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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

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Bloom behavior of the Skeletonema costatum "species-complex", a keystone diatom cluster, in Narragansett Bay (NBay), USA, during a 39-year (1959–1997) time series was statistically related to variations in the path and latitudinal position of the north wall of the Gulf Stream (GSNW). Winter–spring abundance of the Skeletonema complex was ca. 10-fold greater in years when the GSNW was displaced to the south; summer abundance was 3-fold higher in years of southerly displaced GSNW flow. The relationships with the North Atlantic Oscillation (NAO), the influence of temperature on growth and grazing of Skeletonema and the advective connectivity of NBay with contiguous regional waters potentially impacted by GSNW dynamics are evaluated. The two major, regionally coupled ocean–atmosphere systems, the NAO and the GSNW, differ in their seasonal and interannual impacts and do not directly explain the specific causes of the associated variations in bloom behavior of the Skeletonema complex. Summer bloom behavior was correctly forecast in 14 of 17 years based on advanced predictions of GSNW position at its extreme northern (GSNWI $> +0.5$) and southern (GSNW < -0.5) latitudinal limits.

INTRODUCTION

Phytoplankton variability occurs at all levels of behavior, including the timing and abundance of blooms, species succession and community organization, and in various patterns—as ephemeral fluctuations, unusual events, irregular blooms, even chaotically (Smayda, 1998). There are also cycles and trends, and the scales of variability range from daily to seasonal to interannual to decadal. Investigators seeking to explain plankton dynamics and plankton variability often focus on the physical, chemical and biological variables within the bloom habitat—the internal drivers. However, coastal ecosystems are open and sensitive to regional atmospheric and oceanographic signals—external drivers. The external drivers primarily focused on are climatic perturbations, such as phytoplankton behavior in cold versus warm winters, wet versus dry seasons. Long-term variations in "ocean climate" (Dayton *et al.*, 1999) that result from large-scale, low-frequency variations in coupled ocean–atmosphere systems, such as ENSO in the Eastern Pacific (Chavez *et al.*, 2003) and North Atlantic Oscillation (NAO) in the North Atlantic (Barton *et al.*, 2003), are more subtle external drivers that alter phytoplankton abundance, species composition and their succession, upper trophic levels and trophodynamics (Colebrook, 1986; Aebisher *et al.*, 1990; Fromentin and Planque, 1996; Reid *et al.*, 1998;

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Belgrano *et al.*, 1999; Irigoien *et al.*, 2000; Seuront and Souissi, 2002; Drinkwater *et al.*, 2003; among others). In the North Sea, for example, NAO-induced changes in circulation patterns led to shifts in phytoplankton abundance and species composition, followed by changes in the dominant *Calanus* species (Fromentin and Planque, 1996). NAO-altered ecosystem responses, such as year-class failure, can extend beyond the perturbation period (Ottersen *et al.*, 2001).

The interannual variability normal to habitat variables and plankton behavior can conceal the habitat signals and ecological impacts of climate change. Plankton variations driven by external factors, particularly variability driven by coupled atmospheric–oceanographic signals, are not tractable from the measurements of internal variables alone. The relevant external drivers can be operative over decadal time scales, during which they can subtly modify the impacts and behavior of the internal drivers, e.g. nutrients and grazers. Eventually, the long-term cumulative effect can emerge as a recognizable effect of climate change, e.g. as changes in the timing and magnitude of the annual bloom maximum or in dominant species composition. Accordingly, a revised analytical approach from the traditional focus on internal variables is required to analyze the variability and changes in plankton behavior induced by climate change. Central to this analytical approach is the need to incorporate time series of external variables into the analysis.

Allen *et al.* (Allen *et al.*, 2006) have pointed out that correlations with large-scale climate indices such as the position of the Gulf Stream North Wall (GSNW) and the North Atlantic Oscillation Index (NAOI), can serve as probes to help detect climate change effects concealed within a data set. The GSNW is the dominant oceanographic feature of the western North Atlantic. The variability in its path and flow has been reported to influence plankton processes directly, both in the NW and NE North Atlantic, accompanied by the indirect effects of marine–atmosphere interactions and subtle modifications of marine climate (Planque and Taylor 1998; Taylor *et al.*, 2002). Connectivity between coupled Gulf Stream–NAOI (atmosphere) variations and phytoplankton community composition in the North Atlantic is evident on geological and recent time scales. Long-term variations in the GSNW and North Atlantic Drift Current affected dinoflagellate species composition in the Norwegian Sea 48–30 thousand years before present, with dinoflagellate abundance increasing during the warm periods associated with increased GSNW flow (Eynaud *et al.*, 2002). In the western North Atlantic, dinoflagellate abundance on the Scotian Shelf increased during relatively warm periods ca. 9000 YBP, characterized by northward excursions of the GSNW and increased warm core ring (WCR) activity (Mudie *et al.*, 2002). During recent periods, altered wind patterns and changes in mixed-layer depth in the NE Atlantic, driven in part by GSNW variability, promoted shifts in plankton abundance and species composition (Taylor and Stephens, 1980; Taylor, 1995; Frid and Huliselan, 1996; Fromentin and Planque, 1996; Reid *et al.*, 1998; Taylor *et al.*, 2002). Similar impacts on freshwater plankton also have been reported (George and Harris, 1985; George and Taylor, 1995; George and Hewitt, 1999; George, 2000), an association with GSNW variability that must be linked to coupled-atmosphere effects (Allen *et al.*, 2006).

Off the northeast coast of the USA, GSNW dynamics has been reported to influence coastal fish (Hoff and Ibara, 1977; Markle *et al.*, 1980), squid (Dawe *et al.*, 2000) and phytoplankton (French and Hargraves, 1986) populations. The latitude at which the GSNW turns eastward off the east coast of the USA and flows across the North Atlantic varies. Latitudinal migration of the GSNW is linked to atmospheric forcing, with GSNW position co-varying with the NAOI (Joyce *et al.*, 2000) and to forcing from variation in Slope Sea circulation (Rossby *et al.*, 2005). Gulf Stream position is also related to the NAOI through its influence on winter temperature and ice production on the Labrador Shelf, which affects the strength of the southward-flowing Labrador Current off the east coast of the USA (Rossby, 1999; Rossby and Benway, 2000; Rossby *et al.*, 2005). During cold winters, ice production is increased, and the southward flow of the relatively more saline Labrador Current weakens; in warm winters, ice production is reduced and flow of the relatively less saline Labrador Current is strengthened. A strong connection occurs between GSNW position and southern New England terrestrial climate (Colucci, 1976; Hartley and Keables, 1998; Bradbury *et al.*, 2002) and variation in GSNW position has been linked to intensity of US east coast winter storms (Cione *et al.*, 1993). The location of Narragansett Bay (NBay) (41°30′N) at the transition between temperate waters south of Cape Cod and boreal waters to the north of Cape Cod also position NBay in an ideal geographic location for detection of marine climate change. Given this and the impacts of the coupled GSNW–NAO behavior on plankton dynamics summarized above, an influence of GSNW variability on phytoplankton bloom cycles in NBay, located in southern New England on the US east coast (Fig. 1), is hypothesized. The multidecadal plankton time series available for NBay, and the time series of GSNW and NAO indices are suitable for evaluation of this hypothesis.

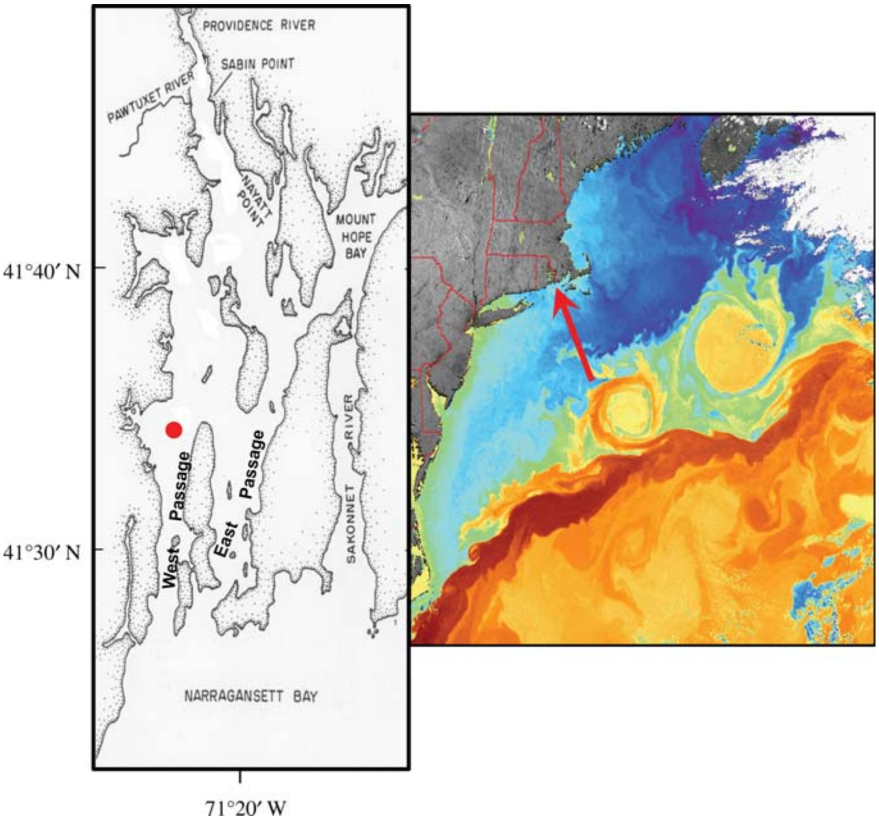

Fig. 1. Location of long-term sampling station (Station II, ~41°30′N, 71°20′W) in lower west NBay, Rhode Island, and thermal image of Gulf Stream relative to NBay (red arrow). Image date: 11 June 1997 (source: http://fermi.jhuapl.edu/avhrr/gallery/sst/eddy_97jun11/eddy.html). GSNW is ca. 400 km south of NBay; the edge of the WCR shown is ca. 230 km south of NBay.

