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Water-column processes in the West Antarctic Peninsula and the Ross Sea: Interannual variations and foodweb structure

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Abstract

The sea-ice zone of the Antarctic exhibits high rates of primary productivity and large interannual variability in plankton and biogeochemical properties, influenced by variations in the timing, extent and duration of sea-ice advance and retreat. In the past decade several interdisciplinary research programs conducted investigations in the sea ice zones of the West Antarctic Peninsula (WAP) and Ross Sea. In this article we synthesize results of these investigations to provide an overview of water-column processes influenced by regional-scale sea-ice dynamics. Primary production (PP) off the WAP varies by nearly an order of magnitude from year-to-year, and its interannual variability is related to the amount of open water within the annual ice pack. The annual sedimentation at 170 m averages about 2% of the overlying PP but is not related to interannual variations in the ice or PP. Rather the interannual variations in sedimentation are related to stocks of krill and salps. Plankton foodwebs in the Ross Sea and WAP exhibit similar annual PP but differ greatly in quantitative foodweb structure. Foodwebs of the WAP are dominated by krill grazing of spring-summer diatom blooms, whereas in the Ross Sea the extensive and early (November) bloom of *Phaeocystis antarctica* is not grazed and ~50% sinks as ungrazed cells. Foodweb reconstructions from inverse models suggest that some functional characteristics of foodwebs in the two regions are quite similar in spite of taxonomic contrasts. Relatively high rates of microbial processing and nutrient recycling characterize both systems, even during years in the WAP when PP differs by an order of magnitude. These similarities indicate broad functional similarities across contrasting foodweb composition in the sea-ice zone.

Keywords: Antarctica; Sea ice; LTER; Foodwebs; Particle flux; Inverse model

1. Introduction

Antarctic coastal waters exhibit high rates of primary production (PP; over $2\,\mathrm{g\,C\,m^{-2}\,d^{-1}}$ and

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100–200 $\mathrm{g\,C\,m^{-2}\,y^{-1}}$) during a limited growing season of about 150–180 days (Smith et al., 1996a, 1998a; Smith and Gordon, 1997; Arrigo et al., 1998b). The phytoplankton growing season is limited by the annual cycle of solar irradiance at high latitude and by the advance, duration, extent and retreat of sea ice (Smith et al., 1996a, 1998c). Sea-ice retreat triggers an annual spring phytoplankton bloom typically dominated by diatoms, but by *Phaeocystis antarctica* in the Ross Sea (Smith and Gordon, 1997; Arrigo et al., 1999). This PP supports large standing stocks of top predators (whales, seals and seabirds; Valiela, 1995) and a rich and diverse benthic fauna (This volume). Benthic and pelagic productivity are linked by gravitational sedimentation of organic matter following the annual spring bloom (Wefer et al., 1988; Honjo et al., 2000). The plankton foodweb is traditionally thought to be characterized by short food chains leading from diatoms to krill to top predators, although more recently the importance of microbial foodwebs and detritus-based trophic exchanges have been recognized (Hewes et al., 1985; Karl, 1993). How coastal Antarctic plankton production can truly satisfy these three demands, viz. supporting top predators, a rich benthos, and a microbial foodweb, remains to be understood, and the relevant trophodynamic pathways to be quantified. We address that problem in this article through a quantitative description of Antarctic foodwebs using an inverse foodweb modeling approach.

In the past decade several large interdisciplinary and long-term studies have made important contributions to our understanding of Antarctic plankton ecology. These include the Joint Global Ocean Flux Study (JGOFS) Southern Ocean Program (Smith et al., 2000), the ROAVERRS Program in the Ross Sea (Arrigo et al., 1998b), Southern Ocean Global Ecosystem Dynamics (Hofmann et al., 2001), and the Palmer Long-Term Ecological Research (PAL-LTER) Program (Ross et al., 1996a). Findings of these large-scale projects emphasize the importance of sea-ice variability for ecosystem functioning, the critical structuring and regulatory roles of krill in the marine ecosystem of the West Antarctic Peninsula (WAP) and of *Phaeocystis* in the Ross Sea, and the linkages between water-column ecology and biogeochemistry. In this article we review some results of these studies as they illuminate the interannual relationships in sea ice, PP, zooplankton stocks and sedimentation in the WAP system, and a comparison of foodweb structure between the diatom-krill-dominated WAP and the *Phaeocystis*-dominated central Ross Sea.

