Pelagic–benthic coupling in the western Barents Sea: Processes and time scales

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ABSTRACT

The link between pelagic and benthic systems has been suggested to be particularly strong on Arctic continental shelves. Differing sampling strategies and the multitude of pelagic and benthic parameters that have been compared, however, make it difficult to determine the limitations of this important ecosystem concept. We sampled across multiple gradients in water mass characteristics, ice cover, productivity regimes, and seasons to test the generality of the pelagic–benthic coupling paradigm during a 3-year study (2003–2005) in the Barents Sea. While benthic community structure varied among stations, biomass was not significantly correlated with sediment oxygen demand (SOD), a finding contrary to some published studies. Average SOD varied from 2.3 to 7.3 mmol $O_2\,m^{-2}\,d^{-1}$, and was (positively) correlated as well with sediment pigments, as it was with the vertical flux of pigments and carbon measured by sediment traps deployed at 90 m. Export flux was also strongly coupled with our measure of benthic carbon cycling (SOD), suggesting that both processes vary on similar, short time scales (days to weeks). In contrast, processes responsible for patterns in benthic biomass reflect a response over longer time scales (several years), and are thus not well coupled with SOD. We conclude that conflicting results of studies assessing pelagic–benthic coupling may not necessarily be due to general inconsistencies in the fundamental relationship, but instead to improper comparisons of parameters or processes that vary over different scales. These findings are particularly relevant for evaluating system processes in ecosystem modeling studies.

1. Introduction

Research performed on Arctic continental shelves over the past 25 years has suggested that benthic and pelagic systems may be more tightly coupled here than in warmer seas (Petersen and Curtis, 1980; Grebmeier and Barry, 1991; Ambrose and Renaud, 1995; Hobson et al., 1995; Piepenburg, 2005). Mechanisms proposed to explain this include reduced importance of the microbial loop, mismatch of zooplankton and phytoplankton population cycles, highly pronounced seasonality, persistently low temperatures, and rapid sinking of pelagic or sympagic (ice-associated) algae (Eilertsen et al., 1989; Graf, 1992; Piepenburg et al., 1997; Wassmann et al., 2003). Despite the apparent generality of this emerging paradigm, some areas have been suggested to be relatively uncoupled (Sauter et al., 2001; Gooday, 2002; Grebmeier et al., 2006b; Tamelander et al., 2006), raising the question of whether the paradigm may be an artifact of timing or location of sampling (e.g., initial focus on productive areas), or if there are fundamental geographical differences in how benthic systems function on Arctic shelves. Since the benthos plays an important role in carbon cycling and nutrient regeneration on these shelves (Grebmeier and McRoy, 1989; Glud et al., 2000; Grant et al., 2002; Renaud et al., 2006), and Arctic shelves have been suggested to be particularly vulnerable to climatic change (ACIA, 2004; Carroll and Carroll, 2003; Renaud et al., 2007a), these inconsistencies are not merely academic curiosities.

A wide range of benthic parameters describing both structure and function of Arctic shelf communities has been studied in the context of pelagic–benthic coupling. These include faunal abundance and biomass, community structure, food-web structure, feeding behavior, oxygen consumption and heat production, sedimentary geochemical profiles, and benthic faunal reproductive cycles (Graf, 1989; Grebmeier and McRoy, 1989; Ambrose and Renaud, 1995, 1997; Hobson et al., 1995). Relationships have been tested among these parameters and data from the pelagic system, including primary production; nutrient concentration; ice cover; and sedimentation rates of carbon, nitrogen, and phytodetritus.

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Clearly, all of these variables reflect processes occurring over different temporal and spatial scales. For example, spatial patterns in benthic community structure are thought to represent a time-integrated response to food inputs over several years or more (e.g., Dunton et al., 2005); while primary production rates or feeding rates of benthic organisms may vary on the scale of hours. It is not clear how coherent different measurements of the strength of pelagic–benthic coupling will be when examined over a spatially heterogeneous range of water mass influence, ice conditions, and depths, compared to being studied within discrete oceanographic features (e.g., polynyas).

The Norwegian-funded CABANERA project ('Carbon flux and ecosystem feedback in the northern Barents Sea in an era of climatic change') investigated the spatial variability, temporal dynamics, and regulation of ecosystem processes during three field campaigns from 2003 to 2005 in the western Barents Sea. The area sampled spans the northern extent of Atlantic Water, through the Marginal Ice Zone, to primarily Arctic-water influence at the Arctic Ocean shelf-break. This area is known to exhibit high spatial and seasonal variability in terms of benthic communities (Zenkevitch, 1963; Piepenburg et al., 1995), primary production rates, and vertical fluxes (Wassmann et al., 2006). Under these conditions, it should be possible to identify differences in functional relationships between the links among water-column and sea floor processes, thus testing the generality of the pelagic–benthic coupling paradigm.

We address both the structure and function (sediment oxygen demand (SOD)) of benthic communities, properties presumed to respond to pelagic variability on different time scales, and ask: how does SOD vary in the western Barents Sea? What is the relationship between SOD and benthic faunal associations? and what is the nature of the coupling between benthic and pelagic processes across the range of conditions found in the western Barents Sea?

2. Methods

2.1. Study area and sampling techniques

The western Barents Sea (Fig. 1) was the study area for an intensive, multidisciplinary ecosystem study that was performed during 2–3 week cruises in July–August during 2003 and 2004, and in May–June 2005. Stations were sampled from the R/V Jan Mayen under conditions ranging from open water to more than 90% cover of primarily first-year ice. See Sundfjord et al. (2007) for a discussion of the general hydrography during this study. Depth ranged from 195 to 503 m (Table 1).