The long-term bloom behavior of the diatom identified as *Skeletonema costatum*, which typically blooms during winter−spring (w-s) and summer in NBay, will be used as the phytoplankton responder. Its persistently high abundance and dominance of the phytoplankton over four decades (1952−1996) of continuous investigation have been documented in numerous papers (Smayda, 1957, 1973; Pratt, 1959, 1965; Karentz and Smayda, 1984, 1998; Borkman and Smayda, 2009; among others). The fluctuations in abundance represent ~70% of the variance in total diatom abundance (Borkman and Smayda, 2009). A large body of literature has described the ecophysiology of natural populations of *Skeletonema* in NBay and strains cultured from local waters (Smayda, 1973; Yoder, 1978, 1979a, b; French, 1984; among others), including its population genetics (Gallagher, 1980, 1982, 1984). In 2005, Zingone *et al.* (Zingone *et al.*, 2005) and Sarno *et al.* (Sarno *et al.*, 2005), based on morphological analyses, concluded that the species in NBay historically reported as *S. costatum* is not that species. They recognized two newly described species within the well known and classical *Skeletonema* morphotype (Braarud, 1962; Hasle, 1973) that characterizes the specimens found in NBay, *Skeletonema grethae* and *Skeletonema japonicum*. We cannot confirm which of these species, if either, identified as *S. costatum* occurred, either seasonally or interannually, and when. The distinctions between these three *Skeletonema* species are based primarily on micro-morphological features that are not apparent when enumerating live cells in field samples under low magnification (×250), as was carried out. Accordingly, in this study, we will use the name *Skeletonema* complex to designate the species historically identified as *S. costatum* in NBay, and making up the time series. Efforts are being made to hindcast the taxonomic identity of the *Skeletonema* population.

METHOD

NBay plankton time series

From January 1959 to May 1997, surface water samples were collected weekly at a long-term monitoring station (41°34′07″N, 71°23′31″W) located in lower NBay (Fig. 1) and analyzed for phytoplankton species composition and numerical abundance (Borkman and Smayda, 2009). Temperature, salinity, Secchi depth, nutrients (NH_4, NO_3, $Si(OH)_4$, PO_4) and zooplankton species composition, numerical abundance and biomass were also determined (Borkman and Smayda, 2009) and will guide interpretation of the analyses in this paper, which focus on the bloom behavior of the *Skeletonema* complex in relation to the variations in GSNW position and WCR activity. The present analyses focus on the 1959–1997 portion of the ongoing NBay plankton time series. Although weekly plankton observations continue through to the present (http://www.gso.uri.edu/phytoplankton/), we have not completed quality-control comparisons of the more recent (1999–present) data that were generated using slightly different methodologies than those employed during 1959–1997. For the 39-year time series (January 1959–May 1997; 1995 weeks) analyzed here, data on phytoplankton abundance 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 the time series averaged one sample every 10 days. Live phytoplankton counts at ×250 magnification were made on the 1430 weekly samples enumerated using a 1 mL Sedgwick-Rafter counting chamber, giving a nominal *Skeletonema* detection level of 1 cell mL^{-1}. The *Skeletonema* complex dominates the phytoplankton in NBay, as documented earlier. The long-term bloom behavior of other important species in NBay is discussed in Karentz and Smayda (Karentz and Smayda, 1984, 1998), Li and Smayda (Li and Smayda, 2000), Smayda (Smayda, 1976, 1984) and Smayda *et al.* (Smayda *et al.*, 2004). Long-term biomass (as chlorophyll) patterns are described in Li and Smayda (Li and Smayda, 1998, 2001), and variability in bloom inception patterns in Smayda (Smayda, 1998).

Gulf Stream index, WCR activity data and NAOI

The monthly and annual GSNW index of Taylor and Stephens (Taylor, 1995, 1996) was used (http://web.pml.ac.uk/gulfstream/inetdat.htm) as an indicator of interannual GSNW variability. This GSNW index, derived from principal component analysis of GSNW position, is a metric of the latitudinal position of the GSNW as it leaves the northeast coast of the USA. The monthly GSNW location has been calculated since 1966 (Taylor, 1995, 1996; Taylor and Stephens, 1998); its behavior is accurately forecast up to 12 months in advance (Taylor and Gangopadhyay, 2001). The annual mean GSNW is used in our analysis because the monthly data are highly variable due to GSNW meandering. The mean path of the GSNW along the northeast coast of the USA lies ~550 km south of NBay, but displays long-term latitudinal fluctuations of 100–200 km (Fig. 1; Rossby and Benway, 2000).

As the GSNW breaks away from the east coast of the USA and flows eastward across the North Atlantic Ocean, meanders develop that fold back on themselves and occasionally pinch off to form isolated, rotating bodies of water known as warm core rings (WCRs) (Gould and Fryxell, 1988). Rings formed north of the GSNW have a central core of warm, saline Sargasso Sea water and, rotating anticyclonically, spin off from the GSNW and move onto the continental shelf with its enclosed phytoplankton community. Long-term variations in watermass properties of the southern New England Bight (SNEB), which is contiguous with NBay, are related to the variable proportions of Shelf Water and Slope Water that enter this Bight (Mountain, 2003) and interact with WCRs which mix slope water onto the shelf (Armstrong, 1998a, b). We used the annual index of WCR activity on the continental shelf south of NBay available for 1974–1983 as an indicator of potential GSNW influence on SNEB waters contiguous with NBay (Fig. 1; Armstrong, 1998a). The WCR index quantifies the duration that WCRs were observed in the SNEB inshore of the shelf-break along the 71°W meridian (Armstrong, 1998a). The NAOI of Hurrell (Hurrell, 1995) (http://www.cgd.ucar.edu/cas/jhurrell/indices.html) was used in combination with related data on the NAO) when analyzing selected aspects of its influence on *Skeletonema* bloom behavior in NBay (Borkman and Smayda, 2009).

Statistical analyses

A statistical method similar to that used by Maberly *et al.* (Maberly *et al.*, 1994) to analyze a 45-year time series of *Asterionellopsis formosa* abundance in Lake Windermere was applied to assess linkages between long-term variations in the timing and magnitude of the annual bloom cycles of the *Skeletonema* complex in NBay and the variations in GSNW location and NAO in regional waters. The timing and abundance of the annual bloom maximum and the bloom cycle patterns of *Skeletonema* were analyzed by assigning to each annual cycle a series of *cardinal characters* (Maberly *et al.*, 1994). The cardinal characters assigned designate *Skeletonema*'s abundance and bloom features at various times of the year; the time of certain bloom features (e.g. start of the w-s and summer–fall (s-f) blooms and the week of greatest cell abundance); the rates of change in cell

Table I: Skeletonema bloom character codes ($n = 21$) used in the analysis (w-s, winter–spring bloom; s-f, summer–fall bloom)

Bloom timing (W) characters (week numbers)
W1 = Week of annual maximum abundance
W2 = Week of w-s bloom start
W3 = Week of w-s bloom peak
W4 = w-s bloom duration [W3-W2]
W5 = Week of s-f start
W6 = Week of s-f maximum abundance
W7 = s-f bloom duration [W6-W5]
Abundance (N) characters (cells mL^{-1})
N1 = Maximum abundance
N2 = Mean annual abundance
N3 = w-s bloom maximum
N4 = First quarter mean abundance
N5 = Second quarter mean abundance
N6 = Third quarter mean abundance
N7 = Fourth quarter mean abundance
N8 = s-f bloom maximum
N9 = % weeks <10 *Skeletonema* per mL
N10 = % weeks >500 *Skeletonema* per mL
N11 = Week 2–5 mean *Skeletonema* abundance
N12 = Week 13–16 mean *Skeletonema* abundance
N13 = Week 25–28 mean *Skeletonema* abundance
N14 = Week 32–35 mean *Skeletonema* abundance

abundance prior to and after seasonal blooms. Twenty-one cardinal characters were assigned (Table I) and examined by plotting each annual cycle, and then recording the week (W) and corresponding *Skeletonema* abundance level (N) for each of the specific bloom and abundance events that comprise the 21 cardinal characters. Weeks of the annual w-s and s-f bloom initiation (W2 and W5, respectively, in Table I) were defined as the first week in a series of two or more weeks when *Skeletonema* exhibited a 2-fold, or greater weekly increase in abundance, i.e. abundance in week $x + 1$ is more than twice the abundance in week x. Bloom termination week was identified as the week when the *Skeletonema* complex ceased to increase in abundance. Bloom duration, in weeks (W4, W7 in Table I), was determined by subtracting the week of bloom initiation from the week of bloom termination, i.e. $W4 = W3 - W2$ for w-s blooms and $W7 = W6 - W5$ for s-f blooms (Table I). Although the calendar year was the time frame used to delineate cardinal characters, the *Skeletonema* bloom cycles were not artificially constrained by the annual boundaries of 52 weeks (i.e. that week 1 begins a year, and week 52 ends the year). When an annual bloom cycle crossed a year-boundary (e.g. the w-s bloom of a given year started in the next to last week of the preceding year), the corresponding weeks in the preceding year were assigned negative week numbers (i.e. week 52 of the prior year was appointed week 0; week 51 was appointed week -1 etc.). The complete suite of 21 cardinal characters could be assigned to 29 of the 38 (1959–1997) years in the time series. Years 1963, 1979, 1982, 1986–1988 and 1992–1994 had incomplete cardinal characters, and 10 cardinal characters were assigned in 1997 when data were available only the first 19 weeks of the year.

