

Sea Ice Variations Influence Benthic Community Growth Rates over Decadal Scales: Evidence from Bivalve Population near the Barents Sea Polar Front

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Running Head: Climate forcing and bivalve growth in the Barents Sea

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Abstract

We examined growth of the Arctic bivalve *Clinocardium ciliatum* from 1977-2006 in the Barents Sea to evaluate the effect of different water masses on growth and to assess the influence of climatic forcing on ecological processes over decadal scales. Analysis of annually-deposited growth lines in shells of 22 individuals from 3 stations allowed us to assess growth conditions for up to 30 years, thus encompassing both warmer and colder climatic phases of the last century. Growth rates of specimens at younger ages (6-13 years) were highest in Atlantic water, resulting in an average size 20% greater compared to similarly aged individuals from Arctic water or at the Polar Front, reflecting warmer sea temperatures and/or presumably greater food supplies in the Atlantic-dominated regions of the Barents Sea. Despite different absolute growth rates, temporal patterns of ontogenetically-adjusted growth (i.e. Standard Growth Index = SGI) had similar features, with below-average but increasing SGI throughout the 1980s and culminating in 1994 or 1995 with the highest SGI. An abrupt decline starting in 1996 led to below-average growth rates for most of the years from the turn of the century to the end of the record in 2006. The decline in growth coincides with abrupt phase shifts in two hemispheric oscillatory indices: the North Atlantic Oscillation (NAO) and the Arctic Climate Regime Index (ACRI). The strongest statistical relationships were found between growth and the ACRI, and its local manifestations through precipitation. The ACRI explained 16.9% and 27.7% of the variation in growth at the Atlantic and Arctic stations respectively while ACRI and annual precipitation together explained 42.1% of the growth at the Polar Front station. Using a two year running mean of the ACRI improved these relationships substantially, indicating a lag in the relationship between index and growth. These results suggest that benthic communities in this area are responding more to regional climate forcing than local parameters and that the predicted increase of Atlantic water in the

Barents Sea in response to climate change will have an impact on at least suspension feeding benthic organisms.

Introduction

The abundance of organisms over a wide range of tropic levels is enhanced by oceanic fronts (Munk et al. 1995; Josefson and Conley, 1997; Hunt and Harrison, 1990; Dewicke et al., 2002; Mendes et al., 2002; Bluhm et al., 2007). These areas typically are the result of two different water masses meeting and are characterized by rapid changes in physical, chemical, and biological conditions over a short horizontal distance. They are commonly observed on a small scale in tidal estuaries, but can also occur on larger, mesoscales on continental shelves. Increased abundances of pelagic organisms associated with fronts is likely a consequence of a combination of increased primary production and the concentration of primary producers into a relatively narrow zone (Floodgate et al., 1981; Creutzberg, 1985; Franks 1992), with a cascade up the food chain to higher order predators. Benthic communities under fronts also receive more food relative to non-front areas because of a combination of higher primary production in the overlying water column and tighter pelagic-benthic coupling (Creutzberg, 1985; Josefson and Conley, 1997). Regardless of the mechanism, high benthic biomass is associated with fronts (Creutzberg et al., 1984; Josefson and Conley, 1997; Bluhm et al., 2007; Carroll et al., 2008). Oceanic fronts are receiving increased attention by oceanographers because they are hot spots of biodiversity and abundance, but the dynamics of polar fronts are still relatively poorly studied. Our lack of knowledge of polar fronts has recently been identified as a gap in our understanding of polar marine systems (ACIA, 2005).

The Polar Front is a well-known feature in the central Barents Sea (Loeng, 1991; Wassmann et al., 2006), and is the zone where relatively warm and saline Atlantic ($> 0^{\circ}\text{C}$, > 34.8 psu) and cold, less saline Arctic ($< 0^{\circ}\text{C}$, < 34.8 psu) water masses meet. The convergence of these two different water masses results in enhanced primary productivity and enriched

pelagic and benthic communities (Carmack and Wassmann, 2006; Carroll et al., 2008). The location of the front moves on the scale of days to centuries, but in the western Barents Sea it appears to be more constrained by topography than where it occurs in Russian waters to the east (Johannessen and Foster, 1978; Harris et al., 1998). Nevertheless, the importance of the Polar Front's position is evident in the relationship between the Front's position and the distribution of capelin in the Barents Sea over decadal and multi-decadal periods (Vilhjálmsón, 1997a,b). The Barents Sea is an area of rapid climate change and the position of the front is expected to change in response to Arctic warming. Under future climate change scenarios, the Barents Sea is predicted to warm and the Atlantic waters in the southern Barents Sea are expected to spread farther north displacing Arctic water (ACIA, 2005). The effect of this shift in the Polar Front and the increased incursion of Atlantic water into the Barents Sea on the Barents Sea ecosystem are unknown.

Sampling Arctic and Atlantic water masses across the narrow Polar Front allows a comparison of the structure and function of the different biological communities these two water masses support and insight into the consequences of a change in the position of the Polar Front due to climate change or other forcing factors. Seafloor communities may be the best location to examine the impact of the Polar Front on the marine ecosystem because in the Arctic there is often a close relationship between water column and benthic processes (Grebmeier et al., 1988; Ambrose and Renaud, 1995; Piepenburg et al., 1997; Wollenburg and Kuhnt, 2000; Dunton et al., 2005). Therefore, long lived, sessile benthic organisms, may be more appropriate monitors of change in the overlying water (e.g. Kröncke et al., 1998, 2001; Dunton et al., 2005) than the more transient pelagic system. Bivalves dominate the benthic biomass of many Arctic shelves (Zenkevich, 1963; McDonald et al., 1981; Gulliksen et al., 1985; Grebmeier et al., 1988; Dayton, 1990; Feder et al., 1994). They also incorporate in their shells a history of environmental conditions at the time of shell formation. This environmental record coupled with the periodic banding, or growth lines, found in many

bivalves (Rhoads and Pannella, 1970; Clark, 1974; Rhoads and Lutz, 1980) makes it possible to develop a chronology of environmental conditions over the life of the individual (Andrews, 1972; Hudson et al., 1976; Jones, 1981; Jones et al., 1989; Witbaard, 1996; Witbaard et al., 1997, 1999; Tallqvist and Sundet, 2000; Schöne et al., 2003; Müller-Lupp and Bauch, 2005; Ambrose et al. 2006).

Temperature and food are the two main factors influencing bivalve growth (Beukema et al., 1985; Jones et al., 1989; Beukema and Cadeé, 1991; Lewis and Cerrato, 1997; Witbaard et al., 1997, 1999; Dekker and Beukema, 1999; Schöne et al., 2005), and both are likely to be influenced by different water masses and the position of the Polar Front. Sampling bivalves from Atlantic and Arctic water masses and close to the Polar Front allows us to assess the impact of these water masses on the growth of a dominant component of the Barents Sea benthic community. Coupled with measurements of environmental conditions over the last 30 years, it also allows us to identify the important factors affecting bivalve growth and make a prediction about future growth in an era of climate change.

Materials and Methods

Sample Collection

Live *Clinocardium ciliatum* (hairy cockle) were collected from three sites in the western Barents Sea. Sites were chosen based on CTD data to represent locations in Atlantic or Arctic water masses or along the polar front separating these two water masses (Fig. 1, Table 1). Samples were collected from the *RV Lance* (Norwegian Polar Institute, Tromsø Norway) between 3 and 7 June, 2007 using a 1 x 1 meter stainless steel triangle dredge dragged on the seafloor for ten minutes. Live, undamaged cockles were sorted from dredged material on deck.

At each site, a Seabird CTD was used to characterize the salinity and temperature of the water column. Data were used to generate TS profiles and these profiles and bottom water temperature and salinity were used to determine if stations were in Atlantic or Arctic water based on criteria established by (Loeng, 1991). Station B-14 had bottom water temperature and salinity representative of Atlantic water ($> 0^{\circ}\text{C}$ and $> 34.9\text{‰}$), station B-12 was clearly in Arctic water ($< -1^{\circ}\text{C}$ and $< 34.5\text{‰}$) and station B-5 had characteristics intermediate between these two (Table 1). An extensive CTD survey in the area made it possible to locate the polar front at the time of sampling (Figure 1).

