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A late Holocene paleo-productivity record in the western Gulf of Maine, USA, inferred from growth histories of the long-lived ocean quahog (*Arctica islandica*)

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Abstract To investigate environmental variability during the late Holocene in the western Gulf of Maine, USA, we collected a 142-year-old living bivalve (Arctica islandica) in 2004, and three fossil A. islandica shells of the Medieval Warm Period (MWP) and late MWP / Little Ice Age (LIA) period (corrected ${}^{14}C_{AMS} = 1030 \pm 78$ AD; 1320 ± 45 AD; 1357 ± 40 AD) in 1996. We compared the growth record of the modern shell with continuous plankton recorder (CPR) time-series (1961-2003) from the Gulf of Maine. A significant correlation ($r^2 = 0.55$; p < 0.0001) exists between the standardized annual growth index (SGI) of the modern shell and the relative abundance of zooplankton species Calanus finmarchicus. We therefore propose that SGI data from A. islandica is a valid proxy for paleo-productivity of at least one major zooplankton taxa. SGIs from these shells reveal significant periods of 2-6 years (NAO-like) based on

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Darling Marine Center, University of Maine, Walpole, ME 04573, USA wavelet analysis, multitaper method (MTM) analysis and singular spectrum analysis (SSA) during the late Holocene. Based on established physical oceanographic observation in the Gulf of Maine, we suggest that slope water variability coupled with North Atlantic Oscillation (NAO) dynamics is primarily responsible for the observed SGI variability.

Keywords Arctica islandica · Shell growth · Climate variability · Paleo-productivity · Gulf of Maine · North Atlantic Oscillation (NAO)

Introduction

The Gulf of Maine is a mid-latitude sea situated in the northwestern Atlantic Basin located along a hydrographic and faunal transition zone that is sensitive to minor climate shifts (Fig. 1) (e.g., marine ecosystem response to climate in the North Atlantic; MERCINA 2001, 2003). The Gulf of Maine is an extremely productive ocean environment that supports a rich and dynamic ecosystem. Because of its geographic location, changes in the strength and/or position of slope water currents (e.g., Labrador Current, Gulf Stream) are thought to significantly affect the oceanography (temperature, salinity, productivity, etc.) in the Gulf of Maine (Dickson et al. 1996; Keigwin and Pickart 1999; Pickart et al. 1999; MERCINA 2001; Greene and Pershing 2001; Conversi et al. 2001). Further, dominant modes of climate variability in the North Atlantic such as the North Atlantic Oscillation (NAO) have been linked to variability in ecosystem dynamics (e.g., Drinkwater and Mountain 1997; Drinkwater et al. 2003). Understanding the mechanisms responsible for the observed interannual-to-decadal changes in zooplankton levels in the Gulf of Maine remains a fundamental research problem (e.g., Pershing et al. 2005). A better understanding of zooplankton dynamics would provide a framework for policy makers to protect and conserve the ecosystem (MERCINA 2001, 2003; Greene and Pershing 2003; Pershing et al. 2004, 2005). Knowledge of past productivity levels in the Gulf of Maine would substantially improve the ability of biological modelers to forecast changes in the Gulf of Maine's ecosystem. In addition, long, continuous environmental records would also allow investigations into the connections among climate, oceanography, and ecosystem dynamics in the Gulf of Maine. Such sclerochronological records extend into a time when there is very little, if any, anthropogenic effect in this environment. Thus a comparison can be made between older (pre-anthropogenic) and newer records to assess, if there are any significant changes associated with increased human activity.