Gulf Stream effects on temperature, salinity and *Skeletonema* bloom characteristics in NBay were initially assessed by correlation or regression analysis. Environmental data (temperature, salinity) and the *Skeletonema* data were checked for serial correlation prior to analysis. The environmental data were found to have significant serial correlation so all correlation analyses with environmental data were corrected for a reduction in effective number of observations (n) by applying the correction of Quenouille (Quenouille, 1952) as cited in Taylor (Taylor, 1995). Statistics were calculated using SAS 9.1 software (SAS, 2002) and GraphPad Prism v. 3.00 software (GraphPad Software, 1999). Data were checked for normality prior to analysis using the Kolmogorov–Smirnov test. For those *Skeletonema* bloom characters having data distributions that deviated significantly from normal, we used the Wilcoxon–Mann–Whitney tests to assess whether the cardinal characters of *Skeletonema* abundance and bloom timing came from significantly different distributions during periods of extreme positive or negative Gulf Stream position, during periods of extreme positive or negative NAO state or warm or cool periods based on mean annual sea surface temperature (SST).

RESULTS

Gulf Stream location and NBay temperature and salinity

Several lines of evidence suggest that patterns of GSNW position and WCR activity influence habitat parameters and *Skeletonema* bloom behavior in NBay. The long-term pattern in mean annual SST at the monitoring station in lower NBay (Fig. 1) and GSNW both had long-term increasing trends during 1959–1997 as judged by the fit of linear models fitted to both mean annual SST and mean annual GSNW (Fig. 2). Mean annual SST increased at a linear rate of 0.31°C per decade during 1959–1997 as judged by linear regression ($\text{SST} = (0.031 \times \text{year}) - 49.52$, $r^2 = 0.42$, $n = 37$, $P = 0.0020$; Fig. 2). However, the relationship between annual GSNW position and NBay mean annual SST variation was not linear with a correlation that was not statistically significant (Pearson $r = 0.36$, $n = 30$, $P = 0.0741$) when corrected for the strong serial correlation in the SST time series. This may be partially related to the decadal periods of temperature

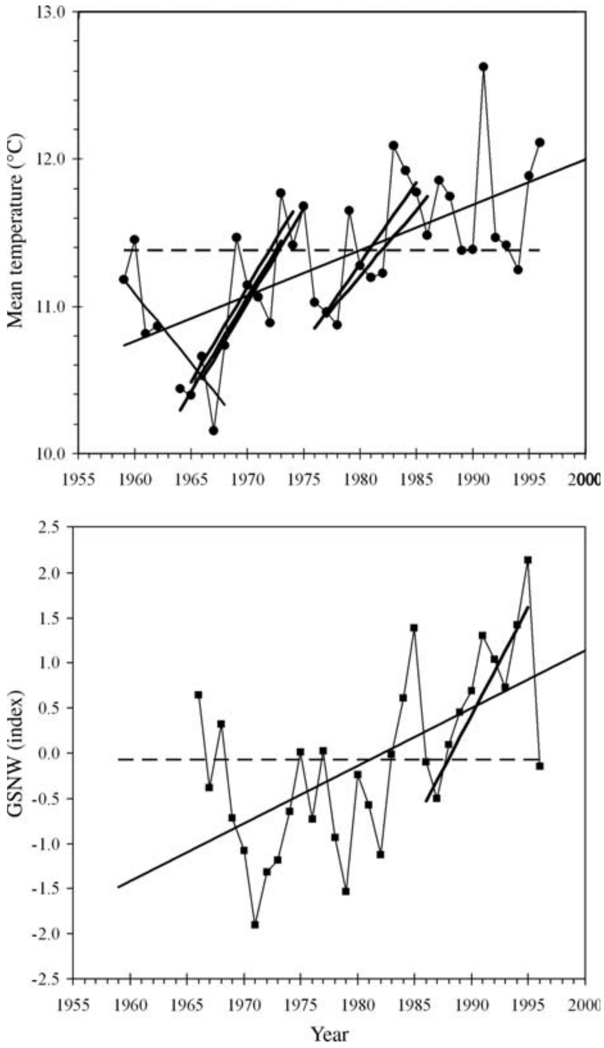

Fig. 2. Top panel: 1959–1996 time series of mean annual sea surface temperature (solid circles) at the NBay long-term sampling station. Horizontal dashed line indicates long-term mean annual SST of 11.38°C. Mean annual surface temperature increased at a linear rate (dark line; SST = (0.031 × year) − 49.58, $r^2 = 0.42$, $n = 37$, $P = 0.0020$) during 1959–1996. Linear regression analysis of SST in 10 year windows indicated that the gradual long-term SST warming trend was interspersed with more rapid decadal cooling (1959–1968) and warming (1964–1973, 1965–1974, 1966–1975, 1976–1985, 1977–1986) periods (light lines). The slopes of the decadal warming trends were not significantly different from each other, with a mean slope of +1.17°C per decade. Bottom panel: time series of mean annual GSNW position (filled squares) during 1966–1996. Horizontal dashed line represents 1959–1997 mean GSNW position. GSNW data are those of Taylor (Taylor, 1995, 1996; available at: http://web.pml.ac.uk/gulfstream/inetdat.htm). The GSNW had a long-term increasing trend as judged by a linear regression (GSNW = +0.064 × year) − 127.2, $r^2 = 0.37$, $n = 31$, $P = 0.0127$) during 1959–1996. Regression analysis of 10-year moving window GSNW indicated a significant decadal increase during 1986–1995 (light line; GSNW = (+0.238 × year) − 473.2; $r^2 = 0.85$, $n = 10$, $P = 0.0002$). At the longitude (71°W) of NBay, there is a ca. 200 km variation in GSNW latitude (Rossby and Benway, 2000) between GSNW = +1 (Gulf Stream displaced northward) and GSNW = −1 (Gulf Stream displaced southward).

decrease (1959–1968) and increases (1963–1975 and 1976–1986) embedded in the long-term temperature record (Fig. 2). The slope of decadal SST increases in the mid-1960s through mid-1970s and again during the mid-1970s through 1986 had slopes that were not significantly different from each other (+1.17°C per decade). However, the rate of these decadal SST increases (+1.17°C per decade) was significantly greater than the long-term rate of SST increase (+0.29°C per decade). A similar decadal analysis of GSNW showed that while GSNW increased (GSNW northward) significantly during 1966–1997 (GSNW = (+0.064 × year) − 127.2, $r^2 = 0.37$, $n = 31$, $P = 0.0127$), the 1986–1995 period was marked by a more rapid northward migration (GSNW = (+0.238 × year) − 473.2; $r^2 = 0.85$, $n = 10$, $P = 0.0002$) of the GSNW (Fig. 2, bottom). A pattern of periods of more extreme warming (i.e. 1964–1975 and 1976–1986) interspersed with periods of no significant SST change is evident.

NBay annual SST responded to extremes in position of the GSNW, with significant differences in mean SST detected when the GSNW was displaced strongly southward compared with mean annual SST during years of strongly northward GSNW displacement. A GSNW threshold of < -0.5 versus $> +0.5$ was detected for mean annual SST, with a significantly different (unpaired *t*-test, $P = 0.0203$) mean annual SST of 11.3°C observed during years (mainly during the 1970s) having southward GSNW displacement (GSNW < -0.5) compared with the SST of 11.8°C observed during years (mainly during the 1990s) of northward displacement (GSNW $> +0.5$). Similar differences in annual mean SST were also detected for greater extremes in GSNW thresholds (i.e. < -1 versus $> +1$), with the above-mentioned $-0.5 <$ GSNW $> +0.5$ GSNW threshold, the minimum detected.