Sample Preparation

Clinocardium ciliatum have a distinct external banding pattern (Fig. 2), which has been use to generate growth curves (Tallqvist and Sundet, 2000). We found external lines hard to interpret. Thus, we compared *C. ciliatum* ages in a subsample of 9 cockles from station B-12 using three methods: (1) external lines, (2) lines in the chondrophore exposed in a cross section of the shell, and (3) exit lines from a cross section of the shell (Fig. 2). Results of this comparison (see below) convinced us that it was necessary to section shells to examine exit lines for an accurate determination of age.

Samples were frozen and shucked after returning to port. A Buehler Isomet low speed diamond saw, running at approximately 90 rpm, was used to cut epoxy-embedded left valves along the line of maximum growth. Samples were polished with 320, 400, and 600 grit sandpaper and finished with a polishing cloth and 0.3 micron polishing powder. The polished samples were imaged using a Nikon stereoscopic zoom microscope SMZ1500 with an attached 2 mega-pixel digital camera at either 1X or 2X magnification. Images of the chondrophore were taken at 4X magnification. Individual magnified images were assembled using Adobe Photoshop into a complete composite image of the clam (Fig. 2).

External lines were clearly visible when a light was shown through the shell. We did not measure the distance between external lines or between chordophone lines, but counted them for comparison with the other measures of age. Exit lines were measured on a digital image from the origin of growth in the chondrophore to where the growth line exited the shell, using high resolution magnification. An exit line was defined as a distinct line stretching across the entire ventral margin. Measurements taken from images were in pixels that were converted to millimeters.

Growth Rates

Shell growth of *Clinocardium ciliatum* was modeled by fitting the von Bertalanffy growth function to age and shell height data for each clam using Excel. The von Bertalanffy function is:

$$SH_t = SH_{\infty} [1 - e^{-k(t-t_0)}]; \quad (1)$$

where t = age in years; SH_t = shell height at age t ; SH_{∞} = maximum, asymptotic shell height, k = growth constant, and t_0 = age when $SH = 0$.

Bivalve growth declines with age, so growth increments within an individual and among individuals of different ages must be standardized before growth among years can be compared. We use the methods of Jones et al. (1989) and Ambrose et al. (2006) to derive an ontogenetically-adjusted measure of annual growth. That method uses the first derivative of the von Bertalanffy function with respect to time:

$$dSH_t/dt = k * S_{\infty} e^{-kt}; \quad (2)$$

where dSH_t/dt = modeled yearly change in shell height. After determining the average yearly changes in shell height based on growth data from all clams, we calculated the expected yearly increase in shell height for each clam for each year. We then divided the measured or observed shell growth for each year by the expected growth for that year to generate a standardized growth index (SGI). This removes the ontogenetic changes in growth and

equalizes the variance for the entire series (Fritts, 1976). Once annual changes in shell growth were standardized, we calculated the mean SGI for each calendar year. The result is a record of year-by-year growth for the *C. ciliatum* sample, with an SGI greater than 1 indicating a better than average year for growth, while a value less than one reflects a worse than average growth year.

The growth rate of individuals at each station was determined by comparing growth curves (age at shell height) for each station. This was done by generating omega (ω) values for each individual at each station. The omega value is derived from the von Bertalanffy growth function (Jones et al., 1989):

$$\omega = S H_{\infty} * k$$

Because *C. ciliatum* growth is linear for early years, slopes of a best fit straight line to size at age relationships were also calculated for individual growth curves.

Environmental Data

We examined relationships between clam growth and other climate indices with potential influence on the region: the Arctic Climate Regime Index (ACRI), the North Atlantic Oscillation (NAO) in winter (December, January, February, March) and the Arctic Oscillation (AO). The AO is the first principal component of the sea level pressure field at latitudes greater than 20° N (Thompson and Wallace, 1998; Stenseth et al., 2003) while the ACRI measures variations in Arctic Ocean and ice circulation based on the sea level height anomaly at the North Pole (Proshutinsky and Johnson, 1997; Johnson et al., 1999; Proshutinsky, pers. comm. for updated index). The sea surface height anomaly at the North Pole is indicative of predominant high-Arctic wind pattern. Data for the NAO, using the sea level pressure difference between Gibraltar and Southwest Iceland (Jones et al., 1997; Osborn et al., 1999), were obtained from (<http://www.cru.uea.ac.uk/cru/data/nao.htm>) and for the AO from (http://www.cpc.ncep.noaa.gov/products/precip/CWlink/daily_ao_index/ao_index.html).

The Barents Sea temperature data (PINRO, Murmansk) is a time series of integrated ocean temperature from 0-200 m along the Kola transect, which runs from the Kola Peninsula northward to the ice edge along the 33° 30'E meridian (Bochkov, 1982; Tereshchenko, 1997). We have used yearly means of Barents Sea temperature in our analysis.

Meteorological data were obtained from the three of the four official weather stations around Svalbard (Longyearbyen, Bear Island, and Hopen) maintained by The Norwegian Meteorological Institute (<http://eklima.met.no>). Daily means of precipitation, pressure, and temperature were used to calculate seasonal and yearly averages.

Ice conditions were estimated from data collected by the Nimbus-7 SMMR and DMSP SSM/I passive microwave satellite (Cavalieri et al., 1997). The spatial resolution of the satellite imagery is 25x25 km, and the cell used for the ice coverage at each station was the one that included the station. The temporal resolution is daily from 1988 to 2006 and every second day from 1978 to 1988. We calculated the ice free days per year as the number of days with ice cover <25% from 1 July to 30 October of a given year; the estimated period of active growth of *C. ciliatum*. Maximum ice coverage occurs in March and data were obtained from: http://nsidc.org/data/seaice_index/archives/index.html.

Statistical analyses

We used both univariate and multivariate statistics to explore relationships between growth and environmental factors. We calculated Pearson correlation coefficients in order to determine basic pair-wise relationships between environmental and physical variables and the SGI. Annual means were compared with environmental variables, and we also investigated the time-dependence between data in consecutive years, leading us to incorporate two data transformations: 2 year-running means were used to reduce the magnitude of interannual variability of both growth rate and environmental data, and a 1-year lag was used to account for the time for physical processes to be reflected in shell growth.

We also used Principal Component Analysis (PCA) (PRIMER version 6, Primer-E Ltd.), a multivariate method, to explore the relationships between SGI and environmental variables (Clarke and Warwick, 2001). Variables used in the PCA analysis were those that had strong correlation coefficients in the pair-wise comparisons.

Finally, we used the best predictors from the univariate correlation analysis and the multivariate PCA analysis in multiple regression models for each station.

Growth rates were compared among stations using a one-way ANOVA on both the omega values and the slopes of the linear regressions, treating each individual as a replicate in the analyses. Prior to conducting the ANOVAs, variances were examined for homogeneity. When an ANOVA was significant ($P < 0.05$), differences among stations were examined using the post hoc Tukey test.

Results

Age Determination

We found substantial differences in cockle ages estimated by the 3 methods used (Table 2). The lines on the chondrophore cross-section were extremely difficult to read in both the first and last few years, resulting in severe underestimation of cockle age. The external lines of whole shells became very difficult to consistently read in the last years of older clams, leading to both underestimation and overestimation of clam ages. Thus despite the ease of using external lines, we conclude that this method is not effective in accurately identifying growth and age in older cockles. The exit lines read from a shell cross section was the most reliable single method, but very early lines (up to 3-4 years), were typically hard to discern. Based on these results, we therefore chose the dual-approach of using external lines to identify very early years, first 1-3 years of growth, and then exit lines revealed in cross

section from that point forward. This combination of approaches proved to be the most effective aging technique, and was used for all age and growth determinations.

Sample Population Characteristics

We analyzed 22 individual *Clinocardium ciliatum*, collected from 3 different sites in the northwest Barents Sea (Table 1). Samples ranged in age from 30 years (B-5) to 20 years (all stations). The lengths of time series from the samples at these stations are 30 years at B-5, 27 years at B-14 and 23 years at B-12 (Fig. 3). The largest individual in our dataset was 37.7 mm, with a corresponding age of 27 years (B-14). While our survey was not exhaustive, the oldest individuals in our sample agree with the observations of Tallqvist and Sundet (2000), suggesting that the maximum age of *C. ciliatum* in the Barents Sea is not much over 30 years.

The overall growth rate, represented by the mean size at age, was identical at each of the sites through age 5, but diverged thereafter (Fig. 3), with the population from station B-14 growing faster from age 5-14 compared to stations B-5 and B-12 which were not different from each other (ANOVA, $P < 0.008$). This significant difference was almost identical using the slope and omega methods to calculate absolute growth (Table 3), suggesting strong agreement of these methods in estimating site-specific growth rates for *C. ciliatum*.