The continuous plankton recorder (CPR) survey is slightly longer than 40 years in the Gulf of Maine and is operated by the National Oceanic and Atmospheric Administration (NOAA). The CPR survey consists of continuous horizontal tows between Boston, Massachusetts and Cape Sable, Nova Scotia at 10 m depth approximately monthly, by ship-of-opportunity (e.g., Pershing et al. 2005). The CPR filters zooplankton via a silk gauze with a 270-µm mesh, collecting zooplankton and relatively large phytoplankton. The resulting CPR dataset contains spatially indexed zooplankton taxa abundances (e.g., Clark



Fig. 1 The general geographic map for the Gulf of Maine (*bottom*), noting Casco Bay, shell location, and Boothbay Harbor (SST record) (*top panel*) is shown. The CPR transect (*dashed black line*) from Boston, Massachusetts to Cape Sable, Nova Scotia, and the northernmost half of the Kaplan Extended SST V2 area are illustrated (*bottom*)

et al. 2001). Because the CPR survey is relatively short, it is necessary to use proxy records to reconstruct productivity prior to the 1960s. Shells of bivalve mollusks serve as important archives of paleoenvironmental information, and can provide high-resolution records of past and present ocean climate variability (e.g., temperature, salinity, productivity, DIC, pCO₂, pollution) (e.g., Schöne et al. 2005a; Shanahan et al. 2005). Shells from the bivalve Arctica islandica (Linnaeus, 1767) (ocean quahog) have been widely used in paleoceanography (Weidman and Jones 1993; Weidman et al. 1994; Witbaard et al. 1994; Marsh et al. 1999; Marchitto et al. 2000; Schöne et al. 2003, 2004, 2005a, b; Scourse et al. 2006; Helama et al. 2007). The ocean quahog is a slow-growing, long-lived bivalve commonly over 100 years old, with individuals reported to be 225, 268 and 374 years old by Ropes and Murawski (1983), Forsythe et al. (2003) and Schöne et al. (2005a) respectively. Growth of the ocean qualog appears to be primarily related to food quality and availability (e.g., depth of the water column, horizontal advection, mixing, etc.) as well as water temperature (Beal and Kraus 1989; Witbaard et al. 1996, 1999). The longevity and the subarctic to mid-latitude distribution of A. islandica in the northern hemisphere make it an extremely useful proxy of past ocean environments. Because A. islandica deposits distinct annual lines in its shell, it is possible to reconstruct past ocean environments at subannual-to-annual resolution (Thompson et al. 1980; Jones 1980, 1983; Ropes et al. 1984; Kraus et al. 1992; Kennish et al. 1994). If the collection date is known, paleoenvironmental reconstructions with an absolute chronology can be created (e.g., Jones 1983; Jones et al. 1989).

In this paper, we investigate environmental variability in the western Gulf of Maine for periods during the late Holocene using growth histories from *A. islandica*. We present an annualized marine-based record of paleo-productivity for intervals of the late Holocene that begins ca. 1000 AD and spans the climate transition between the Medieval Warm Period (MWP) and the Little Ice Age (LIA). Further, we investigate dominant modes of environmental variability and show how those modes vary through time.

Methods and results

Animal collection

One specimen of *A. islandica* was collected alive in the western Gulf of Maine, USA (43°39'22.14"N, 69°48'6.01"W), in 30 m water depth via the fishing vessel FV Foxy Lady on March 14, 2004 during a Maine Department of Marine Resources dredge survey (Fig. 1).

Three well-preserved articulated fossils of *A. islandica* were collected 3 km away (43°41'13.14"N, 69°47'56.34"W) in 38 m water depth via a Rossfelder vibracore (SBVC-9609) on September 29, 1996 (Belknap and Kelley, personal communication) (Fig. 1). Because the animals were collected from the same oceanographic setting (location and water depth), comparisons among the shells to assess changes in ocean conditions through time is thought to be appropriate.

Sample preparation

In preparation for sclerochronological analysis (see Schöne et al. 2005a for details), the left valve from each shell was mounted on a plexiglass block. A quick drying metal epoxy resin (JB KWIK-Weld) was then applied to the surface (inside and out). A thick section (3 mm) of shell was cut from the valve along the axis of maximum growth (Fig. 2a), from the umbo to the shell margin (Fig. 2b), and perpendicular to the annual growth lines with a Buehler Isomet low-speed saw using a 0.3 mm thick diamond wafering blade. Each section was mounted on a glass slide, ground with 800 and 1200 SiC grit, polished with 1 μ m Al₂O₃ powder and cleaned with dehydrated ethyl alcohol.