A significant GSNW influence on salinity in NBay was also detected. For the 10 years (1974–1983) that WCR data are available (Armstrong, 1998a), there was a statistically significant relationship between bottom water salinity in lower NBay and WCR activity quantified as the number of days that rings were present (Fig. 3). WCRs were present in the SNEB (west of the 71°W meridian) for 92 (1983) to 163 (1977) days per calendar year. The mean annual bottom salinity in lower NBay then varied between 29.3 (1983) and 31.5 (1977). Bottom water salinity (31.5) was highest during 1977 when WCR duration was greatest (163 days), whereas the year of least WCR activity (92 days in 1983) coincided with the lowest bottom water salinity (29.3; Fig. 3). There was a statistically significant positive correlation between WCR

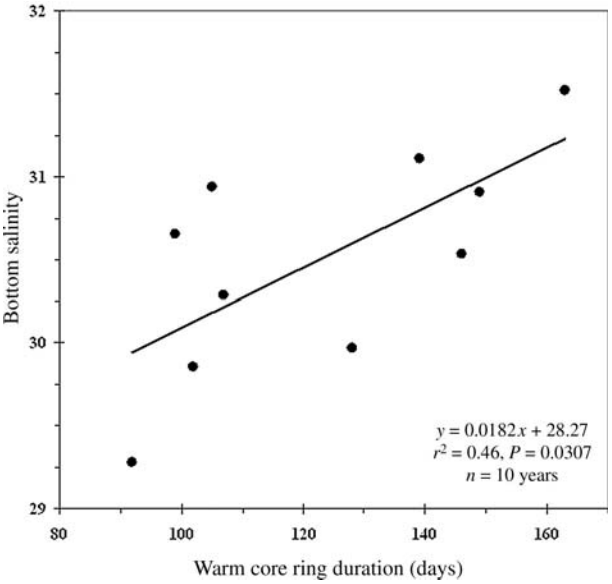

Fig. 3. Scatterplot of WCR duration west of the 71st meridian and bottom salinity at the long-term station in lower NBay during 1974–1983. Mean annual bottom salinity was positively correlated with the degree of WCR activity ($r = 0.68$, $n = 10$ years, $P = 0.0307$).

duration and bottom salinity ($r = +0.68$, $n = 10$, $P = 0.0307$). Salinity was ca. 2 units higher in years when WCRs were present ca. 140–160 days per year compared with years when rings were present only ca. 100 days per year (Fig. 3).

Gulf Stream position, and timing and magnitude of annual *Skeletonema* blooms

Several features of *Skeletonema* bloom timing and magnitude were statistically related to GSNW position during the 39-year time series (Table II). Summer abundance (N6 in Table I) was negatively correlated with GSNW position (Pearson $r = -0.42$, $n = 24$ years, $P = 0.0296$) and summer blooms were less intense in years when the GSNW was displaced to the north (Fig. 4). When the GSNW was positive (northward displacement of GSNW), mean summer abundance of the *Skeletonema* complex did not exceed ca. 3000 cells mL^{-1}; but when the GSNW was negative abundance did not exceed 3000 cells mL^{-1}. The annual bloom maximum of the *Skeletonema* complex shifted from w-s to summer during years when the GSNW had a southward excursion, i.e. the GSNW was negative. For example, during years when the GSNW was < -0.5 the mean annual maximum in August was 9578 cells mL^{-1} ($n = 11$ years). This maximum was significantly greater (unpaired *t*-test, $P = 0.0191$) than the August abundance (2283 cells mL^{-1}; $n = 8$ years) during years when the GSNW was $> +0.5$ (Fig. 5).

Many plankton ecosystem variables do not behave linearly; rapid transitions from one state to another can

Table II: Skeletonema bloom characters having significant differences during different GSNW states during 1966–1996 as tested by Wilcoxon–Mann–Whitney-test

Gulf Stream position differences: bloom character (units, code)	GSNW (−) Mean (*n*)	GSNW (+) Mean (*n*)	*P*-value
Criterion: extreme (+) versus (−) 5 Gulf Stream years			
3Q mean (cells mL^{-1}, N6)	5120 (5)	1563 (5)	0.0283
s-f bloom peak (cells mL^{-1}, N8)	33 500 (5)	14 480 (5)	0.0758
% weeks <10 cells mL^{-1}, N9)	0.15 (5)	0.41 (5)	0.0749
Criterion: Gulf Stream < -1 versus $> +1$			
w-s bloom peak (cells mL^{-1}, N3)	5090 (5)	534 (3)	0.0253
% weeks <10 cells mL^{-1}, N9)	0.15 (5)	0.48 (3)	0.0512
Criterion: Gulf Stream < -0.5 versus $> +0.5$			
s-f bloom start (week, W5)	28.0 (10)	31.6 (8)	0.0731
3Q mean (cells mL^{-1}, N6)	4376 (9)	1313 (8)	0.0161
s-f peak (cells mL^{-1}, N8)	24 754 (10)	10 664 (8)	0.0410
% weeks <10 cells mL^{-1}, N9)	0.20 (10)	0.36 (8)	0.0683
Criterion: Gulf Stream < -0.1 versus $> +0.1$			
% weeks <10 cells mL^{-1}, N9)	0.19 (13)	0.36 (10)	0.0233
Criterion: Gulf Stream <0 versus >0			
% weeks <10 cells mL^{-1}, N9)	0.20 (14)	0.33 (11)	0.0747

GSNW < 0 corresponds to southerly displacement of Gulf Stream path; GSNW > 0 corresponds to northward displacement of Gulf Stream. Bloom characters with significant differences in mean values at $P < 0.10$ shown. Bloom character codes from Table I: w-s, winter–spring; s-f, summer–fall bloom; 3Q, third quarter, e.g. N6.

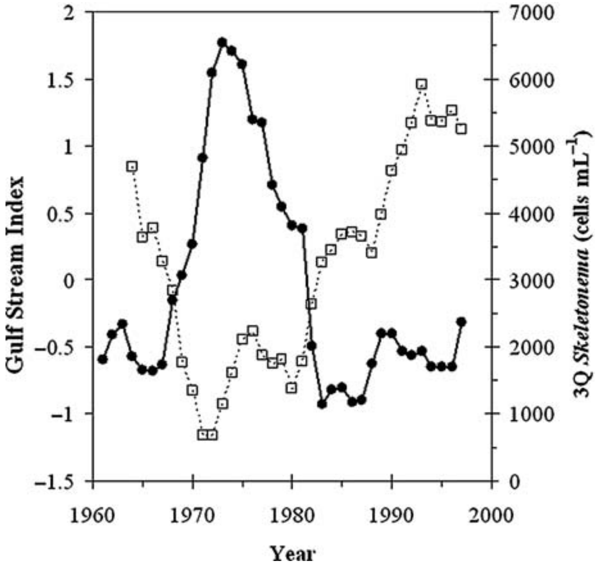

Fig. 4. GSNW position (dashed line with open squares) and mean summer (third quarter) *Skeletonema* abundance (solid line with filled circles). Annual mean data points with 5-year smoothed box-car averages (lines). Pearson correlation between smoothed Gulf Stream position and summer *Skeletonema* abundance was -0.44 ($n = 24$ years, $P = 0.0296$).

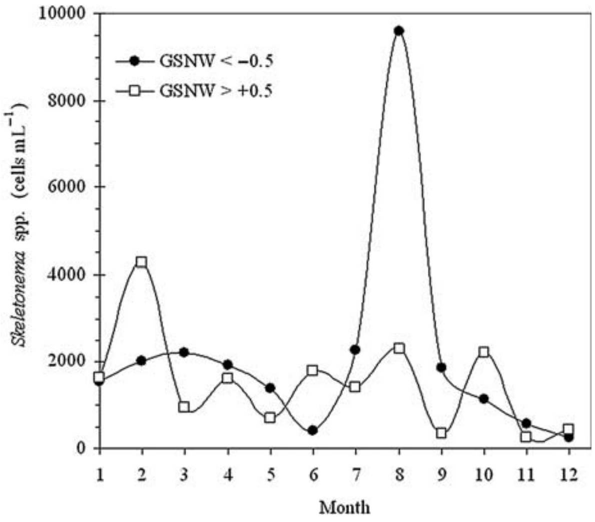

Fig. 5. Mean annual pattern in abundance of the *Skeletonema costatum* "species-complex" during years of Gulf Stream southward displacement ($\text{GSNW} < -0.5$; filled circles) compared with the pattern during years of Gulf Stream northward displacement ($\text{GSNW} > +0.5$, open squares). *Skeletonema* abundance in August was significantly greater ($P = 0.0191$) during $\text{GSNW} < -0.5$ years (9578 cells mL^{-1}, $n = 11$ years) than in years (2283 cells mL^{-1}, $n = 8$ years) when the Gulf Stream was displaced to the north ($\text{GSNW} > +0.5$).

occur (McGowan, 1990; Smayda, 1998). This led us to compare the bloom characteristics of the *Skeletonema* complex during extremely positive and negative GSNW years. The Mann–Whitney test was used to test the hypothesis that the *Skeletonema* cardinal characters (Table I), i.e. its temporal bloom and abundance features differed significantly between the extreme positive and negative excursions of the GSNW. The cardinal characters were partitioned in various ways, e.g. the median value of the cardinal characters in the 5 highest GSNW years versus median cardinal character value during the 5 lowest GSNW years, the cardinal character medians in $\text{GSNW} < 0$ years versus $\text{GSNW} > 0$ years etc. This allowed identification of the threshold levels at which GSNW position affected *Skeletonema* bloom phenology (Table II), if an effect occurred. Peak w-s *Skeletonema* abundance (5090 cells mL^{-1}) was ca. 10-fold greater in years when the GSNW was displaced to the south ($\text{GSNW} < -1$) than in years (534 cells mL^{-1}) when it was displaced to the north ($\text{GSNW} > 1$). Similarly, summer [i.e. third quarter (3Q) in Table II] abundance of the *Skeletonema* complex typically was 3-fold higher in years of southerly displaced GSNW flow (3Q mean 4376 cells mL^{-1}, $\text{GSNW} < -0.5$, $n = 9$ years) than in years of northerly displaced flow (3Q mean 1313 cells mL^{-1}; $\text{GSNW} > +0.5$, $n = 8$ years). During the period (ca. 1972–1980) when the GSNW was displaced southward, summer abundance increased and shifted the annual bloom maximum from w-s to the summer (Fig. 5).