Standardized Growth Index

The von Bertalanffy growth equations yielded high R^2 values ($R^2 = 0.993$ at B-5, $R^2 = 0.990$ at B-12, and $R^2 = 0.986$ at B-14, ($P \approx 0$ for all)), indicating that the von Bertalanffy model was an excellent descriptor of these clams' growth. This allowed us to confidently correct for ontogenetic changes in growth with age and confidently generate the expected growth for each calendar year (Standardized Growth Index = SGI).

SGI varied considerably over the 23-30 year periods covered by the 3 stations (Fig. 4), ranging for individual clams between a low of 0.11 (B-5), 0.22 (B-12) and 0.07 (B-14) in the

poorest growth years (1997, 2005, and 2006 respectively) to highs of 2.99 (B-5) , 3.03 (B-12) and 2.35 (B-14) in the best growth year (1993, 1996, and 1995 respectively). The mean site SGI's ranged from 0.39 (B-5, 2005), 0.62 (B-12, 2004) and 0.31 (B-14, 2006) to 1.51 (B-5, 1994), 2.07 (B-12, 1994) and 1.62 (B-14, 1995) (Fig. 4).

The differences in SGI's among years appear to follow a common cyclic pattern at all sites (Fig. 4). Growth increased through the 1980s and into the mid-1990s, with the highest growth rates occurring in either 1994 or 1995 at all sites. Subsequently, SGI began a sharp decline beginning in 1996 and lasting several years. There was some improvement in SGI, starting around 2000 at B-5 and B-12, but this pattern is not evident at B-14. In fact, using 2-year running means as a low-pass filter, after 1996, only a single site and year (B-12, 2001) exhibited a better than average growth year ($SGI > 1$) (Fig. 5).

Environmental Relationships

SGI is most consistently correlated with the ACRI and there are significant positive correlations at all three stations (Table 4). Only at station B-14 is the correlation between the SGI and the present year ACRI not significant and this station is the only one where a one year lag improves the strength and significance of the correlation. A two-year running mean of the ACRI slightly improves the strength of the correlation and sometimes the significance. A two-year running mean of ACRI explains between 40% and nearly 50% of the variability in a two-year running mean of the SGI's at the three stations and growth tracks even small changes in the ACRI remarkably well (Fig. 5). The only other large-scale climate index related to the SGI at any station is the NAO and it is only significant for B-14 and with a two year running mean at station B-12. The total aerial extent of the Arctic-wide ice cover is the only other large scale environmental parameter we examined and it is significantly positively correlated with the SGI's at stations B-5 and B-14, but not the station in Arctic water (B-12).

Total annual precipitation is the only local environmental parameter related to growth and there is very little difference in whether the precipitation is recorded on Hopen, closest to the stations, or in Longyearbyen; the relationship is always positive and except at the Atlantic water station, B-14, only significant with the two year running mean of the precipitation. The number of ice free days is only significantly related to growth at the Arctic water station, B-5 and the relationship is negative. Temperature, whether air temperature at Longyearbyen or Hopen, or water temperature on the Kola transect is not generally related to growth. The one exception is a negative correlation with the present year's temperature at Longyearbyen and growth at station B-5.

Principal component analysis (PCA) generally confirms the results of the univariate correlation analysis. In PCA, all variables are considered simultaneously. When the results are depicted graphically, the strength of relationship between two variables is related to the cosine of the angle between their vectors, so an angle of 90° indicates no relationship and one of 180° a perfect negative relationship. The length of a vector is the absolute value of the eigenvector and represents the importance of the variable in explaining variation in the data. The first two axes of the PCAs explained approximately 60% of the variability in the data at each of the stations (Fig. 6). The PCAs were nearly identical at Stations B-5 and B-12, and at these two stations the strongest relationship is between SGI and ACRI. The PCA for station B-5 shows a negative relationship between SGI and ice free days which is not quite as strong at Station B-12. There are few strong relationships with SGI revealed by the PCA at Station B-14. SGI is not a strong contributor to variability with a short vector, small eigenvector, on the first PCA axis. SGI is, however, positively related to the temperature along the Kola transect, a relationship not important in the PCAs at the other two stations and not revealed by the Pearson Correlation analyses.

Modeling Growth

We used the same environmental parameters as in the PCA in determining the best multiple regression model for each station. For stations B-5 and B-14 the ACRI is the only parameter that explains a significant amount of variation in the SGI ($R^2 = 0.277$, $P < 0.007$ for station B-5; and $R^2 = 0.169$, $P < 0.004$ for station B-14). In addition to the ACRI, Hopen precipitation is marginally significant in the multiple regression model for station B-12. These two parameters together explain 42.1% of the variation in the SGI ($P < 0.02$ for ACRI, and $P < 0.17$ for Hopen Precipitation). When the observed mean SGI for each year is plotted against the value predicted by our model, it is evident that the model for station B-12 better predicts the measured SGI than models for the other stations (Fig. 7). This is because there is a larger range in the modeled SGI values at B-12 compared to B-5 or B-14.

Discussion

Periodicity of Growth Lines:

We can use shells of bivalves as indicators of climatic processes only if we can properly interpret and chronologically calibrate markers in the shell. Two conditions must be fulfilled in order for a specific bivalve population to be useful in interpreting environmental variability: (1) major increments in the shell must be deposited with a known periodicity, and (2) we must be able to accurately identify each shell band.

The most common markers used in bivalve growth studies are annual growth bands secreted during periods of slow or no growth. In the Arctic, the growth band is likely a result of senescence of the organism during the winter, characterized by cold temperatures and minimal food availability (Sejr et al., 2002; Richardson, 2001; Ambrose et al., 2006). The “winter growth check” then essentially marks the end of a calendar year, as the senescent period encompasses the calendar year boundary.

Growth checks have been demonstrated to be annual in some Arctic species through mark-recapture studies (Sejr et al., 2002), and analysis of oxygen isotopes (Khim et al., 2003), and mineral ratios (Ambrose et al., 2006). Growth checks in *C. ciliatum* have not been investigated for periodicity, and the one previous study of population dynamics and growth of *C. ciliatum* (Tallqvist and Sundet, 2000) assumed that the growth checks were annual. While we did not explicitly examine the periodicity of growth lines in *C. ciliatum*, we do concur, based on several lines of evidence, that these growth checks are annual. First, growth lines are annual in another Arctic species (*Serripes groenlandicus*) in the same family (Cardidae) as *C. ciliatum* (Khim et al., 2003; Ambrose et al., 2006). Second, we have collected *C. ciliatum* from the Barents Sea and Svalbard coastal waters throughout the year, and have observed that the dark annual line is on the outermost margin of shells collected in winter (December-February), while those collected in spring (April and May), immediately following the spring bloom, show clear evidence (e.g. lighter shell color) of new shell growth beyond the last check (Carroll et al., pers. obs.). This evidence strongly suggests that the annual shell growth of *C. ciliatum* begins immediately when fresh food is available, despite water temperatures being at their coldest at this period of the year. Third, if the growth checks were not annual, then they would not be expected to correspond closely to inter-annual patterns of environmental forcing (see below), except by coincidence. Finally, growth patterns of *C. ciliatum* closely match that of *S. groenlandicus* (Fig. 8, discussed further below) which has demonstrated annual growth checks. While these last two lines of evidence are unconvincing by themselves, they do support the other evidence that suggests growth checks are annual in *C. ciliatum*.

Developing schlerochronological records and identifying relationships between growth and environmental variables potentially important in regulating growth rates obviously depends on accurately reading annuli. As schlerochronologies are sequential, errors

in reading lines in any part of the shell record will confound proper assignment of all later dates. Previous work with *C. ciliatum* has been confined to using only external lines (Tallqvist and Sundet, 2000), while the use of cross-sectional exit lines and chondrophore patterns from sectioned shells have been commonly used in other species such as *Arctica islandica*, *Serripes groenlandicus*, and *Mya truncata* (exit lines: Schöne, 2003; Kilada et al., 2007; Chondrophore: Witbaard et al., 1999; Sejr et al., 2002; Amaro et al., 2003; Kilada et al., 2007). Kilada et al. (2007) compared the three methods using *Serripes groenlandicus*, finding that thin sections of the chondrophore revealed the most easily interpretable lines. We found substantial erosion near the umbo of *C. ciliatum* and very close lines at the outer shell margins of adults. We were therefore unsure whether external reading external lines would provide robust and consistent measurements of annual growth. The subsequent comparison of results using external lines, cross-sectional exit lines, and chondrophore lines revealed that external lines were more effective for early years, despite some erosion of the shell (in some cases shell erosion enhanced the visibility of growth lines), and cross-sectional exit lines were most robust for all years after the first three to four years of growth (Figure 2). Combining these two methods proved to be the most effective and reliable method of aging (Table 2). While we found the chondrophore to be a very inaccurate location to measure growth lines in *C. ciliatum*, we did not make thin sections of the chondrophore as Kilada et al. (2007) did in their study of *S. groenlandicus*.