Radiocarbon dating

¹⁴C_{AMS} dating (analyzed at National Ocean Sciences Accelerator Mass Spectrometry Facility, Woods Hole Oceanographic Institution) was used to determine the approximate calendar age of the outermost shell portion (oldest). The periostracum was removed with a razor blade, and approximately 8 mg of shell carbonate was milled from the outer shell layer along the shell margin. Calibrated ¹⁴C ages (cal yr AD) were calculated using Calib 5.01 (Stuiver and Reimer 1993) using a regional Gulf of Maine marine reservoir effect of $\Delta R = 39 \pm 40$ by Tanaka et al. (1990), which included qualog shells (Arctica islandica and Merceneria mercenaria) from museum collections. The calendar age assigned to the entire shell resulted from counting the annual growth layers (Fig. 2c) from the ventral margin back to the umbo region along the greatest growth axis (Jones 1980).

Sclerochronological analyses

We used methods outlined by Schöne et al. (2005a) to resolve annual growth patterns. Polished shell sections were immersed in Mutvei's solution for 20 min at $\sim 38^{\circ}$ C. The treated shell was immediately rinsed with demineralized water and air-dried. The growth patterns of the etched shell were viewed under a reflected light stereomicroscope (Leica Wild M3Z) and digitized using a Nikon Coolpix 995



Fig. 2 Sample preparation and measurements are shown. a Left valve of an *A. islandica* shell, noting the preferred line of section. b A 3-mm thick, cross-section of *A. islandica*. c Enlarged cross-section of *A. islandica* (treated with Mutvei solution) noting the annual lines, measurement of a year's growth, outer shell surface, and the outside and inside shell layers

camera. Annual growth widths, which consist of alternating bands of thin dark lines and relatively thick light portions, were determined to the nearest 1 μ m with Scion Image (version 1.63). Measurements were conducted on the outer shell surface, from one annual band to the next (Fig. 2c). Determination of ontogenetic age was established by counting annual increment layers (Jones 1980; Ropes et al. 1984).

Based on sclerochronological analyses, the modern *A. islandica* shell was 142-years-old and lived from 1863 to 2004 cal yr AD (Fig. 3). The fossils recovered from vibracore SBVC-9609 in the western Gulf of Maine were from 48, 40, and 30 cm core depths, and the sclerochronological ages based on ¹⁴C_{AMS} analyses associated with the fossil shells were 1030–1078 ± 78 AD (48-years-old), 1320– 1355 ± 48 AD (36-years-old), 1357–1470 ± 45 AD (116years-old), respectively.



Fig. 3 a Annual growth of shell SF1 and ontogenetic age (*black dots*). The age-related growth trend was removed with a power growth model (*solid black line*). b Standardized growth index (SGI) for shell SF1 (see text for details) and sclerochronological age

Detrending age-related growth patterns

The growth of A. islandica decreases with increasing ontogenetic age (Fig. 3a), thus long-term growth patterns were removed in order to evaluate environmental signals contained in the annual growth increment time-series. We used a power growth model to detrend the time-series (e.g., Cook and Kairiukstis 1990) (Fig. 3b). The calculated growth indices (GI) were calculated by dividing measured by predicted growth (based on power growth model) values for each year. Indexing removes age-related growth trends from the time-series. Then, the GI data were standardized by subtracting the mean and dividing by the standard deviation of the GI time-series (Fig. 3b). The standardized growth index (SGI) is a dimensionless parameter of how growth deviates from the average growth trend (e.g., Schöne 2003). SGI values were prewhitened with firstorder autoregressive (AR-1) modeling (Box and Jenkins 1976), which successfully removed lag-1 autocorrelation from each SGI time-series. Further, we used a low-pass filter (Savitzky-Goley; window length = 5) on SGI timeseries to emphasize decadal-to-multi-decadal changes in ambient growing conditions.