2. Methods and data sources

The results presented and discussed in this paper are taken principally from the US JGOFS Antarctic Environment and Southern Ocean Process Study (AESOPS, 1996–97) in the Ross Sea and from PAL-LTER in the WAP (1991–present). Other studies are cited appropriately. Methods are described in the US JGOFS (http://usjgofs.whoi.edu/jg/dir/jgofs/) and LTER (http://pal.lternet.edu/data/data_use_policy.php) websites and in cited papers. The data used here were taken from these websites. Southern Ocean Oscillation data were obtained at http://www.bom.gov.au/climate/current/soihtm1.shtml.

2.1. West Antarctic Peninsula

The PAL-LTER project has been making routine observations of local and regional ice extent, plankton stocks and PP and sedimentation since 1991–92. Sea-ice observations for the Peninsula region have been synthesized for the period 1978–present using multi-frequency passive microwave satellite data for the region within the LTER sampling grid (Fig. 1A,B) (Smith et al., 1998b; Stammerjohn et al., 2003). Sea-ice seasons are determined over calendar years. Sea-ice extent is defined as the total ocean area enclosed by the 15% sea-ice concentration contour (Smith et al., 1998b) as determined in the microwave imagery. This region includes areas with $<15\%$ sea-ice cover occurring at subpixel resolution inside the ice pack. Sea-ice area is the ocean area covered only by ice of $>15\%$ concentration, excluding areas of open water within the ice pack. Sea-ice extent and area within the Palmer LTER grid are significantly correlated over the period 1979–2003 ($r^2 = 0.98$, $p = 0.001$; $n = 25$). Open water is the difference between sea-ice extent and area. Ice retreat and advance are the dates of last and first occurrence of $>15\%$ ice concentration from a given pixel in the ice imagery, respectively. The difference between the retreat and advance is the number of ice-free days in a season. Sea-ice retreat and advance were determined for the location of the sediment trap.

Inshore PP rates were measured approximately twice per week at Stations B and E in Arthur

