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PELAGIC-BENTHIC COUPLING, FOOD BANKS, AND CLIMATE CHANGE
ON THE WEST ANTARCTIC PENINSULA SHELF

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"Solid-Phase Oceanography": FOODBANCS scientists and support personnel collect core samples in heavy sea ice on the West Antarctic Peninsula shelf in winter. *Photo by C. Smith*

ABSTRACT. The West Antarctic Peninsula (WAP) shelf is deep and detritus-based (i.e., it is fueled by organic material sinking from intense seasonal cycles of primary production in the water column), leading to pelagic-benthic coupling. The WAP is warming rapidly, yielding increases in seawater temperatures and reductions in sea ice that may fundamentally alter pelagic-benthic coupling and shelf benthic ecosystems. RVIB *Nathaniel B. Palmer* and ARSV *Laurence M. Gould* have provided year-round access to the WAP sea ice zone, facilitating studies of pelagic-benthic coupling and climate change. In the Food for Benthos along the Antarctic Continental Shelf (FOODBANCS) Project, we conducted a 15-month field program to evaluate benthic ecosystem function across the mid-WAP shelf, testing the hypothesis that "phytodetrital material deposited from the summer bloom provides a sustained source of food for benthic detritivores during winter months, when organic-matter flux from the water column is extremely low." We found that the intense seasonality in primary production and food availability in the WAP water column is heavily dampened at the shelf floor by the presence of a "food bank" that sustains benthic ecosystem functions (including sediment-community respiration, deposit feeding, vitellogenesis, spawning, and recruitment of benthos) over the winter; this food bank also influences community structure and life-history strategies of the WAP benthos. The persistence of the food bank may be mediated by low bottom-water temperatures, with the consequence that climate warming might reduce food availability in shelf communities. During the FOODBANCS2 Project, we studied the benthic ecosystem response to the strong latitudinal sea ice gradient along the WAP to explore the ecosystem consequences of sea ice loss from climate change. We found that some aspects of benthic ecosystem structure (e.g., macrofaunal dominance by the polychaete *Aurospio foodbancsia*) covaried with sea ice duration and are likely to be sensitive to sea ice loss. Other benthic parameters (e.g., the standing crop of macro- and megabenthos) exhibited nonlinear responses, with evidence of resilience along much of the sea ice gradient and abrupt change near one end. Still other benthic parameters (e.g., sediment community respiration) changed very little with sea ice duration. We also found that climate warming is facilitating invasion of the WAP shelf by predacious king crabs, with dramatic reduction in benthic biodiversity and altered ecosystem function. In summary, some important benthic ecosystem parameters along the WAP may be resilient to climate-induced changes in pelagic-benthic coupling, while many others may be highly sensitive, responding nonlinearly to sea ice loss. Incorporation of climate change effects into WAP benthic ecosystem models, including the effects of invasive species, will be challenging until mechanisms, nonlinearities, synergies, and tipping points of climate change effects are better understood.

INTRODUCTION

The marine ecosystems of the sea ice zone along the West Antarctic Peninsula (WAP) harbor unusual biodiversity and evolutionary novelty resulting from extreme environmental conditions and millions of years of oceanographic isolation (e.g., Ducklow et al., 2007). Pelagic ecosystem function along the WAP is also remarkable. Here, intense production cycles modulated by extreme seasonal variations in sea ice and light sustain short food webs (e.g., diatoms to krill to birds/mammals; R. Smith et al., 1996; Ducklow et al., 2007). The WAP pelagic ecosystem overlies a large, sediment-covered continental shelf ~ 200 km in width and extending along > 8° of latitude (Figure 1). The water column over the shelf is unusually deep (~ 500 m) due to glacial carving and ice loading on the Antarctic Continent. Consequently, seafloor ecosystems of the WAP shelf are well below the euphotic zone and sustain no in situ primary production. The shelf benthic communities rely on the supply of sinking particulate organic carbon (POC) produced by phytoplankton and sea ice algae in the waters above, through a set of processes known as pelagic-benthic coupling.

The climate of the Antarctic Peninsula is changing profoundly (Ding et al., 2011), with WAP marine ecosystems warming as rapidly as anywhere on Earth. Over the past 50 years, mean winter air temperatures have risen by 6°C (Ducklow et al., 2007) and sea-surface
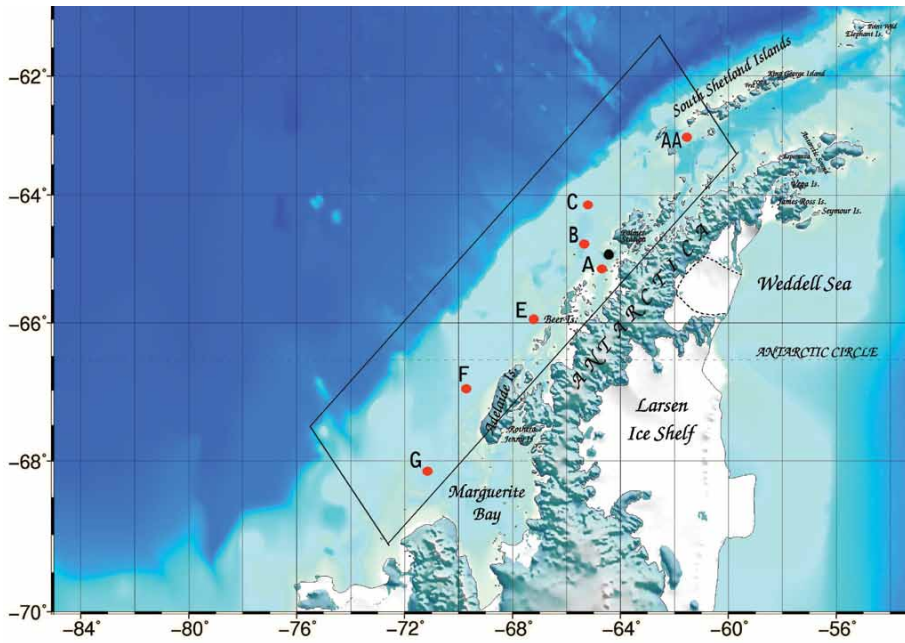
Figure 1. The Antarctic Peninsula region, showing the transect across the West Antarctic Peninsula (WAP) shelf studied during the Food for Benthos along the Antarctic Continental Shelf (FOODBANCS) Project (Stations A, B, and C), the latitudinal transect studied during the FOODBANCS2 Project (Stations AA, B, E, F, and G), and the location of Palmer Deep (black dot). The box outlines the Palmer Long Term Ecosystem Research (PAL-LTER) study area. Depth shading grades from < 500 m (lightest) to > 4,000 m (darkest).

temperatures have risen more than 1°C along the WAP (Meredith and King, 2005). This regional warming has been linked to declines in annual sea ice extent by ~ 15% per decade since 1978 (Ducklow et al., 2007), and to the retreat of 87% of WAP tidewater glaciers over the last ~ 50 years (Cook et al., 2005). Such warming also has the potential to fundamentally change pelagic-benthic coupling and, in turn, the structure and function of WAP shelf benthic ecosystems.