Continuous plankton recorder (CPR) data

The CPR program for the Gulf of Maine is operated by NOAA Fisheries, which began taking CPR transects in 1961 (see Jossi and Goulet 1993 for details). These measurements consist of a single transect between Boston, Massachusetts and Cape Sable, Nova Scotia (Fig. 1) by ship-of-opportunity approximately monthly. Several taxa of zooplankton and relatively large phytoplankton are represented in the CPR data, which are spatially indexed by relative abundance. We used CPR data that focused on the central Gulf of Maine region as outlined by Pershing et al. (2005). The modern shell SGI time-series (SF1) was compared with CPR data (1961–2003) to determine if there is a relationship between zooplankton levels and shell growth.

Relationship between CPR data and shell growth

The comparison between the SGI for the modern shell and the relative abundance of zooplankton species *Calanus finmarchicus* is shown in Fig. 4. A strong relationship between annual shell growth and *C. finmarchicus* abundance is evident ($r^2 = 0.55$; p < 0.0001), and *C. finmarchicus* abundance levels explain 55% of SGI variability. This result demonstrates the potential utility of *A. islandica* as a proxy for paleo-productivity (*C. finmarchicus*) for the western Gulf of Maine. Other zooplankton taxa that showed considerable interannual variability (*Oithono* spp., *Centropages typicus*) did not correlate significantly with the SGI time-series.

Relationship between SST and shell growth

The closest SST record to the shell collection site is in Boothbay Harbor (BBH) (Fig. 1), where the Maine



Fig. 4 Time-series of shell SF1 SGI (*solid black line*) and zooplankton *Calanus finmarchicus* relative abundance (*dashed black line*) are shown. Continuous plankton recorder (CPR) data for the Gulf of Maine was incomplete during 1975, 1976, and 1977

Department of Marine Resources began measuring SST on a daily basis in 1905. This record is available to the public and contains monthly and annual SST averages (Lazzari 2001). The modern shell (SF1) SGI time-series was compared with BBH SST record to assess influences of water temperature on shell growth. There is a weak but significant correlation between annual shell growth and annual SST ($r^2 = 0.04$; p < 0.05) from 1905 to 2003. The highest significant correlation between annual shell growth and seasonal SST values at BBH (1905–2003) was during the fall (SON) and winter (DJF) seasons ($r^2 = 0.11$; p < 0.0009). The fall and winter SSTs at BBH had an equal effect on annual shell growth.

We also compared the modern SGI record with $5^{\circ} \times 5^{\circ}$ SST data outside the Gulf of Maine (37.5–42.5N; 62.5–67.5W) (Kaplan et al. 1998) from 1960 to 1990 (Fig. 1). A significant relationship ($r^2 = 0.17$; p < 0.009) exists between annual SST data outside the Gulf of Maine and the SGI record from 1960 to 1990 with a 1-year lag. This result supports previous findings that indicated water temperature significantly impacts *A. islandica* shell growth (Beal and Kraus 1989; Witbaard et al. 1996, 1999). However, the relationship noted here between shell growth in the western Gulf of Maine and SST outside the Gulf of Maine (Kaplan et al. 1998) suggests that slope water entering the Gulf of Maine is more important to shell growth than water temperature at BBH (Fig. 1).

Relationship with the NAO and shell growth

To test the connection between NAO activity and oceanographic variability in the Gulf of Maine (e.g., MERCINA 2001; Greene and Pershing 2001; Conversi et al. 2001; Drinkwater et al. 2003), we compared the winter (Dec-Mar) NAO index (e.g., Hurrell 1995) with the modern shell SGI record with various lags. We found a statistically significant relationship ($r^2 = 0.29$; p < 0.002) between our modern SGI record and the winter NAO index with a 1-year lag from 1960 to 1990. This result supports a NAO-forcing on zooplankton dynamics in the Gulf of Maine previously discussed.

Calibrated late Holocene SGI time-series

The SGI record from the western Gulf of Maine is shown in Fig. 5. Although the record is not continuous, it offers insights into environmental variability during the late Holocene. There are distinct periods with either high or low shell growth. Five zones are highlighted (Fig. 5), each depicting periods that tend to be in one mode for greater than 10 years. Two periods of relatively low SGI values occur from $\sim 1360-1400$ AD and $\sim 1910-1970$ AD. Three periods



Fig. 5 The late Holocene SGI time-series is illustrated. *Red* highlighted zones represent higher than normal shell growth, while blue highlighted zones represent lower than normal shell growth

of relatively high SGI values occur from $\sim 1450-1470$ AD, $\sim 1864-1890$, and $\sim 1975-2003$. The periods not highlighted exhibit substantial interannual variability in SGI values, but do not exhibit any decadal trends.

