A synthesis of bentho-pelagic coupling on the Antarctic shelf: Food banks, ecosystem inertia and global climate change

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Abstract

The Antarctic continental shelf is large, deep (500–1000 m), and characterized by extreme seasonality in sea-ice cover and primary production. Intense seasonality and short pelagic foodwebs on the Antarctic shelf may favor strong bentho-pelagic coupling, whereas unusual water depth combined with complex topography and circulation could cause such coupling to be weak. Here, we address six questions regarding the nature and strength of coupling between benthic and water-column processes on the continental shelf surrounding Antarctica. We find that water-column production is transmitted to the shelf floor in intense pulses of particulate organic matter, although these pulses are often difficult to correlate with local phytoplankton blooms or sea-ice conditions. On regional scales, benthic habitat variability resulting from substrate type, current regime, and iceberg scour often may obscure the imprint of water-column productivity on the seafloor. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column. However, within a single habitat type, i.e. the muddy sediments that characterize much of the deep Antarctic shelf, macrobenthic biomass appears to be correlated with regional primary production and sea-ice duration. Over annual timescales, many benthic ecological processes were initially expected to vary in phase with the extraordinary boom/bust cycle of production in the water column.

Bentho-pelagic coupling clearly will be altered by Antarctic climate change as patterns of sea-ice cover and water-column recycling vary. However, the nature of such climate-driven changes will be very difficult to predict without further studies of Antarctic benthic ecosystem response to (1) inter-annual variability in export flux, and (2) latitudinal gradients in duration of sea-ice cover and benthic ecosystem function.

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1. Introduction

Connections between ecological processes in the water column and seafloor are widely recognized in
continental-shelf ecosystems (e.g., Graf, 1992) and are called “benthic-pelagic coupling.” In this synthesis, we use the term **benthic-pelagic coupling** to mean a causal relationship (rather than simply a correlation) between water-column and benthic processes. When water-column processes exert control on the benthos, the coupling is said to be “downward.” Common examples of downward coupling include control of seafloor respiration and biomass by the sinking flux of particulate organic matter (Graf, 1992; Smith et al., 1997). “Upward” coupling occurs when benthic processes causally influence ecosystem dynamics in the water column, for example, when organic-matter mineralization or trace-metal entrainment at the seafloor supplies limiting nutrients to the euphotic zone (Sedwick et al., 2000). Here, we will focus on downward coupling although we will briefly consider upward processes.

Many lines of evidence suggest that benthic-pelagic coupling can substantially influence material cycles, community dynamics, and fisheries yields in shelf ecosystems. For example, particle-flux studies in a variety of shelf habitats indicate that 6–60% of net annual primary production can reach the seafloor (Valiela, 1984), providing food for key components of benthic food webs such as suspension feeders, deposit feeders, and sediment microbes. Much of global fisheries yield (roughly 33%, Pauly and Christensen, 1995) and a significant percentage of coastal ecosystem biomass, are composed of demersal or benthic species that utilize energy from this pelagic rain. The deposition of pelagic production (combined with riverine inputs of terrestrial production) cause continental shelf sediments to be major sites of organic matter mineralization and nutrient regeneration in the ocean (Jahnke and Jackson, 1992). The sinking of materials produced in the water column (e.g., downward bentho-pelagic coupling) also allows the shelf floor to accumulate phytoplankton biomarkers and to develop benthic communities that reflect production processes in the waters above. Thus, as a direct consequence of downward coupling, shelf sediments and their biotic communities can provide integrated views in space and time of ecosystem dynamics in the pelagic realm. Consequently, benthic studies may yield important insights into climate-driven changes in coastal pelagic ecosystems.

The vast Antarctic continental shelf, which encompasses roughly 11% of global shelf area (Clarke and Johnston, 2003), has several characteristics that might cause benthic-pelagic coupling to be weak compared to other regions (including the Arctic). The Antarctic shelf is unusually deep (500–1000 m) due to ice loading on the continent (Clarke and Johnston, 2003), and it is characterized by complex topography and ocean circulation (Hofmann and Klinck, 1998; Smith et al., 1999). These properties are expected to reduce the strength of benthic-pelagic coupling by increasing the sinking time and recycling of pelagic production in the water column, and by allowing local benthic habitat variability to obscure pelagic signals. However, other properties of Antarctic shelf ecosystems may enhance the relative importance of bentho-pelagic coupling. For example, summer–winter variations in sunlight, sea-ice cover, and water-column stratification produce extraordinary seasonality in pelagic primary production in Antarctica, yielding intense summer phytoplankton blooms that may yield mass settling of phytoplankton and high export ratios. The accumulation of high algal biomass within sea ice also may favor efficient transport of primary production to the seafloor because algae released from melting sea ice tend to aggregate and sink (Riebesell, 1991). In addition, pelagic food webs in Antarctic shelf waters can be relatively short, with diatom blooms being consumed by krill, which in turn produce fecal pellets that sink rapidly to the seafloor (Wefer et al., 1988; Bathmann et al., 1991). In fact, benthic biomass in Antarctic shelf waters can be very high (Gerdes et al., 1992; Arntz et al., 1994), suggesting efficient transfer of water-column production to the benthos. Because of these opposing factors, it is difficult to say a priori whether bentho-pelagic coupling on the Antarctic shelf should be stronger or weaker than in other regions.

To elucidate the nature of bentho-pelagic coupling on the Antarctic shelf, we will use the existing literature and a new meta-analysis to address six major questions.

1. Are water-column production signals rapidly transmitted to the seafloor?
2. Do benthic parameters (e.g., biomass and respiration) track regional variations in sea-ice cover and water-column production?
3. Do benthic processes vary in phase with seasonal primary production and flux?
4. How do benthic ecosystems respond to particular flux events or seasons?
(5) Are there examples of upward coupling (i.e., of seafloor processes influencing the ecology of the water column)?