Despite the apparent importance of pelagic-benthic coupling and rapid climate change along the WAP, the relative inaccessibility of the region has caused benthic ecosystem structure and function on the open shelf to be very poorly studied into the 1990s. This was in spite of the fact that the width of the WAP shelf, combined with its long north-south extent (> 800 km), provides unusual opportunities around the Antarctic Continent to study pelagic-benthic coupling across and along a strong latitudinal climate gradient. The greater access to the WAP region

provided by the ice-reinforced ARSV *Laurence M. Gould* and the icebreaker RVIB *Nathaniel B. Palmer* beginning in the 1990s has allowed oceanographers to conduct intensive ecological and biogeochemical studies of WAP shelf benthic ecosystems.

THE FOODBANCS PROJECT

In 1998, the Food for Benthos along the Antarctic Continental Shelf (FOODBANCS) project was initiated to evaluate the nature of pelagic-benthic coupling across the mid-WAP shelf (C. Smith and DeMaster, 2008a). At that time, it was well documented that primary production in Antarctic coastal waters followed a highly seasonal boom/bust cycle. Phytoplankton production and food availability in the water column were extremely low during the ice-covered, light-limited winter months, while phytoplankton blooms initiated by sea ice melt and long days yielded very food-rich conditions in the water column during summer (e.g., Holm-Hansen, 1985; R. Smith et al., 1995, 1996; Ducklow et al., 2007). Pelagic time-series studies along the WAP, as part of the Palmer Long Term Ecosystem Research (PAL-LTER) Program, had also established that this seasonality in water-column production yielded enormous variations in POC export from the euphotic zone, causing intense pulses of export in November through March (e.g., Ducklow et al., 2008; Buesseler et al., 2010). Summer POC fluxes into the 150 m deep PAL-LTER sediment traps were among the highest ever measured in the world ocean, whereas winter POC fluxes were among the lowest (e.g., Ducklow et al., 2008).

In addition, it was surmised that many

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benthic ecosystem parameters on the WAP shelf would vary in phase with the extraordinary boom/bust cycle of production and export in the water column. In particular, summer pulses of POC flux were expected to yield strong seasonality in sediment community respiration, microbial biomass, feeding rates of detritivores, and faunal reproduction and recruitment on the deep WAP shelf, as had been observed in the WAP water column and in shallow, hard-substrate benthic systems around Antarctica (for reviews, see Clarke, 1985; Dayton, 1990; Arntz et al., 1994; Arntz and Gili, 2001; C. Smith et al., 2006; C. Smith and DeMaster, 2008b).

Nonetheless, prior to FOODBANCS, the seafloor flux of phytoplankton bloom material, and its influence on the ecology and biogeochemistry of WAP shelf benthic ecosystems, had not been evaluated. FOODBANCS researchers hypothesized that, while POC flux to the WAP shelf floor is highly seasonal, the availability of labile POC (or "food") would be much more persistent at the shelf floor than in the water column. We postulated this because blooms in the Antarctic disappear rapidly due to cell sinking and zooplankton grazing, leaving a food-poor water column after four to eight weeks (e.g., Ducklow et al., 2008). However,

sinking phytodetritus and zooplankton fecal pellets seemed likely to accumulate on the quiescent, soft sediments of the deep shelf where they might provide a rich "food bank" of detritus over much longer periods than in the water column.

Thus, the FOODBANCS Project was designed to address the following key hypothesis: *Sea ice retreat and intense summer phytoplankton blooms yield substantial summer deposition of algal detritus onto the WAP shelf floor; deposited bloom material then provides a sustained source of labile POC (i.e., a "food bank") for benthic detritivores during winter months.*

To test this hypothesis, FOODBANCS scientists conducted an intensive field program to evaluate a broad range of benthic ecological and biogeochemical processes. Field efforts consisted of a grueling cruise schedule of five 21-day cruises (four on the *Gould* and one on the *Palmer*) across Drake Passage, distributed over a 15-month period. Our field program was designed to sample a full seasonal cycle plus a second summer bloom season, with cruises occurring (1) in November/December 1999 at the beginning of summer bloom season, (2) in March 2000 at the end of the summer bloom, (3) in June 2000 during the oligotrophic early winter when sea ice

was forming, (4) in October 2000 at the end of the winter season during sea ice retreat, and (5) in February/March 2001 near the end of a second summer bloom season (Figure 2; C. Smith et al., 2008).

The FOODBANCS program focused on a three-station transect crossing the WAP shelf south of Anvers Island (Stations A, B, and C in Figure 1), with stations selected to represent regional conditions on the inner, middle, and outer WAP shelf in the central PAL-LTER study area (Figure 1). A broad range of environmental parameters were measured using near-bottom moored sediment traps, core sampling (for sediment organisms and geochemistry), radiochemical profiling (both in the water column and sediments), sediment respirometry, and bottom photography (Figure 2). These measurements provided the first insights into (1) seafloor deposition and lability of POC, (2) patterns of labile POC consumption and sediment mixing by detritivorous benthos, and (3) seasonal and interannual variations in biotic abundance, biomass, reproductive condition, recruitment, and sediment community respiration on the WAP shelf.
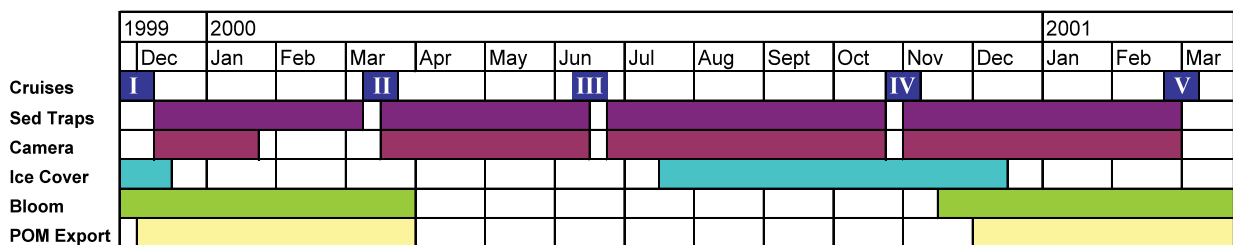

Figure 2. Time lines of research activities and general environmental conditions on the WAP shelf during the FOODBANCS Project. "POM Export" indicates the approximate expected time of export of organic matter from the euphotic zone, based on sediment-trap studies in the region (Karl et al., 1996; Ducklow et al., 2006; C. Smith et al., 2008).

