



## Bivalve growth rate and isotopic variability across the Barents Sea Polar Front

Michael L. Carroll<sup>a,b,\*</sup>, William G. Ambrose Jr.<sup>a,c</sup>, William L. Locke V<sup>c</sup>, Stuart K. Ryan<sup>c</sup>, Beverly J. Johnson<sup>d</sup>

<sup>a</sup> Akvaplan-niva, Fram Centre for Climate and Environment, N-9296 Tromsø, Norway

<sup>b</sup> CAGE – Centre for Arctic Gas Hydrate, Environment, and Climate, UiT The Arctic University of Norway, N-9037 Tromsø, Norway

<sup>c</sup> Bates College, Department of Biology, Lewiston, ME 04240, USA

<sup>d</sup> Bates College, Department of Geology, Lewiston, ME 04240, USA

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### ABSTRACT

Analysis of bivalve shell increments provides a means to reconstruct long-term patterns in growth histories and assess factors that regulate marine ecosystems, while tissue stable isotopes are indicators of food sources and trophic dynamics. We examined shell growth patterns and tissue stable isotopic composition ( $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$ ) of the hairy cockle (*Ciliatocardium ciliatum*) in the northwest Barents Sea to evaluate the influence of different water masses and the Polar Front on growth rates and food sources and to assess the influence of climatic variability on ecological processes over seasonal to decadal scales. Shell growth rates were highest in Atlantic water, intermediate in Arctic water, and lowest at the Polar Front. Temporal patterns of ontogenetically-adjusted growth (SGI) were negatively correlated with the Atlantic Multidecadal Oscillation (AMO), local precipitation and ice-free days. The highest growth occurred during colder periods with more sea ice, while lower growth was associated with warmer periods and less sea ice. Stable isotope values of lipid-extracted tissues from Atlantic water cockles were enriched in  $\delta^{13}\text{C}$  by up to 2.1‰ and  $\delta^{15}\text{N}$  by 1.5‰ compared to animals from Arctic waters. Distinct seasonal and water mass variations in stable isotopic values reflect spatial and temporal variability in food supplies to the bivalves in this region on small spatial scales. Overall, Atlantic waters supported the highest growth rates, the most complex trophic webs, and the greatest sensitivity to interannual variability in environmental conditions. Bivalves from Arctic waters were the most distinct of the three groups in their response to regional climate forcing and local environmental manifestations of those conditions. The Polar Front exhibits growth and isotopic characteristics predominantly of the Atlantic domain.

These results demonstrate that integrating results of sclerochronological and stable isotopic analyses of benthic bivalves provide independent, corroborative lines of evidence and added insight into the ecological function of these systems when assessing potential effects of changes in water mass distributions in the Barents Sea.

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### 1. Introduction

Oceanic fronts are generally thought to support enhanced abundances of organisms over a wide range of trophic levels compared to nearby non-frontal areas (Bluhm et al., 2007; Dewicke et al., 2002; Hunt and Harrison, 1990; Josefsen and Conley, 1997; Mendes et al., 2002; Munk et al., 1995). Frontal areas resulting from the convergence of two different water masses are characterized by rapid changes in physical, chemical, and biological conditions over small spatial scales. They are commonly observed on a small scale in tidal estuaries, but can also occur on mesoscales on continental shelves and on even larger scales in the open ocean. Increased abundance of pelagic organisms associated with fronts is likely a consequence of a combination of increased primary production and/or the concentration of primary

producers into a relatively narrow zone (Creutzberg, 1985; Floodgate et al., 1981; Franks, 1992), with a cascade up the food chain to higher-order predators. Benthic communities under fronts can also receive enhanced food supplies 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; Josefsen and Conley, 1997). Regardless of the mechanism, high benthic biomass is often associated with fronts (Bluhm et al., 2007; Carroll et al., 2008; Creutzberg et al., 1984; Josefsen and Conley, 1997). Polar oceanic fronts, despite being generally recognized as hotspots of biodiversity and abundance, 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 (Harris et al., 1998; Loeng, 1991) and is the boundary between relatively warm and saline Atlantic ( $>0\text{ }^{\circ}\text{C}$ ,  $>34.9$ ) and cold, less saline Arctic ( $<0\text{ }^{\circ}\text{C}$ ,  $<34.7$ ) water masses. The location of the Front moves on the scale of hours to centuries, but in the western Barents Sea it appears

\* Corresponding author at: Akvaplan-niva, Fram Centre for Climate and Environment, N-9296 Tromsø, Norway. Tel.: +47 7775 0318; fax: +47 7775 0301.