Growth rates:

There was a significant difference in overall growth rate among stations, with station B-14 exhibiting faster growth, and therefore larger size at a given age, compared to stations B-5 or B-12 (Table 3, Fig. 3). This is likely related to the different water masses dominating at the different stations. Station B-14 is located in Atlantic water along the slope between the Hopen Trench and Spitsbergen Bank. Station B-12, although geographically near to station B-

14, is located in Arctic water that dominates the top of Spitsbergen Bank, while station B-5 is farther north and located very near to the Polar Front, which runs in a southwest-northeast orientations following the bathymetry of the Bank (Table 1, Fig. 1).

Bivalve growth rates are principally regulated by temperature and food availability (Beukema et al., 1985; Beukema and Cadée, 1991; Jones et al., 1989; Lewis and Cerrato, 1997; Dekker and Beukema, 1999; Witbaard et al., 1997, 1999; Schöne et al., 2005). The extent to which each regulates growth of *C. ciliatum* in the Barents Sea is impossible to determine from our study because they strongly co-vary: Atlantic water is both warmer (Loeng, 1991; Sundfjord et al., 2007a,b) and more productive (Slagstad and Wassmann, 1997; Wassmann et al., 2006; Hodal and Kristiansen, 2008) than Arctic water of the Barents Sea. Wassmann et al. (2006) estimated that while the Barents Sea as a whole has an average primary production of $93 \text{ gC m}^{-2} \text{ yr}^{-2}$, primary production in the Atlantic water-dominated areas was nearly twice that of Arctic water areas (130 vs. $70 \text{ gC m}^{-2} \text{ yr}^{-2}$).

Sediments under Atlantic water in the Barents Sea also have higher concentrations of plant pigments than sediments under Arctic water (Cochrane et al., submitted), suggesting that more food reaches the benthos under Atlantic vs. Arctic water. These differences between water masses in delivering potential food to the suspension feeding *C. ciliatum* are reflected in growth rates. Cockles at the Atlantic station (B-14) grew substantially faster than in those at the stations in Arctic water or the Polar Front even when these stations are in close proximity to each other. This result is different than found by Tallqvist and Sundet (2000), who reported faster growth of *C. ciliatum* in an Arctic water mass in Storfjord, Svalbard compared to the Barents Sea or in an Atlantic water-influenced region north of Svalbard. The difference they reported was however simply a qualitative assessment of the relative growth curves for different year classes without any supporting statistical analyses. This calls into question

whether their reported difference is supportable and causes difficulty in comparing results between these studies.

The higher growth at station B-14 compared to the other stations is even more remarkable because the bottom depth at station B-14 is much greater (187m) than the other stations (99-117m). Despite tight pelagic-benthic coupling on Arctic shelves (Grebmeier et al., 1988; Ambrose and Renaud, 1995; Tamelander et al., 2006; Renaud et al., 2007), benthic communities at greater depths generally receive less food than those nearer the surface. For example, Witbaard et al. (1999) demonstrated that bivalve growth rates in boreal and Arctic waters declined with depth. Further, *C. ciliatum* in Disko Bay, west Greenland, grow only 25% as fast at 100m compared to 25-40m (Høpner-Petersen, 1978). Thus, our result demonstrating the fastest growth rate of *C. ciliatum* occurring at the deepest station is noteworthy and is likely related to elevated food supplies associated with Atlantic water masses.

It is surprising that growth rates at station B-5 are not higher than at station B-12. Station B-5 is located near the Polar Front, which would be expected to be a region of enhanced productivity and export to the sea bottom (e.g. Josefson and Conley, 1997; Carroll et al., 2008). In the same region of the Barents Sea as the present study, Carroll et al. (2008) found increased macrofaunal abundances and higher species diversity at the Barents Sea Polar Front compared to Atlantic and Arctic locations. An explanation may be found in the variability in the location of the Polar Front in this region of the Barents Sea. While the locations of water masses in the Barents Sea are well defined on a large geographic scale, on a small scale the location of the frontal boundary between Atlantic and Arctic water is variable due to tidal forcing and other instabilities, resulting in variable water mass properties along the frontal boundary (Drinkwater et al., unpublished data). Thus, while station B-5 was located near the Polar Front at the time of sampling in June 2007, it was on the Arctic “side”

of the Polar Front, and likely experiences substantial periods of time under the influence of the Arctic water mass.

Temporal Patterns:

Despite differences in the overall growth rates between stations located in different water masses, the temporal patterns of their SGI's are similar. At each station the SGI steadily increased from the start of the chronology in the late 1970's or early 1980s up until the mid-1990s. This trend was most dramatic at station B-12, but was evident at all stations (Fig. 4). Perhaps the most distinctive feature of the temporal pattern is the abrupt decline in the SGI starting in 1996 and lasting for 3 or 4 years, which resulted in SGI's below 1.0 by 2000. This distinct shift in *C. ciliatum* growth rates in the middle of the mid-1990's corresponds precisely in time with a well-known phenomenon in which a number of both physical and biological components of North Atlantic and Arctic ecosystems marine exhibited a regime shift at that time. Analysis of sea surface temperature anomalies indicate that a major regime shift took place in the North Atlantic between 1995 and 1996, with widespread ecological effects on various components of the marine ecosystem including phytoplankton, zooplankton, fish and birds (Reid et al., 1998; Beaugrand et al., 2002; Durant et al., 2004; Richardson and Schoeman, 2004; Hátún et al., 2005; Heath, 2005; Perry et al., 2005; Hansen and Samuelsen, 2008). On western Svalbard, marine benthic species diversity and abundance patterns in Kongsfjorden exhibited strong shifts between 1994 and 1996 after years of relative stasis (Beuchel et al., 2006). These regional phenomena were attributed largely to the influence of the North Atlantic Oscillation Index (NAO), which shifted abruptly from a strong positive phase in 1995 to a strong negative phase in 1996. There is evidence of the influence of the NAO on ecological components in both the terrestrial and marine ecosystems (Ottersen et al., 2001), including the bivalve *Arctica islandica* from the North and Norwegian seas (Schöne et al., 2005), and the 1995/96 shift was a strong signal. Even though we did not

detect a universal or strong influence of NAO on the SGI of *C. ciliatum* in the Barents Sea (see below), we did detect a corresponding strong shift in the SGI from highly positive to negative at all stations between 1995 and 1996, suggesting a regional controlling mechanism. Further evidence for the regional nature of the strong phenomenon occurring in 1995-1996 is seen from the growth patterns of *Serripes groenlandicus* from Rijpfjord, a high-Arctic fjord in northeast Svalbard with teleconnections to the Arctic Ocean (Ambrose et al., 2006). The overall SGI pattern from the *S. groenlandicus* population from Rijpfjord is substantially similar to Barents Sea *C. ciliatum* over the last 20 years and also exhibits a strong shift from highly positive to negative SGI's in 1995-1998 (Fig. 8).

Environmental Regulation:

The similar temporal SGI pattern at all stations (Figs. 4, 5), suggests some commonality in environmental forcing that regulates growth patterns. Indeed, the correlations (Table 4) indicate that the ACRI is consistently the parameter most strongly related to the SGI. There is strong coincidence between the temporal pattern of the ACRI and the SGI at all stations (Fig. 5, left panels). This is reflected in a very consistent relationship between ACRI and SGI at the 3 stations (Fig. 5, right panels), with R^2 ranging between 0.41 and 0.48 and the slopes being almost identical.

Only at B-14, the Atlantic water station, does NAO have a stronger relationship to SGI than ACRI (which is still significant). While the NAO is widely considered to have a fundamental structuring influence on the climate and marine ecosystems in the North Atlantic (e.g. Ottersen et al., 2001), the strength of its influence seems to diminish in the more Arctic regions of the Barents Sea and Svalbard, giving way to more polar-oriented forcing functions. Ambrose et al. 2006, found a much stronger relationship between the SGI of *Serripes groenlandicus* in the high-Arctic Rijpfjord (northeast Svalbard) and the ACRI compared to

the NAO. In the present study, the ACRI also predominates as the driver at the Arctic and Polar Front stations (B-12 and B-5, respectively), while the NAO shows up at the Atlantic-dominated station (B-14).