PELAGIC-BENTHIC COUPLING ACROSS THE WAP SHELF

To test the food bank hypothesis, we addressed a series of questions concerning pelagic-benthic coupling on the WAP shelf.

1. Is the flux of POC to the shelf floor as seasonally variable as export production from the euphotic zone? As predicted, the flux of POC and chlorophyll *a* (a tracer of fresh phytoplankton detritus) to the near-bottom FOODBANCS sediment traps exhibited dramatic seasonal variability, with mean fluxes over the three months of summer exceeding winter three-month fluxes by up to 12-fold (C. Smith et al., 2008). Interannual variability in these fluxes was also intense, with ~ 10-fold higher fluxes of POC and chlorophyll *a* in summer of 2000–2001 than in 1999–2000. Time-lapse photographs of the seafloor, taken at 12-hour intervals from November 1999 to March 2001, indicated that the high summer flux in 2000–2001 was accompanied by pulsed accumulation of 1–2 cm of greenish phytodetritus over > 30,000 km² of continental shelf (Figure 3; C. Smith et al., 2008). Similar summer accumulations of phytodetritus have been documented for other parts of the wide Antarctic shelf that are characterized by low current velocities comparable to those on the WAP (Gutt et al., 1998; Beaulieu, 2002). As can often be the case for phytoplankton production in the WAP water column, the large flux of POC and accumulation of phytodetritus on the shelf floor during FOODBANCS was not well correlated with the regional disappearance of sea ice, which receded months before the largest POC pulses. POC flux into the near-bottom FOODBANCS sediment traps (160 m above the seafloor), when corrected for lateral advection, was similar to the flux of POC over the same time interval into the PAL-LTER trap just below the euphotic zone (C. Smith et al., 2008). This observation suggests that virtually all of the export production during the FOODBANCS study was efficiently transferred to the deep WAP shelf floor in our study area, providing food for the benthic ecosystem. In summary, the fluxes of POC, chlorophyll *a*, and phytodetritus to WAP shelf sediments varied intensely on seasonal to interannual timescales, with efficient export through the water column yielding dramatic temporal variability in the flux of labile organic material onto the WAP shelf floor (C. Smith et al., 2006, 2008).

2. Does labile phytodetritus material (i.e., detritivore food) persist in WAP shelf sediments following the summer bloom? Sediment inventories of chlorophyll *a* and enzymatically hydrolyzable amino acids (EHAAs, which are important nutritional components of the sediment for deposit feeders; Mayer et al., 1995) were measured for all stations and cruises as indicators of food availability for detritivores. Inventories of chlorophyll *a* in the top 2 cm of sediment were moderate to high throughout the 15 months, and exhibited much less interannual variability than the chlorophyll *a* flux into near-bottom sediment traps (Mincks et al., 2005; C. Smith et al., 2008). Sediment concentrations of EHAAs were enriched relative to other marine sediments and penetrated deeply (> 5 cm) into the sediment column, varying little with season (Mincks et al., 2005), suggesting persistent food
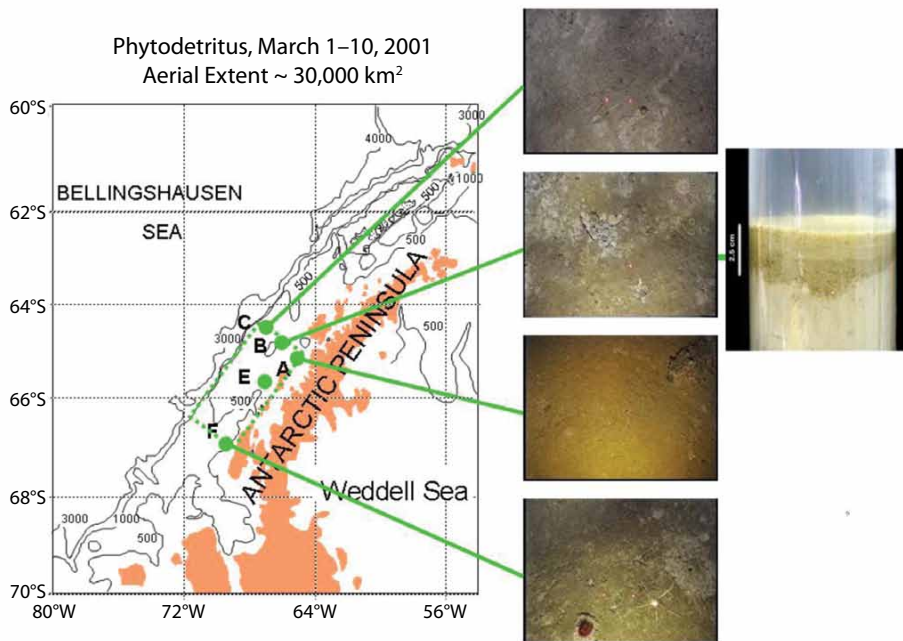

Figure 3. Representative images of the seafloor obtained from March 1–10, 2001, at Stations A–C and F during the FOODBANCS Project illustrating summer accumulation of greenish phytodetritus material over ~ 30,000 km² of the WAP shelf floor. The tube at right, from a megacore sample collected at Station B during the same time interval, illustrates seafloor accumulation of ~ 2.0 cm of phytodetritus. *Modified from C. Smith et al. (2008)*

availability for deposit feeders during winter months. There was a distinct gradient in the $\Delta^{14}C$ content of the organic matter in the upper 8 cm of the WAP sediments (−210 to −285‰), probably resulting from the preferential decomposition of labile organic matter ($\Delta^{14}C$-rich material) in surface sediments. Based on ^{234}Th particle bioturbation coefficients (~ 22 cm^2 yr^{-1}; McClintic et al., 2008) and the $\Delta^{14}C$ gradient in the sediment column, the turnover time for the labile organic material in WAP shelf sediments was estimated to be ~ 01.2 yr, allowing labile organic material deposited during summer blooms to survive microbial degradation over the winter (DeMaster et al., 2011). These ^{14}C results are consistent with estimated turnover times of EHAA and with chlorophyll *a* turnover times in the surface sediments (0.25–0.67 yr), indicating that labile organic matter deposited during the summer may provide a food source (or food bank) for detritivores during winter months when primary production is extremely low (Mincks et al., 2005).

