1.067×+1194; r^2=0.69, n=30, p<0.0001).

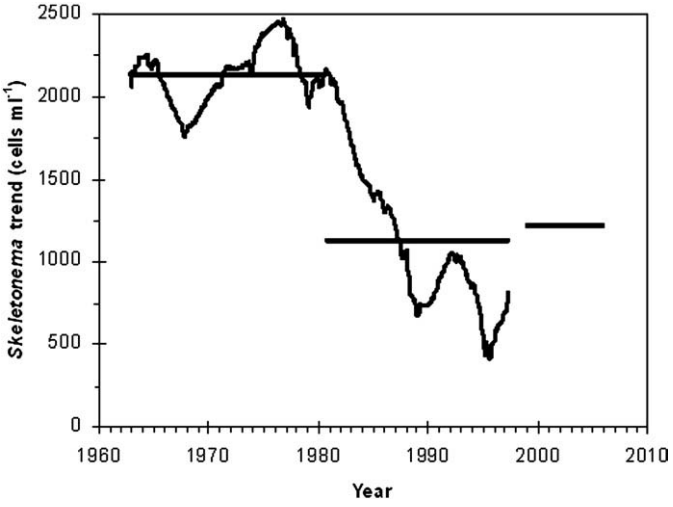

Fig. 3. Long-term (1959–1997) lower Narragansett Bay *Skeletonema* spp. trend derived from time series analysis (continuous line). Mean *Skeletonema* abundance levels (2137 cells ml^{-1}) prior to, and after (1128 cells ml^{-1}) an August 1980 change point, and the mean abundance during 1999–2005 (1220 cells ml^{-1}) all shown as horizontal lines.

This *ca.* 50% reduction in *Skeletonema* abundance during the 1980s was not evenly distributed throughout the year. Analysis of monthly *Skeletonema* abundance indicated that *Skeletonema* declines after the 1980 change point were greatest during the winter–spring and autumn months. Six months of the year (January, March, May, September, October, and November) displayed significant differences in *Skeletonema* abundance after the 1980 change point (Table 1). *Skeletonema* abundance during March declined nearly 5-fold from 3281 cells ml^{-1} (95% C.I.=1584–4978 cells ml^{-1}; n=21) prior to the 1980 change point to 708 cells ml^{-1} (95% C.I.=0–1607 cells ml^{-1}; n=12) after the change point (Fig. 4). Monthly *Skeletonema* abundance declined in all months showing significant change, except during October when its abundance increased post-1980 (Table 1), primarily due to an October, 1999 bloom of *ca.* 18,000 cells ml^{-1}. The sharp post-1980 decline in March *Skeletonema* abundance marked the demise of the prolonged (January–April) *Skeletonema* winter–spring bloom often observed prior to 1980.

The long-term, declining trend in *Skeletonema* abundance (Fig. 3) was statistically associated with several environmental parameters

Table 1
Comparison of monthly mean *Skeletonema* spp. abundance before and after an August 1980 change point. Abundance values are monthly means for the periods prior to and after the change point year. p-value is for Wilcoxon 2-sample test comparing mean abundance before and after change point. Ratio of mean abundance after:before change point year given

Skeletonema spp. abundance (cells ml^{-1})				
	Before	After		Ratio
Month	Mean (95% C.I.; n)	Mean (95% C.I.; n)	p-value	(after/before)
January	4687 (1561–7813; 21)	1586 (0–3779; 12)	0.0414	0.34
February	2909 (1691–4168; 22)	3173 (0–8158; 12)	0.1170	
March	3281 (1584–4978; 21)	708 (0–1607; 12)	0.0014	0.22
April	2424 (964–3883; 21)	908 (0–1866; 11)	0.0519	
May	1461 (797–2129; 20)	908 (0–2393; 12)	0.0186	0.62
June	284 (67–500; 21)	1410 (0–3387; 12)	0.5874	
July	1529 (416–2642; 20)	1262 (0–2783; 10)	0.8431	
August	7687 (3977–11,400; 20)	4280 (1662–6897; 12)	0.2509	
September	2001 (911–3091; 20)	453 (0–928; 12)	0.0009	0.23
October	848 (38–1658; 20)	1512 (0–4489; 13)	0.0487	1.78
November	311 (0–688; 20)	177 (0–537; 11)	0.0390	0.57
December	358 (122–595; 21)	242 (0–531; 12)	0.1497	

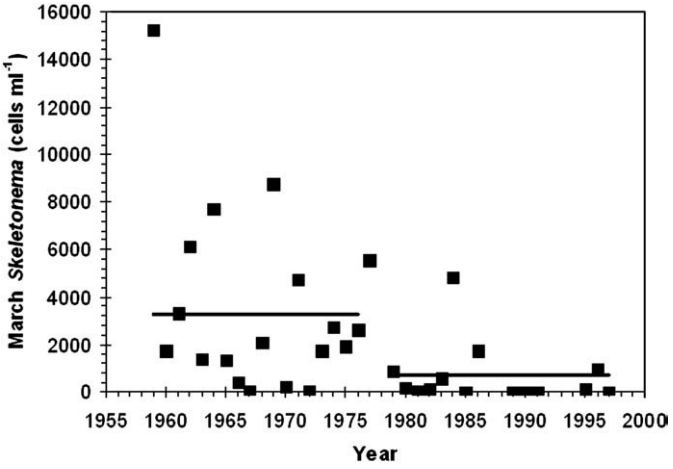

Fig. 4. Long-term (1959–1997) March abundance of *Skeletonema* abundance (data points), horizontal lines indicate mean March *Skeletonema* abundance prior to (3281 cells ml^{-1}) and after (708 cells ml^{-1}) a 1980 change point in *Skeletonema* abundance.