Of the local manifestations of the large-scale drivers, precipitation (at Hopen and/or Longyearbyen) sometimes gave strong relationships, ice cover at the sites was important only at station B-5, and yet maximum Arctic-wide ice cover had a significant relationship at 2 of 3 sites. In these offshore, relatively deep locations, we doubt that precipitation *per se*, has such a strong direct influence on growth rates as indicated in the correlations. We infer however, that precipitation is probably the measurable local manifestation of the environmental regulation occurring at these locations. For example, periods of low NAO are associated with a greater frequency of stormy conditions in the Arctic, with both higher precipitation and stronger wave action. These factors could substantially affect food availability to the benthos through maintenance or disruption of the pycnocline with a resulting influence on primary production (Josefson and Conley, 1997; Sakshaug, 1997, 2004) or via resuspension of food-containing bottom sediments (Witbaard et al., 2005). Even at the depths of these stations, there are episodic events of bottom currents strong enough to resuspend sediments (Sternberg et al., 2001). There was not a strong signal between local ice cover and growth rates, with ice free days being related to growth only at the Polar Front station (B-5). We view this result as indicative of the strong heterogeneity of both the bathymetry, the distribution of bottom sediments, and the variability in hydrographic processes. These all interact to provide a complex environmental situation and obscuring a strong signal of sea ice on growth rates. Tallqvist and Sundet (2000) also found no relationship between local ice cover and either overall growth rates or annual relationship to relative growth, and suggesting that the ice cover was decoupled from food supply in the region.

There was however a significant relationship between the maximum extent of winter ice in the Arctic and relative growth at two of three sites, providing further support for the conclusion of overriding regulation of bivalve growth by large-scale (hemispheric) environmental phenomena.

The multiple regression analysis in order to develop a model of *C. ciliatum* growth for each site yielded variable success in terms of variance explained and tightness of fit between observed and modeled values for each year. At two sites (B-5 and B-14), a single variable only, ACRI, had a significant explanatory value on SGI, while at B-12, the model included ACRI and precipitation. While significant, the two sites with only ACRI had a much lower proportion of variance in SGI explained by the model (28 and 17%), compared to the site with both ACRI and precipitation as predictors (42%). This is also evident when comparing the observed vs. modeled SGI values for each year (Fig. 7). Sites which included only a single predictor (B-5 and B-14) had modeled values which were constrained in a much smaller range than the observed values, while the site whose model both the large-scale and local factor (B-12) had a much better reflection of the observed values. This both limits the predictive capability of the models of these populations, given the present set of environmental variables and leads to the conclusion that while the large scale climatic regulation of these populations is evident, this overriding influence by itself is inadequate to understand all the influences leading to growth patterns in the Barents Sea.

The Barents Sea shelf is complex both bathymetrically and hydrographically, with myriad factors interacting at different spatial and temporal scales that ultimately lead to a growth rate of *C. ciliatum* in a given year. But given this complexity it is remarkable that a single large scale factor, the ACRI, consistently is the most reliable overriding influence on *C. ciliatum* growth in the Barents Sea. While there is a clear effect of water mass, with populations in Atlantic water growing faster than their Arctic brethren, the importance of the Polar Front on

growth was not evident in this study. One reason for this may be related to the larger geographic area covered by the three sites in the present study, which may obscure patterns over a much smaller spatial scale commensurate with the variability in the Polar Front location. Therefore, a follow-up study focusing on a much more limited geographic area crossing the Polar Front would provide substantially better information on the influence of this hydrographic feature would seem warranted.

Our results, taken together, suggest changes in benthic communities will occur as a result of climate change. Given the demonstrated strong linkage between bivalve growth rates and hemispheric climatic phenomena, if the positive phase of the ACRI and NAO (represent warmer and wetter conditions) are reflective of future conditions then we can also expect the benthos to be affected. If climate change results in increased Atlantic water regions in the Barents Sea as predicted, the result will clearly be increased growth of *C. ciliatum*. If the higher growth rate of cockles we observed at station B-14 compared to the Polar Front and Arctic water stations is a consequence differences in food, then other components of the benthic community, particularly, suspension feeders, can also be expected to respond to the change in water mass distribution.

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Tables and Figures

Table 1. Station information for the three collection sites of *Clinocardium ciliatum* in the northwest Barents Sea.

Station	Location	Latitude (°N)	Longitude (°E)	Water Depth (m)	Bottom Water Temp. (°C)	Bottom Salinity (psu)	Water Mass	No. Analyzed	Date Collected (2007)
B-5	East Hopen Bank	76°30.33	27°29.87'	117	-0.90	34.63	Polar Front	11	3 June
B-12	Spitsbergen Bank	75°39.80	24°01.14'	99	-1.05	34.49	Arctic	8	6 June
B-14	Spitsbergen Bank	75°00.06	25°05.82'	187	0.68	34.86	Atlantic	3	7 June

Table 2. Comparison of ages determined for *Clinocardium ciliatum* from Station B-12 by analyzing growth lines from three different methods (exit lines on cross-section, external lines of whole shell, and chondrophore from cross-section).

Sample	Exit Lines	External Lines	Chondrophore	Both External and Exit Lines ^{1,2}
B12-1	19	21	13	20
B12-2	23	21	17	23
B12-4	23	20	13	21
B12-5	21	22	18	23
B12-6	19	21	16	22
B12-7	22	17	12	22
B12-8	18	23	12	20
B12-9	21	N.A. ³	19	21

¹ Using external lines on umbo for the first few years of growth until agreement is found between the exit and external lines, and then using exit lines for the remainder.

² Method used for statistical analysis.

³ Shell was too eroded to analyze.

Table 3. Comparison of mean growth rates among stations. Comparisons were assessed in two ways; from the mean slope of the samples at each station from 0-12 years of age (the period in which growth was linear), and from the omega parameter derived from the von Bertalanffy equation. In both types of comparisons, statistical results are from post-hoc pairwise comparisons (Tukey test) following a significant one-way ANOVA ($p > 0.05$).

Site	Slope	SD	ANOVA (P=0.008)	Omega	SD	ANOVA (P=0.007)
B5	1.73	0.19	B	2.66	0.43	B
B12	1.82	0.21	B	2.67	0.43	B
B14	2.18	0.13	A	3.65	0.46	A

Table 4. Coefficients from Pearson correlations relating *Clinocardium ciliatum* standard growth index (SGI) to various environmental variables at each site, 1977-2006. The first column of coefficients at each site is from present year data. The second column has the environmental data lagged by 1 year with respect to growth. The third column shows relationships using 2-year running means (previous and present year) of environmental data. Bold lettering denotes a significant correlation at the $P < 0.01$ level. The levels of the significant correlations are: * $P < 0.01$, ** $P < 0.001$

Environmental Variable	B-5			B-12			B-14		
	Present Year	Lagged	Running Mean	Present Year	Lagged	Running Mean	Present Year	Lagged	Running Mean
NAO ¹	0.33	0.21	0.37	0.29	0.50	0.53*	0.61*	0.38	0.68**
AO ²	0.36	0.27	0.39	0.27	0.46	0.47	0.51	0.29	0.52
ACRI ³	0.59*	0.46	0.67**	0.63*	0.38	0.65*	0.52	0.62*	0.71**
Precipitation (Hopen) ⁴	0.46	0.35	0.48*	0.49	0.50	0.56*	0.72**	0.51	0.69**
Temperature (Hopen) ⁵	-0.47	-0.19	-0.37	0.17	0.17	0.19	-0.40	-0.32	-0.41
Precipitation (Longyearbyen) ⁶	0.38	0.35	0.53*	0.48	0.32	0.58*	0.34	0.43	0.56*
Temperature (Longyearbyen) ⁷	-0.49*	-0.18	-0.39	0.11	0.06	0.10	-0.49	-0.45	-0.53
Kola Transect Temperature ⁸	0.03	0.09	-0.03	0.12	0.30	0.20	0.19	-0.08	-0.01
Ice Free Days ⁹	-0.52*	-0.12	-0.37	-0.16	-0.07	-0.13	0.24	0.29	0.20
Max Arctic Ice Extent ¹⁰	0.52*	0.42	0.49*	-0.10	-0.11	-0.14	0.59*	0.75**	0.58*