Benthic sampling was performed using replicate multicorer or box corer casts. Only cores with intact surface layers, indicated by surface 'fluff' or delicate epifauna, were used. Replicate subcores (10 cm diameter × 20–25 cm deep with as much overlying water preserved as possible) were taken from each cast for estimating the respiration of the entire infaunal sediment community. Additional subcores were taken for sediment pigment concentration, and these were sectioned into 1 cm intervals. While subcoring may be viewed as pseudoreplication (Hurlburt, 1984), our analyses indicated that variance in respiration rates and chemical composition among subcores from the same box core deployment was not significantly different from the variance among cores from different deployments at the same station (unpublished data).

2.2. Oxygen demand measurements

Incubation cores (5–12 per station) were filled with bottom water collected using the ship's rosette, and bubbled for at least 2 h to saturate the overlying water with oxygen. Core tubes without sediment were filled with bottom water and bubbled, and
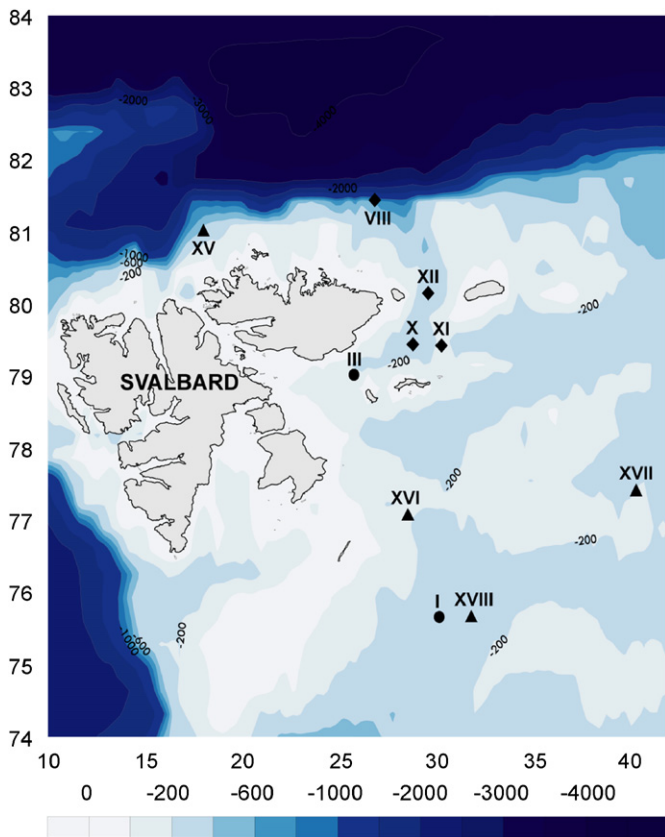

Fig. 1. Map of western Barents Sea indicating sampling stations. Circles: sampled summer 2003; diamonds: sampled summer 2004; triangles: sampled spring 2005.

Table 1
Location, depth and sampling dates for Barents Sea stations sampled for benthic process studies in 2003–2005

Station no.	Location	Latitude °N	Longitude °E	Depth (m)	Date
I	Hopen Trench	75°40.0′	30°10.0′	345–352	11 July 2003
III	Erik Eriksenstredet	79°01.2′	25°46.3′	198	16 July 2003
VIII	N. Kvitøya Trench	81°16.7′	26°51.2′	503	28 July 2004
X	N. Kong Karlsland	79°48.4′	28°48.4′	303	29 July 2004
XI	NE. Kong Karlsland	79°56.6′	30°17.0′	195	01 Aug 2004
XII	Kvitøya Trench	80°09′	29°36.0′	286	02 Aug 2004
XV	Questrenna Shelf	81°01.5′	18°01.1′	311	21 May 2005
XVI	N. Hopen Trench	77°05.2′	28°33.0′	206	26 May 2005
XVII	E. Storbanken	77°25.6′	40°18.3′	208	29 May 2005
XVIII	Hopen Trench	75°40.8′	31°48.7′	340	30 May 2005

acted as controls for methodological effects and for respiration of water-column biota. Cores were always kept in the cold room under reduced light at 0–2 °C. At the beginning of the oxygen-demand assays, cores were sealed using tops that provided constant stirring without sediment resuspension. Oxygen concentrations were monitored every 3–6 h during the incubations using a polarographic oxygen probe (YSI) inserted into a small sampling port in the core top. Incubations were terminated when 15–30% of the oxygen had been consumed (usually after 30–48 h).

2.3. Faunal analysis

After incubations were completed, sediment cores were gently sieved on 1-mm mesh and the sieve residue was fixed with buffered 10% formaldehyde with Rose Bengal stain added. These samples were later sorted to coarse taxonomic groups and transferred to 70% ethanol. Experts at the Zoological Institute of the Russian Academy of Sciences identified all organisms to the lowest practical taxonomic level, usually species. Species lists were compared with data bases at Akvaplan-niva and the European Register of Marine Species (http://www.marbef.org/data/erms.php) to insure compatibility with other studies performed in this area. Blotted wet biomass was determined for each taxon in each sample. Shells are included in biomass values, but tube structures are not included for polychaetes or crustaceans.