(Table 2). Strong significant positive correlation was found between the declining *Skeletonema* trend and declining chlorophyll concentration; between *Skeletonema* and winter (1Q) irradiance, and between *Skeletonema* and winter (1Q) wind speed. Strong negative correlation was found between the *Skeletonema* trend and several metrics of copepod (*Acartia tonsa*) abundance, between *Skeletonema* and the winter NAO index, and between *Skeletonema* and second quarter (April–June) water temperature. Note that nutrient concentrations and *Skeletonema* were only moderately associated, and of these, only P and Si were significantly associated with the *Skeletonema* trend. Many of the environmental parameters related to the long-term *Skeletonema* decline were seasonally restricted to winter (1Q) or spring (2Q) mean values, indicating the importance of winter–spring events in the environmental regulation of long-term *Skeletonema* abundance in Narragansett Bay.

Table 2
Significant ($p<0.05$) associations (Pearson correlation coefficients) between the long-term *Skeletonema* trend and annual or quarterly means of environmental variables. 1Q, 2Q, 3Q, 4Q refer to first through fourth quarter mean values; integrated chlorophyll and nutrient values calculated from surface, mid-depth and bottom observations; *n* refers to number of years or quarters in each comparison

Correlation between *Skeletonema* trend and:	Pearson correlation coefficient	*n*	*p*-value
1Q surface chlorophyll (μg l^{-1})	+0.62	25	0.0008
Mean annual irradiance (W m^{-2})	+0.54	38	0.0005
2Q integrated chlorophyll (mg m^{-2})	+0.53	24	0.0082
1Q irradiance (W m^{-2})	+0.53	38	0.0007
Mean annual integrated chlorophyll (mg m^{-2})	+0.52	19	0.0212
1Q wind speed (m s^{-1})	+0.50	38	0.0013
Mean annual surface chlorophyll (μg l^{-1})	+0.49	20	0.0270
2Q surface chlorophyll (μg l^{-1})	+0.47	24	0.0202
2Q irradiance (W m^{-2})	+0.35	38	0.0332
Mean annual wind speed (m s^{-1})	+0.34	38	0.0350
2Q integrated phosphate (mg m^{-3})	−0.40	27	0.0364
4Q Secchi depth (m)	−0.41	24	0.0441
2Q surface silica (μM)	−0.44	31	0.0131
1Q SST (°C)	−0.44	38	0.0057
Gulf Stream index	−0.45	31	0.0119
Mean annual Secchi depth (m)	−0.45	24	0.0164
2Q SST (°C)	−0.49	38	0.0017
1Q *Acartia tonsa* (# m^{-3})	−0.49	19	0.0332
NAOI winter index	−0.54	38	0.0005
1Q Secchi depth (m)	−0.58	25	0.0024
3Q *A. tonsa* (# m^{-3})	−0.65	15	0.0084
Mean annual *A. tonsa* (# m^{-3})	−0.68	15	0.0056

3.2. Skeletonema annual bloom pattern

Three types of *Skeletonema* annual bloom patterns were identified by cluster analysis of the de-trended monthly residuals derived from the time series decomposition. A bi-modal (winter–spring and summer blooms) bloom pattern with the winter–spring bloom greater (Group 1); a unimodal pattern with reduced winter–spring bloom and a large summer bloom (Group 2); and a pattern of peak *Skeletonema* abundance in the autumn (Group 3). In 12 of the years the winter–spring bloom was the dominant feature of the annual *Skeletonema* cycle (Group 1; 1959, 60, 61, 62, 64, 66, 68, 69, 71, 76, 84, 96; Fig. 5a). Ten of the 25 years classified had an annual cycle dominated by a summer *Skeletonema* bloom (Group 2; 1965, 67, 70, 72, 74, 75, 83, 89, 91, 95; Fig. 5b), and three of the 25 years (Group 3; 1973, 85, 90; Fig. 5c) were 'autumn bloom' years in which *Skeletonema* abundance was below the long-term trend for the first seven months of the year, followed by above average abundance in August, followed by an autumn bloom during October. There were significant differences in monthly mean *Skeletonema* abundance levels among the three different bloom patterns in five of the winter–spring months (January