(6) Will the patterns of benthic-pelagic coupling in the Antarctic be altered by climate change?

2. Question (1): Are water-column production signals rapidly transmitted to the shelf floor?

Clearly, downward bentho-pelagic coupling could be especially strong on the Antarctic shelf if the melting of sea ice and the intense, but often short-lived, summer phytoplankton blooms cause rapid export of particulate organic carbon (POC) to the shelf floor. Time-series sediment traps provide one means to assess the timing and intensity of POC flux from the water column; Sediment traps have been deployed extensively at depths $\geq$150 m, i.e. below the euphotic zone, on the open continental shelf of Antarctica. Major studies have focused on the western Antarctic Peninsula region (von Bodungen et al., 1986; Wefer et al., 1988; Karl and Tien, 1991; Karl et al., 1996, unpublished data; Palanques et al., 2002; Ducklow et al., 2006; Smith et al., in review), the Ross Sea (Dunbar et al., 1989, 1998; Nelson et al., 1996; Collier et al., 2000) and the Weddell Sea (Bathmann et al., 1991). All these studies document dramatic summer pulses of particulate-organic-matter flux to deep shelf waters and, by inference, to the shelf floor. Peak summer fluxes, when integrated over timescales of weeks, frequently exceed winter lows by 1–3 orders of magnitude, with summer flux patterns punctuated by brief events lasting a few weeks and varying in timing and intensity from year to year (Fig. 1). Thus, there is strong evidence that the Antarctic shelf benthos experiences a seasonal boom/bust cycle of POC flux resembling the boom/bust patterns of primary production and phytoplankton biomass in the water column (Smith and Sakshaug, 1990; Karl et al., 1996; Smith et al., 1996; Smith et al., 1998). It is important to note, however, that while POC flux and primary production on the Antarctic shelf share similar scales of temporal variability, flux pulses to the shelf floor frequently are not obviously coupled to local sea-ice disappearance or overlying phytoplankton blooms. For example, in 1990–1992, Dunbar et al. (1998) found maximum particle fluxes in the Ross Sea occurring from two to as many as 10 weeks after local surface waters became ice free, and Collier et al. (2000) found peak flux in 1997 occurring in late fall even after sea ice had returned (Fig. 2). This poor coupling between sea-ice disappearance, phytoplankton blooms, and flux events to the shelf floor should not be surprising because the factors controlling phytoplankton

Fig. 1. Particulate carbon flux at 150 m depth in the Palmer LTER study area on the western Antarctic Peninsula shelf showing extreme seasonal and interannual variability (D. Karl, unpublished data). Note that many of the flux pulses occur late in the summer season in February and March, i.e. 1–2 months after the disappearance of sea ice in waters overlying the trap.
blooms and export flux in the Antarctic are remarkably varied. Some of the processes that may decouple flux events from ice disappearance or from phytoplankton blooms include the following: (1) Wind-driven dispersal of sea ice prior to its melting (this prevents local release of ice algae, which tend to aggregate and sink (Riebesell et al., 1991)). (2) Spatial and temporal complexity in phytoplankton bloom dynamics and advective processes on local scales (1–100 km) (Smith and Sakshaug, 1990; Smith et al., 1996, 1998; Ditullio et al., 2000). (3) Variability in the occurrence, development, and die-off of nekton and zooplankton grazer assemblages (including krill, salps, and copepods) that can “pelletize” and cause sedimentation of phytoplankton blooms, or, alternatively, intensify water-column recycling (Leventer and Dunbar, 1987; Bathmann et al., 1991; Loeb et al., 1997; Dunbar et al., 1998; Atkinson, 1998; Collier et al., 2000; Zhou et al., 2004). (4) Wind-driven deep mixing, which can inhibit primary production early in the summer season (Dunbar et al., 1998; Ducklow et al., 2006) and cause abrupt bloom termination with mass phytoplankton deposition later in the summer (Gleitz et al., 1994). Thus, while we can conclude that intense pulses of POC flux are transmitted to the Antarctic shelf floor, these pulses are not always tied tightly (in space and time) to local sea-ice conditions or phytoplankton blooms overhead.

3. Question (2): Do benthic parameters (e.g., biomass and respiration) track regional variations in water-column processes, such as sea-ice cover and primary production?

Most of the Antarctic shelf floor is substantially deeper than the bottom of the euphotic zone.
et al. (1979) found the abundance of macrofauna prevented by the absence of sunlight, Bruchhausen seaward edge), where phytoplankton production is/C24 production. For example, under the center of the strong reflect regional patterns of phytoplankton benthic parameters on the Antarctic shelf do flux from the water column, such as the abyssal equatorial Pacific (Smith et al., 1997). Indeed, regional co-variance between phytoplankton production and benthic community parameters has been documented for other deep seafloor habitats that depend on detrital community structure of epibenthic megafauna at 55

At the extremes of water-column productivity, benthic parameters on the Antarctic shelf do strongly reflect regional patterns of phytoplankton production. For example, under the center of the ~400 m thick Ross Ice Shelf (475 km from its seaward edge), where phytoplankton production is prevented by the absence of sunlight, Bruchhausen et al. (1979) found the abundance of macrofauna and epibenthic megafauna to be extremely low relative to similar depths in the open Ross Sea where summer phytoplankton blooms occur. In addition, Bruchhausen et al. (1979) saw no bioturbation features in the muddy sediments beneath the ice shelf, indicating that the abundance and activity of infaunal megabenthos were also extremely low. Similarly, macrobenthic abundance on the oligotrophic west side of McMurdo Sound in the Ross Sea is an order of magnitude lower than on the eutrophic east side (Dayton and Oliver, 1977). Waters on the west side of the Sound flow northward from beneath the Ross Ice Shelf and have levels of plankton biomass and productivity only 10–50% of those in the eastern Sound, where waters flow southward from the relatively productive Ross Sea Polynya (Barry and Dayton, 1988).