3. Does summer-bloom phytodetritus serve as a source of labile POC (or as a "food bank") for the WAP benthic ecosystem over the winter?

A number of lines of evidence indicate sustained feeding by shelf detritivores during winter months as well as muted seasonality in benthic ecosystem function and structure on the WAP shelf. Excess ^{234}Th activity, a 24-day half-life tracer for feeding activity (e.g., C. Smith et al., 1993; Box 1), was detected in the gut contents of a variety of deposit-feeding megafauna (sea cucumbers, burrowing urchins, echiuran worms, and sipunculan worms) during all sampling times (spring, summer, fall,

winter), indicating that large deposit feeders on the mid-WAP shelf continue to feed throughout the austral winter (McClintic et al., 2008). Labile phytoplankton pigments were also present in detritivore guts and WAP shelf surface sediments at all sampling times (Wigham et al., 2008), indicating feeding on labile food material throughout the year. Bioturbation rates of excess ^{234}Th showed no significant seasonal variability, indicating that community-level particle mixing processes, which are dominated by deposit feeding (Wheatcroft et al., 1990), continued at similar rates over the summer and winter (McClintic et al., 2008). In addition, stable isotopic analyses (δ^{13}C and δ^{15}N) of deposit

feeders and their food sources revealed no evidence of seasonal variability in food material or trophic position for either surface or subsurface deposit feeders, and stable-isotope signatures of surface sediments exhibited little temporal variability (Mincks et al., 2008). All these lines of evidence indicate year-round labile food availability and detritivore feeding on the WAP shelf, providing strong evidence of the presence of a persistent seafloor "food bank."

Sediment microbial-community biomass and respiration, which are expected to be particularly responsive to variations in the availability of labile organic matter, also revealed relatively little seasonality (Mincks et al., 2005). Microbial

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BOX 1 | USING THE PARTICLE TRACER, ^{234}TH, TO ASSESS CONTINUITY IN SEDIMENT DEPOSIT FEEDING

^{234}Th is a naturally occurring radioisotope with a 24 day half-life. This tracer is produced from the decay of uranium in seawater and quickly adsorbs onto the surface of settling particles, producing an "excess" activity (an activity in excess of that supported by decay of uranium contained in the particles). Most of ^{234}Th excess activity in the water column is associated with settling particles relatively rich in labile organic matter. Consequently, particles rich in ^{234}Th activity reach the seabed, tagging the sediment particles of relatively high nutritional value. The vertical profile of ^{234}Th in the seabed can be used to assess the bioturbation intensity (or sediment particle mixing rate) in the seabed (McClintic et al., 2008) and the relative rates of seasonal deposition on the seafloor (see discussion later in this article).

In addition, ^{234}Th also can be used to assess seasonal variations in deposit feeding (i.e., the feeding activities of animals that ingest sediments and digest off the labile organic material). If a deposit feeder were to cease feeding for several months during the winter, the ^{234}Th excess activity in its gut sediment would quickly decay away because of ^{234}Th's short half-life. During the FOODBANCS Project, the ^{234}Th gut contents of deposit feeders were measured during the spring, summer, fall, and winter at stations A,B, and C and there was no appreciable decrease in ^{234}Th activity in the gut sediment of any deposit feeders during the winter season. Thus, the ^{234}Th gut sediment measurements indicate that the deposit feeders at 64°S (near Palmer Station) are likely to feed continuously throughout the summer and winter, which is consistent with "food bank" concept, in which nutritional organic matter is available in the surface sediments on a year-round basis (Mincks et al., 2005; McClintic et al., 2008).

(ATP) biomass in sediments was high at all stations to 5 cm depth throughout the year, with seasonal variability restricted to the upper 2 cm (Mincks et al. 2005). Sediment-community respiration (essentially, microbial degradation of organic carbon by oxygen consumption), as measured by core incubations and oxygen porewater profiles, exhibited much less seasonality than POC flux into the sediment traps (Hartnett et al., 2008). Sediment community respiration rates and denitrification rates continued at substantial levels throughout winter months, indicating the presence of labile (i.e., easily degraded) organic matter in the sediments. The year-round presence of labile organic material in the WAP sediments is highly consistent with a winter sediment food bank integrating seasonal fluctuations in seafloor deposition of labile POC.

The population densities and reproduction patterns of the sediment-dwelling fauna also exhibited muted seasonality, suggesting only moderate "bottom-up" forcing from seasonal POC deposition. Macrofaunal community abundances varied little seasonally, and most polychaetes (which constitute the bulk of benthic macrofaunal abundance and diversity) were either marginally seasonal or nonseasonal recruiters, with small juveniles present at the seafloor year-round (Mincks and Smith, 2007; Glover et al., 2008). Among deposit-feeding megafauna, the most abundant burrowing urchin (*Amphineustes lorioli*) showed no seasonal variation in the biochemical composition of gonad and gut (energy-storage) tissues, and exhibited year-round spawning (Galley et al., 2005). The two dominant deposit-feeding holothurians also spawned and recruited throughout the year (Galley et al., 2008; Sumida et al., 2008). These patterns of year-round reproduction and recruitment are consistent with a persistent food bank of labile organic material in WAP shelf sediments, allowing the processes of reproduction and recruitment on the WAP shelf to be largely decoupled from seasonal bloom dynamics in the water column.