Spectral analyses

To assess persistent patterns in shell growth (SGIs), we employed three independent techniques of spectral analyses; wavelet analysis (Torrence and Compo 1998), multitaper method (MTM; Thompson 1982, Mann and Lees 1996) and singular spectrum analysis (SSA; Vautard and Ghil 1989). Each of these methods offer distinct advantages over traditional Blackman-Tukey analysis, which is susceptible to aliasing and requires several window lengths to extract dominant frequencies, and Fourier transforms, which are ineffective on nonstationary timeseries. Wavelet analysis decomposes a time-series into time-frequency space, which allows one to visualize dominant modes of variability and how those modes vary through time (Torrence and Compo 1998). Further, wavelet transforms can be used to evaluate time-series that are nonstationary and contain a variety of frequencies (Daubechies 1990). SSA enables a time-series decomposition into trend, oscillating, and noise components by analyzing its covariance matrix (Vautard and Ghil 1989). MTM is a refined Fourier-based analysis that offers better resolution and decreased spectral leakage (Thompson 1982).

We performed wavelet analyses (Morlet; m = 6) on the SGI time-series that were greater than 100 years long to determine dominant modes (periods) in both records, and how those modes varied through time (Torrence and Compo 1998) (Fig. 6). Both records were normalized relative to a global wavelet spectrum in order to compare relative power of the signals temporally, and significance at the 95% confidence interval (CI) was determined against a



Fig. 6 Wavelet spectrums for shells SF1 (*top*) and SBVC9609-30 cm (*bottom*) using the Morlet (m = 6) wavelet. The power has been scaled by the global wavelet spectrum. The *cross-hatched* region is the cone of influence, where zero padding has reduced the variance. *Black contour* is the 5% significance level, using a *red-noise* (autoregressive lag1) background spectrum (Torrence and Compo 1998)

red-noise (autoregressive lag1) background spectrum. The modern shell record (SF1) showed significant periodicities in the 2–16 years range from the 1860s–1900. Also, from \sim 1970–1985 a shorter period (2–3 years) was significant (Fig. 6, top). The longest paleo-shell (SBVC 9609-30 cm) showed significant periods of 2–4 years after 1400 AD (Fig. 6, bottom). Further, at the end of the record there is a shift to longer periods (8–16 years). Both SGI time-series exhibit non-stationary tendencies, which suggest that the forcing mechanism (s) may also be non-stationary.

We used MTM and SSA to determine persistent patterns in SGI values. For both techniques, significance at the 95% C.I. was determined using a red-noise (autoregressive lag1) background spectrum using KSpectra (SpectraWorks, version 2.2). The spectral features for modern shell (SF1: 1864-2003 AD) are shown in Fig. 7. MTM analysis produced significant periods of ~ 2.1 , 3.5, and 4.7 years (Fig. 7, top). SSA produced significant periods of 4.7 and 5.0 years (Fig. 7, bottom). The common signal between both techniques is 4.7 years (Fig. 7). The spectral features for paleo-shell (SBVC9609-30 cm; $1357-1470 \pm 40$ AD) are shown in Fig. 8. MTM analysis produced significant periods of 2.0, 3.8, 4.5, 4.8, and 57.0 years (Fig. 8, top). SSA produced significant periods of ~ 2.1 and 3.9 years (Fig. 8, bottom). The common signals between both techniques are ~ 2.1 and 3.8–3.9 years (Fig. 8). The shorter shell records (SBVC-9609-48, 1030 ± 78 AD; SBVC-9609-40, 1320 ± 45) yielded signals of 6.6 years and 5.5 years respectively based on MTM analysis and SSA. All four SGI records have significant NAO-like periods in the 2-6 years range.