With less extreme contrasts of ice duration and water-column productivity, regional correlations between water-column and shelf-floor processes become more difficult to detect, especially if the comparisons are made across divergent benthic habitat types. For example, as part of the Research on Ocean–Atmosphere Variability and Ecosystem Response in the Ross Sea (ROAVERRS) Project, Barry et al. (2003) studied the abundance and community structure of epibenthic megafauna at 55 stations at depths of 270–1173 m in the southwest Ross Sea and explored the strength of bentho-pelagic coupling. Their stations included a broad range of habitat types (crest, bank, slope and basin), current regimes, and sediment organic-carbon content. Barry et al. (2003) found that megabenthic abundance, diversity and faunal groupings were far more strongly associated with benthic habitat parameters than with water-column factors such as sea-ice duration or summer primary productivity (evaluated by CO2 drawdown in the water column), although they did find a weak association between primary productivity and the numbers of trophic groups and echinoderm classes. The habitat parameter “depth” and co-varying factors such as water flow explained the greatest amount of variance in the abundance of a variety of taxa and trophic groups, with a shift from suspension-feeding assemblages at shallower depths (e.g., crests and banks with higher flow) to deposit feeders at deeper stations (e.g., basins with lower flow). Barry et al. (2003) conclude that in their Ross Sea study region, the complex spatial distribution of banks and basins interacts with bottom currents to yield local zones of erosion and deposition, obscuring the footprint of regional primary productivity. These authors speculate that on temporal scales of years or greater, megafaunal secondary production in the Ross Sea may be coupled to primary production in the water column.

Similar control of megafaunal distributions by local habitat characteristics (e.g., current intensity, bottom relief, sediment type, depth, and iceberg scour), rather than by regional primary production patterns, has been inferred from photographic studies on the continental shelves of the Weddell and Bellingshausen-Amundsen Seas (Starmans et al., 1999; Gutt, 2000). Once again, a very broad range of habitat types was considered (including banks and troughs, zones of high and low flow, and soft and hard substrates), potentially masking water-column signals.

If the analysis of bentho-pelagic coupling is restricted to a single, depositional seafloor habitat type, in particular muddy sediments, do we see stronger correlations between pelagic processes (e.g., sea-ice duration or primary productivity) and benthic parameters? Consideration of bentho-pelagic coupling in muddy habitats is highly relevant because much (perhaps most) of the Antarctic shelf below a depth of ~200 m consists of silt-clay sediments (personal observations).
At least two sets of data allow us to address benthic pelagic coupling in muddy habitats on the Antarctic shelf. Grebmeier et al. (2003) tested the hypothesis that sediment oxygen consumption, pigment concentrations, and δ13C values can be used as long-term indicators of overlying primary production and sea-ice dynamics. As part of the ROAVERRS Project, their general study area was similar to that of Barry et al. (2003), encompassing a 400 × 600 km region of the southwest Ross Sea; however, because Grebmeier et al. (2003) worked only at sites where plexiglass cores could be inserted into sediments for oxygen consumption measurements, all their stations were dominated by silt-clay (or muddy) sediments. Over broad scales (50–100 km), Grebmeier et al. (2003) found sediment oxygen consumption and chlorophyll-a (chl-a) concentrations to be highest in regions where annual polynyas opened earliest (i.e. where sea-ice duration was shortest) and primary production was greatest. δ13C values in surface sediments were also highest beneath productive polynya waters; this pattern is expected with downward coupling because phytoplankton from areas of high productivity in the Ross Sea are typically enriched in 13C relative to 12C (Villinski et al., 2000). Furthermore, concentrations of characteristic pigments (fucoxanthin and hexanoyloxyfucoxanthin, respectively) in surface sediments matched the general pattern of diatom-dominated production in the western part of the study area and Phaeocystis dominance in the east. Thus, Grebmeier et al. (2003) demonstrate that benthic processes and sediment parameters on the muddy Ross Sea shelf reflect large-scale, multi-annual patterns of sea-ice cover and phytoplankton production in the water column.

A second data set allowing examination of benthic-pelagic coupling on regional scales on the muddy Antarctic shelf comes from Mühlenhardt-Siegel’s (1988) study of macrobenthic biomass in soft sediments from 62° to 67.5°S along the western Antarctic Peninsula. Because Antarctic macrobenthos, especially larger species that dominate biomass, appear to have generation times of years to decades (Arntz et al., 1994), we expect macrobenthic biomass to integrate patterns of sea-ice cover, primary production and export flux over time-scales of roughly 5–10 years. Mühlenhardt-Siegel (1988) evaluated macrofaunal biomass in 1985 and 1986, using box cores or Van Veen grabs, at 13 stations on the open WAP shelf between depths of 100–500 m (i.e. from just below the euphotic zone to the average shelf depth; Fig. 3, Table 1). To explore correlations between benthic biomass and primary productivity, we used Smith et al.’s (1998, Fig. 3) satellite-based estimates of net primary production in the WAP region for the period 1978–1986, i.e. for the 7–8 years preceding Mühlenhardt–Seigel’s sampling. Specifically, we compiled annual averages of the Smith et al. (1998) estimates of primary production along each of the Palmer Long-Term Ecological Research (LTER) grid lines (Fig. 3), and then used linear regression to derive a general equation predicting primary production as a function of distance along the WAP shelf (Fig. 4). We then used the regression equation to estimate regional annual primary production at the position of each of the stations sampled by Mühlenhardt-Siegel (1988) (Table 1).