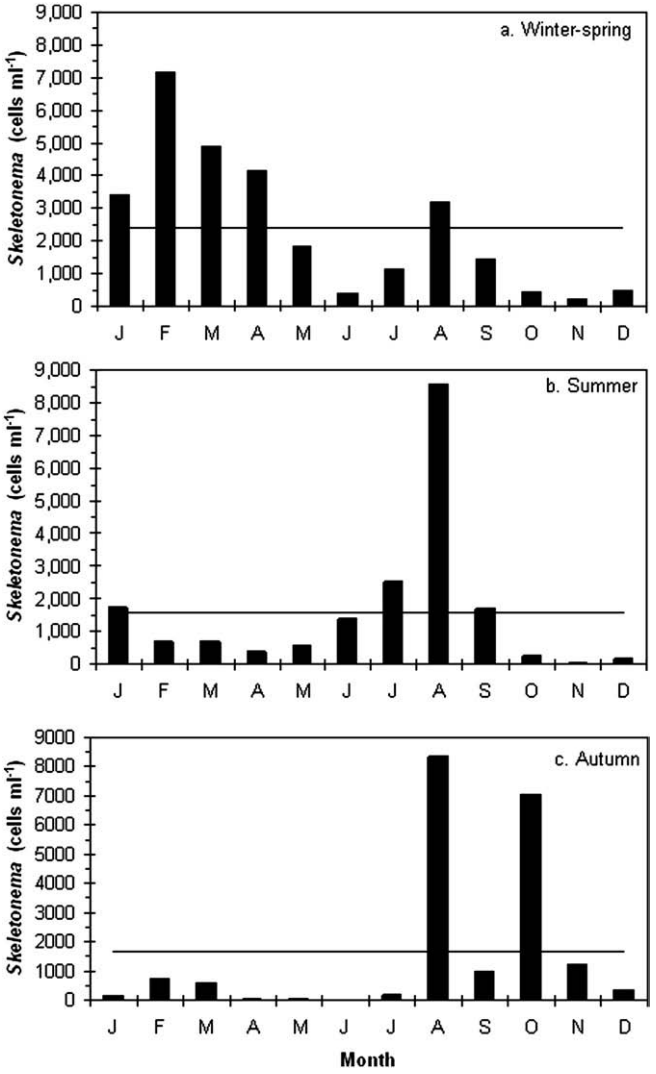

Fig. 5. Three types of patterns in Narragansett Bay *Skeletonema* spp. annual abundance as identified by cluster analysis. Mean monthly *Skeletonema* abundance in years having winter–spring (a.), summer (b.) and, autumn (c.) bloom pattern. The mean annual *Skeletonema* abundance during winter–spring (2393 cells ml^{-1}), summer (1550 cells ml^{-1}) and, autumn (1655 cells ml^{-1}) bloom years are indicated by horizontal lines.

Table 3
Monthly mean *Skeletonema* spp. abundance (cells ml^{-1}) and 95% confidence intervals for three bloom patterns (winter–spring, summer, autumn) identified by cluster analysis. Values in bold are maxima within each month. Differences between monthly bloom pattern means were tested by Kruskal–Wallis test; with *p*-value and Kruskal–Wallis *H* statistic given. Months having significantly different ($p<0.1$) values were tested with Dunn's multiple comparison post-tests. Results of significantly different pairings given in post test column; post test notation: 1=winter–spring, 2=summer. 3=autumn bloom pattern

Annual bloom pattern					
	Winter–spring	Summer	Autumn		
Month	(95% C.I.)	(95% C.I.)	(95% C.I.)	*p*-value (*H*)	Post test
January	3392 (1417–5367)	1726 (0–4302)	131 (48–215)	0.0579 (5.70)	1–2, 2–3
February	7163 (2862–11,460)	711 (0–1641)	718 (48–2462)	0.0003 (16.04)	1–2, 2–3
March	4887 (2230–7544)	711 (21–1401)	586 (0–3083)	0.0015 (13.01)	1–2, 1–3
April	4148 (1945–6350)	399 (0–1009)	28 (0–126)	0.0003 (16.58)	1–2, 1–3
May	1816 (312–3319)	579 (0–1187)	34 (0–105)	0.0321 (6.88)	1–3, 2–3
June	392 (7–777)	1408 (0–3831)	5 (0–16)	0.0312 (6.93)	1–3, 2–3
July	1143 (0–2344)	2521 (0–4825)	203 (0–1065)	0.1459 (3.85)	
August	3184 (1475–4894)	8564 (3542–13,170)	8354 (0–36,190)	0.1258 (4.83)	
September	1435 (332–2538)	1715 (0–3806)	980 (0–4980)	0.4706 (1.51)	
October	433 (0–924)	253 (0–592)	7029 (0–30,630)	0.2415 (2.84)	
November	235 (0–558)	56 (0–137)	1221 (0–6442)	0.6251 (0.94)	
December	487 (82–892)	162 (0–333)	363 (0–1710)	0.4383 (1.65)	
Annual mean	2393 (1948–2872)	1550 (999–2188)	1655 (0–5119)	0.0813 (4.83)	1–2

through June; Table 3). This suggests that winter–spring bloom dynamics were highly influential in structuring *Skeletonema's* annual cycle. The annual mean abundance that *Skeletonema* achieved in different bloom pattern years was significantly different. In winter–spring dominated years (Group 1=2393 cells ml^{-1}, $n=12$ years), annual mean *Skeletonema* abundance was significantly different (Kruskal–Wallis test $p=0.0183$) than in the summer (Group 2=1 550 cells ml^{-1}, $n=10$ years) and autumn bloom-peak years (Group 3, 1655 cells ml^{-1}, $n=3$ years). Applications of Dunn's multiple comparison post tests indicated that this was due to the difference between the elevated mean annual *Skeletonema* abundance achieved during winter–spring bloom years and repressed annual mean abundance achieved during summer bloom years.