NAOI and annual *Skeletonema* blooms

NBay is located in the region where North Atlantic atmospheric circulation patterns strongly influence SST and wind/weather patterns, as quantified by the NAOI (Cayan, 1992; Hurrell, 1995). Years with high (positive) winter (December–February) NAO indices tend to have strong southern wind flow and mild winters; years with low (negative) NAO state have colder, windier winters (Hurrell, 1995; Hawk, 1998). Thus, plankton dynamics in NBay are subject to at least two large-scale, regional drivers—the NAO and the GSNW. Linkage to GSNW dynamics has been described above; the influence of the NAO on the *Skeletonema* bloom cycles has been partly described in Smayda *et al.* (Smayda *et al.*, 2004) and Borkman and Smayda (Borkman and Smayda, 2009).

During the 39-year time series, abundance of the *Skeletonema* complex ranged from 0 to 108 750 cells mL^{-1}. Mean annual abundance varied from 134 to 3525 cells mL^{-1} and, particularly noteworthy, the decadal mean abundance declined from ca. 2200 cells mL^{-1} during the 1960s and 1970s to ca. 1500 cells mL^{-1} the following two decades. Some features (cardinal characters) of the long-term bloom behavior of the *Skeletonema* complex during the extremes of the NAOI and Gulf Stream conditions are compared in Table III to illustrate the extent to which these two climatic indices contributed to the observed bloom behavior. A clear influence of the NAO on w-s bloom dynamics is evident. The duration,

Table III: Skeletonema annual bloom cycle characteristics relative to NAOI and GSNW position and compared with Mann–Whitney test (w-s, winter–spring; s-f, summer–fall)

Cardinal character	Mean of (−) years (*n*)	Mean of (+) years (*n*)	*P*-value
Criterion: greatest and least 5 NAOI years			
Week of annual maximum	12.6 (5)	29.6 (5)	0.0465
w-s bloom duration (weeks)	9.2 (5)	4.0 (5)	0.0255
w-s bloom maximum (cells mL^{-1})	24 967 (5)	1713 (5)	0.0090
1Q mean abundance (cells mL^{-1})	5536 (5)	399 (5)	0.0163
2Q mean abundance (cells mL^{-1})	2578 (5)	166 (5)	0.0090
Criterion: Gulf Stream < -0.5 versus $> +0.5$			
3Q mean abundance (cells mL^{-1})	4376 (9)	1313 (8)	0.0161
s-f bloom maximum (cells mL^{-1})	24 754 (10)	10 664 (8)	0.0410

maximum and mean abundance of the w-s *Skeletonema* bloom differed significantly between NAOI positive (+) and negative (−) phases. During the cold, windy and bright conditions of NAOI (−) years, the mean duration of the w-s bloom was 9 weeks, twice that (4 weeks) during the five maximum NAOI (+) (=warm) years. Maximum abundance during the five most NAOI (−) years (=cold) was ca. 23 000 cells mL^{-1} greater than that during the five NAOI (+) (=warm) w-s periods (1713 cells mL^{-1}). These differences in mean abundance between cold [NAOI (−)] and warm [NAOI (+)] w-s periods were sustained during the 1Q and 2Q of that season and remained statistically significant (Table III). The week of the annual maximum was also affected. During the five minimum winters [NAOI (−), cold] the annual maximum occurred in week 13 (late March), on average; but during the five maximum winters [NAOI (+), warm], it was delayed until week 30 (late July)—a 4-month displacement and shift in the annual maximum from a w-s to a summer event.

The cardinal characters listed in Table I were examined for correlation with the NAOI. The winter NAOI correlated positively ($r = +0.35$; $n = 33$, $P = 0.0474$) with the week of the w-s bloom initiation (W2 in Table I); i.e. the lower the NAOI and temperature, the earlier the bloom began. This effect of temperature was confirmed by the negative correlations found between the winter NAOI and the duration of the w-s bloom (W4; $r = -0.41$, $n = 33$, $P = 0.0329$); i.e. the bloom was shorter during warm winters. There was no correlation with the NAOI either for the week of the annual maximum (W1) or the week of the w-s bloom maximum. A negative correlation occurred between the NAOI and mean annual abundance of the *Skeletonema* complex (N2 in Table I; $r = -0.39$, $n = 32$, $P = 0.0466$), 2Q mean abundance (N5; $r = -0.60$; $n = 32$, $P = 0.0318$) and mean abundance during weeks 2−5, weeks 13−16 and weeks 25−28 (N10, N11, N12; $r = -0.36$ to -0.64; $P = 0.0003$ to 0.0376). Correlations were not found between the NAOI and the other cardinal characters of w-s abundance (N1, N3, N4) and summer bloom behavior of *Skeletonema* (N6−N9, N13, N14).

The results indicate that the influence of the NAOI on the *Skeletonema* complex was confined to its w-s bloom dynamics; the signal was lost during the summer when the GSNW impacted its bloom behavior. The sensitivity of *Skeletonema* complex bloom behavior to variations in the location of the GSNW is illustrated in Table III. Mean *Skeletonema* abundance when the GSNW was displaced farthest to the north (>+0.5 threshold) is compared with abundance during its most southerly displacement (<−0.50). Summer (3Q) abundance typically was 3-fold greater (4376 cells mL^{-1}) in years when the north wall was more southerly (GSNW < −0.5). When the GSNW was displaced farther north, the s-f maximum (24 754 cells mL^{-1}) was lower by ca.14 000 cells mL^{-1} (40%) than that in years when the north wall was farther south (Table III). The virtually identical abundance during the w-s and s-f bloom maxima (ca. 25 000 cells mL^{-1}) is striking. They are associated, respectively, with cold winters (−NAOI) and southerly displacement of the GSNW (GSNW < −0.5), two distinct but related ocean-climate conditions.

In contrast, w-s abundance of the *Skeletonema* complex during warm NAOI (+) winters was reduced, the reduction much greater (by ca. 12.5-fold) and to a lower level (1713 cells mL^{-1}) than during the reduction in the s-f peak (10 664 cells mL^{-1}) associated with northward migration (GSNW > +0.5) of the north wall relative to its southerly positioning (Table III). This pattern suggests bloom dynamics of the *Skeletonema* complex, at least those aspects influenced by the NAO, are more sensitive to changes in the NAOI than to the variability in GSNW behavior, which becomes more important during the s-f period. There were fewer correlations between cardinal characters designating the timing (W5−W7) and abundance (N6−N10, N13, N14) of the summer *Skeletonema* blooms and the GSNW. A positive correlation with GSNW was found only with the number of weeks that *Skeletonema* abundance was <10 cells mL^{-1} (N9; $r = +0.59$, $n = 24$, $P = 0.0068$). That is, when the GSNW was in a positive (+) phase, the north wall was more northerly and the number of weeks of <10 cells mL^{-1} of *Skeletonema* was greater. Negative correlation was found between the GSNW and 3Q abundance of *Skeletonema*, N6 ($r = -0.44$; $n = 24$, $P = 0.0296$), i.e. migration of the north wall northward was accompanied by decreased summer *Skeletonema* abundance.

Annual SST had a mean value of 11.4°C and varied over a 2.4°C range from 10.2°C (1967) to 12.6°C (1991) during 1959−1997. We applied a similar threshold analysis to mean annual SST to discern whether an SST influence on *Skeletonema* bloom patterns could be detected independent of GSNW or NAO. We examined the effects of mean SST on *Skeletonema* by comparing bloom characters observed in years having SST thresholds of <11.4°C versus >11.4°C (i.e. greater than or less than the long-term mean) and by comparing the coolest 5 years versus the warmest 5 years. Mean annual SST effects were detected only in the comparison of extreme cold and warm years, and only for *Skeletonema* w-s bloom features. No SST effects were detected for summer or autumn bloom features. Significant differences in w-s bloom initiation (W2) and w-s bloom duration (W4) were detected in comparison of the coolest 5 years (1964–1968) and the warmest 5 years (1983, 1984, 1991, 1995 and 1996). w-s *Skeletonema* bloom initiation shifted from a mean of late December (week 1.7) during extreme cold years (mean annual SST of 10.7°C) to late January (week 4.8) in extreme warm (mean annual SST of 11.9°C) years ($P = 0.0099$, unpaired *t*-test). This earlier bloom initiation contributed to an increase in *Skeletonema* w-s bloom initiation which increased significantly ($P = 0.0032$, unpaired *t*-test) from 2.4 weeks duration in the five warmest years to 9.7 weeks duration in the 5 coldest years.