When we compare the regional estimates of primary production to the log of macrobenthic biomass from Mühlenhardt-Siegel (1988), we find a highly significant regression relationship (Fig. 4).
Stepwise multiple regression analysis using productivity and depth as independent variables demonstrates that productivity explains the greatest percentage of variance in biomass (52%, Fig. 4), and that the addition of depth does not significantly improve the regression relationship ($p > 0.40$). We interpret the significant relationship between primary productivity and biomass to mean that macrobenthic biomass on the muddy western Antarctic Peninsula shelf is controlled to a substantial degree by regional primary productivity in the water column. It is noteworthy that the regression relationship implies that a $\frac{1}{3}$-fold increase in regional primary production leads to a $\frac{1}{10}$-fold increase in macrobenthic biomass. We speculate that this greater rate of increase in benthic biomass may be driven by a strong positive relationship between regional production and export ratio (i.e. the proportion of primary production exported to the shelf floor) over the range of production levels studied here (49–123 g C m$^{-2}$ yr$^{-1}$), as suggested by empirical (Lampitt and Antia, 1997) and modeling studies (e.g., Laws, 2004). Overall, we suspect that the regional imprint of water-column production on macrobenthic biomass on the muddy WAP shelf is actually stronger than indicated in our meta-analysis because the Mühlenhardt-Siegel (1988) and Smith et al. (1998) studies were not designed to resolve the effects of benthic-pelagic coupling.

Based on the results of Grebmeier et al. (2003) and our meta-analysis of the Mühlenhardt-Siegel (1988) data, we conclude that a number of benthic biological parameters in muddy Antarctic shelf habitats are likely to reflect regional patterns of water-column primary production. These benthic parameters are also very likely to be correlated with processes that control mean levels of regional primary production, such as annual sea-ice duration.

4. Question (3): Do major benthic processes vary in phase with seasonal primary production and POC flux?

As discussed earlier, Antarctic shelf ecosystems experience extraordinary seasonal variability, with phytoplankton production and export flux potentially changing by orders of magnitude between summer and winter (Figs. 1 and 2). Because of the intense seasonal variability in POC flux and phytoplankton availability in the water column, it was initially expected that many benthic processes would vary in phase with the pelagic production cycle. Data now exist to explore seasonal variability in a number benthic processes on the Antarctic shelf, including sediment-community oxygen consumption, suspension feeding, deposit feeding, life histories, reproduction, and benthic recruitment from the water column.

4.1. Sediment oxygen consumption

Three studies have examined seasonal patterns of sediment-community oxygen consumption on the
Antarctic shelf and all three exhibit weak seasonality compared to the pelagic production regime. At 8–9 m depths at Signy Island, Nedwell et al. (1993) found that while particulate-organic-matter flux varied ~80-fold from summer to winter, sediment community oxygen consumption varied 5-fold or less. In addition, sediment-oxygen consumption was only weakly coupled to organic-matter flux, and exhibited much stronger inter-annual than seasonal variability (Fig. 5). At 160 m in Port Foster (Deception Island), Baldwin and Smith (2003) found similarly modest seasonal variability (2.7-fold) in sediment-community oxygen consumption (sediment trap failures prevented a direct comparison with POC flux in this study). Finally, in our FOODBANCS (FOOD for Benthos on the ANt-Arctic Continental Shelf) study at 500–600 m on the western Antarctic Peninsula shelf near Anvers Island (discussed in more detail below), we found no significant seasonal difference in sediment oxygen consumption for 1999–2000, even though immediately overlying sediment traps recorded a ~4-fold seasonal difference in POC flux when averaged over 3-month intervals (Smith et al., in review). Thus, it appears that sediment-community oxygen consumption on the Antarctic shelf shows substantially less seasonal variability than primary production in the water column, and sediment oxygen consumption does not necessarily vary in phase with seasonal POC flux. In particular, the dampened response of sediment oxygen consumption to seasonal POC flux suggests that sediment community respiration on the Antarctic shelf has substantial “inertia”.

4.2. Suspension feeding

Because of the extreme summer/winter contrasts in primary production and chlorophyll concentrations in the water column, the traditional view has been that benthic suspension feeders on the Antarctic shelf should be extremely resource limited during the winter (Clarke, 1988; Barnes and Clarke, 1995). In particular, it was expected that suspension feeders would experience long periods of starvation, and cease feeding (e.g., “hibernate”) beneath winter sea ice (Clarke, 1988; Barnes and Clarke, 1995). Barnes and Clarke (1995) conducted the first intensive seasonal study of a broad range of suspension feeders in the Antarctic and found that winter conditions (i.e. sea-ice cover and low water-column chlorophyll concentrations) persisted for about 6 months at their Signy Island sites (2–45 m water depths). Nonetheless, many species continued to suspension feed for all but 2–3 months in midwinter, and at least one species (a bryozoan) fed throughout the year (Fig. 6). Barnes and Clarke (1995) suggest that many of these suspension feeders may consume low concentrations of nanoplankton during much of the winter, freeing them from complete reliance on the summer bloom. They suggest that the Antarctic winter may not be as harsh for many Antarctic benthos as once believed.