3.3. Environmental control of the annual bloom pattern

To determine if there were differences in planktonic habitat associated with different *Skeletonema* bloom patterns, 22 environmental parameters (including meteorological [temperature, wind speed, irradiance, river flow, NAO index], nutrient [NH4, NO3, PO4, SI (OH),] and biological [chlorophyll *a*, *Acartia* abundance]) sampled synchronously with *Skeletonema* were compared by Kruskal–Wallis tests. Annual and quarterly means of these variables were compared for the different bloom patterns (Table 4). Significant differences were found in winter (first quarter, 1Q), autumn (fourth quarter, 4Q) and mean annual environmental variables. First quarter irradiance and wind speed were higher and first quarter temperature was lower in winter spring bloom years than in summer or autumn bloom years (Table 4), this suggests that bright, windy, cold winters favored winter–spring *Skeletonema* blooms. First quarter water column integrated silica was higher in years with dominant summer blooms (98.7 µmol m^{-2}) compared to first quarter silica in winter–spring bloom (50.6 µmol m^{-2}) and autumn bloom (35.3 µmol m^{-2}) years, primarily due to the elevated first quarter silica concentration observed during summer bloom years.

Fourth quarter (4Q) nutrient concentrations were lower during fall *Skeletonema* bloom years than in winter–spring or summer bloom years. For example, the mean 4Q surface nitrate level was 2.1 µmol in fall bloom years compared to 4Q nitrate levels of 5.6 µmol and 7.5 µmol in winter–spring and summer bloom years, respectively. 4Q phosphate and ammonia levels were also reduced during autumn bloom years. Water temperature (surface temperature) in the 4Q was *ca.* 1.5 °C higher (11.2 °C) in fall bloom years than in winter–spring (4Q SST=9.7 °C) and summer (4Q SST=10.1 °C) *Skeletonema* bloom years, with post tests indicating that the significant difference was attributable to the elevated 4Q temperature associated with the autumn *Skeletonema* bloom pattern.

Although the 95% confidence intervals around some of the estimated mean environmental values in years with different *Skeletonema* bloom patterns were large (Table 4), winter–spring *Skeletonema* bloom years

Table 4
Mean values and 95% confidence intervals of environmental variables having significantly different ($p<0.10$) means during winter–spring, summer and autumn bloom years. Mean values in winter–spring, summer, or autumn bloom pattern years were compared by Kruskal–Wallis test. 1Q, 2Q, 3Q, 4Q refer to first through fourth quarter mean values; integrated nutrient values calculated from surface, mid-depth (*ca.* 4 m) and bottom (*ca.* 8 m) observations. *p*-value and Kruskal–Wallis *H* statistic and significantly different pairings as indicated by Dunn's multiple comparison post tests are shown for each variable; post test notation: 1=winter–spring, 2=summer. 3=autumn bloom pattern

Skeletonema spp. bloom pattern					
	Winter–spring	Summer	Autumn		
Variable (units)	Mean (95% C.I.)	Mean (95% C.I.)	Mean (95% C.I.)	*p*-value (*H*)	Post test
1Q irradiance (W m^{-2})	55.9 (51.9–59.1)	49.3 (45.5–52.6)	48.2 (42.8–53.6)	0.0213 (7.70)	1–2, 1–3
1Q surface temperature (°C)	1.7 (1.3–2.1)	2.6 (1.9–3.3)	2.5 (0.6–4.4)	0.0500 (5.99)	1–2, 1–3
1Q wind speed (m s^{-1})	5.3 (5.1–5.7)	5.0 (4.9–5.2)	4.9 (4.8–5.0)	0.0158 (8.30)	1–2, 1–3
1Q integrated silica (mmol m^{-2})	50.6 (19.8–81.4)	98.7 (49.3–148.1)	35.3 (0–123.9)	0.0433 (6.28)	1–2, 2–3
1Q *Acartia hudsonica* (# m^{-3})	4 609 (0–24 420)	11 867 (8 906–15 101)	5 871 (0–12 160)	0.031 (6.91)6	2–3
Winter NAO (index)	−1.4 (−2.5–+0.1)	+1.1 (−0.4–+3.1)	+1.7 (0–+1.8)	0.0531 (5.82)	1–3
4Q surface temperature (°C)	9.7 (8.6–10.6)	10.1 (9.7–10.5)	11.2 (10.3–11.8)	0.0679 (5.19)	1–3, 2–3
4Q *A. hudsonica* (# m^{-3})	3483 (1016–5950)	1404 (465–2343)	892 (0–2237)	0.0863 (4.90)	1–3
4Q integrated ammonia (mmol m^{-2})	27.9 (0–63.8)	54.8 (36.7–73.0)	26.2 (0–54.6)	0.0373 (6.58)	2–3
4Q surface ammonium (µmol)	3.7 (0–10.5)	6.9 (5.5–8.4)	3.1 (0.3–5.9)	0.0320 (6.89)	2–3
4Q surface nitrate (µmol)	5.6 (2.6–8.5)	7.5 (4.6–10.4)	2.1 (0–6.6)	0.0778 (5.11)	2–3
4Q surface phosphate (µmol)	1.7 (1.2–2.1)	1.8 (1.3–2.2)	1.1 (0.9–1.3)	0.0549 (5.80)	1–3, 2–3
Annual irradiance (W m^{-2})	76.8 (74.3–79.2)	73.7 (71.4–76.1)	71.8 (69.9–73.7)	0.0627 (5.54)	1–3