In summary, it would appear that the two most prominent regional (external) and coupled atmosphere–oceanic systems, the NAO and the Gulf Stream, influence bloom dynamics of the keystone *Skeletonema* species-complex in NBay, with seasonal and long-term consequences. The NAO is a more important driver of w-s bloom dynamics, with no evident signal of an NAO impact on summer *Skeletonema* bloom behavior. Temperature alone had less influence on *Skeletonema* bloom patterns, and the mean annual SST signal was evident only in w-s bloom dynamics. Conversely, the GSNW and WCR behavior are more important drivers of the summer bloom dynamics of the *Skeletonema* species-complex, with no evident signal of a GSNW impact on w-s bloom dynamics.

DISCUSSION

Gulf Stream position and *Skeletonema* bloom cycles in NBay

The statistically significant differences in the bloom phenology of the *Skeletonema* species-complex related to variations in NAO and GSNW position along the northeastern coast of the USA suggest that regionally coupled ocean–atmosphere behavior influences plankton dynamics in NBay. This influence is in addition to regulation by internal drivers such as vertical mixing, nutrient availability, grazing pressure etc. However, the processes and mechanisms by which regionally coupled atmosphere–ocean systems impact plankton dynamics in local, coastal embayments, such as NBay, are obscure. The issue needing resolution is whether the associations found between GSNW position, temperature and long-term *Skeletonema* bloom cycles have an ecological basis or should be discarded as statistical artifacts. If ecologically realistic, do they directly explain their putative impacts on *Skeletonema* or do the GSNW and NAO elements proxy the mechanisms actually involved? This is the focus of the following discussion.

The *Skeletonema* observations analyzed here were made during a sustained warming period from the late 1960s through the 1990s. SST in NBay was cooler than the long-term (1959–1996) mean from 1959 to the late 1960s (Fig. 2). This decade of below-mean temperature was followed in the 1970s by SST increasing to near mean levels, after which mean SST increased dramatically during the period from 1976–1986. The position of the GSNW and SST followed a parallel long-term increasing (northward migration) trend during 1959–1997, with a period of rapid GSNW northward migration during 1986–1995 (Fig. 2). This parallel GSNW–SST behavior is consistent with the pattern of long-term fluctuations reported for GSNW heat transport. Poleward heat transport was relatively low during the mid-1960s (Sato and Rossby, 1995; Sato and Rossby, 2000)—the period when NBay was relatively cool. The timing of the inflection points in the SST record (1968–1969 and 1982–1983) is also consistent with the pattern of temperature change recorded for the North Atlantic basin (Rodionov and Krovnin, 1992). A SST regime shift, featuring an increase in annual SST range (i.e. summer maxima to winter minima) in the continental shelf waters offshore of southern New England was detected in the mid-1980s (Friedland and Hare, 2007). The 1980s NBay SST increase then appears to be part of a larger, regional-scale change. Mean NBay SST was ca. 1°C warmer (estimated from regression; Fig. 2) in the 1990s compared with the 1960s, and SST has remained at this elevated level through the 2000s. Increasing water temperature has been linked to changes in *Skeletonema* bloom phenology in the North Sea where a ca. 0.9°C increase in SST was linked to a shift, to later in the year, in the timing of the *Skeletonema* annual peak (Edwards and Richardson, 2004). Our analysis of NBay *Skeletonema* bloom phenology showed no mean annual SST effect on the timing of annual bloom peak, but that SST effects were confined to the w-s only. In extreme cold years, the *Skeletonema* w-s bloom began earlier (late December) and lasted longer (9.7 weeks) compared with warm years when the w-s bloom began in late January and was of shorter duration (2.4 weeks).

Temperature influences phytoplankton community structure in NBay (Karentz and Smayda, 1984) and has been shown experimentally to modify *in situ* growth rates of natural populations of *Skeletonema* during w-s (Smayda, 1973). These temperature-dependent relationships suggest that temperature-related changes in *Skeletonema* physiology and ecological processes accompanied the influence of GSNW and contributed to the statistical association found between the latitudinal position of the GSNW and bloom behavior of the

Skeletonema complex. SST during 1959–1996 ranged from −2°C to 26°C. The mean 3Q (summer) temperature for all summers during the 1959–1997 time series was 20.9°C; it varied by only 2.7°C between the recorded extremes of 19.4°C (1967) and 22.1°C (1996). The *Skeletonema* complex is eurythermal, and capable of growth (μ) between (at least) 0°C and 30°C (Smayda, 1973; Suzuki and Takahashi, 1995). Within the μ–temperature relationship, growth rate is most sensitive to temperatures below 15°C, i.e. during the w-s bloom period when NAO effects rather than a GSNW influence are more pronounced. The *in situ* growth of the *Skeletonema* complex decreased 6-fold, from $\mu = 3.0$ to 0.5 per day, over a ca. 12°C decrease (from 13°C to 0.9°C) during the seasonal temperature decline from November to February (Smayda, 1973). The Q_{10} (=rate of change over a 10°C temperature increase) for growth of the *Skeletonema* complex between 5°C and 15°C is $Q_{10} = 3$, but between 20°C and 30°C growth (during the exponential phase) is relatively constant and μ is high ($\mu = 4.5$ per day^{-1}) (see Figure 6A in Smayda, 1973). Suzuki and Takahashi (Suzuki and Takahashi, 1995) found a similar constancy in μ (1.2–1.4 per day) between 15°C and 25°C for *S. costatum* isolated from Tokyo Bay. The relative constancy of μ over the temperature range that corresponds to the summer temperatures, and therefore is likely to be influenced by GSNW position, is more significant in the present context than the actual growth rate at those temperatures.

The modest year-to-year differences in mean summer temperature ($\Delta = 2.7$°C) in NBay are not expected to affect significantly interannual differences in growth rate, nor do they alone explain the GSNW–*Skeletonema* bloom phenology association found. The number of weeks annually that mean summer temperature exceeded 20°C varied more than the spread in the interannual difference (2.7°C) in mean summer temperature. The period when surface water temperature was ≥20°C ranged from 4 to 14 weeks per year, with an overall mean of 9.7 weeks. The 10-week spread in the duration that ≥20°C waters were present is considerable. It may be an aspect of temperature variability that is important to species whose life cycle, growth and related processes are enhanced and dependent upon a prolonged period of high temperature. We have not examined the potential relationship between the annual duration of the ≥20°C summer temperature window and the GSNW location–temperature–*Skeletonema* association found. However, we do not expect the duration of the ≥20°C threshold to have significantly impacted *Skeletonema* growth rate and bloom performance, given the μ–temperature relationship for the *Skeletonema* complex (Smayda, 1973; Suzuki and Takahashi, 1995).

At least two *Skeletonema* species—*S. tropicum* and *S. menzelii*—are potentially available for transport into NBay via GSNW dynamics from their subtropical habitats, the northern extension of which for *S. tropicum* is along the east coast of the USA at Cape Hatteras at 30°N (Hulburt and Guillard, 1968) and the western Sargasso Sea for *S. menzelii* (Guillard *et al.*, 1974). Since neither species has been reported from NBay, their appearance would be directly indicative of a GSNW contribution to temperature-altered bloom behavior. Both species are eurythermal and grow rapidly, similar to the *Skeletonema* complex, but their μ–temperature windows are narrower. This would restrict their potential appearance and growth in NBay to the summer period. *Skeletonema tropicum* does not grow below 13°C; its μ increasing from 0.3 to 3.0 per day over the range from 13°C to 33.8°C (Hulburt and Guillard, 1968). *Skeletonema menzelii* grows between 12°C and 27.8°C, with its μ increasing from ca. 0.7 to 3.0 per day over that temperature range (Guillard *et al.*, 1974). Failure of *S. tropicum* and *S. menzelii* to bloom allochthonously in NBay, despite favorable summer temperatures may indicate that their propagules are not being seeded, rather than an ecological barrier. We conclude that it is unlikely that temperature alone explains the association between GSNW position and *Skeletonema* bloom dynamics based on the growth (μ)–temperature relationship for the *Skeletonema* complex and summer temperatures in NBay.

We cannot link the GSNW, temperature and *Skeletonema* association to changes in summer zooplankton abundance in NBay; the supporting evidence is either lacking or contradictory. The copepod, *Acartia tonsa*, remained dominant during the time series without apparent competition from newly introduced species or replacement by indigenous species (Smayda, unpublished), although Sullivan *et al.* (Sullivan *et al.*, 2007) reported that a long-term decline in its abundance has accompanied warming. We do not exclude that GSNW location in regional waters somehow altered summer zooplankton (herbivorous) grazing dynamics and contributed to the GSNW–temperature–*Skeletonema* relationship found (Fig. 2; Tables II and III). Gulf Stream variation along the Northumberland coast (UK) strongly influenced summer zooplankton dynamics, unlike in winter (Taylor *et al.*, 2002). Modest changes in water temperature can alter seasonal grazing rates and patterns, with large impacts on species composition, biomass levels and ecosystem processes (Southward *et al.*, 1995; Sanford, 1999).

