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Benthic infauna of the seasonally ice-covered western Barents Sea: Patterns and relationships to environmental forcing

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ABSTRACT

The northwestern Barents Sea and Svalbard archipelago are influenced by both warm Atlantic and cold Arctic water masses. We investigated infaunal benthic community structure in Atlantic- and Arctic-dominated areas, and at the Barents Sea Polar Front in order to assess the patterns of variability and to examine the influence of environmental variables on benthic fauna in this region. As part of the CABANERA program, we sampled 14 stations between 2003 and 2005 for benthic infaunal community composition, density, and biomass. Stations were in offshore shelf locations with soft sediments ranging in depth from 200 to 500 m, and encompassed different water mass characteristics and a wide range of other environmental conditions. Benthic biomass averaged 66 g WW m^{-2} (range 10–152 g WW m^{-2}), mean density was 4340 ind. m^{-2} (1970–7896 ind. m^{-2}), and species richness varied from 71–192 taxa $stn.^{-1}$. Community structure was reflective of large-scale oceanography, as stations clustered in groups related to predominant water masses. Patterns in faunal density and biomass were largely determined by sedimentary characteristics, with water temperature, depth, and annual primary production also influencing some community parameters. Organism density and species richness were 86% and 44% greater at stations located near the Polar Front, compared to stations located in either Atlantic- or Arctic-dominated water masses. This pattern is coincident with elevated primary production at the Polar Front (48% compared to Atlantic- or Arctic-dominated water), suggesting a direct link between food availability in the Barents Sea and the benthic community structure. This leads to the conclusion that benthic communities in northwestern Barents Sea region are food-limited, and strongly dependent on predictable, albeit episodic, delivery of organic matter from the water column. Climatic processes leading to long-term changes in the location of the Polar Front will therefore have impacts on community structure and function on the sea floor.

1. Introduction

Benthic fauna are considered good indicators of environmental conditions. Their predominantly sessile existence and relatively long lives are characteristics amenable for detection of a time-integrated response to external forcing, either individually or collectively as a community. Thus, changes in benthic communities over time have been used as indicators of environmental changes resulting from both natural variations (Kröncke, 1995; Kröncke et al., 1998, 2001) and anthropogenic disturbances (Pearson and Rosenberg, 1978; Underwood, 1996; Carroll et al., 2003) in marine systems.

Benthic faunal community structure is regulated through both abiotic factors, such as water depth and sediment characteristics (i.e. grain size), food availability (Gray, 1974, 1981; Snelgrove and Butman, 1994; Kendall, 1996), and biotic interactions with other fauna, including predation and competition (Peterson, 1979; Ambrose, 1984; Wilson, 1990; Olafsson et al., 1994). Animals living on the sea floor below the euphotic zone away from riverine inputs are totally reliant on material from the water column sedimenting to the sea floor for their energetic requirements (Klages et al., 2004). In the Arctic, primary production is highly variable in time and space, and benthic food supply is often in the form of episodic pulses of pelagic- and ice-related organic carbon (i.e. the spring bloom) (review in Carmack and Wassmann (2006)). Although the fate of primary production in Arctic shelf seas depends upon numerous water-column processes related to the spatial and temporal variability in both the production regime and pelagic grazers (Eilertsen et al., 1989; Wassmann et al., 1996;

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Andreassen and Wassmann, 1998; Falk-Petersen et al., 1999; Carroll and Carroll, 2003), the amount and quality of this organic material reaching the sea bottom is strongly related to the overlying primary production regime. Wassmann (1991) estimated that 48–96% of photosynthesized carbon in the water column reaches the sea floor, emphasizing the coupling between pelagic and benthic systems. The result of this pelagic–benthic coupling in the short term is seasonally and locally elevated concentrations of chlorophyll and fatty acids (correlates of primary production) on the sediment surface (Bauerfeind et al., 1997; Stephens et al., 1997; Sun and Wakeham, 1999; Renaud et al., 2008a) and associated increases in benthic processing (Rysgaard et al., 1998; Gooday, 2002; Clough et al., 2005; Moodley et al., 2005; McMahon et al., 2006; Sun et al., 2007; Renaud et al., 2008a). But benthic community parameters (biomass, organism density, and diversity), which integrate over longer temporal and spatial scales such as years or even decades, have also been found to reflect the overlying primary production regime (Grebmeier et al., 1988; Highsmith and Coyle, 1990; Ambrose and Renaud, 1995; Piepenburg et al., 1997; Dunton et al., 2005).

Tight pelagic–benthic coupling seems to be particularly amplified at mesoscale features in the Arctic such as polynyas, fronts, and the marginal ice zone, where episodic but intense pulses of primary production favor export of pelagic material to the sea bottom (Hobson et al., 1995; Smith and Barber, 2007 and references therein). The Barents Sea continental shelf is bathymetrically and hydrographically complex, resulting in high spatial and temporal variability (i.e. patchiness) in the physical (Elverhøi et al., 1989; Fredriksen et al., 1994) and biological (Engelsen et al., 2002) features influencing the benthic environment. Increased biomass and density of benthic communities are associated with the summer marginal ice zone of the Barents Sea (Zenkevich, 1963; Antipova, 1975; Denisenko, 2002), but these studies have not specifically examined the influence of the more stable Polar Front region on benthic communities.