2.4. Sedimentary pigment analysis

Triplicate subcores for sediment pigments (5 cm diameter) were taken from each station. Pigments from the top 2 cm were analyzed fluorometrically according to Holm-Hansen et al. (1965). In the laboratory, this sediment was thawed and 20 mL of 100% acetone was added. Pigments were extracted in the freezer in the dark, during which tubes were shaken periodically. After 48 h, sediment was centrifuged (4000 rpm for 10 min) and the supernatant was analyzed in a Turner Designs model 10-AU fluorometer before and after acidification with 10% HCl. In 2004, pigment content was determined 2–3 weeks following collection, while these values were measured on board in 2005. Pigment samples for fluorometric analysis were not taken in 2003.

2.5. Statistical treatment

Respiration rates were determined as the (negative) slope of the regression of oxygen concentration (mmol O_2) on incubation time (days) and scaled to $1\,m^2$ (Clough et al., 2005). If control cores exhibited significant oxygen consumption ($p < 0.05$), the mean of these values was subtracted from the slope of each sediment incubation core. Dry biomass of infauna ($g\,DM\,m^{-2}$) was calculated from: (1) family-level DW/WW (including shells, where applicable) conversion factors if available in the compiled list of conversion factors by Brey (2001), (2) the higher-taxonomic-level factors from Ricciardi and Bourget (1998) since most of these factors were determined from a larger number of taxa than those of Brey (2001), and (3) assuming dry mass to be approximately 20% of wet mass (Rowe, 1983) if the taxon was not available from either of the first two sources. SOD was normalized for infaunal biomass by dividing the SOD of each core by the core's computed dry biomass of macrofauna. Values of this ratio that are <1 have been noted to be normal at many Arctic shelf sites at depths <500 m, a result suggested to indicate dominance of respiration by macrofauna (Clough et al., 2005).

Faunal communities were analyzed using nonmetric multi-dimensional scaling (MDS) of the Bray–Curtis similarity matrix calculated from species-abundance data. Analyses were run on untransformed data and on the same data set following presence/absence transformation. Comparison of the results is useful for assessing the relative importance of dominant or rare species in generating the observed patterns. An analysis of similarities (ANOSIM) was performed on the data to compare communities among stations. ANOSIM is a resampling technique that can identify significant differences in species composition among groups of samples (stations), after which pairwise comparisons can be conducted (Clarke and Gorley, 2006). Similar analyses were performed for the species-biomass data. Faunal data were not available from station XI.

Linear correlation analyses were performed to investigate the relationships among sediment carbon, sediment pigments, SOD, infaunal biomass, and vertical flux estimates of carbon and chlorophyll. Vertical flux measurements were performed by Reigstad et al. (2008), and we used data from 90-m traps, as this depth was common to all stations where we had SOD and other sediment data, it is sufficiently below the euphotic zone at all sites, and is far enough above the sea floor that resuspension is unlikely to have a major impact on estimates. Flux data of Reigstad et al. from station XIV were assumed to approximate flux at our nearby station XV, and were collected within 24 h of our sampling.

3. Results

3.1. Benthic faunal communities

Community structure based on species abundances was significantly different among all stations sampled (ANOSIM: $p < 0.001$). The MDS plot (Fig. 2) visualizes the ANOSIM result, indicating that replicate cores were generally much more similar within a station than they were to cores from other stations. However, it is important to note that axes in the MDS plot are dimensionless so it is less clear how different they are. In fact, we sampled a similar bottom type (sandy mud to mud) within a relatively narrow depth range in the Barents Sea (Table 1), so it is somewhat surprising that stations were so distinct. Results for the untransformed and severely transformed data sets gave identical results (ANOSIM: $p < 0.001$), indicating that patterns are robust to biases against or for rare species in the different techniques. Only results for analysis of the untransformed data are presented here.
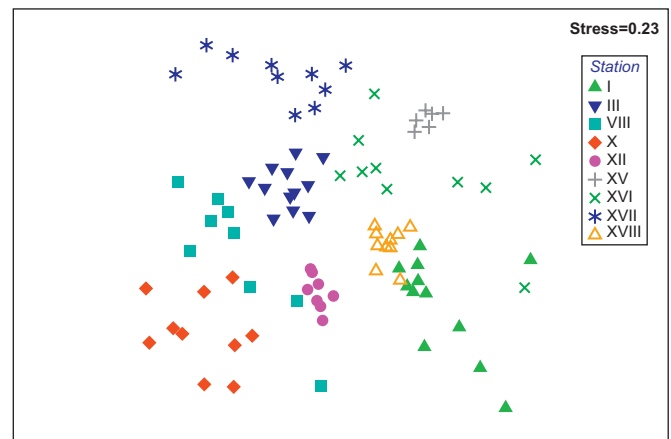

Fig. 2. Multidimensional scaling of benthic macroinfaunal communities from Barents Sea stations during 2003–2005. Results are for untransformed abundance data, and each point represents an individual core. Stations indicated by each symbol are identified in the legend. All stations are significantly different from each other by ANOSIM at alpha = 0.05. Foraminiferans were excluded from data.