We examined the potential influence of GSNW position on zooplankton regulation of *Skeletonema* bloom cycles through top-down grazing by gelatinous zooplankton. Gelatinous zooplankton abundance increased on Georges Bank (Brown *et al.*, 2005) and in the North Sea (Lynam *et al.*, 2005) during GSNW intrusions. In NBay, the ctenophore *Mnemiopsis leidyi* is a voracious predator on zooplankton. Its grazing down of summer copepod populations leads to increased *Skeletonema* abundance (Deason, 1980; Deason and Smayda, 1982). During the 1990s when the GSNW was to the north of its mean path and NBay was warmer (Fig. 2), the seasonal presence and summer abundance of *M. leidyi* increased. Sullivan *et al.* (Sullivan *et al.*, 2001) attributed this to the rise in temperature, and recently concluded (Sullivan *et al.*, 2007) that *A. tonsa* abundance has "plummeted" because of intensifying predation by *M. leidyi*, now thriving because of warming. During this positive GSNW period in the 1990s, and given the top-down grazing of *M. leidyi* on *A. tonsa*, an increase in summer abundance of *Skeletonema*, as Deason and Smayda (Deason and Smayda, 1982) found, would have been expected to accompany the decline in abundance of *A. tonsa* reported (Sullivan *et al.*, 2007) and, hence, reduced grazing on *Skeletonema*. That dynamic would be consistent with the parallel trends found statistically in the GSNW location, temperature and *Skeletonema* bloom patterns (Fig. 2, Tables II and III). However, the opposite association was found—summer *Skeletonema* abundance decreased during GSNW (+) years, especially during August (Fig. 5). This negates the hypothesis that the GSNW–temperature–*Skeletonema* relationship in NBay is the result of GSNW-mediated increase in ctenophore abundance and grazing on *A. tonsa*.

Regional circulation and physical–chemical impacts on NBay

A direct, temperature-mediated effect on cellular growth and grazing affecting the seasonal blooms cycles of the *Skeletonema* complex in NBay driven by GSNW location seems unlikely. However, there are indirect pathways through which regional GSNW dynamics, including the spin off of WCRs, potentially can impact ecological behavior in NBay. NBay is an open embayment in oceanographic exchange with contiguous regional waters impacted by GSNW location. These source waters transport heat, salt, nutrients and organisms into NBay; probably also alter its "water quality", and admix the regional waters through which they move (Gould and Fryxell, 1988). An east to west alongshore current from the SNEB region driven by the prevailing southwesterly winds flows across the entrance into NBay and delivers offshore water into the bay through its East Passage (Fig. 1; Kincaid and Pockalny, 2003). The regional flow of "new" coastal water is influenced by wind conditions, and its influx into NBay is highly seasonal, being persistent during summer and largely absent during winter (Kincaid and Pockalny, 2003). A time series analysis showed that surface temperature at an offshore site and bottom water temperature in NBay were virtually identical, indicating the bottom water layer originated at the surface in Rhode Island Sound (Fox *et al.*, 2000). A significant, summer (July) cooling event that decreased surface temperature 5°C in Rhode Island Sound at the mouth of Buzzards Bay appeared 4 days later in the bottom waters of NBay, indicating (for that event) an offshore to inshore NBay transport time of ca. 4 days.

The summer circulation pattern near the entrance into NBay is integrated into the complex, and variable southwesterly along-shelf flow over the mid- to outer continental shelf (Kincaid and Pockalny, 2003). The water entering the bay from the SNEB and Rhode Island Sound (Kincaid and Pockalny, 2003) is composed of variable proportions of Shelf Water and Slope Water that flow into the SNEB (Bigelow, 1933; Wright, 1976; Kincaid and Pockalny, 2003; Mountain, 2003), contributions modified by interactions with WCRs (Armstrong, 1998a, b). The temperature and circulation patterns offshore south of NBay are highly variable (Armstrong, 1998a, b; Ingham, 1998; Kincaid and Pockalny, 2003), reflecting the variable location and degree of mixing between coastal and oceanic water masses on the southern New England continental shelf (Bigelow, 1933; Wright, 1976; Mountain, 2003). Winter (February) bottom water temperature, for example, at the 100 m isobath near 71°W (ca. 120 km south of NBay) exhibited a 10°C range (5–15°C) during a 10-year period (1974–1983) of monitoring (Armstrong, 1998b). Variations in temperature (and salinity) are influenced by WCR activity, which transports relatively warm, high salinity water onto the shelf during passage (Armstrong, 1998b). During the decade from 1974 to 1983, WCRs were present 92–163 days per year (Armstrong, 1998a). There was a significant positive relationship between the mean annual bottom salinity at the long-term monitoring station in lower NBay (Fig. 1), which ranged from ca. 29.5 to 31.5, and Armstrong's (1998a) WCR duration index (Fig. 3). In years of greater WCR activity, bottom water salinity tended to be higher.

NBay is also open to an influx of nutrients from offshore. A positive correlation occurs between the long-term patterns in bottom water salinity, residence time and nitrate concentration (Borkman and Smayda, 2003). Bottom water salinity is an important determinant of NBay residence time (Officer and Kester, 1991). Summer influx into the bay taps bottom water in Rhode Island Sound shown to contain elevated dissolved inorganic nitrogen concentrations (Kincaid and Pockalny, 2003), an input consistent with nitrate reductase profiles in lower NBay (Culver-Rymsza, 1988). Nixon *et al*. (Nixon *et al*., 1995) have suggested that ca. 20% of the total phosphorus loading and ca. 70% of the total nitrogen loading (both relative to terrestrial discharge) are supplied from offshore. Changes in "water quality" that affect phytoplankton growth are possibly another modification that might accompany the influx of offshore water into NBay. Johnston (1963) carried out an extensive bioassay study using *S. costatum* in waters collected in the region extending from Iceland to the North Sea and experimentally enriched with various nutrient concentrations and chelated mixtures. There was considerable seasonal and spatial variability in the capacity of the inshore, coastal and oceanic watermass types bioassayed to support the growth of *S. costatum*. Labile, unknown "growth factors" and chelated trace metals were particularly important factors determining growth success. The long-term temperature and salinity patterns and evidence of nutrient influx linked to regional circulation patterns demonstrate the advective openness of NBay to potential, indirect impacts from regional GSNW behavior and WCR activity. The connectivity between oceanographic climate on the southern New England shelf and the ecology of NBay appears to be captured in the statistically significant associations found among GSNW location and the seasonal bloom cycles of the *Skeletonema* complex.

Regional circulation and advection of phytoplankton

Gulf Stream behavior has been reported to influence phytoplankton distributions and interannual abundance in regional Slope waters (Garcia-Moliner and Yoder, 1994; Ryan *et al*., 1999), including through intrusions that pump nutrients into slope and shelf waters (Lohrenz *et al*., 2002; Schollaert *et al*., 2004). The mean path of the Gulf Stream is ~550 km south of NBay and displays latitudinal fluctuations of 100–200 km (Rossby and Benway, 2000). Transport time from the continental shelf region through Rhode Island Sound to the mouth of NBay (Fig. 1) varies from one to four days (French and Hargraves, 1986; Fox *et al*., 2000). The initiation of "brown tide" blooms in nearby Long Island estuaries has been linked to fluctuations in the "oceanographic climate" of southern New England shelf waters, specifically through modified residence time and nutrient concentrations (Vieira and Chant, 1993). French and Hargraves (French and Hargraves, 1986) attributed rapid increases in summer abundance of *Leptocylindrus danicus*, a common diatom bloom species in NBay (Karentz and Smayda, 1984, 1998), to seeding from Gulf Stream WCR and Slope Water populations. This potential source is validated by Gould and Fryxell (Gould and Fryxell, 1988) who found *L. danicus* in a WCR that remained distinct for 4–5 months while embedded within slope water, and during which it was prominent in the successional cycle and became dominant during a June bloom. However, blooms of *L. danicus* in NBay do not require external seeding—there is an indigenous population that blooms in late-spring (Karentz and Smayda, 1984, 1998). The potential for blooms of both indigenous and introduced populations to occur in coastal embayments is not usually considered when dealing with species succession. Although summer temperature conditions might favor survival and dispersion of the WCR flora in regional waters, barriers against successful invasion exist, as illustrated by the failure of *S. tropicum* and *S. menzelii* to appear in NBay.

Prodigious w-s blooms of the boreal meroplanktonic diatoms, *Detonula confervacea* and *Thalassiosira nordenskioeldii*, develop in NBay (Smayda *et al*., 2004; Smayda, unpublished), but their resting spores are not found in the bottom sediments (Hargraves and French, 1975, 1983). Since the phytoplankton assemblages entrained within the WCRs derive from the Sargasso Sea (Gould and Fryxell, 1988), they do not include the boreal and temperate species that bloom in NBay (Karentz and Smayda, 1984, 1998). The *D. confervacea* and *T. nordenskioeldii* blooms that occur presumably are seeded by excysted propagules dispersing from offshore metapopulations other than WCRs. The sources of the propagules are unknown. Most of the species that bloom in NBay also bloom in contiguous, offshore waters; but the w-s bloom in those waters develops later (Conover, 1956; Riley, 1952, 1967; Riley and Conover, 1967), being dependent on watermass stratification unlike in the well mixed, shallower waters of NBay where light-limited growth is a lesser problem (Hitchcock and Smayda, 1977). It is unknown whether resting cysts of *D. confervacea* and *T. nordenskioeldii* occur in the sediments of Rhode Island Sound or whether the bloom behavior of these species in those waters also require external seeding. Nonetheless, the bloom behavior of *D. confervacea* and *T. nordenskioeldii* provides additional, indirect evidence that NBay is open to seeding of diatom species from offshore. This can be extrapolated to the prospect that blooms of the eurythermal *Skeletonema* complex, which is holoplanktonic, are possibly seeded by propagules derived from both indigenous and allochthonous populations, similar to the behavior circumstantially evident for *L. danicus*.