E-mail address: [mc@akvaplan.niva.no](mailto:mc@akvaplan.niva.no) (M.L. Carroll).

to be relatively more constrained by bathymetry than in Russian waters to the east (Harris et al., 1998; Johannessen and Foster, 1978). The Barents Sea is an area of rapid climate change and the position of the Barents Sea Polar Front may be expected to change in response to stronger inflows of Atlantic water and displacement of Arctic water (ACIA, 2005; Loeng and Drinkwater, 2007). The effects of such a shift in the Polar Front and the increased incursion of Atlantic water into the Barents Sea on the ecosystem are unknown.

The convergence of these two different water masses has been assumed to be a location of enhanced primary productivity (Wassmann et al., 2006), with enriched pelagic and benthic communities (Carmack and Wassmann, 2006; Carroll et al., 2008). The spatial distribution of capelin in the Barents Sea has been associated with the location of the Polar Front over decadal and multi-decadal periods (Vilhjálmsón, 1997a,b), and benthic biomass is higher in the frontal zone compared to adjacent Arctic and Atlantic locations (Carroll et al., 2008). There has, however, not been a multidisciplinary study specifically examining the production at the Barents Sea Polar Front, and associated ecological processes in the pelagic and benthic communities.

Stable isotopic signatures are useful tools in assessing dietary sources, identifying trophic relationships, and constructing marine food webs (Hobson et al., 1995; Iken et al., 2010; McConnaughey and McRoy, 1979; Wada et al., 1987). This is because relative proportions of heavy and light isotopes of carbon and nitrogen fractionate in a predictable manner between producer and consumer and with each subsequent trophic link (DeNiro and Epstein, 1981; Minagawa and Wada, 1984; Wada et al., 1987). The trophic enrichment of  $^{13}\text{C}$  is rather low, <1‰ across consecutive trophic levels (Fry and Sherr, 1984; Post, 2002), so differences in  $^{13}\text{C}$  are generally reflective of different food sources, while consumer tissues become progressively enriched in  $^{15}\text{N}$  by 3–4‰ per link so  $^{15}\text{N}/^{14}\text{N}$  can be used to estimate trophic levels of organisms in the community (Hobson and Welch, 1992; Hobson et al., 1995; Søreide et al., 2006; Wada et al., 1987). In the Barents Sea, dietary sources, food web structure and coupling between different ecological compartments (ice-associated, pelagic, and benthic) have been elucidated with stable isotope techniques (Søreide et al., 2006, 2008; Tamelander et al., 2006, 2008).

Seafloor communities are ideal systems 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 (Ambrose and Renaud, 1995; Dunton et al., 2005; Grebmeier et al., 1988; Piepenburg et al., 1997; Tamelander et al., 2006; Wollenburg and Kuhnt, 2000). Therefore, long-lived, sessile benthic organisms may be excellent monitors of change in the overlying water (e.g. Dunton et al., 2005; Galkin, 1998; Kröncke et al., 1998, 2001) compared to the more transient pelagic system. Further, bivalves dominate the benthic biomass of many Arctic shelves (Dayton, 1990; Feder et al., 1994; Grebmeier et al., 1988; McDonald et al., 1981; Zenkevich, 1963). They also incorporate in their shells a history of environmental conditions at the time of shell synthesis (Richardson, 2001). This environmental record coupled with the periodic banding, or growth lines, found in many bivalves (Clark, 1974; Rhoads and Lutz, 1980; Rhoads and Panella, 1970), makes it possible to develop a chronology of environmental conditions over the life of the individual (Andrews, 1972; Butler et al., 2009, 2011; Hudson et al., 1976; Jones, 1981; Jones et al., 1989; Müller-Lupp and Bauch, 2005; Schöne et al., 2003; Witbaard, 1996; Witbaard et al., 1997, 1999). Comparing bivalve chronologies across climatic gradients provides understanding of how climate and local environmental conditions interact and are linked to biological systems.