4. What feeding strategies do benthic deposit feeders use to ingest and assimilate labile organic matter from the WAP food bank throughout the year? The novel use of ^{14}C activity as a tracer during the FOODBANCS project allowed the tracking of labile organic matter through the WAP benthic food web. The ^{14}C content of most deposit-feeding megafauna (e.g., *Molpadia musculus*, *Bathyplotes rubipunctatus*, *Protelpidia murrayi*, *Peniagone vignioni*, and irregular urchins) was fairly uniform (Δ^{14}C of –120 to –130‰), similar to the ^{14}C activity of surface waters and plankton (Berkman and Forman, 1996), and enriched by 70 to 140‰ relative to surface sediments (–200 to –275‰). Surface sediments contained an old carbon fraction, which was not assimilated into megafaunal tissue. By comparing the ^{14}C abundance in the gut sediments of megafauna to that in their body tissues, it was clear that some deposit feeders (e.g., echiuran worms and the holothurian *Peniagone*) acquire their ^{14}C enrichment via very selective particle ingestion (Purinton et al., 2008). Other megafaunal deposit feeders (e.g., the head-down holothurian *Molpadia* sp., the holothurian *Protelpidia murrayi*, and various burrowing urchins) feed much less selectively at the seafloor, but acquire ^{14}C enrichment in their tissues relative to the ambient sediments by selective digestion and assimilation of labile organic carbon from sediments within their guts (foregut ^{14}C content ≤ –172‰ but a body ^{14}C content of –125‰; Purinton et al., 2008). The megafauna that ingested sediments less selectively clearly assimilated only a subset of the organic material they took in, as corroborated by a down-gut decline in organic-carbon Δ^{14}C content of their gut sediments (foregut > midgut > hindgut). Thus, the old isotope adage from food web analyses that *"you are what you eat"* does not necessarily apply to the WAP shelf deposit feeders; a more correct statement is *"you are what you assimilate"* (i.e., selection for key nutritional components in deposit feeders can occur after the material is ingested via selective digestion and assimilation of material from the gut).

The Cause and Significance of a Benthic Food Bank on the WAP Shelf

Diverse measurements provide strong evidence of a benthic food bank that maintains benthic ecosystem function and structure on the WAP shelf year-round, despite extraordinarily intense seasonality in primary production and POC export from the water column (Figure 4). Evidence of benthic food banks have also been detected on other Antarctic shelves, including in the Weddell and Ross Seas (Isla et al., 2006; Norkko et al., 2007). How is a benthic food bank (i.e., a relatively large inventory of labile organic material) maintained in WAP shelf sediments over the winter? Why is it not consumed and respired to much lower concentrations

by the high-biomass sediment microbial community? One possibility is that the low temperatures of the WAP shelf (as low as –1.8°C) may reduce the efficiency of microbial hydrolytic exoenzymes, requiring higher substrate concentrations (i.e., greater concentrations of labile POC) to maintain a particular community-level rate of organic matter mineralization (Arnosti and Jørgensen, 2003; Mincks et al., 2005; Weston and Joye, 2005). Under this "temperature-substrate limitation hypothesis," labile organic material builds up in the WAP shelf sediments to relatively high levels (forming a detritivore food bank) before sediment microbial respiration can balance the annual flux of labile POC to the seafloor. The mineralization of organic matter in low-temperature tundra soils appears to follow similar dynamics, with labile organic material building up to high levels before microbial respiration can balance organic carbon inputs (Schlesinger, 1997).

If correct, the temperature-substrate limitation hypothesis has important implications for the effects of climate warming on carbon storage and benthic trophodynamics on the Antarctic shelf (Mincks et al., 2005; C. Smith et al., 2006; Norrko et al., 2007; Clarke et al., 2009). Warming of Antarctic shelf bottom waters by a few degrees could significantly enhance the efficiency of microbial remineralization (Arnosti and Jørgensen, 2003) and increase sediment POC mineralization rates (Robador et al., 2010), leading to a decrease in the concentration of labile organic material in Antarctic shelf sediments. This situation could, in turn, reduce food availability for benthic detritivores by decreasing the size of the "food bank," altering food
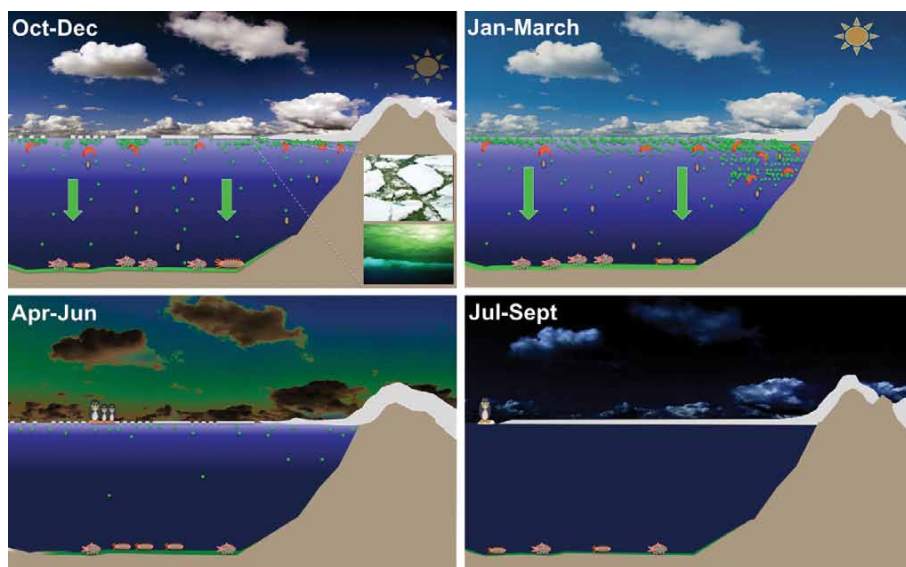

Figure 4. Schematic of the food-bank hypothesis, describing pelagic-benthic coupling along the mid-WAP shelf. OCTOBER–DECEMBER (SPRING): Days are lengthening, sea ice melt is releasing ice algae and causing stratification, phytoplankton blooms are initiating settlement of fresh phytodetritus to seafloor, and benthic detritivores (illustrated as holothurians on the seafloor) are still primarily consuming the benthic "food bank" accumulated during the previous summer. JANUARY–MARCH (SUMMER): Days are long, sea ice has receded, and intense phytoplankton blooms yield sedimentation and accumulation of a phytodetrital carpet that provides fresh food for benthic detritivores and replenishes the benthic food bank. APRIL–JUNE (FALL): Days are shortening rapidly to a minimum, sea ice is forming, diminishing phytoplankton blooms yield little phytodetrital flux to the seafloor, and benthic detritivores continue to feed on the sediment food bank of labile organic material that accumulated over summer. JULY–SEPTEMBER (WINTER): Days are short, but lengthening; heavy sea ice cover limits light penetration and phytoplankton production; the water column is food poor; and benthic detritivores continue to feed on the sediment food bank that persists from the previous summer's blooms.

webs, and reducing the rate of carbon sequestration in Antarctic shelf sediments. If the temperature-substrate limitation hypothesis is correct, continuation of the current trend of climate warming in the Antarctic Peninsula region (Ducklow et al., 2007) could have great impacts on the function and structure of detritus-based ecosystems on the WAP shelf (C. Smith et al., 2006, 2008).