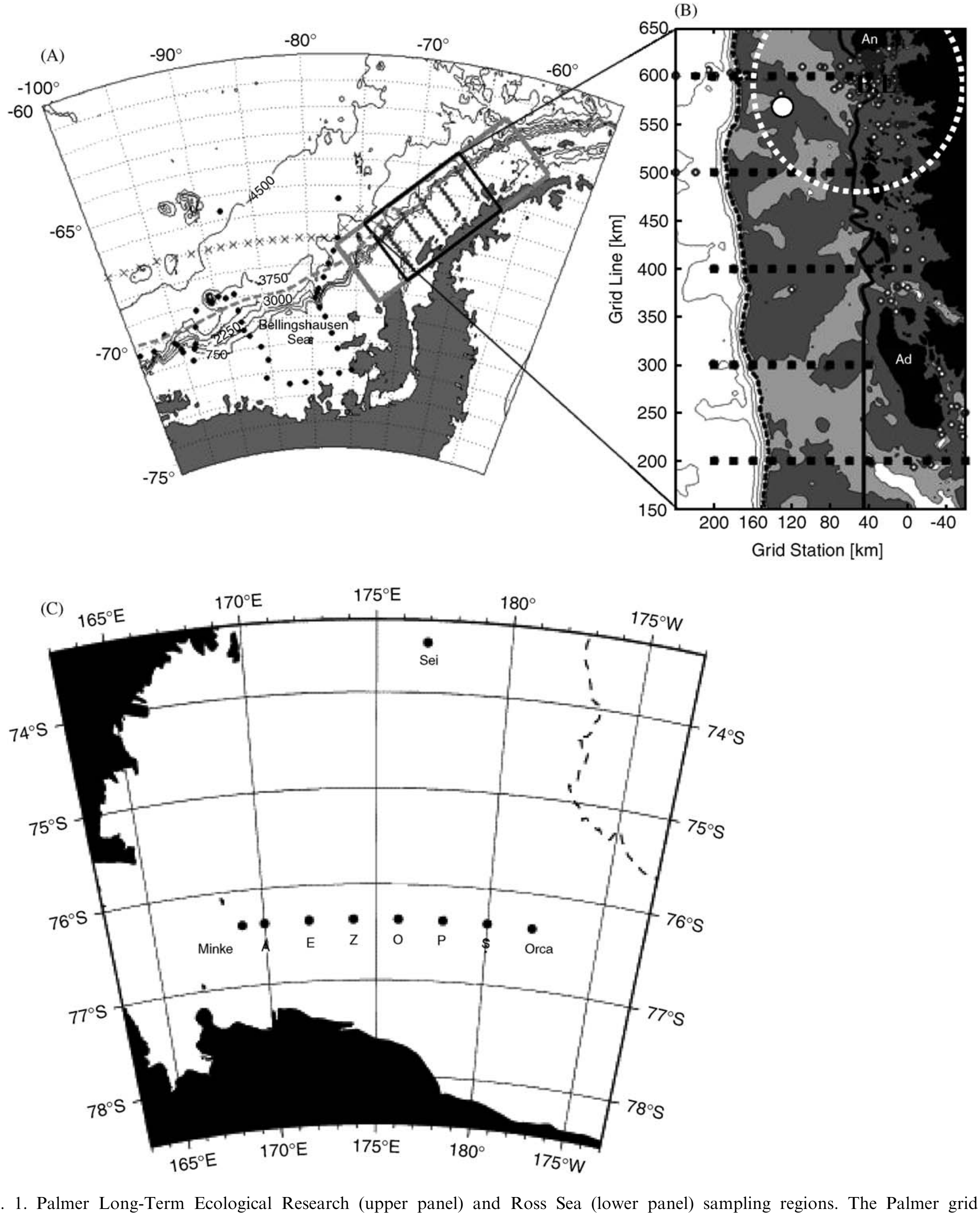

Fig. 1. Palmer Long-Term Ecological Research (upper panel) and Ross Sea (lower panel) sampling regions. The Palmer grid of hydrographic stations includes 10 onshore-offshore lines 100 km apart with individual stations at 20 km intervals, extending from the inshore region beyond the shelf break (water depths 200–4000 m). The location of the penguin foraging area around Palmer Station (dashed circle) and the sediment trap mooring (solid circle) are also depicted.

Harbor near Palmer Station (lat. 64.7 S; 64.0 W). These rates were integrated through a 180-day growing season (October 15–April 15) to obtain total annual production. Offshore PP rates were determined on annual January cruises in the LTER sampling grid (Fig. 1). Sedimentation rates were measured with a McLane Mark IV-time series sediment trap (McLane Research Labs, Falmouth, MA), deployed in each calendar year (mid-January–mid-January) at 170 m depth (lat 64.48 S; long 66.04 W) in 350 m depth over the midshelf (Fig. 1). The daily sedimentation rates were integrated for each calendar year to obtain annual fluxes. Since the annual peak in sedimentation happens between November and February (Fig. 4), this integration splits each annual peak between 2 years. Integration from July to July would place each annual peak within 1 year, but because of breaks in the data record, it misses 2 years covered by the calendar year integration. Integrals following each time slice were significantly correlated ($r^2 = 0.98$, $p < 0.001$; $n = 7$).

Zooplankton stocks were derived from net collections along the 500 and 600 lines of the sampling grid (stations 60–200 km offshore), judged to be the region where zooplankton would most likely contribute to sedimentation into the trap. Zooplankton climatologies were calculated using delta-transformed abundances (R. Ross and L. Quetin, pers. commun.).

Interannual variability in sea ice and ecological properties was characterized using the standardized anomaly, S:

$$S = (X_i - \bar{X})/\bar{X}, \qquad (1)$$

where the X_i are the annual means and $\bar{X}$ is the average of the X_i over some specified period (in this case, usually 1992–2004).

2.2. Year designation

Years in which different observations were made are termed according to a sequence of events defining the response of the ecosystem to ice retreat. Ice advance, extent and retreat are defined for each calendar year, as is the integrated annual total sedimentation. However, the sedimentation year corresponds to the preceding ice year (see Section 4). Graphs are plotted by ice years.