tended to be bright, windy, cold, and have lower *Acartia hudsonica* abundance in the first quarter, and were cool and had high *A. hudsonica* abundance in the fourth quarter. In contrast, during summer and autumn *Skeletonema* bloom years, first quarters were darker, warmer, and less windy, and accompanied by higher *A. hudsonica* abundance. The fourth quarters were warm and had low *A. hudsonica* abundance. The 1Q environmental differences between winter–spring and summer–fall bloom years (*i.e.*, temperature, wind) may be partially regulated by changes in weather induced by large-scale atmospheric circulation patterns. The NAO index was lower (mean = −1.4) in winter–spring bloom years than in autumn (mean = +1.7) *Skeletonema* bloom years. Conditions associated with a winter–spring *Skeletonema* bloom pattern (*i.e.*, bright, cold winters, negative NAO index, fewer zooplankton) were typical of the 1960s, while habitat conditions associated with the summer bloom pattern (cloudy, warm winters, positive NAO index, increased winter zooplankton abundance) were more frequently observed during the 1990s.

4. Discussion

4.1. Long-term Skeletonema decline

Long-term changes in an organism's abundance may be indicative of changes in the control mechanisms limiting that population. The long-term pattern of *Skeletonema* abundance in Narragansett Bay exhibited a 22 year period (1959–1980) of relatively stable, elevated (*ca.* 2100 cells ml^{-1}) abundance, followed by a period of rapid decline subsequent to a change point detected in August 1980, and a second post-1990 relatively stable period of reduced (*ca.* 1100 cells ml^{-1}) abundance. The *ca.* 50% decline in *Skeletonema* abundance during the 1980s is consistent with observations that a similar decline in total phytoplankton biomass occurred in lower Narragansett Bay during the 1980s (Li and Smayda, 1998). The long-term decline in *Skeletonema* abundance appears to be part of a 're-oligotrophication' (Hase et al., 1998) response in Narragansett Bay (Nixon et al., 2008). This response has included decreasing phytoplankton biomass (Li and Smayda, 1998; Fulweiler et al., 2007) and a related increased in water clarity and *in situ* light levels (Borkman and Smayda, 1998). The variation in *Skeletonema's* long-term annual abundance pattern explained *ca.* 70% of the variance in total diatom abundance during 1959–1996 (*i.e.*, Fig. 2).

Skeletonema's contribution to the long-term phytoplankton biomass (chlorophyll) decline in Narragansett Bay was estimated using the light-dependent chlorophyll content data of a local *Skeletonema* clone (Langdon, 1987) and *in situ* light levels during 1972–1997. Applying this, the estimated amount of chlorophyll in the lower bay attributable to *Skeletonema* declined by *ca.* 40% from a mean of 1.5 μg l^{-1} prior to an August 1980, to 0.9 μg l^{-1} after the August 1980 change point. This decline parallels the overall decrease in chlorophyll from *ca.* 7 μg l^{-1} during the 1970s to *ca.* 4 μg l^{-1} in 1990 observed by Li and Smayda (1998), and is consistent with chlorophyll levels observed in the 2000s (URI GSO monitoring data; Smayda, unpublished; Fulweiler et al., 2007). The decline in *Skeletonema* chlorophyll is made up of two components: the decline in abundance related to the decreasing number of cells present, and the physiological component related to the chlorophyll content per cell. As with most diatoms, the cellular chlorophyll content of *Skeletonema* cells is partially dependent on ambient light levels, with a *ca.* 2.5-fold decrease in chlorophyll content developing in response to increases from low to high ambient light levels (Langdon, 1987; Anning et al., 2000). Based on the recent increases in lower bay water clarity (Borkman and Smayda, 1998) and the physiological response to this, the cellular chlorophyll content of *Skeletonema* is estimated to have decreased *ca.* 10% from *ca.* 0.60 pg chlorophyll $cell^{-1}$ during the 1970s to 0.55 pg chlorophyll $cell^{-1}$ during the 1990s. It is not known if this decline in cellular chlorophyll content is applicable to all diatoms in the bay, but diatoms generally decrease their chlorophyll content in response to increasing *in situ* light (Sakshaug and Andresen, 1986; Langdon, 1988; Falkowski and Raven, 1997; Goericke and Montoya, 1998).

While the effects of local factors such as changing anthropogenic nutrient input on plankton communities are difficult to discern from the effects of long-term climate variation (Greve et al., 1996), our analysis of *Skeletonema's* long-term abundance and bloom patterns suggests an important role of climate-related variables (NAO index, temperature, irradiance). The drastic decrease in *Skeletonema* abundance that began in 1980 parallels changes in oceanic/atmospheric circulation patterns in the North Atlantic that also began in the early 1980s. Northwestern Atlantic SST and wind/weather patterns are strongly influenced by North Atlantic atmospheric circulation patterns (Cayan, 1992), as summarized by the NAO index. In the northeastern US, years with high (positive) winter (December to February) NAO indices tend to have strong southern wind flow and mild winters; years with a low (negative) NAO state are characterized by colder winters (Hurrell, 1995). Beginning in the early 1980s, and through 1995, the NAO index was in an elevated state (see Hurrell, 1995), and concomitant increases in Narragansett Bay water temperature, especially winter temperatures, have been observed. Winter water temperatures in Narragansett Bay increased between 2.5 °C to 3.0 °C (Cook et al., 1998; Keller et al., 1999; Smayda, unpublished) during the 1959–1997 portion of the *Skeletonema* time series.