Orejas et al. (2000, 2003) built on the work of Barnes and Clarke (1995) and suggested that there may be two end-member suspension feeding adaptive patterns in the Antarctic. A “fast” (or seasonal)
feeding pattern may focus on the large phytoplankton of the summer bloom, with feeding and metabolic adaptations to ingest at high rates, and to rapidly accumulate biomass and energy reserves during summer months. Species with this “fast” pattern, which appear to include some gorgonians (e.g., *Tubularia ralphii*), encrusting bryozoans, and suspension-feeding holothurians, would then cease feeding for extended periods during the Antarctic winter (Orejas et al., 2000). An alternative “slow” (or continuous) suspension-feeding adaptive pattern may focus on smaller microplankton and resuspended sediment particles, with adaptations to feed and meet low metabolic costs at very low food concentrations throughout most (or all) of the Antarctic winter (Orejas et al., 2000). Species with the “slow” pattern may not have the metabolic potential to exploit the very high concentrations of macrophytoplankton during summer blooms. Orejas et al. (2003) demonstrate that two species of Antarctic octocorals can indeed feed on low concentrations of microplankton (e.g., ciliates, dinoflagellates, and other small phytoplankton) and on fine particles resuspended from the seafloor in a manner consistent with the “slow” pattern. They also postulate that the resuspension of

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**Fig. 5.** (A) Flux of particulate organic matter into sediment traps (open circles), and sediment-community oxygen consumption (closed circles), over time at 8–9 m depth near Signy Island. (B) Sediment organic-matter content at the same station. Open circles indicate the 0–0.5 cm depth layer, and closed symbols indicate the 1–2 cm depth layer. Panels (A) and (B) modified from Nedwell et al., (1993).
phytodetritus deposited during summer months may contribute substantially to food availability for suspension feeders over the winter (Orejas et al., 2003). In summary, it appears that the feeding of benthic suspension feeders may be strongly or weakly coupled to summer phytoplankton blooms on the Antarctic shelf, depending on divergent suspension-feeding and metabolic adaptations.

### 4.3. Deposit feeding

Relatively few studies are available from the Antarctic shelf to evaluate seasonality in deposit feeding. The most extensive data come from studies of the sea urchin *Sterechinus neumayeri* at Adelaide Island at 67.5°S along the Western Antarctic Peninsula (Brockington et al., 2001; Brockington and Peck, 2001). At study sites ranging in depth from 6 to 30 m, Brockington et al. (2001) found that *S. neumayeri* ceased egesting sediments, and had empty guts, for 4–5 winter months when water-column chlorophyll concentrations were extremely low. Chlorophyll concentrations in surface sediments (0–5 mm) also declined substantially during winter months (although total sediment organic content in this layer showed little seasonal variation). Metabolic rates and body-tissue (especially gut-tissue) mass in *S. neumayeri* declined during the non-feeding period, indicating that the winter was a time of starvation.

Brockington et al.’s (2001) results contrast substantially with our seasonal studies of deposit feeding on the western Antarctic Peninsula shelf during the FOODBANCS (FOOD for Benthos on the ANtarctic Continental Shelf) project. At 500–600 m depths near Anvers Island (64°S), Galley (2003 and Galley et al., 2005) found no evidence of winter cessation of feeding, or decline in energy reserves in gut and other tissues, for the deposit feeding echinoids *Sterechinus antarcticus* and *Amphipneustes lorioli*, or for the holothurian *Protelpidia murrayi*. The holothurian *Peniagone* cf. *Vignioni* also appeared to feed throughout the winter, although the gut tissue did exhibit a slight but significant seasonal variation in protein and lipid composition (Galley, 2003). DeMaster et al. (submitted) found similar evidence of winter deposit feeding during the FOODBANCS study on the western Antarctic Peninsula shelf, with four species of surface deposit feeders and two subsurface deposit feeders containing recently deposited sediment in their guts during all seasons sampled.
Excess $^{234}$Th activity, which has a 24-day half-life and is used as a tracer for sediments with high food value (Lauerman et al., 1997; Miller et al., 2000; Demopoulos et al., 2003), remained relatively high in the guts of many of the deposit feeders even in winter (i.e., June and October, see Fig. 7). In addition, $^{14}$C measurements of gut sediments indicated the consumption of relatively young, labile organic carbon throughout the year Purinton et al., accepted. Finally, $\delta^{13}$C and $\delta^{15}$N measurements suggested incorporation of fresh phytodetritus, as well as microbially reworked sedimentary organic matter, into deposit-feeder tissues year round (Mincks et al., accepted). Thus, a broad suite of deposit feeders on the western Antarctic Peninsula shelf at 500–600 m depths exhibit strong evidence of (1) feeding throughout the year, and (2) ingesting high-quality material even in winter. One potentially important difference between the FOODBANCS and Brockington et al. (2001) study sites may be related to hydrodynamic regime; based on 15 months of time-lapse photography, the muddy FOODBANCS sites have low flow velocities with little evidence of sediment resuspension Smith et al., in review, whereas Brockington et al.’s (2001) sites appear to be characterized by hard bottoms or coarser sediments and more energetic flow regimes. Thus, summer-bloom phytodetritus may accumulate and provide a sediment “food bank” during much of the year at our FOODBANCS sites, while summer bloom material may be advected into deeper waters from Brockington et al.’s (2001) relatively shallow (6–30 m) sites.