1. Winter North Atlantic Oscillation Index (from December, January, February, March).

2. Winter Arctic Oscillation Index (from December, January, February, March).

3. Arctic Climate Regime Index (Annual)

4. Total Annual Precipitation from Hopen Island.

5. Average annual temperature from Hopen Island.

6. Total Annual Precipitation from Longyearbyen.

7. Average annual temperature from Longyearbyen.

8. Average Annual sea temperature on the Kola Transect

9. Number of days with ice concentration <25% at the sampling site

10. The total aerial extent of the Arctic-wide ice cover at its maximum extent (March).

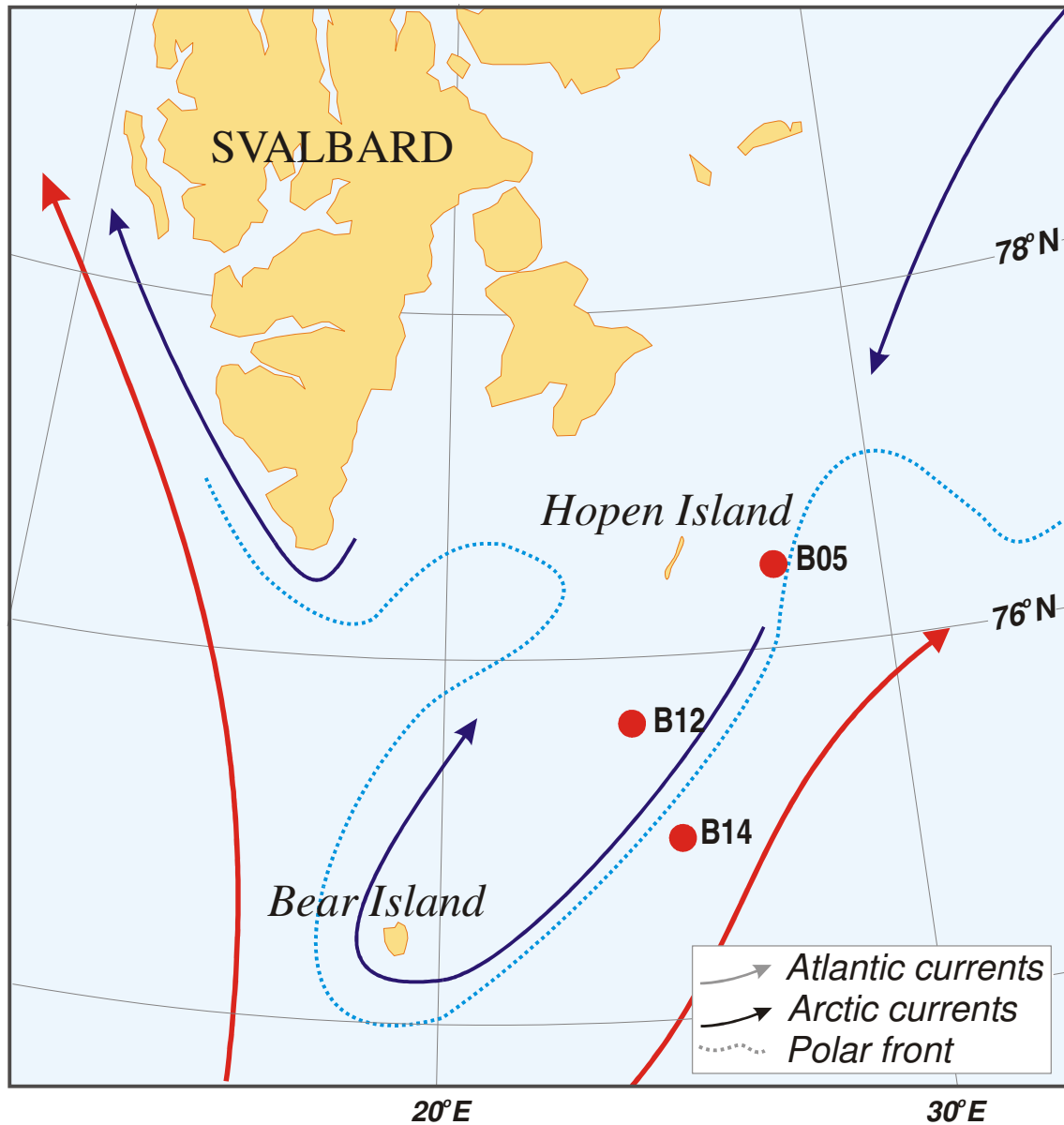


Figure 1. Map of the study region showing the western Barents Sea and part of the Spitsbergen Archipelago. Collection locations of *Clinocardium ciliatum* are indicated, as are general current patterns and the generally assumed location of the polar front, which coincides with the limit of maximum ice cover in late winter.

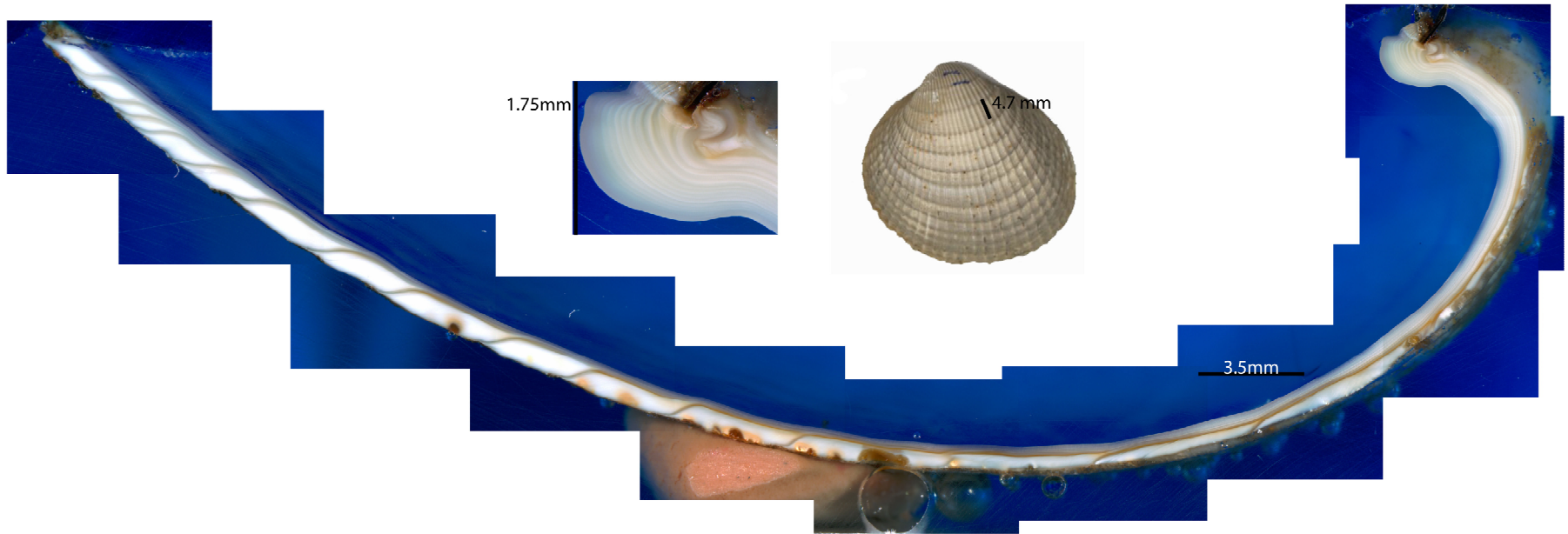


Figure 2. Three images of *Clinocardium ciliatum*, illustrating the different counting methods. The main image of a section of a whole sample is a composite of several images of different locations of the shell section (2X magnification) and clearly shows the exit lines. The insets are of a chondrophore at 5X magnification (left) and whole shell with externally visible lines (right).