Small changes in temperature have been associated with dramatic changes in the abundance of phytoplankton in the eastern North Atlantic where qualitative sampling (CPR ocean colour) of North Sea phytoplankton has suggested that a mid-1980s step-wise increase in phytoplankton abundance may have occurred in response to warmer sea temperatures (Reid et al., 1998). In Narragansett Bay, Keller et al. (1999) showed that winter–spring phytoplankton abundance and grazer activity affecting the fate of phytoplankton production are sensitive to relatively small differences in winter water temperature. In mesocosm experiments, a winter (December through February) temperature decrease of 3 °C resulted in significantly decreased standing stocks of zooplankton and significantly higher chlorophyll concentrations in the cold treatment compared to the 3 °C warmer treatment. Keller et al. (1999) also showed, for the 1977 to 1997 period, that winter–spring water temperature was an accurate predictor (explaining *ca.* 60% of the variance) of winter–spring peak chlorophyll. The *Skeletonema* time series also exhibited a significant inverse relationship between mean first quarter (1Q) temperature and mean 1Q *Skeletonema* abundance. 1Q (January, February, and March) water temperature explained about 20% of the variance in *Skeletonema* 1Q abundance between 1959 and 1997.

Changes in the abundance and composition of planktonic communities have been associated with changes in far-field drivers of atmospheric and oceanic circulation such as the position of the north wall of the Gulf Stream and the NAO index (Colebrook, 1986; George and Taylor, 1995; Frid and Huliselan, 1996; Taylor, 1995, 1996; Reid et al., 1998; Planque and Reid, 1998). There is increased understanding of the linkages between formation of 18 °C Sargasso Sea water, Labrador Sea and Greenland Sea convection, and Gulf Stream position, with concomitant effects on the NAO (Dickson et al., 1996; Dickson, 1997; Taylor and Stephens, 1998). Although the effects of Gulf Stream position and NAO on weather (Rodwell et al., 1999), and subsequent effects on aquatic systems are best known for the eastern side of the North Atlantic (Planque and Fromentin, 1996; Planque and Reid, 1998; Weyhenmeyer et al., 1999; Livingstone, 1999), the effects of NAO index variability have also been detected along the east coast of North America. In Narragansett Bay, an inverse correlation between NAO state and peak winter–spring bloom chlorophyll has been reported (Hawk, 1998; Keller et al., 1999), and in nearby Massachusetts Bay, long-term zooplankton (Turner et al., 2006) and phytoplankton (Keller et al., 2001) abundance patterns have been linked to NAO state.

4.2. Environmental regulation of annual bloom pattern

Analysis of *Skeletonema's* seasonal bloom patterns identified three distinct annual bloom patterns: 1: bimodal, with a large winter–spring and smaller summer–autumn bloom peaks; 2: unimodal, with a small winter–spring and larger summer–autumn bloom peaks; 3: unimodal, having either a late summer or autumn bloom peak. These annual patterns, their interannual variations and long-term trends are responses to annual and long-term variations in climate, which affect temperature, light, freshwater input and wind speed/direction. A climatic driver (NAO), with its intrinsic variability, appears to intermittently push the system towards one of these bloom patterns. There is a continuum in *Skeletonema* annual bloom patterns found along the biogeographical gradient on the Atlantic coast of North America. An annual *Skeletonema* bloom pattern dominated by the winter–spring bloom occurs in the northern Gulf of Maine, and a summer bloom dominated *Skeletonema* annual cycle is often observed in the region south of Narragansett Bay (Marshall and Cohn, 1983; Marshall, 1988). Inter-annual variations in climate may drive a given annual *Skeletonema* bloom pattern in Narragansett Bay towards the characteristic pattern typically observed elsewhere within its latitudinal distribution. In the cool years, typical of the early 1960s in the time series, *Skeletonema's* seasonal pattern was dominated by winter–spring blooms, while in warmer years (more typical of the later part of the series) summer or fall blooms prevailed. The mechanisms driving the variation in the seasonal bloom pattern are not fully known. Pre-bloom nutrient concentrations (Martin, 1965) and zooplankton abundance (Keller et al., 1999) have been shown to be important in influencing winter–spring bloom magnitude in Narragansett Bay. Analysis of a 22-year subset of the weekly time series revealed that the phytoplankton community shifted from a winter–spring annual maxima in the 1960s to a summer phytoplankton maxima in the 1970s (Karentz and Smayda, 1998). The decline in winter–spring *Skeletonema* bloom prominence identified in our study paralleled their results. Karentz and Smayda (1998) also noted that decreasing light levels during the 1960s to 1980s were important in structuring the phytoplankton community. This decline in *in situ* light is consistent with the shift from *Skeletonema's* winter–spring bloom years, which tended to occur in the brighter 1960s, to summer bloom *Skeletonema* years which prevailed in the 1980s and 1990s.