The FOODBANCS project, and several other time-series studies on the Antarctic shelf, suggest that numerous processes, including sediment respiration, deposit feeding, larval development, and recruitment, often are poorly coupled to the summer bloom, due in

part to the accumulation of a persistent sediment food bank that buffers the benthic ecosystem from the seasonal variability in the water column (Arntz and Gili, 2001; C. Smith et al., 2006; Norrko et al., 2007; C. Smith and DeMaster, 2008a or b). As a consequence, a variety of benthic parameters (sediment respiration, inventories of labile organic matter, macrobenthic biomass) may act as "low-pass" filters for pelagic-benthic coupling, smoothing seasonal water-column signals and responding primarily to longer-term (e.g., decadal) trends in the quantity and quality of primary production and POC export. These benthic ecosystem parameters are relatively easily

monitored and could provide very useful indicators of trends in export production and pelagic-ecosystem function on the Antarctic shelf that result from regional climate warming (C. Smith et al., 2006; Ducklow et al., 2007).

FOODBANCS2: SEA ICE DURATION AND PELAGIC-BENTHIC COUPLING

One major consequence of climate warming along the WAP is a dramatic decline in sea ice cover (Ducklow et al., 2007). For example, along the mid WAP at 66°S, annual sea ice duration has declined from seven months to four months in recent decades (Jacobs and Comiso, 1997). We know that sea ice plays a central role in pelagic ecosystems of the sea ice zone, and that large changes in sea ice duration may reorganize pelagic food webs, altering rates of primary production, community structure of phytoplankton and grazing zooplankton, and the quantity and quality of export flux (e.g., Atkinson et al., 2004; Moline et al., 2004; Clarke et al., 2007; Thomas and Dieckmann, 2010). We also know that the quantity and quality of export flux from the euphotic zone through pelagic-benthic coupling influence the structure and function of shelf benthic ecosystems along the WAP. In particular, export flux fuels a broad range of benthic organisms and processes, contributing to a WAP sediment food bank that nourishes detritivores during winter months (see discussion above). Thus, some aspects of benthic ecosystem function and structure may be highly sensitive to changes in annual sea ice duration, while others may be resilient. Elucidating the response of the shelf benthos to differences in annual sea

ice duration is fundamental to predicting the effects of climate warming on WAP marine ecosystems.

To help address the potential effects of sea ice loss on pelagic-benthic coupling on the WAP shelf, the FOODBANCS2 Project was developed to test the following hypothesis: *Large latitudinal differences in sea ice duration along the WAP shelf are correlated with substantial changes in benthic ecosystem structure and function.*

To address this hypothesis, we studied the benthic ecosystem along a five-station transect running down the mid-WAP shelf from 63° to 68°S latitude (Figure 1). Stations were selected to be similar in depth (550–600 m) and physical characteristics (i.e., they were situated on flat, muddy sediments with no evidence of sediment resuspension and well below the effects of iceberg scour). The transect spans a large latitudinal gradient in mean annual sea ice duration (averaged over the five years prior to our study) ranging from 1.4 mo yr^{-1} at our northernmost station to 7.6 yr^{-1} at our southernmost station (Figure 5). We conducted cruises along the transect in the summers of 2008 and 2009 using ARSV *Laurence M. Gould*, and in winter 2008–2009 (in sea ice) aboard RVIB *Nathaniel B. Palmer*, to evaluate seasonal and interannual variability in key benthic ecosystem parameters.

Benthic Ecosystem Response to the Latitudinal Sea Ice Gradient

Our synthesis of shelf ecosystem response to the sea ice gradient is just emerging, and it is surprisingly complex. As expected, some basic benthic parameters vary monotonically along the transect and are strongly correlated with sea

ice duration: sediment deposition rates over decadal scales (based on excess ^{210}Pb inventories) and sediment inventories of the labile phytodetritus tracer chlorophyll *a* (r = –0.750, p = 0.001) (Figure 5). Certain aspects of benthic faunal structure also covary with sea ice duration. In particular, sediment macrofaunal community abundance becomes increasingly dominated (up to 45%) by the spionid poychaete *Aurospio foodbanscia* as annual sea ice duration increases (r = 0.93, p < 0.05) (Figure 5). *Aurospio foodbancsia* was first described in 2009 (Mincks et al., 2009), yet it is almost certainly the most abundant macrofaunal species on the WAP shelf; it appears to be especially well adapted to the extremely seasonal pelagic-benthic coupling associated with long annual sea ice duration on the southern WAP shelf. This newly described Antarctic polychaete seems very likely to decline in abundance along the WAP, with macrofaunal species evenness increasing, as sea ice duration wanes due to climate warming.

Other benthic ecosystem parameters change significantly along our latitudinal transect, but the change is distinctly nonlinear. These parameters include total community abundance and species richness for both macrofauna and epibenthic megafauna, as well as megafaunal trophic structure (Figure 5). Community abundance (or "standing crop") for both size classes is relatively high at the northernmost station and relatively low to the south, suggesting that increased sea ice duration may cause a nonlinear decrease in food availability (i.e., in labile POC flux) to the benthos over the general times (years to decades) characteristic of these faunal size classes (see C. Smith et al., 2006, 2008).

Megafaunal trophic structure shifts from an overwhelming predominance of suspension feeders in the north to deposit feeders and omnivores in the south. This shift is consistent with a strong decline in the duration of the summer bloom, and availability of food in the water column, at the southernmost latitudes. All these results suggest that the quantity and quality of export flux to the shelf floor, as well as food availability for suspension feeders, may respond nonlinearly to sea ice duration as suggested by the water-column studies of Montes-Hugo et al. (2009). Alternatively, local forcing on benthic ecosystem structure along our transect may overwhelm regional forcing related to variations in sea ice duration.