Table 2
Sediment oxygen demand (SOD) and other sediment parameters from benthic stations sampled for process studies

Station	SOD (mmol O_2 m^{-2} d^{-1})	Infaunal biomass (g dry m^{-2})	SOD/biomass (mmol O_2 g dry^{-1} d^{-1})	Sediment chlorophyll (mg m^{-2})	Sediment phaeopigment (mg m^{-2})	Flux of chlorophyll (mg m^{-2} d^{-1})	Flux of phaeopigments (mg m^{-2} d^{-1})	Flux of carbon (mg m^{-2} d^{-1})
I	2.7 (0.6)	12.3 (6.3)	0.22	No data	No data	0.11 (0.01)	0.28 (0.01)	123 (31)
III	2.3 (0.5)	6.8 (9.1)	0.34	No data	No data	1.63 (0.12)	1.70 (0.24)	222 (24)
VIII	5.5 (1.9)	6.0 (8.4)	0.91	2.4 (2.7)	12.2 (7.7)	No data	No data	No data
X	2.6 (0.7)	2.8 (2.2)	0.91	0.6 (0.3)	13.1 (2.2)	1.85 (0.07)	2.98 (0.43)	117 (4)
XI	6.7 (4.9)	No data	No data	12.9	30.7	2.48 (0.26)	3.33 (0.49)	219 (9)
XII	5.6 (0.2)	13.5 (4.9)	0.41	1.6 (0.8)	21.8 (4.4)	No data	No data	No data
XV	7.3 (2.1)	11.8 (5.9)	0.61	40.2 (5.4)	79.3 (5.3)	6.22 (0.24)	4.44 (0.63)	351 (31)
XVI	5.1 (0.9)	11.2 (19.1)	0.45	17.8 (12.9)	29.9 (14.2)	3.48 (0.06)	3.15 (0.44)	208 (15)
XVII	3.2 (1.0)	3.4 (5.7)	0.93	0.7 (0.3)	4.7 (2.2)	0.98 (0.07)	2.02 (0.19)	80 (10)
XVIII	4.0 (0.8)	13.3 (6.5)	0.30	13.0 (2.1)	22.0 (4.6)	13.58 (0.13)	8.59 (0.15)	720 (51)

Data represent means (1 standard deviation). Pigment data are from the top 2 cm of sediment. Flux data are from Reigstad et al. (2008). See text for sample size and other pertinent information.
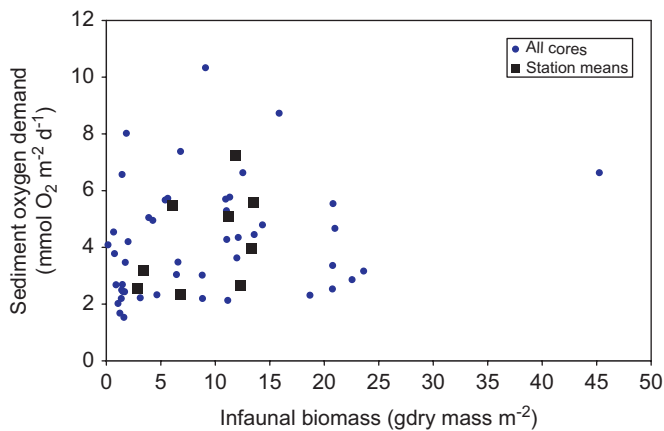

Fig. 3. The relationship between biomass of macrofauna from incubation cores and sediment oxygen demand from those cores for all stations. Small circles indicate values for individual cores, while squares represent station means. Linear correlations for both sets of points are nonsignificant ($p \gg 0.05$).
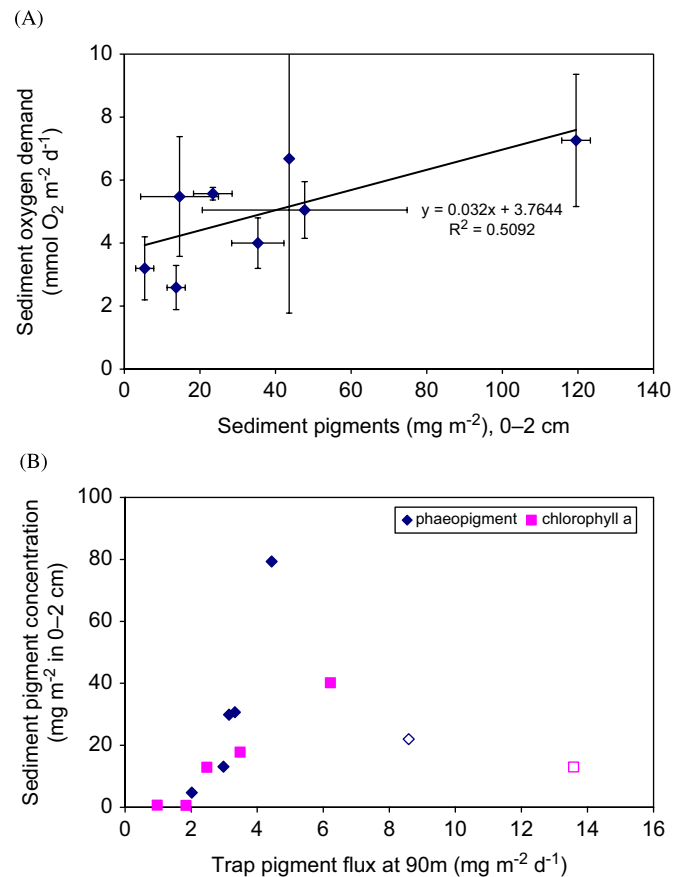

Fig. 4. Regressions indicating the relationship between (A) sediment oxygen demand and sediment pigments (total from top 2 cm), and (B) sediment pigment concentration (from top 2 cm) and pigment flux calculated from sediment traps at 90 m. In (B) chlorophyll and phaeopigments are presented separately, and the Station XVIII (open symbols) is excluded from the regression analyses. Regression lines not added in (B) to retain clarity; but see Section 3.3 for more details of these statistically significant relationships. SOD values represent stations means of 4–12 replicates; pigment values are means of 2–3 replicates.