Years (1959–1962, 1964, 1966, 1968–1969, 1971, 1976, 1984, 1996) when *Skeletonema's* primary bloom occurred during winter–spring were brighter and colder, especially in the 1Q, and were also low NAO-state years, with reduced 1Q zooplankton abundance than in those years (1965, 1967, 1970, 1972, 1974–75, 1983, 1989, 1991, 1995) when the primary bloom occurred in summer or early autumn (Table 4). Inception of the winter–spring bloom, in some years, accompanies reduced grazing pressure (Pratt, 1965; Martin, 1965, 1970). A detailed experimental analysis of the 1972 winter–spring *Skeletonema* bloom in Narragansett Bay showed that temperature, light, nutrients, grazing, possibly phytoplankton species interactions and hydrographic disturbances affected its day-to-day changes in bloom dynamics and overall bloom pattern (Smayda, 1973). In experiments, *Skeletonema* was preferentially grazed by *Acartia hudsonica* in mixed diatom communities, with grazing on larger diatoms (*Guinardia* (formerly *Rhizosolenia*) *delicatula*) beginning after *Skeletonema* abundance decreased below *ca.* 50 to 300 cells ml^{-1} (Smayda, 1973; Martin, 1970). *Acartia* grazing is not constant: both its grazing rate and abundance increase with the vernal increase in temperature, reflecting *A. hudsonica's* optimum filtering temperature of 15 °C (Deason, 1980). Increased winter–spring water temperatures, typical of the latter part of this time series, leading to decreased zooplankton development times (Durbin and Durbin, 1981) and a concomitant reduction in the temporal mismatch between phytoplankton and zooplankton abundance peaks as well as increased grazing rates (Deason, 1980), may depress winter–spring phytoplankton biomass in Narragansett Bay (Keller et al., 1999). Changes in the timing and magnitude of the temperate winter–spring bloom, which often sinks ungrazed to the bottom sediments, are expected to influence upper trophic levels because of changes in the magnitude of phytoplankton carbon deposition to the benthos (Townsend and Cammen, 1988; Townsend et al., 1994). During the 1980s, phytoplankton carbon deposited by the winter–spring bloom was depleted by benthic organisms in Narragansett Bay by the end of summer (Rudnick and Oviatt, 1986). Declines in phytoplankton production in the Wadden Sea were coincident with decreases in benthic filter feeder abundance and a subsequent decrease in the abundance of birds that feed on these benthic organisms (Philippart et al., 2007). The *ca.* 50% decline in *Skeletonema* abundance that has occurred since 1980 is expected to decrease the transfer of phytoplankton carbon to the benthos, a reduction that may have impacted higher trophic levels.

Following its winter–spring bloom, *Skeletonema* growth becomes nutrient- and grazing-limited (Smayda, 1973; Vargo, 1976; French, 1984). In the transition from a diatom-dominated winter–spring flora to a flagellate dominated summer flora, a 'clear-water' or open niche phase of reduced phytoplankton in May and June often occurs (Smayda and Villareal, 1989). The diatom-to-flagellate transition may be partially explained by a temperature-mediated shift from nitrate uptake by diatoms in cool water (<15 °C) to ammonium uptake by flagellates as the water warms (Lomas and Glibert, 1999). The May–June 'clear-water' period is also often a period of increased zooplankton biomass, with both *A. hudsonica* and *A. tonsa* present (Durbin and Durbin, 1981). The 'clear water' phase was especially pronounced for *Skeletonema* in years with large winter–spring blooms. No correlation was found between summer environmental variables, with the exception of a negative correlation between 3Q *Acartia* abundance and the long-term *Skeletonema* trend. *Skeletonema* abundance during 1959 to 1996 declined primarily in winter and spring, with *ca.* 50% declines in January, March, and May when water temperature showed the largest increases (Cook et al., 1998; Keller et al., 1999). This suggests that after the initial, physically controlled (*i.e.*, weather and temperature) winter and spring period, summer *Skeletonema* dynamics are largely influenced by biological forces such as grazing and competition for rapidly recycled nutrients (Furnas, 1982, 1983), or allelochemic competition (Tomas, 1978). *Acartia* abundance was the only summer variable statistically associated with the long-term 1959 to 1996 trend in *Skeletonema* abundance ($r = -0.65$, $n = 15$, $p = 0.0084$). This is in agreement with the observations of Deason and Smayda (1982a,b) who quantified the role of *A. tonsa* abundance, as modulated by ctenophore (*Mnemiopsis leidyi*) grazing, in controlling summer *Skeletonema* blooms.

The timing and magnitude of the *Skeletonema*-dominated late summer–fall bloom in southern New England waters have been described as 'unpredictable' (Pratt, 1959). Increased nitrate availability (Riley, 1967), ctenophore regulation of copepod abundance (Martin, 1970; Durbin and Durbin, 1981; Deason and Smayda, 1982a,b) and water column stability-light limitation (Riley, 1967; Hitchcock and Smayda, 1977) have been cited as mechanisms regulating the fall bloom. While the mechanisms regulating fall blooms are not fully known (see French, 1984), a late summer or fall bloom of *Skeletonema* is an intermittent feature in Narragansett Bay. The three *Skeletonema*-dominated 'fall bloom' years (1973, 1985, and 1990) captured in the time series occurred in years that had *ca.* 6% less mean annual incident irradiance (71.8 W m^{-2}) than years when winter–spring blooms were prominent (76.8 W m^{-2}). Larger differences were seen in 1Q light levels: fall bloom years had 1Q light levels of 48.2 W m^{-2} compared to 1Q light of 55.9 W m^{-2} during winter–spring bloom years and 1Q light levels of 49.3 W m^{-2} in summer bloom years (Table 4). While such small differences in light are likely physiologically insignificant, we suggest that the differing light levels associated with each bloom pattern may be symptomatic of different weather patterns in those years. Autumn *Skeletonema* blooms occurred in years with sharply

reduced or absent winter–spring and summer *Skeletonema* blooms. However, on a mean annual basis, a large summer or autumn bloom did not compensate for a reduced winter–spring bloom. For *Skeletonema* in Narragansett Bay, failure of the winter–spring bloom represents a 'missed opportunity' for growth that is not reclaimed later in the year by increased summer or autumn blooms.