2.3. Ross Sea vs. WAP

Models of foodwebs in the Ross Sea and WAP were constructed using the inverse approach first employed by Vézina and Platt (1988). Methods of data input, computation and overall approaches used here are described in detail in Richardson et al. (2004) and Daniels et al. (2006). The model is designed to recover rates of specified processes, but not standing stocks, which are normally specified as inputs. For the WAP, data were taken from January 1996, a year with high PP relative to the long-term mean (see Daniels et al., 2006, for discussion). This year was chosen principally because it was used in other analyses and was close to the Ross Sea sampling year. Below, we show that most foodweb properties were similar in a low-productivity year (1999). Data were selected from the January, 1996 LTER grid stations within the 115-km foraging radius of Adélie penguins nesting near Palmer Station (Fig. 1A), as estimated from satellite transmitters mounted on individual penguins (W.R. Fraser, pers. commun.). For the Ross Sea, data were taken from the November 1997 JGOFS cruise (NBP97-8; http://usjgofs.whoi.edu/jg/dir/jgofs/southern/nbp97_8/) (Fig. 1C) because this period was deemed to be most analogous to the January period in the WAP (Daniels et al., 2006). Where multiple observations were available, we used a range defined by the standard deviation of the available data. The data used in our models are presented below.

3. Results

3.1. Sea ice, PP, and sedimentation in the WAP, 1992–2004.

Sea-ice extent, PP, and sedimentation all exhibited substantial interannual variations during the decade of LTER observations. The annual sea ice extent in the 200,000 km^2 observation grid (Fig. 1) averaged 92,234 km^2 or about 50% coverage (Table 1). The sea ice retreated from the site of the sediment trap mooring on the average on day 310 (06 November) but varied by ~35 days earlier or later (Table 1). The local PP at Palmer Station averaged 176 $\mathrm{gC\,season}^{-1}$ (Fig. 2; 0.98 ± 0.60 $\mathrm{gC\,m}^{-2}\,\mathrm{d}^{-1}$). The daily variability in PP at Palmer Station averaged 72% of the mean for 1994–2001, and the average magnitude of the standardized anomalies for this period was 0.5. Both PP and

Table 1
Sea-ice extent, day of ice retreat, seasonal primary production and sedimentation at 170 m depth near Palmer Station, Antarctica

Pri. prod. season	Ice year (calendar)	Sedimentation year (calendar)	Sea-ice extent (km^2)	Sea-ice retreat[a] (day of year)	Primary prod. (gC m^{-2})	Sedimentation (gC m^{-2} y^{-1}) (% of PP)
1991–92	1991	1992	107,753	na	250	na
1992–93	1992	1993	106,750	315	120	1.64
1993–94	1993	1994	96,733	314	60	1.70
1994–95	1994	1995	103,164	320	177	3.98
1995–96	1995	1996	96,765	324	351	2.60
1996–97	1996	1997	84,627	301	212	0.14
1997–98	1997	1998	99,872	327	106	3.37
1998–99	1998	1999	74,213	272	47	4.13
1999–00	1999	2000	79,780	314	63	2.96
2000–01	2000	2001	78,005	306	293	na
2001–02	2001	2002	69,932	282	212	1.94
2002–03	2002	2003	109,396	319	176	2.18
2003–04	2003	2004	83,776	301	266	2.02
2004–05	2004	2005	101,447	340	125	na
Mean	—	—	91,112	310	176	2.42

[a] The day of sea ice retreat is defined as the day sea declines to below 15% ice cover for any given pixel in the SMMR imagery.

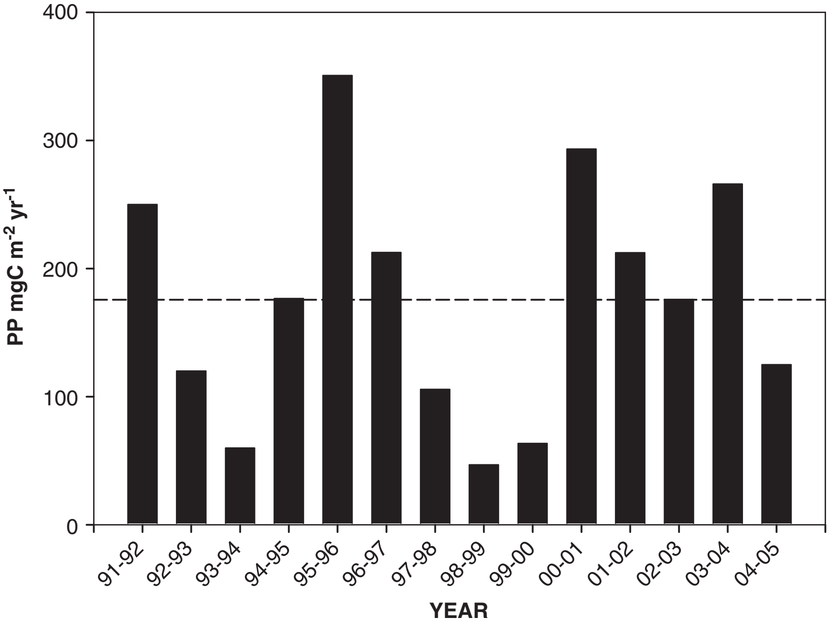

Fig. 2. Multiyear record of annual primary production (October–April) at Palmer Station.