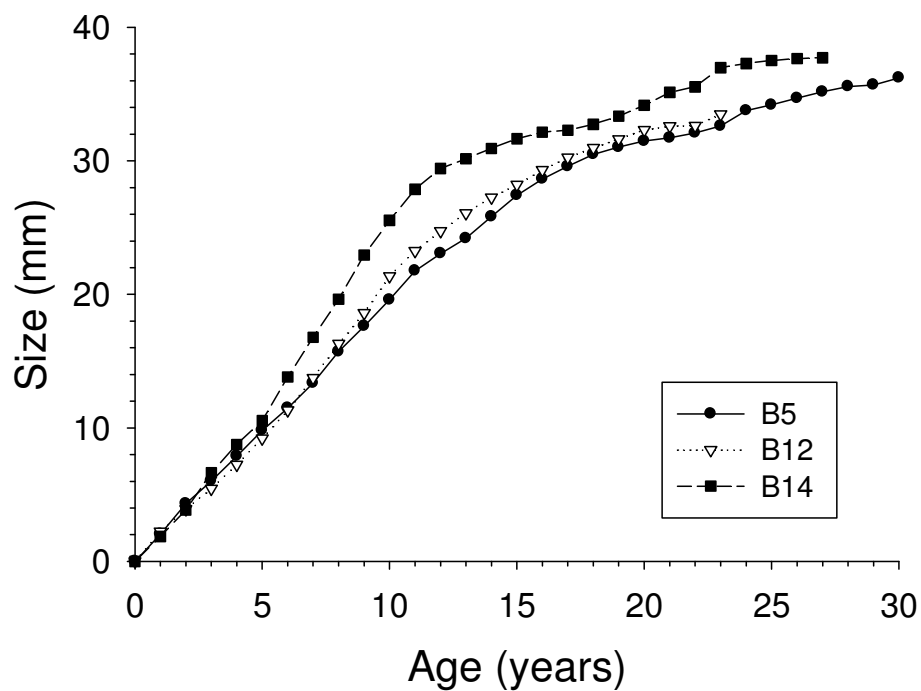


Figure 3. Mean size at age for populations at each sampling site. See Table 1 for sample sizes. Error bars excluded for graphical clarity.

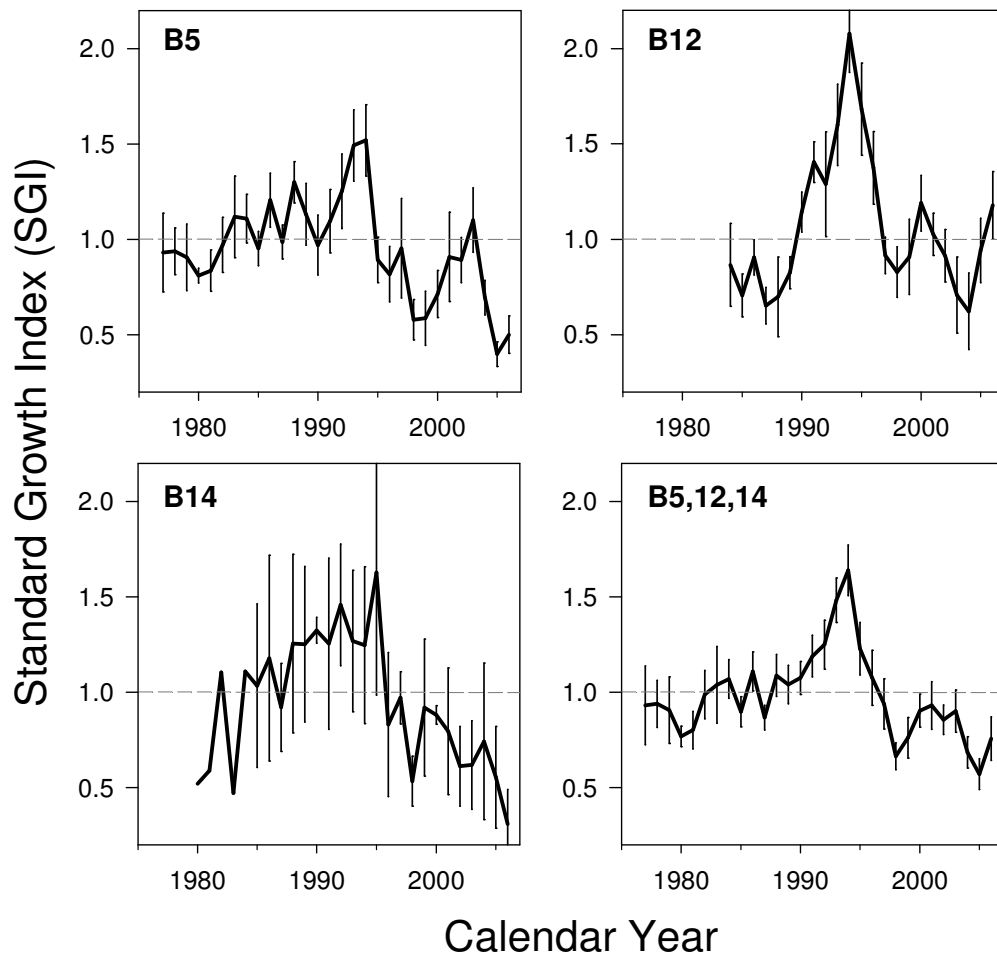


Figure 4. Mean Standard Growth Index (SGI), $\pm$ standard error, of *Clinocardium ciliatum* from 3 sites in the Barents Sea collected live in 2007. Growth increments were calculated by measuring both internal and external lines, and von Bertalanffy growth curves were used to remove the ontogenetic trend and standardize populations for comparison. An SGI greater than 1 is considered a relatively good growth year while less than 1 is a relatively poor growth year.

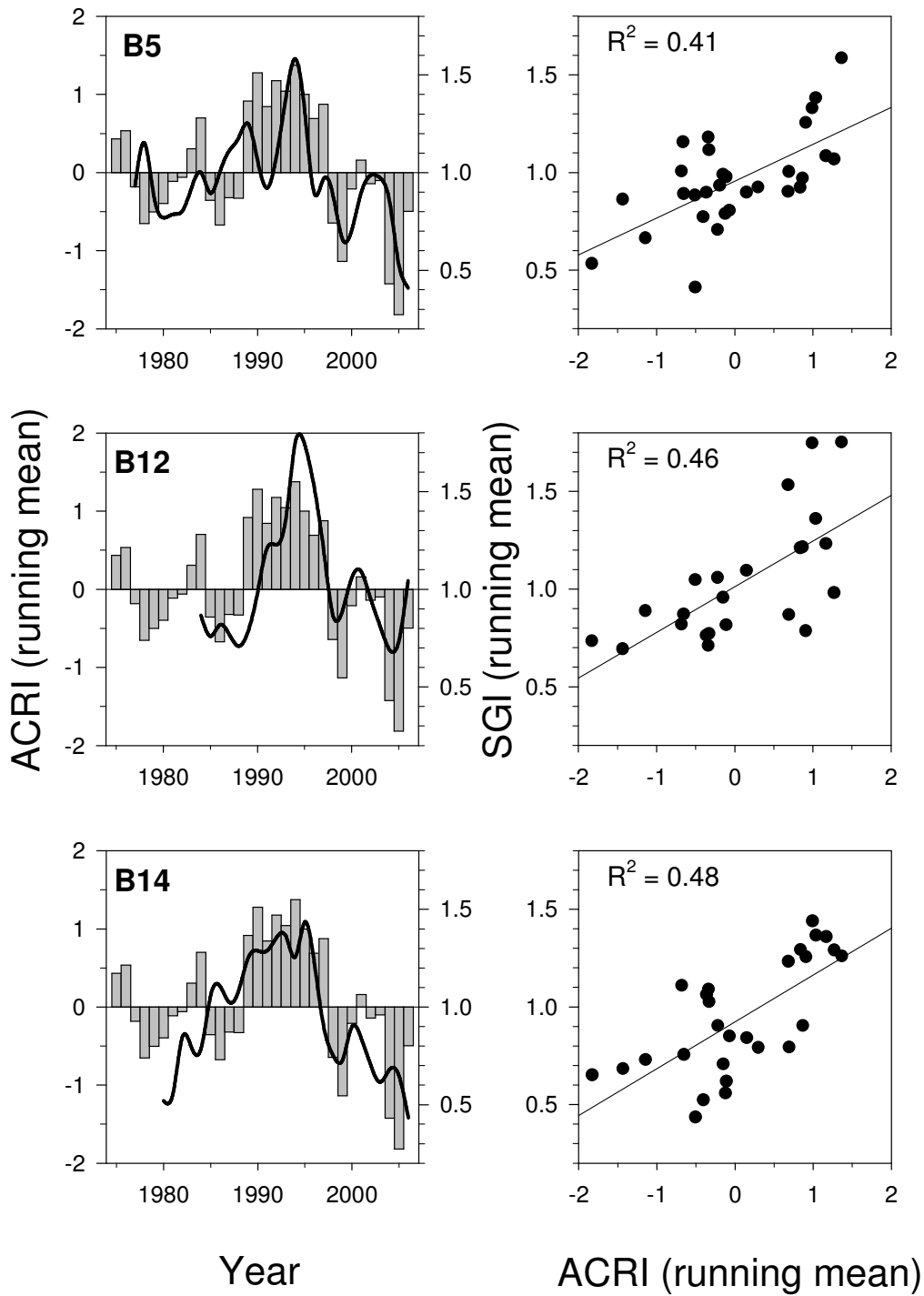


Figure 5. Relationship between Arctic Climate Regime Index (ACRI) and *Clinocardium ciliatum* SGI at each of the 3 stations. Temporal pattern of ACRI, bars, with *Clinocardium ciliatum* SGI, line, superimposed (left panels), and regressions of ACRI vs. SGI (right panels). Both SGI and ACRI are 2-year running means of raw data.