### 4.4. Life histories and reproduction

Patterns of reproduction and life history have been moderately studied, and widely discussed, for Antarctic macro- and megabenthos, especially for echinoderms and gastropods (Bosch and Pearse, 1990; Pearse, 1994; Clarke, 1996; Poulin and Feral, 1996; Galley, 2003; Galley et al., 2005). Two general patterns have emerged. (1) Direct and lecithotrophic development modes are overwhelmingly dominant, with planktotrophy relatively rare compared to lower latitudes (Clarke, 1996; Poulin and Feral, 1996; Galley, 2003). For example, the combined data of Poulin and Feral (1996) and Galley (2003) suggest that 43/61 (or 70%) of echinoids with known developmental modes are brooders in Antarctica versus only 28% in Monterey Bay, California (Clarke, 1996). Benthos with direct development feed at the seafloor throughout their life cycle, and the larvae of lecithotrophs are generally assumed to obtain all or most of their nutrition from energy reserves provided with the egg by a benthic mother (but see Jaeckle and Manahan, 1989, and Manahan, 1990 for exceptions). (2) While many Antarctic benthos may spawn during the summer season, many others (including species with planktotrophic larvae) do not, leading to larval presence in the water column throughout the year.
Thus, most Antarctic macro- and megabenthos studied have developmental types (direct and lecithotrophic) that rely directly on benthic energy resources and might be considered, at best, to be only indirectly coupled to the water column and its summer bloom. In addition, many species that do exploit water-column resources (i.e. those with planktotrophic larvae) produce larvae that remain in the water column at times removed from the summer bloom. This pattern suggests that the reproduction and life histories of many Antarctic benthos are not necessarily tightly coupled to, or in phase with, the summer phytoplankton bloom.

4.5. Benthic recruitment

Although the data are very sparse, recruitment of benthos with pelagic larvae also may be only weakly coupled to the summer phytoplankton blooms on the Antarctic shelf. For example, Stanwell-Smith and Barnes (1997) conducted settling-plate studies for 21 months at 5-25 m depths at Signy Island and concluded that the dominant settling taxa (bryozoans and spirorbid polychaetes) recruited essentially continuously at low rates throughout the year. Similarly, McClintock et al. (1988) concluded that the common asteroid *Odontaster validus* recruits year round. Most recently, Bowden (2005) conducted the first detailed study of recruitment of benthos within the Antarctic Circle (67.5°S, Adelaide Island). He found a total of 39 taxa from nine phyla settling onto his plates, with dominance by bryozoans and spirorbid polychaetes. Most species settled throughout the year, but with a clear seasonal pattern. Perhaps unexpectedly, the peak in the number of recruiting taxa occurred in late winter, indicating decoupling of recruitment from the summer phytoplankton bloom. Furthermore, recruitment of Antarctic benthos in Bowden's study exhibited less seasonality than for similar communities in temperate latitudes, where the general pattern is one of summer recruitment.

In summary, most benthic ecological processes on the Antarctic shelf were initially expected to vary in phase (or in “lock-step”) with the extraordinarily seasonal boom/bust cycle of production in the water column. In fact, many processes, including sediment-community oxygen consumption, suspension and deposit feeding, reproduction, larval development, and recruitment, often appear to be poorly coupled to the summer phytoplankton bloom. Why might this be the case? The best insights are likely to be obtained from integrative, time-series studies of benthic ecosystem response to seasonal and inter-annual variations in water-column production and export flux. In the next section we discuss results from the few integrative time-series studies available for the Antarctic shelf.

5. Question (4): How do benthic ecosystems respond to particular flux events or seasons?

Several benthic case studies provide time-series measurements of multiple ecosystem parameters across seasons and years on the Antarctic shelf. We will focus on our FOODBANCS (FOOD for Benthos on the ANtarctic Continental Shelf) program, in which a broad range of parameters were studied over a 15-month period at three stations along a transect across the western Antarctic Peninsula shelf south of Anvers Island (Fig. 8). These stations were chosen to be representative of broad areas of the mud-covered Antarctic shelf at its typical depth of 500–600 m.

Sediment traps deployed ∼150 m above the seafloor at FOODBANCS Station B indicated strong seasonal, and even stronger inter-annual, variability in chl-a and POC flux to the western Antarctic Peninsula shelf floor (Fig. 9). In particular, chl-a and POC flux (averaged over the 3–4 month intervals of trap deployments) varied 3–4 fold from summer to winter in 2000, and 4–11 fold between the summers of 2000 and 2001 (Fig. 9; Smith et al., in review). Time-series photographs of the seafloor at Station B indicated that the very high flux period during summer of 2001 was characterized by pulsed accumulation of greenish phytodetrus on the seafloor (Fig. 9). Nonetheless, benthic response to this seasonal and inter-annual variability in flux was relatively muted. For example, sediment inventories of chl-a varied only 3-fold between summers (Fig. 10), versus an 11-fold inter-annual difference in trap chl-a flux. Other labile organic components of the sediment, in particular enzymatically hydrolysable amino acids (EHAA), also remained high and relatively constant at all our sampling times (Mincks et al., 2005), and surface deposit feeders were able to ingest young, apparently labile organic matter throughout the year (Purinton et al., accepted; DeMaster et al., submitted). In addition, sediment-community oxygen
consumption at Stations A through C varied roughly 2 to 3-fold between any of our five sampling times while POC flux varied up to 12-fold. (Hartnett et al., in revision; Thomas et al., submitted). Finally, sediment microbial biomass and macrofaunal abundance remained high and relatively constant across all our sampling times (Mincks et al., 2005; Smith et al., in review). We conclude that despite highly pulsed POC flux in summer months, labile organic matter accumulates in western Antarctic Peninsula sediments to yield a predictable “food bank” for detritivores during low-productivity winter periods. Stable isotopic analyses suggest that some of this food-bank material may be passing through a sediment microbial loop, with microbial processing enhancing the food quality (e.g., organic-nitrogen content) for detritivores (cf. Lovvorn et al., 2005; Mincks et al., accepted). As a consequence of this sediment food bank, many benthic processes, including sediment-community oxygen consumption, deposit feeding, and even bioturbation intensity (McClintic, 2002), exhibit substantial “inertia” on the western Antarctic Peninsula shelf, varying modestly across seasons.