Biomass varied between 2.8 g DM m^{-2} on the eastern end of the Storbanken to 13.5 g DM m^{-2} in the Kvitøya Trench (Table 2). Fauna was dominated by polychaetes, crustaceans, and bivalves on both abundance and biomass bases. Parallel samples were taken for more detailed community analysis and are presented by Carroll et al. (2008). MDS and ANOSIM based on faunal-biomass data indicated broad community differences among stations, just as it did for species-abundance data. Station pairs X/XII, X/XV, and XII/XV were not significantly different from each other, while all other pairs (32/35) were distinct (global ANOSIM: $p < 0.001$; pairwise ANOSIM: $p < 0.05$).

3.2. Sediment oxygen demand

SOD (station means) varied by a factor of about 3, between 2.3 and 7.3 mmol O_2 m^{-2} d^{-1} (Table 2). Macrofaunal biomass was not an accurate predictor of SOD. Linear correlations of the two variables on either a per-core or a per-station basis were non-significant ($p \gg 0.05$; Fig. 3). SOD also did not correlate significantly with depth ($p > 0.05$). For all stations, the biomass-normalized SOD was <1 mmol O_2 consumed g-dry-mass^{-1} d^{-1} (0.22–0.93) (Table 2).

3.3. Coupling with sedimentary parameters and vertical flux

Sediment pigment concentration (chlorophyll a (chl a) and phaeopigments in the top 2 cm) varied by more than an order of

magnitude across all stations, from a low of 5.4 mg m^{-2} at station XVII to 119.5 mg m^{-2} at station XV (Table 2). Chl a comprised between 4% and 37% of the total pigment content. Variation in sediment pigment concentration explained half of the variability in SOD ($p < 0.05$), despite high core-to-core variability at each station (Fig. 4A). Pigment concentrations at the sediment surface were highly correlated with measured pigment flux at 90 m, even
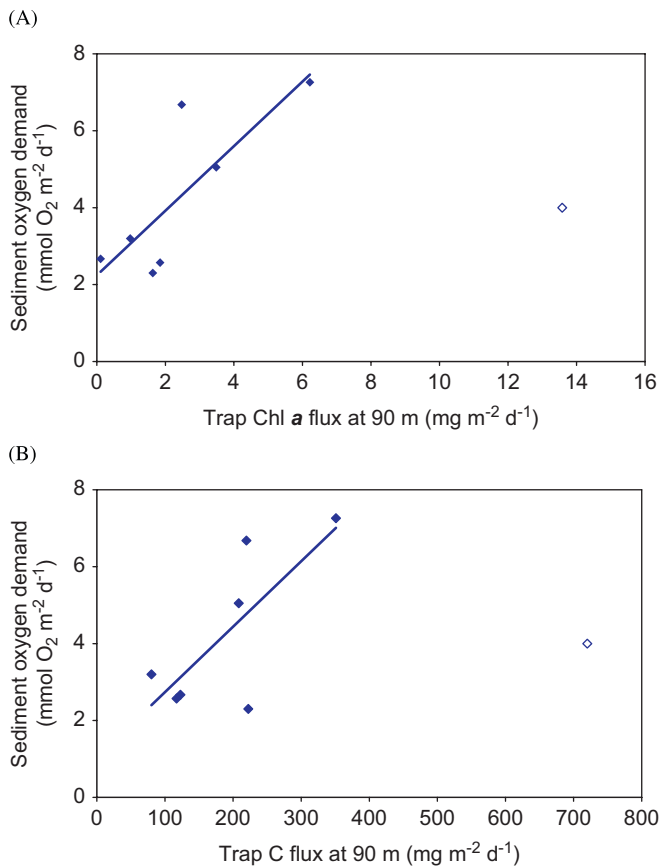
(A)

(B)

Fig. 5. Regressions indicating the relationship between sediment oxygen demand and (A) chlorophyll *a* flux and (B) carbon flux calculated from sediment traps at 90 m. Data for the Station XVIII (open symbols) are presented, but were omitted from regression analyses (see Section 3.3 for details). SOD values represent stations means of 4–12 replicates.

though total depths ranged from 195 to 503 m. Vertical flux at 90 m explained 87% and 96% of the variability in sediment phaeopigments and chl *a*, respectively, when station XVIII (open symbols) was excluded (Fig. 4B; $p < 0.01$ for each).

The sediment community responded quickly to the arrival of fresh food, or proxies thereof, from surface waters. Sinking chl *a* and carbon at 90 m depth explained 58% and 47% of the SOD, respectively, (Fig. 5A and B; $p < 0.03$ and 0.06, respectively). Again, station XVIII was excluded from these regressions (Section 4.3.1). A positive intercept of the *y*-axis in the regression of SOD on carbon flux indicates a tentative value for a 'baseline' respiration level of sediment community in the absence of any vertical flux $(1.04 (\pm 1.4) \, \mathrm{mmol} \, O_2 \, m^{-2} \, d^{-1}$, corresponding to a carbon remineralization rate of $0.88 \, \mathrm{mmol} \, C \, m^{-2} \, d^{-1}$, assuming 1:1 stoichiometry and a respiration coefficient of 0.85; Smith 1978). This value needs to be further clarified from more stations from this region and around the Arctic.