sedimentation varied by nearly an order of magnitude over the observation period (Table 1). The annual average sea-ice extent corresponded to the southern oscillation index (SOI; Ropelewski and Jones, 1987) (Fig. 3). Positive sea-ice anomalies corresponded to negative SOI (ENSO events), and low sea-ice years occurred during positive SOI phases.

The annual pattern of sedimentation is characterized by a summer–autumn peak lasting 50–100 days and reaching upwards of ~50 mgC m^{-2} d^{-1} in most years (Fig. 4). Sedimentation at 170 m averaged

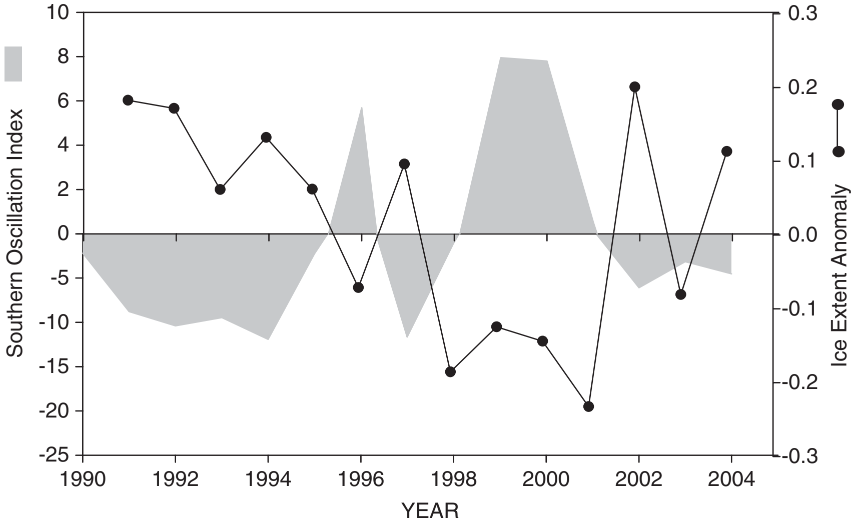

Fig. 3. Relationship between Southern Oscillation Index and ice extent within the LTER study area.

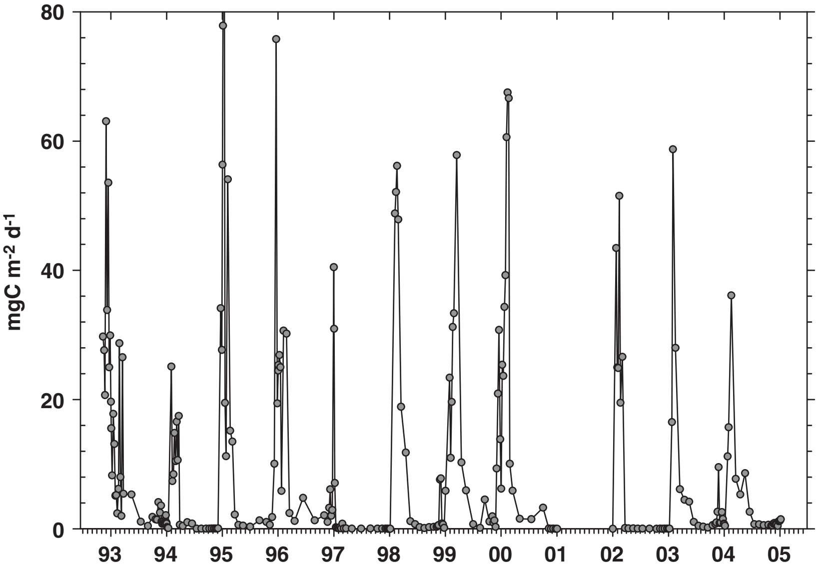

Fig. 4. Multiyear record of annual sedimentation within the LTER study area.