4.3. Recent changes in Narragansett Bay and Skeletonema regulation

One difficulty with long-term monitoring is that it is not possible to monitor all aspects of a particular system, and that 'overlooked' components of the system may be driving observed changes. The *Skeletonema* time series presented here is part of an ecosystem-based plankton monitoring program that examined a comprehensive set of plankton habitat variables, including chemical (N, P, Si nutrients), physical (temperature, salinity, irradiance), meteorological (rainfall, river flow, climatic indices), and biological (phytoplankton and dominant copepod abundance) metrics. However, the possibility remains that the observed *Skeletonema* decline was driven by unmeasured factors. Narragansett Bay has strong benthic–pelagic coupling, with filter-feeding bivalves dominating benthic grazing (Pratt and Campbell, 1956). There has been a serial colonization of introduced filter feeding ascidians (tunicates or sea squirts) in lower Narragansett Bay during the past 30 years (Auker, 2006). The most recent exotic colonial ascidian (*Didemnum* spp.) was first detected in lower Narragansett Bay in 2000, and has since rapidly increased to cover *ca.* 20% of the bottom cover in this region by 2005 (Auker and Oviatt, 2008). A similar situation has been observed in contiguous Long Island Sound, where long-term monitoring detected three species of introduced filter-feeding colonial ascidians were present in the mid-1970s through the late 1980s (Stachowicz et al., 2002; Osman and Whitlatch, 2007). The impact of these invasive filter feeding organisms on phytoplankton abundance and species composition is unknown. On a weight-corrected basis, ascidian clearance rates during summer may rival those of some common Narragansett Bay shellfish (*i.e.*, *Mytilus edulis*; Petersen, 2007). A rapid decline in phytoplankton biomass due to increasing top-down control of phytoplankton abundance occurred during the 1980s in San Francisco Bay following the introduction and rapid population increase of a filter feeding clam (Cloern, 1982, 1996). An undetected change in the quantity and species composition of the benthic grazers may have occurred in the late 1970s–1980s in Narragansett Bay, with subsequent increases in benthic grazing that may explain some of the observed long-term decline in *Skeletonema* abundance beginning in 1980. This hypothesis remains difficult to test without long-term quantification of the benthic component of the ecosystem.

Lower Narragansett Bay has experienced considerable change during the course of this time series, including a phytoplankton biomass decline (Li and Smayda, 1998), increasing water clarity (Borkman and Smayda, 1998), increasing water temperature (Cook et al., 1998), changes in phytoplankton bloom patterns (Smayda, 1998; Keller et al., 1999; Smayda et al., 2004), altered zooplankton dynamics (Sullivan et al., 2001; Costello et al., 2006), and changing fish communities (Jeffries and Terceiro, 1985; Collie et al., 2008). However, the levels of nitrogen nutrient loading to Narragansett Bay have remained relatively constant for the past 50 years (Hamburg et al., 2008; Nixon et al., 1995, 2008). Ambient, lower bay nutrient levels were not closely associated with the long-term decline in *Skeletonema* abundance. Our analysis suggests that changes in weather patterns, especially winter weather (as indicated by the NAO index), were closely associated with the long-term pattern of *Skeletonema* abundance and annual pattern. There appeared to be a threshold effect, with cold, stormy winter weather (during years winter NAO index of <-1.4) favoring a relatively abundant and winter–spring bloom dominated *Skeletonema* pattern. In contrast, warm winter weather (winter NAO index of $>+1.1$) was associated with a summer bloom pattern and reduced annual *Skeletonema* abundance. In other systems, NAO-related weather variability has been identified as a selective mechanism influencing the contribution of diatoms to the winter–spring bloom (Irigoien et al., 2000). Low frequency (decadal scale) shifts in plankton abundance and community structure have been associated with weather-driven changes in marine climate (Cloern et al., 2007). Long-term variation in marine climate, with its manifold effects on the phytoplankton habitat, influences phytoplankton community composition, abundance levels and annual patterns. We suggest that in Narragansett Bay phytoplankton abundance levels are influenced by long-term variations in far-field marine climate, and that this influence can be detected in the long-term annual bloom and abundance patterns of *Skeletonema* abundance.

Acknowledgements

This research was funded by the EPA's Science to Achieve Results (STAR) program, supported by EPA grant R82-9368-010 awarded to T. Smayda, and grant RD83244301 awarded to T. Smayda and D. Borkman. A National Science Foundation grant (OCE 953020) awarded to T. Smayda also supported this research. We thank all the GSO 'Bunker C' students and staff who assisted in field sampling and laboratory analyses for the long-term monitoring effort.

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