Finally, the mean values of several key ecosystem parameters changed little along the FOODBANCS2 latitudinal gradient. These parameters include sediment community respiration (with relatively little difference between latitudes and seasons), sediment microbial (ATP) biomass, and bioturbation rates based on ^{234}Th excess activities (integrating 100-day timescales). All of these parameters may have relatively short response times (on the order of months) with the consequence that seasonal and interannual "noise" obscures latitudinal trends. Nonetheless, the lack of major differences in the means of these parameters along the transect suggest that important aspects of benthic ecosystem structure and function may be quite resilient to substantial climate-induced reductions in sea ice duration along WAP shelf.

In summary, some aspects of benthic ecosystem structure (e.g., dominance by *Aurospio foodbancsia*) covaried with sea ice duration along the FOODBANCS

transect and are predicted to be sensitive to climate warming-induced sea ice loss. Other benthic parameters (including the standing crop of macro- and megabenthos) exhibited nonlinear responses, with little change (i.e., evidence of resilience) along much of the latitudinal range,

and abrupt change near one end of our transect. Still other benthic parameters (e.g., sediment microbial biomass) changed very little along the latitudinal transect, or varied nonmonotonically. Thus, benthic ecosystem parameters are likely to exhibit variable responses
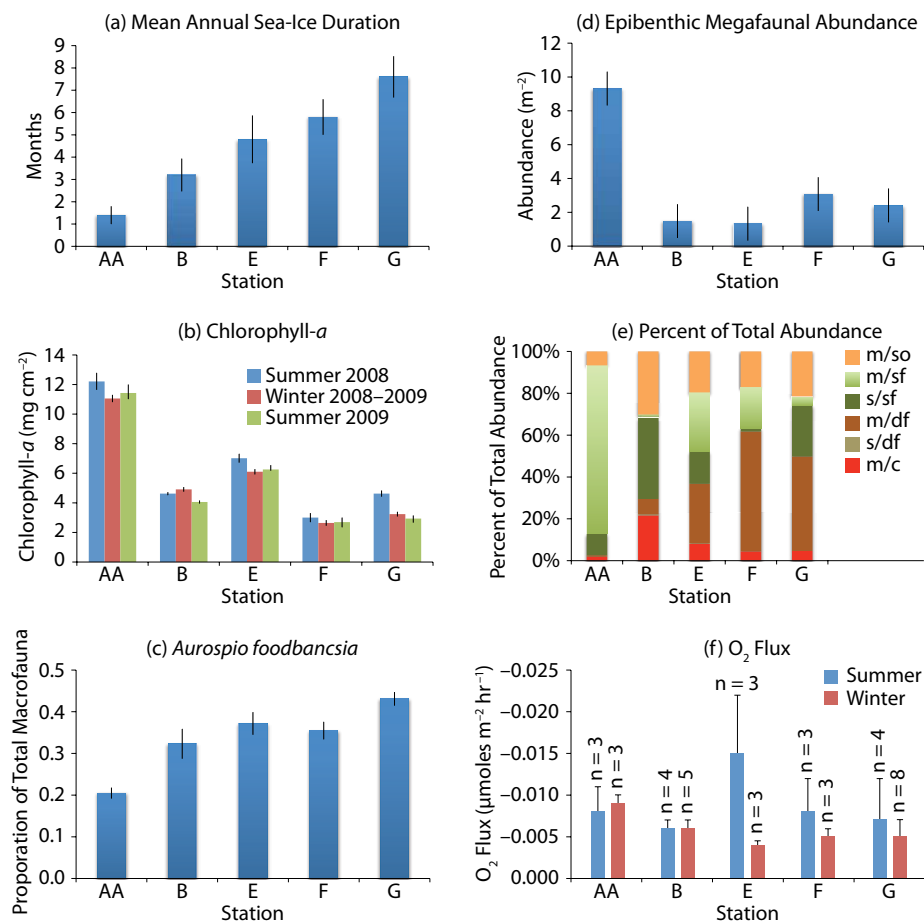

Figure 5. Variation in marine-ecosystem parameters at stations AA, B, E, F, and G along the FOODBANCS2 latitudinal gradient (see Figure 1 for station locations). (a) Mean (±1 s.d.) annual sea ice duration (defined as average number of months per year with an ice concentration > 50%) for the period 2004–2008 (recent work of author Sršen and colleagues, based on NSIDC data). (b) Inventories of chlorophyll *a* (mean ±1 s.e.), based on fluorometry, in the top 4 cm of sediment during summer (February–March) and winter (August) (recent work of author Smith and colleagues). (c) Mean (±1 s.e.) proportion of total macrofaunal abundance comprised of the polychaete *Aurospio foodbancsia*, averaged over the summer and winter FOODBANCS2 cruises (recent work of author Sršen and colleagues). (d) Mean abundance (±1 s.d.) of epibenthic megafauna based on seafloor photographic surveys, averaged across the summer and winter FOODBANCS2 cruises (recent work of author Smith and colleagues). (e) Trophic-group composition of epibenthic megafauna. m/so = mobile scavengers/omnivores. m/sf = mobile suspension feeders. s/sf = sessile suspension feeders. m/df = mobile deposit feeders. s/df = sessile deposit feeders. m/c = mobile carnivores (recent work of author Smith and colleagues). (f) Mean (+1 s.d.) sediment-community respiration in summer and winter based on shipboard sediment-core incubations (recent work of author Thomas and colleagues).

to climate change and sea ice loss, with those parameters having multiyear to decadal response times (e.g., those derived from macrofauna and mega-fauna) exhibiting higher signal to noise ratios (Figure 5).

RESPONSE OF WAP SHELF BENTHOS TO RISING SEAWATER TEMPERATURES: POTENTIAL INVASIVE EFFECTS OF KING CRABS

Antarctic shelf waters, including those along the WAP, have been cold (< 1°C) and oceanographically isolated by the Antarctic Circumpolar Current for at least 14 million years (Aronson et al., 2007). These low temperatures are thought to have excluded king crabs and other large crushing predators from the Antarctic shelf, allowing the development of endemic, species-rich epifaunal communities potentially highly vulnerable to invasion by crushing predators (Aronson et al., 2007). King crabs occur widely in the warmer waters of the continental slope around Antarctica (Hall and Thatje, 2010), so climate warming of WAP shelf waters (Meredith and King, 2005) may soon allow the invasion of these temperature-limited predators onto the Antarctic shelf (Aronson et al., 2007; Thatje et al., 2008).