Given a large, metabolically active microbial community in sediments at our FOODBANCS study sites (as indicated by high microbial biomass and sediment respiration), why do pools of labile organic matter, such as chl-α and EAA, persist at high concentrations? We have hypothesized that high organic-matter concentrations persist because at very low temperatures typical of the Antarctic shelf, microbial communities require higher substrate concentrations to sustain a particular level of heterotrophic activity (see Mincks et al., 2005, for development of the hypothesis). This may result, in part, from low temperatures causing reduced substrate affinities in extracellular enzymes (Nedwell, 1999; Yager and Deming, 1999; Arnosti and Jorgensen, 2003). Such temperature induced substrate limitation may then cause labile organic matter to build up in sediments to relatively high levels before microbial community respiration rates can balance the sinking flux of labile POC to the seafloor (Mincks et al., 2005).

Similar muted response by benthic ecosystems to pulsed POC flux has been seen in other Antarctic shelf locations. As mentioned previously, at 9 m depth at Signy Island, Nedwell et al. (1993) found that monthly POC flux to the seafloor varied roughly 80-fold between summer and winter, while sediment community oxygen varied less than 6-fold over the same period (Fig. 5). Particulate organic matter concentrations in the top 5 mm of sediment varied even less, changing by a factor of 2 between seasons and years (Nedwell et al., 1993). In another example, Baldwin and Smith (2003) found that, at 160 m depths inside the Deception Island caldera, seafloor POC flux could vary seasonally on the order of 10-fold, while sediment-community oxygen consumption varied seasonally less than 2-fold during the year studied. Finally, Isla et al. (2006) document the presence of a large, persistent pool of labile organic matter in sediments at 200–400 m on

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Fig. 8. Map of the Antarctic Peninsula region showing the locations of the primary FOODBANCS Project stations A, B and C. The sediment trap and time-lapse camera moorings were located near station B.
the Weddell shelf, and postulate that this provides food of high nutritional value to detritivores during winter months.

We conclude that benthic ecosystem response to summer flux pulses on the Antarctic shelf has substantial inertia, in part due to the presence of a sediment food bank. As a consequence, many benthic ecosystem parameters influenced by the availability of labile organic matter, e.g., respiration rates, levels of biomass, and rates of deposit feeding and bioturbation, may be buffered from the intense seasonal variability in production occurring in the water column. These parameters are likely to act as “low-pass filters,” primarily recording longer-term (i.e. inter-annual) trends in water-column production processes as influenced, for example, by climate-driven changes in sea-ice cover (Jacobs and Comiso, 1997; Smith et al., 2001).

Fig. 9. (A) Particulate organic carbon flux into sediment traps moored 150–170 m above the seafloor at FOODBANCS Station B. Means ± 1 s.e. are given. (B) Chl-a flux into the FOODBANCS sediment traps (left Y-axis) and phytodetritus “score” (right Y-axis) from time-lapse seafloor photographs versus time after initial camera deployment on 8 December 1999. Phytodetritus scores are as follows: 1 = no visible greenish phytodetritus on seafloor, 2 = light dusting of phytodetritus visible, 2 = moderate to heavy cover of phytodetritus over 50–80% of the seafloor, 3 = heavy phytodetritus cover over >80% of the seafloor. Data from Mincks et al. (2005) and Smith et al. (in review).
6. Question (5): Are there examples of upward coupling (i.e. of seafloor processes influencing the water column)?

Because of the great depth of the Antarctic continental shelf (typically $\geq 500$ m), one might expect upward bentho-pelagic coupling to be relatively weak. Nonetheless, there are some important examples of upward coupling.

As a consequence of energetic bottom currents, complex topography, and weak density gradients, it seems quite feasible that micronutrients regenerated at the shelf floor could be mixed up into the euphotic zone. For example, sediments in the Ross Sea may be routinely resuspended to $>100$ m into the water column (Collier et al., 2000). Further, Sedwick et al. (2000) argue that phytoplankton production in the Ross Sea is iron-limited, and that the upwelling of iron-enriched waters from the seafloor enhances phytoplankton production, especially that of *Phaeocystis*. Regeneration of micronutrients from the seafloor is likely to be facilitated by the frequent occurrence of a poorly stratified water column, allowing enhanced vertical mixing (Barry, 1988; Sedwick et al., 2000). Thus, phytoplankton production in the Ross Sea and other Antarctic regions may be substantially influenced by micronutrient regeneration (especially of iron) in shelf sediments.

Other examples of upward coupling include pelagic or bentho-pelagic predators exploiting benthic prey. For example, Arntz et al. (1994) reviewed data suggesting that gentoo penguins and cormorants obtain 26% and 19%, respectively, of their food resources from benthic amphipods. In addition, Weddell and elephant seals feed on benthic octopus, and nototheniid and bathydraconid fish consume benthic amphipods, polychaetes, ophiuroids and isopods (Arntz et al., 1994). Furthermore, Gutt (2000) describes an upward trophic link mediated by krill that feed at the seafloor and then are consumed by pelagic fish or mammals.

We conclude that, despite an unusually deep shelf, there is significant evidence of upward bentho-pelagic coupling in Antarctica. We suspect that exploitation of benthic prey by pelagic predators may be especially important on the Antarctic shelf during ice-covered winter months, when water-column production is very low. The importance of upward bentho-pelagic coupling, and its variation as a function of season and sea-ice cover, clearly merits substantial further study on the Antarctic shelf.

7. Question (6): Will patterns of bentho-pelagic coupling on the shelf be affected by climate change (e.g., by warming of the Antarctic Peninsula)?