2.42 gC m^{-2} yr^{-1} or 2% of the PP at Palmer Station (Table 1).

Interannual anomalies for ice-related properties were generally somewhat lower than the anomalies for biogeochemical processes of PP and sedimentation (Fig. 5). Anomalies for ice extent, area and open water (Smith et al., 1998b) ranged from −0.25 to +0.25. The ice extent was above average for 1991–95, then generally below average for 1996–2001, reflecting a declining trend in sea-ice coverage over the past 25 years. The day of ice retreat near the trap mooring varied less, with no trend. PP and sedimentation varied from −0.7 to +1 and −0.9 to +0.7, respectively. Zooplankton stocks fluctuated widely from −1 (i.e., zero abundance) to +3.

3.1.1. Relationships

Ice extent covaried strongly (in most years) with the date of ice retreat from the sediment trap site

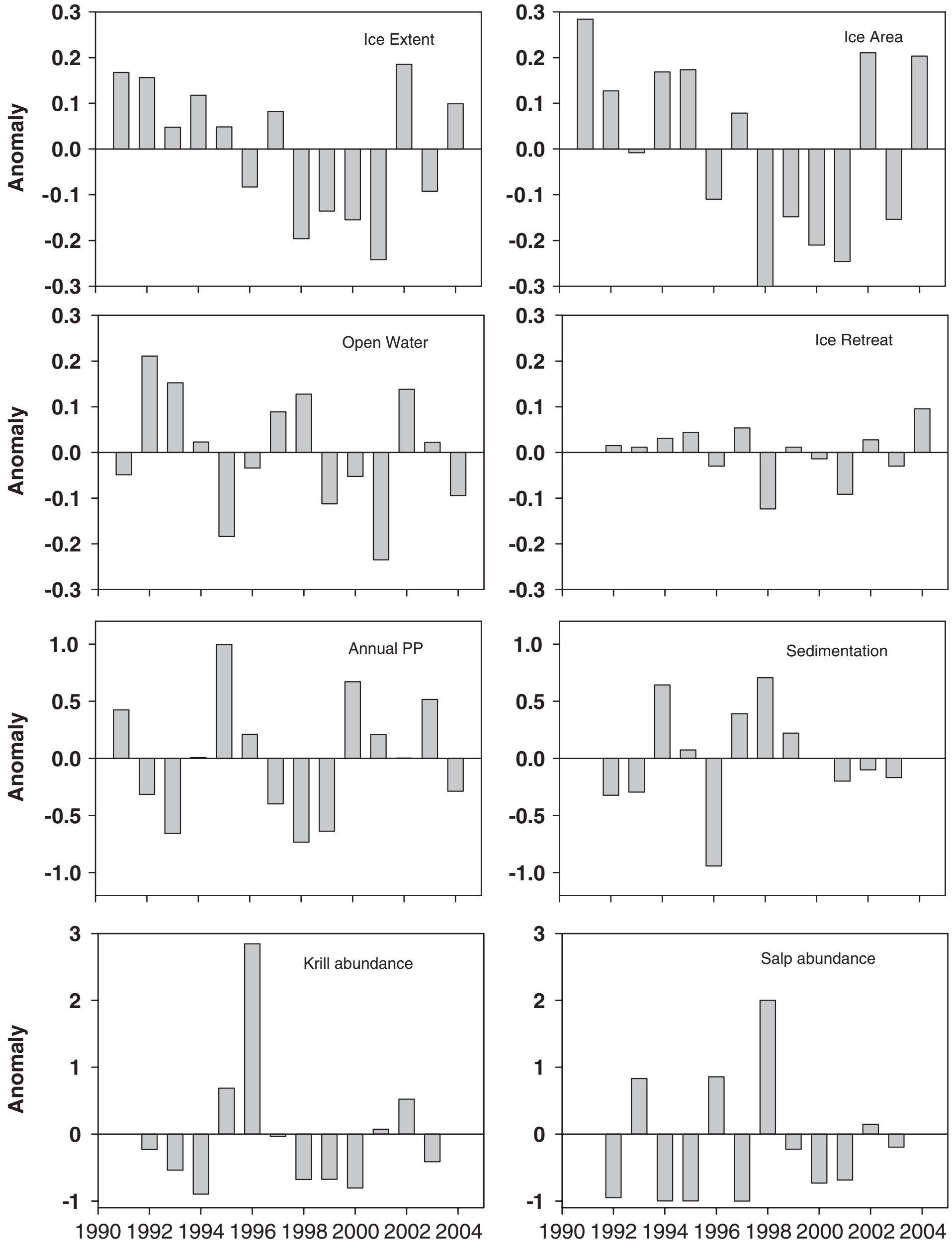

Fig. 5. Interannual standardized anomalies for ice and ecological properties within the LTER study area.