Additional evidence that NBay and its phytoplankton are open and coupled to regional circulation patterns comes from a bloom of the toxic dinoflagellate *Alexandrium fundyense*. Initiated in the Gulf of Maine, its bloom progressed along the southern New England coast over a 7-week period from May to July 2005 (Anderson *et al*., 2005). The prevailing currents transported cells of *A. fundyense* south of Cape Cod into the offshore waters of Rhode Island, a pathway of dispersal matched by the trajectories of surface drifters deployed (see Fig. 6 in Anderson *et al*., 2005). During this period, cells of *A. fundyense*, which is not indigenous in NBay, were found in very low abundance at a monitoring station located near its entrance into the East Passage (Fig. 1; Borkman, unpublished). These lines of evidence show that direct advection of phytoplankton populations from the SNEB into NBay do occur and that variability in the offshore marine climate via interannual variability in GSNW location and WCR activity may be a mechanism for long-term variability in *Skeletonema* bloom patterns.

NAO and *Skeletonema* bloom cycles: contrast with Gulf Stream influence

During the 1959–1996 time series, air temperature along the Atlantic coast of the USA increased (Ford, 1996), and winter temperature in NBay increased 2–3°C (Cook *et al*., 1998; Keller *et al*., 1999; Fig. 2). The increase in winter temperature correlated positively with a prolonged, positive phase (+) of the NAOI and was accompanied by notable changes in long-term phytoplankton behavior: a decline in w-s abundance (Hawk, 1998; Keller *et al*., 1999; Smayda, unpublished); a shift in the annual *Skeletonema* bloom maximum from w-s to summer (Borkman and Smayda, 2009); changes in the dominant w-s species (Smayda *et al*., 2004; Borkman and Smayda, 2009); a decline in biomass (as chlorophyll) since the early 1970s (Li and Smayda, 1998) and (in some years) reduced w-s production (Oviatt *et al*., 2002). The cumulative effect of these long-term changes in phytoplankton abundance and bloom timing, led by changes in *Skeletonema* (Borkman and Smayda, 2009), appears to have altered the deposition rate of organic matter to the NBay benthos with impacts on benthic nitrogen flux (Fulweiler *et al*., 2007). The segment of the annual phytoplankton cycle most impacted by the progressive increase in winter warming linked to the NAO was the w-s bloom phase, whereas no effect of GSNW and WCR behavior on w-s *Skeletonema* dynamics was detected. In contrast, the impacts of the NAO and GSNW location on summer *Skeletonema* dynamics were reversed. Summer bloom behavior was not correlated with the NAO, whereas there was strong connectivity with GSNW behavior, with *Skeletonema* abundance varying with the latitudinal position of the GSNW. In years when the GSNW was displaced to the south ($GSNW < -0.5$), abundance of the *Skeletonema* complex during August was ca. 4-fold greater (9578 cells mL^{-1}; $n = 11$) than that in years (2283 cells mL^{-1}; $n = 8$) when the GSNW was displaced (migrated) to the north ($GSNW > +0.5$). Although *Skeletonema* bloom behavior is impacted by the two major and regionally coupled ocean–atmosphere systems found, the seasonal and interannual effects of the NAO and GSNW differ.

Taylor and Gangopadhyay (Taylor and Gangopadhyay, 2001) identified a connection between the NAOI and the GSNW that allows prediction of the GSNW position 1 year in advance. Our analyses indicate that summer abundance of the *Skeletonema* complex could be predicted based on knowledge of the annual mean GSNW position. Applying the GSNW criterion of $GSNW < -0.5$ versus $GSNW > +0.5$ (Table III) as a threshold for differentiating increased (>2000 cells mL^{-1}) versus repressed (<2000 cells mL^{-1}) mean 3Q abundance, nine large (>2000 cells mL^{-1}; mean) and 8 small summer bloom years are predicted during the 1959–1996 time series. The prediction of a large summer bloom based on the criterion of extreme southern displacement of the GSNW ($GSNW < -0.5$) was correct in 7 of the 9 years (78%). A reduced summer bloom year was correctly predicted in 7 of the 8 (88%) years when the GSNW was displaced to the extreme north ($GSNW > +0.5$).

Significance of the relationships

The statistically significant associations found between GSNW position and the long-term bloom behavior of the *Skeletonema* complex appear to be ecologically feasible and should not be treated as a statistical artifact. This conclusion is supported by the various lines of evidence presented that NBay is open, and subject to habitat and ecological modification by the offshore dynamics of regional waters, including GSNW and WCR behavior that affect temperature, salinity, nutrients, phytoplankton seeding, abundance and bloom cycles. Notwithstanding, we conclude that the long-term patterns and altered bloom behavior of the *Skeletonema* complex (see also Borkman and Smayda, 2009) are not causally linked to the GSNW or NAO. Rather, the GSNW position and NAO are proxies for the linkages between long-term variations in the regionally coupled atmosphere–oceanographic system and bloom dynamics of the *Skeletonema* complex. The specific mechanisms and processes of this far-field "oceanographic climate" (Dayton *et al*., 1999) driving the linked variability in *Skeletonema* behavior are multivariate and remain obscure.

Transcending local relevance to NBay, the ecological feasibility of the relationships points to the general need to consider regionally coupled ocean−atmosphere systems when evaluating the regulation of phytoplankton dynamics in local habitats and not to restrict analyses to within-system parameters—internal drivers, such as nutrients, grazers etc. (see also Smayda, 1998). The results, particularly the seasonal differences in the impact of the NAO, GSNW and WCRs on bloom behavior, suggest that three types of external forcing can occur during an annual cycle (or over the long-term) and need to be recognized—a weather-sensitive phase and a transport-sensitive phase, and an anthropogenic nutrient phase that sometimes accompanies the two ocean−atmosphere elements. Transport sensitive refers to the sum total of the physical, chemical and biological characteristics of the advected watermass modifying recipient waters; it is not restricted to propagule delivery. Allen *et al*. (Allen *et al*., 2006) also distinguished between weather- and transport-sensitive phases, which they specifically linked to the NAO and the GSNW, respectively. With regard to NBay and the NAO regulated weather-sensitive phase, its effect is rather narrow, such as the effect of temperature on w-s bloom dynamics. As Allen *et al*. (Allen *et al*., 2006) pointed out; some components of plankton-based ecosystems are not directly affected by NAO-driven climate change.

The transport-sensitive period dominates the summer season when advective processes within the regional circulation pattern increasingly exchange heat, salt, nutrients, populations and impact "water quality", such as proxied by the GSNW and WCR dynamics in the present study. Allen *et al*. (Allen *et al*., 2006) studied the effects of long-term climate change proxied by the NAO and the GSNW on the production of dimethylsufide. They concluded that the GSNW signal is propagated through climatic conditions, whereas the NAO signal is generated from the persistence of winter conditions. This also generally applies to phytoplankton behavior in NBay linked to these two climatic indices. In contrast to weather-sensitive dynamics, multiple variables are affected during the transport-sensitive phase, which have wider trophic consequences. The anthropogenic nutrient phase, when present, may be seasonal or continuous, as it is in the inner reaches of NBay (Smayda and Borkman, 2008). The exogenous supply of nutrients from the watershed is also weather influenced, particularly during rainy periods, with secondary contributions accompanying influxes during the transport-sensitive period. The distinction among the three types of external drivers is relevant to ecosystem-based management proposals, such as being developed for NBay (Desbonnet and Costa-Pierce, 2008). In the latter case, the focus is on internal drivers in developing strategies to modify anthropogenic nutrient loading to prevent and reverse ecological degradation, including undesirable blooms and hypoxia. However, management and other models that consider internal drivers only and neglect externally driven weather and transport sensitive behavior are vulnerable to low-frequency ocean−atmospheric forcing that can alter thresholds, ecophysiological processes and ecosystem dynamics.

Concluding remarks

This study reveals that the multi-decadal NBay time series is suited to detect climate-related changes in phytoplankton dynamics and also demonstrates that the location of NBay, which lies at the transition between temperate waters to the south of Cape Cod (41.7°N) and boreal waters to the north, is ideally positioned geographically to detect the effects of climate change (Fig. 1). It is exactly in such ecotones where changes induced through climate modification are expected to first appear and become quantifiable. The connectivity between oceanographic climate on the southern New England shelf and the ecology of NBay captured in the statistically significant association with blooms of the keystone *Skeletonema* complex most likely spreads broadly through meteorological variables that impact a range of ecosystem components, i.e. phytoplankton, zooplankton, growth and grazing. In effect, two distinct modalities in oceanographic-climate regulation of plankton processes in NBay are revealed by the long-term *Skeletonema* behavior—the GSNW signal is propagated in summer through climatic conditions, whereas the NAO signal is generated from the persistence of winter conditions, during which temperature plays a primary role (Borkman, 2002; Smayda *et al*., 2004; Borkman and Smayda, 2009). This differential, external driving of plankton behavior compounds the difficulty in quantifying plankton dynamics when considering only internal drivers.

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