Discussion

A paleo-productivity proxy- SGI and *Calanus finmarchicus* abundance levels

It is assumed that growth histories from *A. islandica* reflect important changes in water column processes, including



Fig. 7 Spectral analysis for 142-years-old shell SF1 using MTM (*top*) and SSA (*bottom*) using KSpectra (version 2.2) is shown. The *black dashed contour* (*top*) and the *black vertical bars* (*bottom*) are the 5% significance levels, using a *red-noise* (autoregressive lag1) background spectrum



Fig. 8 Spectral analysis for 116-years-old shell SBVC9609-30 cm using MTM (*top*) and SSA (*bottom*) using KSpectra (version 2.2) is shown. The *black dashed contour* (*top*) and the *black vertical bars* (*bottom*) are the 5% significance levels, using a *red-noise* (autoregressive lag1) background spectrum

primary production and sedimentation rates (Witbaard et al. 1997), because A. islandica is an active suspension feeder in the benthic zone primarily relying on phytoplankton supply (Cargnelli et al. 1999). The strong positive relationship between the relative abundance of zooplankton C. finmarchicus and shell growth ($r^2 = 0.55$; p < 0.0001) suggests that it is appropriate to use SGIs from A. islandica to reconstruct at least one major component of productivity in the western Gulf of Maine. However, the connection between C. finmarchicus and A. islandica growth is still poorly understood (e.g., Planque and Fromentin 1996; Witbaard et al. 2003). Planque and Fromentin (1996) proposed a food-web-competition model to explain the significant negative relationship between C. finmarchicus abundance and A. islandica growth in the northern North Sea. In the Planque and Fromentin (1996) model high C. finmarchicus levels (related to local ocean conditions) would lead to low phytoplankton levels due to predation by C. finmarchicus, which would result in less export of phytoplankton into the benthic zone, and less A. islandica shell growth. However, we propose a hydrographic-based model to link C. finmarchicus levels and A. islandica growth in the Gulf of Maine. Greene and Pershing (2001) suggested that C. finmarchicus is a deepwater zooplankton species derived from a North Atlantic source that is subject to advective transport processes. We suggest that *C. finmarchicus* is a tracer of slope water input from the North Atlantic, and the hydrographic properties (temperature, salinity, nutrients, etc.) are significantly affecting primary productivity (e.g., phytoplankton) in the Gulf of Maine. Therefore, increased phytoplankton abundance would lead to greater *A. islandica* growth. Further, this idea is supported by a significant relationship ($r^2 = 0.17$; p < 0.009) between annual SST data outside the Gulf of Maine (Kaplan et al. 1998) and the SGI record from 1960 to 1990 with a 1-year lag, indicating a slope water connection. Therefore, we believe that *C. finmarchicus* levels are associated with slope water properties and are potential proxies of primary production in the western Gulf of Maine.

C. finmarchicus dynamics and SST outside the Gulf of Maine explain most of the SGI variability from the modern shell record. Fall and winter SST at BBH explains $\sim 11\%$ of SGI variability from 1905 to 2003. Other local mechanisms that may be responsible for part of the SGI variability include river discharge (nutrients), coastal currents changes (e.g., Eastern Maine Coastal Current, Western Maine Coastal Current), stratification during the summer months, and winter mixing.

North Atlantic climate variability and ecosystem dynamics in the Gulf of Maine

A strong relationship is documented between NAO variability and changes in various trophic levels of the North Atlantic marine ecosystem (Drinkwater et al. 2003). Drinkwater et al. (2003) reported that NAO variability affected abundance, biomass, distribution, species assemblages, growth rates, and survival rates for phytoplankton, zooplankton, benthos, fish, marine diseases, whales and seabirds. However, the relationships among climate variability, NAO variability and the oceanographic response in the Gulf of Maine are still unresolved. The oceanography of the region is, in part, influenced by fluctuations in the cold polar waters from the northeast, and the warm temperate waters from the south, and freshwater input via rivers (Loder et al. 1998; Pettigrew et al. 1998). To the northeast, the Labrador Current (LC), which is primarily a buoyancy-driven coastal current formed in the Labrador Sea, flows southeastward over the continental shelves and slopes of Labrador and Newfoundland and mixes along the Scotian Shelf (Lazier and Wright 1993; Loder et al. 1998). The sources for the LC are from the Nordic Sea and Canadian Archipelago (Loder et al. 1998). The LC-derived current brings cold (4-8°C), relatively fresh and nutrient poor (Petrie and Yeats 2000; Drinkwater et al. 2003; Thomas et al. 2003; Townsend et al. 2006) water to the