There is strong evidence on the Antarctic shelf that the amount of annual primary production, as well as the nature of water-column grazing and particle export, is heavily influenced by the annual extent and duration of sea-ice cover (Smith and Sakshaug, 1990; Loeb et al., 1997; Smith et al., 1998, 2001; Clarke and Harris, 2003). Climate warming, in turn, has yielded significant reductions in sea-ice cover along the Antarctic Peninsula (Jacobs and Comiso, 1997; Smith et al., 2001), and there is reason to believe that this warming and
sea-ice reduction will continue (IPCC, 2001). Because benthic biomass on regional scales is correlated with water-column production, it is hard to imagine that climate-induced changes in sea-ice duration and primary production would not alter benthic-pelagic coupling, and in turn the structure and dynamics of benthic communities. Conceivable warming-induced changes in benthic-pelagic coupling driven by shorter sea-ice duration include the following: (1) a community shift among suspension-feeder to favor species with the “fast” (or seasonal) feeding pattern (Orejas et al., 2003) as the summer bloom season becomes longer; (2) a shift in benthic recruitment patterns to more closely resemble those of the temperature zone, specifically with stronger summer peaks in recruitment (cf. Bowden, 2005); and (3) a decrease in the importance of benthic prey to pelagic predators as the water column remains highly productive for a greater portion of the year. Nonetheless, the specific effects of climate change on coupling are extremely difficult to predict because they will be influenced not only by changes in primary production, but also by poorly constrained changes in the structure of the pelagic food web and the intensity of water-column recycling (Loeb et al., 1997; Ducklow et al., 2006). Sufficient to say that changes in pelagic ecosystem structure, in particular those modulated by long-term trends in sea-ice cover (for example, a shift from krill- to salp-dominated grazer assemblages; Loeb et al., 1997), will undoubtedly influence the benthos. In fact, we suggest that because many benthic processes act as “low-pass filters” in the face of high-frequency (i.e. seasonal) oscillations in export flux, benthic parameters such as biomass in various size classes of benthos, and labile organic-matter inventories in sediments, may be especially useful indicators of long-term trends in ecosystem dynamics in the water column over the Antarctic shelf (cf. Grebmeier and Barry, 1991; Hannides and Smith, 2003).

8. Conclusions

As expected in the highly seasonal Antarctic pelagic ecosystem, large summer pulses dominate POC flux to the Antarctic shelf floor. However, on local scales, these seafloor pulses often are offset in time and space from overlying plankton blooms as a consequence of the complex suite of processes controlling export flux.

Over regional scales (~100 km) and across all benthic habitat types (from rocky crests to sedimented basins), patterns of water-column primary production are only weakly imprinted on the shelf floor. However, in the muddy habitats that abound on the deep shelf, a variety of benthic parameters, including sediment oxygen consumption, sediment pigment concentrations, and macrofaunal biomass, can be correlated with large-scale spatial patterns of water-column production and sea-ice cover. At present, these regional correlations are based only on two studies in which benthic parameters and water-column production were measured over the same time interval. Clearly, if we wish to understand the processes driving regional patterns of production, biomass and biogeochemical cycling on the Antarctic shelf floor, additional regional studies of benthic-pelagic coupling are needed.

In contrast to initial expectations, many benthic processes and parameters, including sediment respiration, deposit feeding, reproduction, recruitment to hard substrata, and biomass levels, often do not vary in phase with seasonal patterns of water-column production. In fact, much of the soft-bottom benthic ecosystem is characterized by substantial “inertia,” in part due to the accumulation of a sediment food bank that extends the availability of labile organic material beyond the summer months (Mincks et al., 2005; Isla et al., 2006). Because of this inertia, many benthic processes may act as low-pass filters, removing seasonal “noise” and responding to longer-period, inter-annual trends in the flux of organic matter to the seafloor. Thus, a number of benthic ecosystem parameters, in particular biomass levels and inventories of labile organic matter, potentially could provide useful indicators of long-term trends in export production and pelagic ecosystem function on the Antarctic shelf.

Major regions of the Antarctic shelf appear to be undergoing rapid climate change; in particular, the Antarctic Peninsula has sustained substantial warming in the past few decades (Smith et al., 2003; Clarke and Harris, 2003). Such climate change will clearly alter pelagic ecosystems (e.g., by reducing the prevalence of sea ice) and in turn change benthic ecosystems through benthic-pelagic coupling. However, these climate-induced changes are extraordinarily difficult to predict because we have limited understanding of benthic ecosystem response to the normal, often intense, inter-annual variability in primary production and carbon flux typical of the Antarctic shelf; i.e. we know little of shelf community resistance and resilience in the face of natural
perturbations. The presence of a substantial food bank in Antarctic shelf sediments (Mincks et al., 2005) is likely to confer relatively high resistance in benthic foodwebs to short-term variations in primary production and export flux. However, the resilience of Antarctic shelf ecosystems in the face of climate warming (i.e. their speed of recovery once substantially perturbed by climate change) could be very low, especially if warming reduces the size of the benthic food bank by raising bottom water temperatures (Mincks et al., 2005) or by increasing the efficiency of water-column recycling.

Climate varies substantially with latitude along the Antarctic shelf, offering exciting opportunities to explore the effects of climate change on bentho-pelagic coupling and benthic ecosystem function. For example, annual sea-ice duration ranges from roughly 2–3 months at 64°S to ~10 months at 69°S along the western Antarctic Peninsula (Jacobs and Comiso, 1997). Well-designed studies of benthic ecosystem responses to both (1) inter-annual variability in export flux, and (2) latitudinal gradients in pelagic ecosystem function are urgently needed to elucidate the impending effects of climate change on bentho-pelagic coupling in the Antarctic.

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