4. Discussion

4.1. Patterns in SOD

SOD measured over the range of biological and hydrographic conditions sampled in 2003–2005 in the western Barents Sea was within the range of values recorded for other shelf areas across the Arctic (Table 2; Clough et al., 2005; Grebmeier et al., 2006a). Higher (2–4x) values have been found in 'hot spots' on shallow shelf areas well under 100 m. The measured SOD values are

underestimates of actual carbon mineralization by the sediment community as they do not take into account either metabolic activity by epifauna or anaerobic respiration. In the Barents Sea, epifauna can be abundant and may account for up to 75% of sediment community oxygen consumption (SCOC), although such values are usually restricted to depths shallower than 150 m (Piepenburg et al., 1995). Epifauna also have been found to be responsible for up to 25% of SCOC in the Chukchi Sea (Ambrose et al., 2001), and over 40% of SCOC in the Beaufort Sea (Renaud et al., 2007b). While we do not have epifaunal density estimates from the stations we sampled, most stations were deeper than 200 m. At these depths, Piepenburg (2005) estimated the contribution of epifauna to be around 4% in the Barents Sea. The contribution to carbon mineralization by anaerobic bacteria has been shown to be important in Arctic fjords (Rysgaard et al., 1998; Glud et al., 2000), but less so in the open waters of the Barents Sea (Vandieken et al., 2006).

Variability in SOD in time and space in the Arctic has been suggested to reflect an interaction among quality and quantity of carbon supply (Grebmeier and McRoy, 1989; Piepenburg et al., 1997; Cooper et al., 2002; Renaud et al., 2006; Morata and Renaud, 2008), benthic community structure (Piepenburg et al., 1995), and sediment organic-carbon content (Grebmeier et al., 2006a). Other physical and biological parameters (ice cover, sediment grain size, integrated water-column chlorophyll, depth) act through one or more of the above parameters. Interannual variability in SOD has been suggested to be an indicator of climate-driven changes in ecosystem structure (Grebmeier et al., 2006b), although there has been little documentation of the temporal scales of variability in SOD (but see Renaud et al., 2006 for a study at 230 m in the Beaufort Sea). A 7-year study at a deep (4100 m) station in the North Pacific showed considerable seasonal and interannual variability in SCOC (Smith and Kaufmann, 1999). Renaud et al. (2006) have noted a 10-fold increase in SOD over a time span of several weeks at a single location, and Wenzhöfer and Glud (2004) observed a 7-fold variability over a diel cycle. These studies suggest that it is important to determine what is driving SOD, and over which time scales these drivers operate in benthic communities, especially if changes in SOD are to be used as indicators of climate change.

4.2. Role of faunal communities

The structure of benthic infaunal communities was distinct at each station (Fig. 2), despite sampling areas with similar sediment types on the Barents shelf. This was the case whether abundance data were transformed or not, and was also consistent if species-biomass data matrices were used instead of species-abundance matrices. A companion study using a VanVeen grab at the same stations revealed a similar biomass range; and these faunal community patterns are discussed in more detail, and in relation to environmental parameters at these stations, by Carroll et al. (2008).

Communities with different composition and biomass may be expected to process food arriving at the sea floor in different manners. This has been shown in studies in the Bering and Chukchi Seas where SOD and macrofaunal biomass were significantly (positively) correlated (Clough et al., 2005; Grebmeier et al., 2006a). In this study, however, there is no direct statistical link between SOD and macrofaunal biomass, either on a per-core or per-station basis (Fig. 3). There are different arguments that can be used to explain this finding. It is possible, for example, that macrofauna are not responsible for the bulk of the oxygen consumption measured in our study (the Barents Sea). Multiple lines of evidence, however, suggest that macrofauna are, in fact, dominating SOD on some Arctic shelves (e.g., Piepenburg

et al., 1995). Additionally, Clough et al. (2005) propose that biomass-specific respiration rate can be a useful indicator of the relative importance of macrofauna versus microbial processes, and suggest that a value less than 1 indicates dominance by macrofauna. This metric is less than 1 for all stations sampled in our study (Table 2), indicating that macrofauna are likely to be important contributors to SOD. Grebmeier et al. (2006a) also suggest that macrofauna are dominating sediment oxygen consumption in their study area, citing several supporting works from that region. It seems likely, therefore, that macrofaunal respiration comprises the majority of the oxygen consumption on the Barents shelf. A second possible explanation is that this study samples from depths (approximately 200–500 m) where infauna are less important, and SOD is relatively low. This is probably important when comparing our results to those from areas of the highly productive and very shallow Chukchi Sea. As mentioned above, however, SOD measured in this study are similar to the general range found throughout the Arctic, including in shallow areas (<200 m) of both the Beaufort and Laptev Seas (Schmid et al., 2006; Renaud et al., 2007a, and references within).

We maintain that macrofauna are dominating SOD in our study, and that the published significant correlations between SOD and macrofaunal biomass on Arctic shelves with episodic deposition of phytodetritus do not reflect direct causal links between the two. We propose a modification to the current view of pelagic–benthic coupling on Arctic shelves. A change in macrofaunal community structure, including biomass, is a response to long-term (interannual) trends in organic carbon deposition (e.g., Blacker, 1957; Grebmeier et al., 2006a), while SOD may respond rapidly to pulsed arrival of food to the sea floor (e.g., McMahon et al., 2006; Renaud et al., 2006). Therefore, finding a positive correlation between macrofaunal biomass and SOD may be a fortunate coincidence of sampling during a peak (or at least representative) time of deposition. Most stations in the Grebmeier et al. (2006a) study, and all shelf stations evaluated by Clough et al. (2005), were sampled in June–July, the time of highest primary production over the Chukchi shelf. The Barents Sea region is characterized by high variability in bloom conditions. Stations sampled in our study span a period of early to late phytoplankton bloom (Hodal and Kristiansen, 2008). It is likely, then, that many of the stations had not received their representative annual pulse in food supply. We suggest, then, that SOD and biomass respond to processes acting on significantly different time scales and should not be expected to correlate *a priori*. Admittedly, our findings are not conclusive, but are supported by both the stations sampled in this study and many of the studies for which relevant system-level data is available.