Gulf of Maine region (Loder et al. 1998). To the south, the warm (8-12°C), relatively saline and nutrient rich (Townsend et al. 2006) waters of the Atlantic Temperate Slope Water move northward along the continental slope toward the Gulf of Maine region (Drinkwater et al. 1999), and is thought to vary in accordance with the location of the Gulf Stream (Taylor and Stephens 1998; Loder et al. 2001). The MERCINA working group (2001) reported that fluctuations in the ocean-climate system are reflected in the changes in composition and relative distributions of phytoplankton. Low concentrations of phytoplankton in 1998 were coincident with negative anomalies in sea surface temperatures (SST) and followed the intrusion of the nutrient poor LC possibly induced by the sudden negative shift in the NAO in 1996 (Thomas et al. 2003). Greene and Pershing (2001, 2003) showed that the NAO is positively correlated with changes in zooplankton (C. finmarchicus) abundance at lags of 2-4 years. Conversi et al. (2001) also reported significant positive correlations between the NAO index and C. finmarchicus abundance ($r^2 = 0.25$) with a 4years lag, and winter SST (derived from the comprehensive ocean-atmosphere data set (COADS)) ($r^2 = 0.22$) with a 2-years lag over a 30-years period (1961-1991) in the Gulf of Maine. Because phytoplankton and zooplankton are at the base of the food chain, and C. finmarchicus alone represents more than 70% of the region's springtime zooplankton biomass, it is crucial to understand the possible causes in their fluctuations. Zooplankton changes in marine ecosystems offer an essential connection between primary producers and higher trophic levels. Many marine animals, such as planktivirous fish, marine mammals, and seabirds depend upon C. finmarchicus as their primary nutrition (Greene and Pershing 2003). Drinkwater et al. (2003) suggested the abundance of herbivorous zooplankton, such as C. finmarchicus, usually follows local phytoplankton patterns, but with a slight lag. The NAO phase and distribution of zooplankton relationship is opposite in the northeast Atlantic than in the northwest Atlantic (Conversi et al. 2001). This out-of-phase relationship between the northwestern and northeastern Atlantic and the NAO high phase was described by Drinkwater et al. (2003) as a result of colder conditions in the eastern Atlantic Basin, causing zooplankton levels to decrease, whereas they increased in the western Atlantic due to warmer conditions. Recently, Pershing et al. (2004, 2005) reported that C. finmarchicus dynamics in the Gulf of Maine are coincident with the NAO index at times, but substantial zooplankton community shifts have occurred independent of NAO activity. Further, Pershing et al. (2005) suggested that slope water variability (i.e., advective transport processes) is a viable mechanism that links North Atlantic climate and C. finmarchicus levels in the Gulf of Maine.

Relationship between the NAO and shell growth

There is a statistically significant relationship ($r^2 = 0.29$; p < 0.002) between our modern SGI record and the winter (Dec-Mar) NAO index (e.g., Hurrell 1995) with a 1-year lag from 1960 to 1990. It appears that NAO activity is in part controlling shell growth via advective processes between the North Atlantic and the western Gulf of Maine. In addition, Greene and Pershing (2001) suggested that a substantial part of the stock is derived from inputs from populations off the continental shelf, because C. finmarchicus prefers deepwater during autumn and winter. Therefore, it is possible that C. finmarchicus levels are subject to climate forcing mechanisms (NAO) outside the Gulf of Maine. If advection processes into the Gulf of Maine are more important in controlling C. finmarchicus levels than local processes such as mixing, stratification, or salinity, then a relationship between the NAO and C. finmarchicus levels would be expected (e.g., Drinkwater et al. 2003). We suggest that the relationship noted here between SST outside the Gulf of Maine (Kaplan et al. 1998) and shell growth are linked to NAO dynamics as reported by Drinkwater et al. (2003), and that the SGI record is composed of a mixed signal, with origins in the North Atlantic and locally within the Gulf of Maine. In addition, we propose that positive (negative) SGI values represent relatively more input of Atlantic Temperate Slope Water (LC-derived water) into the Gulf of Maine, based on the previous nutrients studies (e.g., Petrie and Yeats 2000; Drinkwater et al. 2003; Thomas et al. 2003; Townsend et al. 2006).