The Barents Sea shelf is key region of the Arctic, the largest of the pan-Arctic shelves and a nexus of hydrological, biological, and geological transformation and exchange processes. It is characterized by high average productivity (93 $\mathrm{g\,C\,m^{-2}\,yr^{-1}}$), and supports 49% of the total Arctic shelf primary production and vigorous geochemical cycling (Sakshaug, 2004; Wassmann et al., 2006a). Hydrologic and ecologic processes occurring in the Barents Sea affect the entire Arctic Ocean (Carmack and Wassmann, 2006). The primary production and trophic links support large populations of higher trophic levels and, including fisheries, birds, and marine mammals (Wassmann et al., 2006a).

However, in this region of the Arctic, studies of benthic community composition have been concentrated on the west coast of Svalbard (Blacker, 1957, 1965), both within the western fjords (Holte and Gulliksen, 1998; Wlodarska-Kowalczuk et al., 1998; Hop et al., 2002; Kendall et al., 2003; Wlodarska-Kowalczuk and Pearson, 2004; Renaud et al., 2007b) and across the shelf break in Fram Strait (Weslawski et al., 2003; Wlodarska-Kowalczuk et al., 2004). Benthic faunal studies in the Barents Sea and the shelf-slope north of Spitsbergen are far less common (but see Piepenburg et al., 1995; Cochrane et al., 1998; Kröncke, 1998; Kröncke et al., 2000). The most widespread studies that have been carried out in the Barents Sea were conducted by the Russians during the Soviet period (Brotskaya and Zenkevich, 1939; Zenkevich, 1963; Antipova, 1975), and only recently have become accessible to non-Russian speakers (Galkin, 1998; Denisenko, 2001, 2002, 2004; Wassmann et al., 2006a). Further, most of the benthic faunal studies in the Svalbard–Barents Sea region have been descriptive studies focused on documenting spatial patterns of species distributions or faunal community types, without investigating the external processes responsible for regulating the observed patterns. In the present era of changing climate in the Arctic, it is essential to understand not only the composition of benthic communities, but also how they are linked to environmental processes, if we hope to be able to anticipate the consequences of climate change to these systems.

Our study, part of the interdisciplinary Norwegian-funded CABANERA ecosystem study, examined benthic communities over a continuum of environmental conditions in the western Barents Sea. The transect spanned 75–82°N from the Atlantic-dominated water mass of the west-central Barents Sea, through the Polar Front and the Arctic water east of Spitsbergen and extended just past the Arctic Ocean shelf-break north of Svalbard. Our goals were to document general patterns of community structure over the wide range of environmental conditions in the Barents Sea as well as to understand environmental forcing of benthic community structure, rather than a focus on distributions of specific species. We placed particular emphasis on examining community structure at the Polar Front region of the Barents Sea in order to identify how benthic community parameters compared to non-Polar Front locations. To achieve this, we compared benthic community parameters and species distributions to the physical and biological characteristics of the system most likely to influence benthic communities on short and long time scales.

2. Materials and methods

2.1. Study sites

Three sampling expeditions were carried out through the CABANERA program on the R/V *Jan Mayen* (University of Tromsø): 7–23 July 2003, 20 July–3 August 2004, and 18 May–5 June 2005. A total of 14 stations were sampled for benthic fauna from the western Barents Sea, north Svalbard shelf, and Nansen Basin of the Arctic Ocean (Fig. 1). The stations were oriented roughly in a transect along 30°E latitude from 75°N to 82°N, from the Atlantic-dominated water mass of the west central Barents Sea, through the Polar Front and the Arctic water east of Spitsbergen and extending just past the Arctic Ocean shelf-break north of Svalbard. Most, but not all, stations had at least some ice present at the time of sampling; ice concentrations ranged from 0% to 90% during our work at the station. All stations except XVIII were ice-covered at some point during the winter preceding sampling. The station network for the benthic sampling was similar to the pelagic stations sampled during the CABANERA field program in order to facilitate studies spanning both benthic and pelagic components (Tamelander et al., 2006; Morata and Renaud, 2008; Renaud et al., 2008a) and to provide a framework for more general inferences about the overall marine ecosystem at specific locations within the Barents Sea. But it was not always possible to conduct benthic sampling at exactly the same locations as pelagic or ice-related work (Table 1).

2.2. Field sampling and laboratory analyses

Samples were collected at each station with a van Veen grab (0.1 $\mathrm{m^2}$), with lead-weighted arms and hinged, lockable, rubber-covered inspection ports. Five replicate van Veen grabs were collected sequentially with the ship held in position. Sediment in the grab from each cast was viewed on deck through inspection ports for washout, and rejected if the jaws were not fully closed, if uneven penetration was detected or if the grab was less than two-thirds full.

Samples were washed through a 0.5-mm sieve, then all material retained was fixed in 4% buffered formalin with Rose