4.3. Pelagic–benthic coupling

4.3.1. Quantitative evidence: vertical flux, sediment inventories, and SOD

Correlation analysis suggested that half of the variability in SOD in our incubations can be explained by pigment concentrations in the top 2 cm of the sediment (Fig. 4A). This finding is consistent with other studies from the Arctic (Grant et al., 2002; Clough et al., 2005), and even from a tropical deep-sea site (Smith et al., 2002). Phytodetritus is the major carbon source to the benthos on Arctic shelves lacking significant riverine inputs, and processes affecting its delivery to the benthos are likely to be linked with benthic stocks and processes. Despite water depths at our stations being between 195 and 503 m, vertical pigment flux measured in traps 100–410 m above the sea floor explained over 85% of the variance in surface chl *a* and phaeopigments concentrations (Fig. 4B). This implies that material must be

sinking quickly, and that the 90 m trap accurately estimates export production. Strong correlation of fluorometrically determined chl *a* data with both chl *a* and fucoxanthin analyzed by HPLC (Morata and Renaud, 2008) suggests the majority of the phytodetrital input is from diatoms.

Wexels Riser et al. (2008), working at the same stations, found that 30% of the carbon flux at 90 m was in the form of fast-sinking fecal pellets from large copepods. Fast-sinking phytodetritus and a responsive benthic community suggest that these two processes are linked in both biological significance and in time scale. Not surprisingly then, both chl *a* and carbon flux measured in 90 m traps had strong relationships with SOD, each explaining more than 45% of the variance in this benthic process (Fig. 5). Clearly, the rate of delivery to the benthos will vary over the season depending on bloom stage, phytoplankton cell size, and pelagic grazing dynamics. Most of the flux, however, will occur during or around the spring bloom period, and approximately 45% of primary production during the spring bloom is exported below 90 m (Wexels Riser et al., 2008) and sinks with relatively little degradation from there to the sea floor. Although primary production by ice algae is considerably less than that by phytoplankton in the Barents Sea (Wassmann et al., 2006), ice algae can be a locally important additional food source for the benthos (McMahon et al., 2006; Tamelander et al., 2006), the more so as they presumably sink with greater efficiency than phytoplankton (Carroll and Carroll, 2003). This suggests that a large part of net annual primary production sinks to the benthos in the productive Barents Sea and is rapidly processed by resident fauna.

We must point out several caveats in the interpretation of these data. Our results demonstrate statistical correlations and not direct causal relationships. Therefore, they do not necessarily indicate that chl *a* or carbon is the factor cuing benthic activity. Other biochemicals (amino acids, fatty acids, etc.) may stimulate benthic activity, and may even be the material immediately assimilated by the deposit-feeding macrofauna. In addition, activity by bacteria and meiofauna, while assumed to represent a lower proportion of total oxygen demand on Arctic shelves than that by macrofauna (e.g., Piepenburg et al., 1995), may also respond to food inputs. In a study in the Beaufort Sea, however, meio- and micro-fauna increased their respiration rates by a factor of ~2 in response to ice algal deposition, while macrofaunal respiration increased by more than a factor of 10 (Renaud et al., 2006).

Finally, regressions involving trap data (Figs. 4B, and 5) were performed excluding station XVIII where flux values were 2–3 times higher than at any other station. This is probably due to a 48-h storm that reached the station just after our arrival, completely homogenizing the previously stratified water column. Increased vertical transport estimates may be real, caused by increased flocculation and/or active transport, or an artifact of resuspension and/or lateral advection off nearby bank sediments. Since C:chl *a* and C:N ratios suggest that the trap material is fresh (Reigstad et al., 2008), flocculation and active transport seem to be the most likely possibilities. Regardless, this event shows that while pelagic–benthic coupling is robust across a wide variety of water masses and bloom conditions, local dynamics may override its importance under some conditions.

4.3.2. Temporal and spatial scales

Time scales of benthic response to food inputs are not well studied, especially at high latitudes. Our evidence, and that by Renaud et al. (2006) from a January–July study in the Beaufort Sea, suggests that the benthic community is capable of rapid increases in activity (measured as SOD). Resolution of the time scale is difficult, but statistical links between vertical flux and

both sediment pigments and SOD imply that response is on the order of days to a very few weeks. These scales agree with the days to weeks identified for faunal response to bloom sedimentation (Graf, 1989, 1992) or experimental addition (McMahon et al., 2006), and the one-month lag between arrival and disappearance of a phytodetrital pulse on the sea floor off Northeast Greenland (Ambrose and Renaud, 1997). In a review of benthic response to seasonal flux, Gooday (2002) grants that macrofauna may react quickly in productive waters of the continental margins. In the deep-sea, however, rapid response may be limited to smaller size fractions of the benthos (Gooday, 2002), or may not be identifiable at all (Sauter et al., 2001).