Chronologies of bivalve growth have proven useful in linking ecological processes via growth rates to climatic variability around Svalbard and the Barents Sea. Tallqvist and Sundet (2000) first examined annual growth patterns of the bivalve *Ciliatocardium ciliatum* (hairy cockle) in the Norwegian Arctic (Svalbard area). Ambrose et al. (2006) developed the first growth chronology of the Greenland Smooth Cockle (*Serripes*

*groenlandicus*) in a high Arctic site in northeast Svalbard and linked growth cycles to climatic variability. Carroll et al. (2009) identified a mechanistic relationship between *S. groenlandicus* growth in the south-east Barents Sea and the North Atlantic Oscillation index via river discharges to the White Sea. Further, Carroll et al. (2011a,b) also found enhanced growth rates of *S. groenlandicus* and *C. ciliatum* populations in Atlantic water over relatively large spatial scales, even while environmental regulation was similar.

Carroll et al. (2011a) developed growth chronologies of *C. ciliatum* and identified relationships between growth and environmental variability in different water masses in the Barents Sea. In the present work we build upon the earlier results of Carroll et al. (2011a) by: (1) comparing the growth rates of *C. ciliatum* over a much smaller spatial scale but still spanning Arctic and Atlantic water masses, as well as specifically pinpointing sites in the Polar Front, (2) lengthening the chronologies by collecting older individuals, and (3) examining tissue stable isotopic concentration in the same samples as those whose shells are used in the growth analyses, thus allowing an assessment of food source variability to the benthos at these locations.

We simultaneously examine the effect of water masses and climate variability on growth rates, growth patterns, and isotopic concentration of *C. ciliatum*, as a part of the International Polar Year program NESSAR (Norwegian Component of the Ecosystem Studies of Subarctic and Arctic Regions) examining physical and ecological properties at the Barents Sea Polar Front. We specifically test the hypothesis that bivalve growth rates are higher at the Polar Front as a result of assumed enhanced primary production and/or export to the sea bed in this location compared to immediately adjacent Arctic and Atlantic water masses.

## 2. Materials and methods

### 2.1. Site description and sample collection

Five stations were selected on a 70 km transect running from near the top of Spitsbergen Bank eastward along the slope of Hopen Trench (Fig. 1, Table 1). Stations were 12–15 km apart at 20 m depth intervals, from 95 m depth at B26 to 182 m depth at B30. Samples for the growth rate and stable isotopic analyses were collected from the RV 'Jan Mayen' (University of Tromsø, Norway) on 2 May 2008, while additional samples for isotopic analysis were collected from same stations with the RV 'Lance' (Norwegian Polar Institute; Tromsø, Norway) on 29 September 2009.

Live *C. ciliatum* (hairy cockles) were collected at each site using a  $1 \times 1 \times 1$  meter triangle dredge dragged on the seafloor for 10 min. Live, undamaged cockles were sorted from dredged material on deck. Samples were immediately dissected on board to separate shells and tissues. Tissues were immediately frozen ( $-20\text{ }^{\circ}\text{C}$ ) for later isotopic analysis, while shells were air-dried.

At each station, a Seabird CTD was used to profile the salinity and temperature of the water column. Temperature and salinity profiles were used to identify the water mass at the station based on criteria of Loeng (1991), where Atlantic water is  $>0\text{ }^{\circ}\text{C}$  and  $>34.9$  and Arctic water is  $<-1\text{ }^{\circ}\text{C}$  and  $<34.7$ . During both sample collections, extensive CTD surveys were carried out in the area so the water mass characteristics are thoroughly described (see Fer and Drinkwater, this volume).

### 2.2. Growth rates

Ages of *C. ciliatum* were determined from the shell banding pattern following the methodology described in Carroll et al. (2011a). Briefly, a combination of external (near the umbo) and internal lines was used to establish the shell size at each annual increment throughout its lifetime. Increments have been experimentally determined to be annual markers (Ambrose et al., 2012). This allowed us to generate growth curves for each individual. Chronologies from individual samples at each site were visually compared and cross-matched in order to identify

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