In March 2010, remotely operated vehicle surveys conducted from the *Palmer* discovered a large, reproductive population of king crabs (estimated to be 1.55 million individuals) living 120 km onto the WAP shelf (C. Smith et al., 2012). The crab (*Neolithodes yaldwyni*), found to be abundant (~ 10,600 km^{-2}) at 950–1,410 m depth in Palmer Deep, had never been observed during extensive trawling and imaging surveys of the surrounding shelf over previous decades (C. Smith et al., 2012). Thus, this is the first evidence that king crabs have crossed the WAP shelf. In the crab depth zone (> 950 m) in Palmer Deep, crab traces were abundant, echinoderms (e.g., brittle stars, asteroids, crinoids) wholly absent, and megafaunal diversity drastically reduced, suggesting that the crabs have major invasive ecological impacts (Figure 6; C. Smith et al., 2012). The Palmer Deep king crabs appear to be acting as major ecosystem engineers, with their walking and foraging activities potentially modifying the bioturbation regime and sediment geochemistry, and with their removal of habitat-forming echinoderms. If *N. yaldwyni* is currently limited by cold temperatures as suspected (Hall and Thatje, 2010), the rate at which WAP shelf waters are warming could allow this invasive predator to spread to shallower depths on the WAP shelf (400–600 m) within one to two decades, leading to major loss of benthic
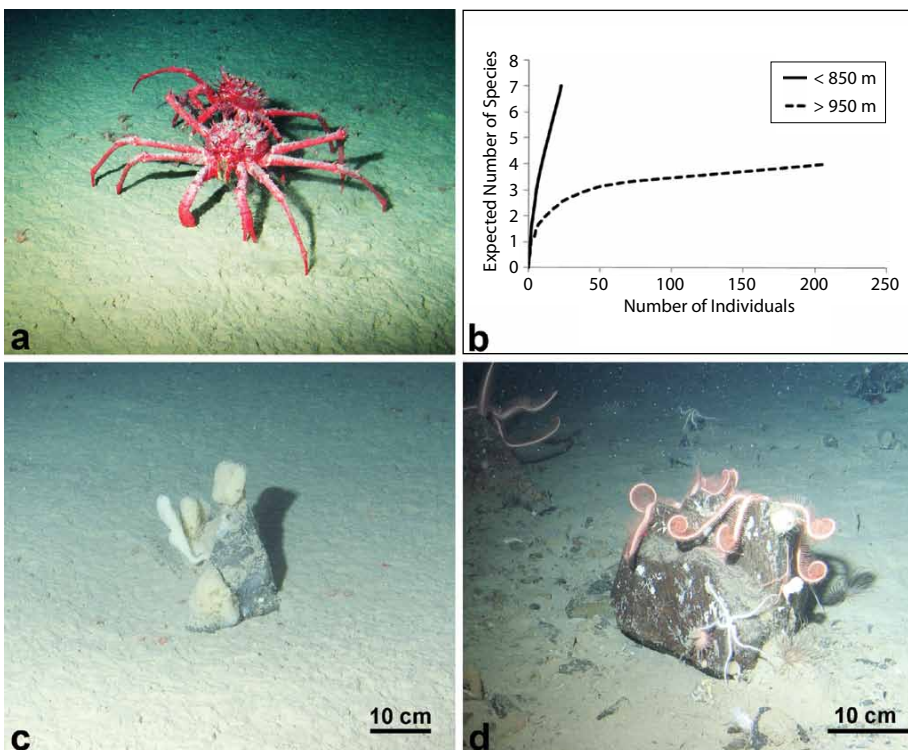

Figure 6. (a) *Neolithodes yaldwyni* foraging on the Palmer Deep floor. Gashes and puncture marks in the sediment were caused by the walking and feeding activities of the crabs. (b) Rarefaction diversity curves for the sediment dwelling mega-fauna in Palmer Deep at depths of more than 950 m (where *N. yaldwyni* and its traces were abundant; dashed line) and less than 850 m (where *N. yaldwyni* and its traces were absent; solid line). Note that species diversity measured with rarefaction is dramatically lower within the crab zone than above it. (c) Example of a drop stone from the *N. yaldwyni* depth zone in Palmer Deep (> 950 m) with only hexactinellid sponges and serpulid worm tubes visible. Note crab traces in the sediments around the stone. (d) Example of a drop stone from above the *N. yaldwyni* depth zone (< 850 m), with brisingid asteroids, ophiuroids, an echinoid, hexactinellid sponges, and serpulid worm tubes visible. *Modified from C. Smith et al. (2012)*

biodiversity and altered sediment geo-chemistry (C. Smith et al., 2012). Thus, the warming of the WAP shelf water column appears to be facilitating invasion by cold-intolerant crushing predators, potentially leading to abrupt (highly nonlinear) shifts in benthic biodiversity and ecosystem function (as predicted by Aronson et al., 2007).

OVERALL CONCLUSIONS

Our intensive, all-season studies of pelagic-benthic coupling along the WAP have been made possible by the ice-breaking capabilities of the *Palmer* and the ice-strengthened nature of the *Gould*. The FOODBANCS studies indicate that the intense seasonality in primary production, food availability, and export flux in the WAP water column is heavily dampened at the shelf floor by the presence of a benthic food bank. This food bank of labile organic material sustains benthic ecosystem functions (e.g., sediment community respiration, deposit feeding, vitellogenesis, spawning, and recruitment of benthos) throughout the winter, and is likely to fundamentally influence the community structure and life-history strategies of the WAP shelf benthic fauna. Very low bottom-water temperatures may mediate the presence of the food bank, with the consequence that climate warming may reduce the food storage capacity of shelf sediments and substantially alter ecosystem structure and function along the WAP.

Our latitudinal studies down the strong sea ice gradient along the WAP suggest that sea ice loss due to climate change will have complex effects on WAP benthic ecosystem structure and function. Key shelf benthic species (e.g., *Aurospio foodbancsia*) appear likely to decline with sea ice loss, and important aspects of ecosystem structure (e.g., macro- and megabenthic abundance and trophic composition) could undergo abrupt nonlinear changes when tipping points are reached. Warming-mediated invasions of the WAP shelf by predacious king crabs have the potential to dramatically reduce benthic biodiversity and alter seafloor ecosystem function. Nonetheless, some benthic ecosystem parameters, for example, sediment community respiration and microbial biomass, may be quite resilient in the face of climate-induced changes in sea ice duration in WAP shelf ecosystems. Incorporation of climate change effects into WAP benthic ecosystem models, including the effects of invasive species, will be highly challenging until mechanisms, nonlinearities, synergies, and tipping points of climate change effects are more thoroughly understood.

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