A recent study around Antarctica tracked the seasonal signal of phytodetrital fluxes, sediment pigments, and SOD from shelf (to 600 m) environments (Smith et al., 2006). The authors found a strong seasonal pulse in vertical flux, but little response in SOD or sediment chl a integrated over the top 10 cm, and interpreted this as indicating that respiration responds to long-term trends in productivity, and sediment pigment inventories are evidence of poor coupling of benthic and pelagic processes. These results appear to be in sharp contrast to ours, and certainly the conclusions are divergent. As discussed above, benthic communities below a deeper water column may be expected to show less of a response to seasonal signals than those in shallow water (cf. Gooday, 2002). The depth of the Antarctic shelf may result in the most labile material being consumed during vertical transit. Additionally, POC flux may be intercepted by communities of epifaunal suspension feeders that Smith et al. (2006) observed feeding throughout most of the year. The sediment inventories of Smith et al. (2006) were considerably lower than those seen in our study: the largest concentration is less than half the smallest value that we found. It is unclear how such a low concentration could be seen as a buffer for the system (as they suggest) unless benthic fauna have particularly low food requirements. In fact, Stephens et al. (1997) found 43–89% of sediment pigment inventory to be "poorly degradable," perhaps bound to sediment particles (Keil et al., 1994) and thus unavailable to consumers, despite appearing to be labile. The overwhelming majority (99%) of the flux material from the deep equatorial Pacific was found to have a half-life of days to a few months (Stephens et al., 1997). It is possible that the Antarctic shelf, especially at depths up to 600 m, operates in a fundamentally different manner than many other areas of the world ocean; and, clearly, different studies show different rates of benthic response to sedimenting organic material. It is left to further investigation, however, how respiratory processes should reflect a long-term supply trends in communities of organisms generally considered to be opportunistic.

Perhaps what the contrasts between our study and that of Smith et al. (2006) best show is just how little spatial variability in patterns and process in the benthos has actually been investigated. Spatial patterns are difficult to identify as they are almost always accompanied by temporal (including, e.g., bloom stage; Tamelander et al., 2008) variability. Still, over multiple studies, spatial patterns in benthic activity are identifiable (Grebmeier et al., 2006a), and these can be linked to pelagic processes on similar (meso-) scales.

Our findings of a tight link between benthic and pelagic processes highlight a second aspect of spatial scale. The high correlation ($r^2 > 0.85$) between vertical pigment flux at 90 m and surface-sediment pigments indicates a rapid sinking of some fraction of suspended particulate organic matter. Sinking matter does not fall straight downward, of course, but is advected laterally by currents. What our results indicate is that either vertical flux estimates are representative for a large area surrounding the study site, or trapped material sinks very quickly,

or both. Similar results have been found on Arctic shelves (Ambrose et al., 2005; see Renaud et al., 2006 for a longer discussion), suggesting that point measurements (opposed to time-integrated values) in surface waters are valid for assessing pelagic–benthic coupling at these depths.

4.4. Designing studies of pelagic–benthic coupling

A paradigm such as pelagic–benthic coupling is only valuable if we can use it as a tool to more effectively conduct research and make predictions about the functioning of ecosystems. This study points to the need for a common interpretation of the paradigm such that deviations from its predictions are interpretable and are neither dismissed as flawed nor used to invalidate a principle based on considerable data. What then is pelagic–benthic or benthic–pelagic coupling? Hargrave (1973) has described it as a fundamental relationship between the pelagic and benthic regions, while Gooday (2002, p. 312) defines it as "the deposition on the seabed of organic-rich particles originating in the upper water column." Already, these two quite general definitions differ importantly in that one points to the existence of a relationship, and the other describes a process by which this occurs. Pelagic–benthic coupling has been used synonymously with benthic–pelagic coupling by some, but the order of the wording should represent the predominant direction of transfer (in this case, pelagic productivity to benthic respiration would be pelagic–benthic coupling). Even within this context, pelagic–benthic coupling has also been used to describe the attenuation of vertical carbon flux in the top approximately 200 m of the water column without the mention of a specific benthic stock or process this attenuation is impacting (Wassmann et al., 2003; Carmack and Wassmann, 2006). We choose to use the more general definition for the relationship between benthic and pelagic processes (Hargrave, 1973), and let each investigator decide which processes to study.

We maintain, however, that the only valid studies of pelagic–benthic coupling are those comparing processes (or stocks) that can reasonably be expected to vary on similar temporal and spatial scales. This study shows that benthic standing stock, a parameter that most investigators agree reflects an integrated response to food supply over interannual scales (e.g., Dunton et al., 2005), is not directly connected with SOD, a process varying on the scale of days to several weeks. SOD is, however, tightly linked to pelagic flux processes that vary over similar short time scales.

We conclude that correlative studies investigating coupling of processes mismatched in temporal scale can lead to misinterpretation of observed patterns. Numerous examples exist in the literature (see reviews by Grebmeier and Barry, 1991; Graf, 1992; Piepenburg, 2005), and a comprehensive reassessment of these studies may be enlightening. This revised view is not intended to discount the value of these studies, but to suggest a new perspective in which to view the results. The coherence of rates of water-column and sea-floor processes described in this study confirms the generality of the pelagic–benthic coupling paradigm, since time scales are matched. Matching scales of time and space when looking for coupling may make studies more complex, but it will provide meaningful tests of where and when systems are coupled, and give useful insights into processes that may interfere with this fundamental relationship. Knowledge about potential influences of, for example, relative importance of pelagic consumption/retention of organic carbon, advection and vertical mixing events, benthic boundary-layer processes, or lag time in responses, are valuable in understanding ecosystem functioning and how it may vary in time and space. This is the ultimate value in using paradigms as conceptual models in ecological studies.

Acknowledgments

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