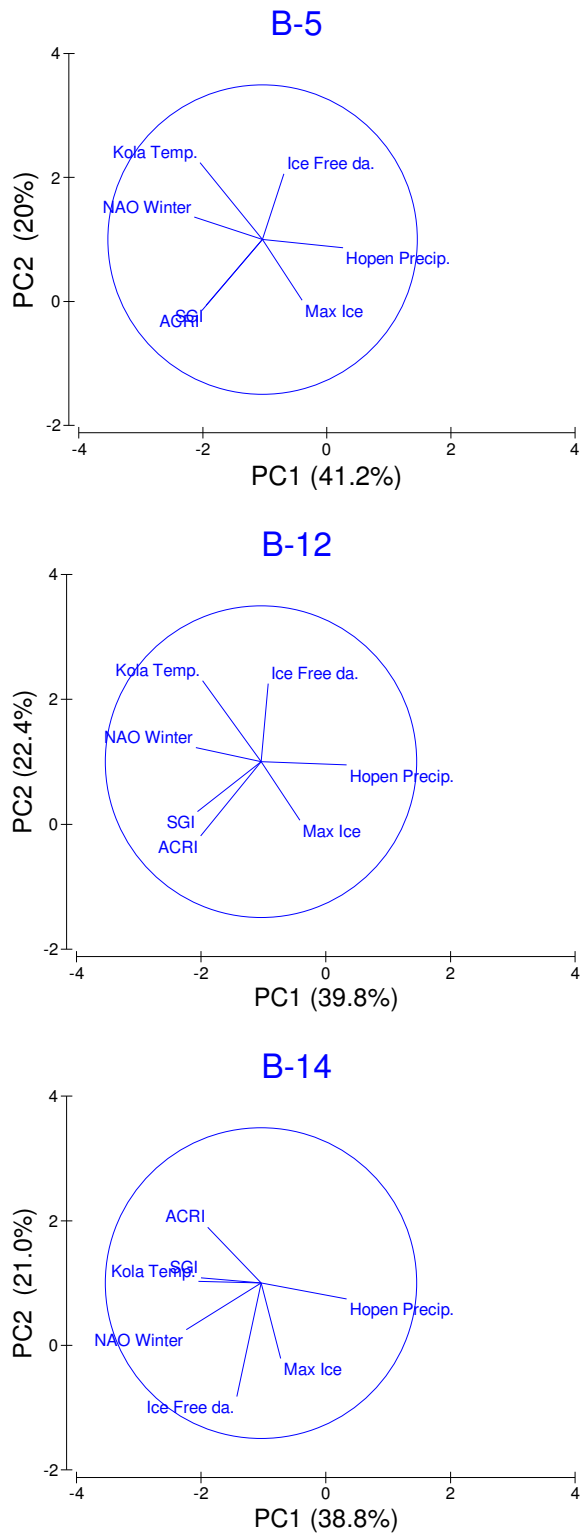


Figure 6. Results of Principle Component Analysis (PCA), relating environmental variables to *Clinocardium ciliatum* growth (SGI) for the each site. Only environmental variables with significant correlations are included in the analysis.

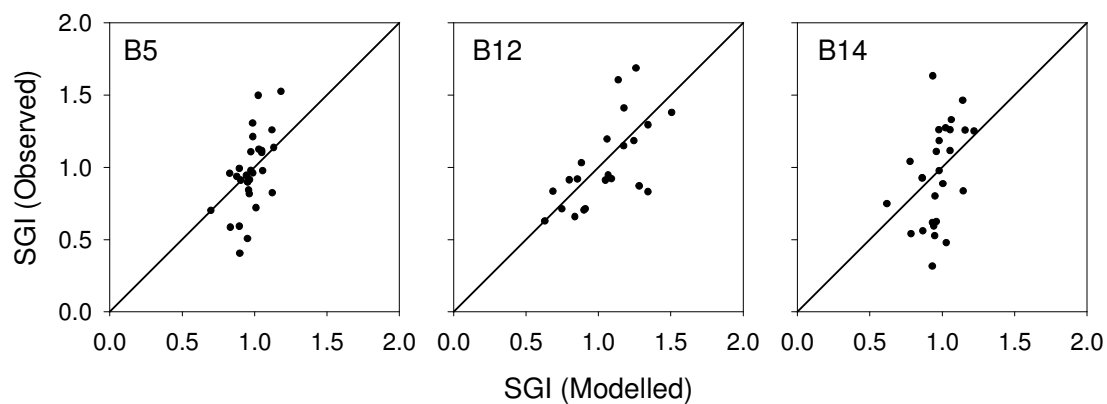


Figure 7. Scatterplot of observed vs. modeled SGI from each site (1977-2006). The model is the result of a multiple regression at each site, and line in each plot represents a perfect prediction by the model of actual growth rates of the *Clinocardium ciliatum* population.

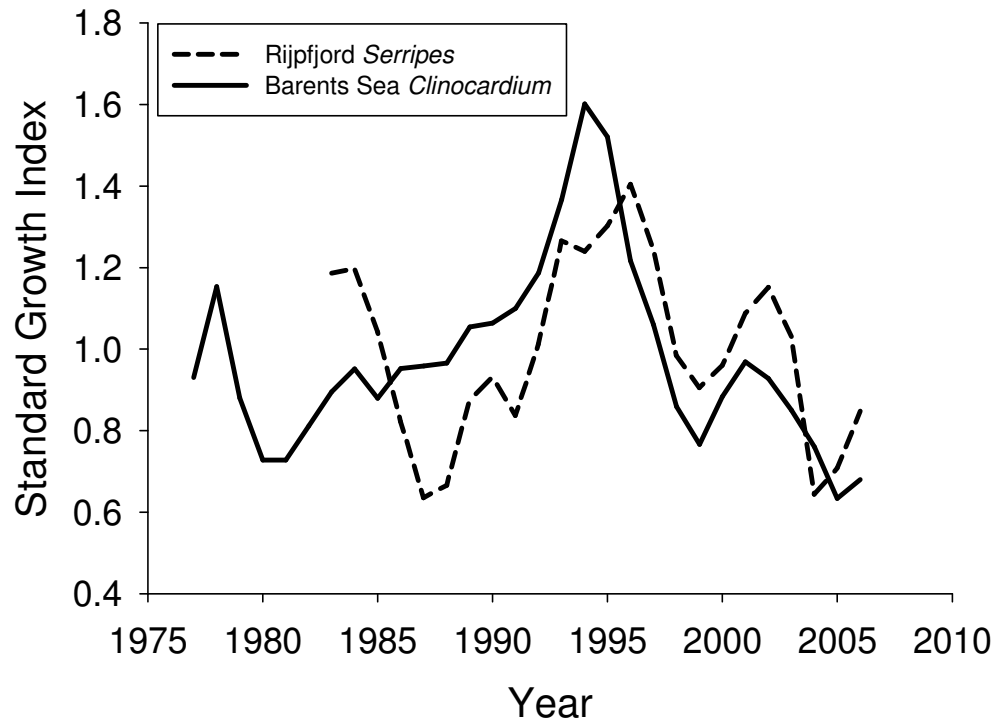


Figure 8. Comparison of the SGI temporal pattern between *Clinocardium ciliatum* populations from the three Barents sites from the present study (combined) and a *Serripes groenlandicus* population from Rijpfjord, northern Svalbard. *Serripes* data are from Ambrose et al. (2006), with updates. Presented data are 2-year running means of the annual data.