Interannual-to-decadal SGI variations

The modern (SF1) and paleo-shell (SBVC9609-30 cm) SGI records are dominated by significant (above 95% C.I.) high frequency oscillations in the 2-5 years periods (NAOlike). This result is based on robust spectral techniques, including wavelet analysis, MTM, and SSA. This suggests the mechanism responsible for the 2-5 years period noted in the SGI records (productivity) has not changed since \sim 1350 AD. Evident patterns in SGI variability exist throughout much of the record, and the SGI record tends toward long periods of either relatively fast (more productive) or slow (less productive) growing conditions (Fig. 4). These decadal patterns in shell growth exist from \sim 1350–1470 AD and during the modern period $(\sim 1864-2003 \text{ AD})$, but they are not evident in the shorter SGI record. The SGI records during the MWP (SBVC-9609-48, 1030 ± 78 AD) and late MWP (SBVC-9609-40, 1320 ± 45) are dominated by 6.6 and 5.5 years periods, respectively. Neither of these paleo-SGI records produced the higher frequency period of 2 years noted in the longer shell records. The absence of the higher frequency signal may be attributed to milder and less variable ocean conditions during the MWP.

Conclusion and future work

We present a preliminary proxy for at least one major component of paleo-productivity (Calanus finmarchicus abundance) in the western Gulf of Maine based on growth records (SGIs) from A. islandica. The late Holocene SGI record has substantial interannual-to-decadal variability. We propose that slope water variability coupled with North Atlantic Oscillation (NAO) dynamics is primarily responsible for the observed SGI variability. SGIs from these shells reveal significant periods (95 % C.I.) of 2-6 years (NAO-like) based on wavelet analysis, MTM analysis and SSA during the late Holocene. Spectral analyses on SGI records indicate a shift in periodicity from 5-6 years to 2-5 years after ~ 1350 AD, possibly related to the MWP/LIA transition. Further, decadal trends in SGI variability are clearly noted, and likely related to long-term changes in slope water properties in the northwestern Atlantic basin. This record should improve the understanding of past environmental variability in the Gulf of Maine beyond the CPR instrumental record. The development of a new paleoproductivity proxy is promising for this region. Although there is a strong relationship between the growth in the modern shell and environmental data presented here, we recognize that this study is preliminary because we have not replicated our findings with multiple shells. Ongoing work is addressing this weakness. Further, although it is safe to say that "food" dynamics is the major controlling factor on shell growth today for this region and others (e.g., Witbaard et al. 1996, 1999), different factors in the past, such as water temperature, salinity, seasonality, pathogens, etc., may have played more important roles on shell growth. Thus further work is necessary to better understanding of the dynamics driving shell growth. A major goal is to complete a 1,000-year continuous SGI record, based on a large number of shell replicates (e.g., Helema et al. 2007) and cross-matching techniques (e.g., Scourse et al. 2006), from the region to assess multi-decadal-tocentennial components of the coupled ocean-biology-climate system. Further this sclerochronological record will provide the foundation to conduct detailed geochemical studies (e.g., elemental ratios, oxygen isotopes) on the shell material. This added geochemical information would substantially improve the use of such archives, as well as improving environmental reconstructions. Paleoenvironmental information derived from the shells of A. islandica provides a framework for both climate and marine biological modelers to improve their understanding of past environmental conditions. The longevity and geographic distribution of the bivalve *A. islandica*, and its utility as an ocean proxy offers significant advances in paleoceanography, especially in mid-to-high latitudes.

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