(Fig. 6). This correspondence reflects the expected relationship between ice retreat from some location within the pack ice and the overall area of ice coverage in any given year. The greater the area covered by sea ice, the later the retreat past a location in the ice pack. The annual PP at Palmer Station and the January production over the sampling region were both inversely related to the area of open water within the icepack but not to the date of ice retreat from the trap (Table 2). Offshore production in January was more strongly influenced by interactions among ice area, open water, and ice retreat (Table 3; $r^2 = 0.94$, $p = 0.008$).

Interannual variation in krill abundance over the northern shelf was not directly related to the patterns of ice extent and duration; however, salp abundance was significantly and inversely correlated with ice area, retreat, and offshore PP. Salp

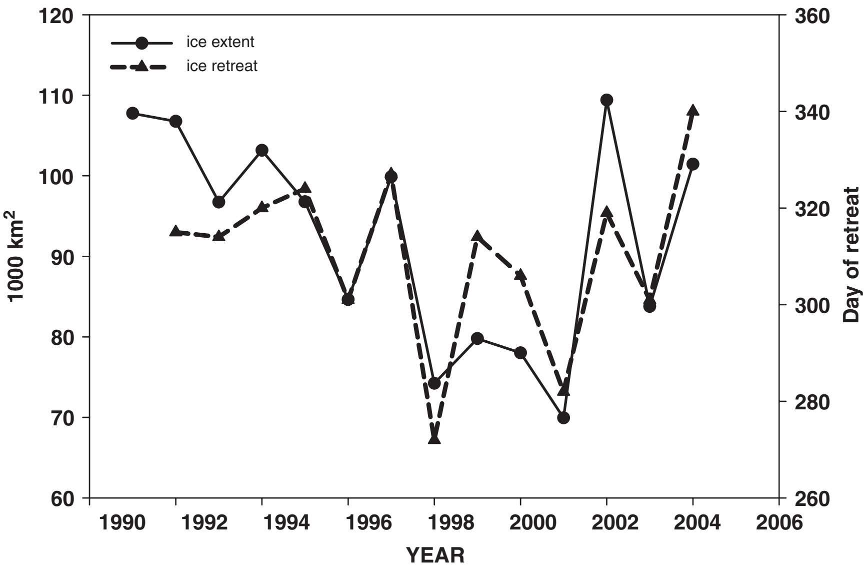

Fig. 6. Multiyear record of relationship between sea-ice extent in the LTER study region and ice retreat from the sediment trap-mooring site (north shelf sector).

abundance anomalies also were directly related to the number of ice-free days at the trap site (Tables 2 and 3).

Sedimentation was not related to the ice indices nor to the PP. Sedimentation anomalies were inversely correlated with krill abundance (Fig. 7) over the full observation period. Sedimentation anomalies were not correlated with salp abundance over the full period, but were directly and strongly correlated during 1998–2004 (Fig. 7). In 1996, sedimentation was lowest in the observation period, and krill were highest. Salps were also high in 1996, weakening the relationship over the full period. This pattern suggested that krill and salps affect sedimentation in opposing directions, and this hypothesis is supported by a significant relationship among the three variables ($r^2 = 0.52$, $p = 0.05$; Table 3).

3.2. Foodweb structure in the WAP and Ross Sea

3.2.1. Input flow structure and observations

The inverse solution method we used selects a best-fit system of trophic exchanges (carbon flows) consistent with observed flows and specified biological constraints (e.g., biomass-specific maintenance respiration, growth efficiencies etc.) for a predefined network of compartments. Our network includes separate compartments for small ($<5\,\mu$m) and large ($>5\,\mu$m) phytoplankton and three size classes of grazers including protozoans, microzooplankton and mesozooplankton. The small and large phytoplanktons represent nanoflagellates and diatoms, respectively, while the mesozooplankton includes copepods and krill. For the Ross Sea a third phytoplankton compartment represents colonial *Phaeocystis*. There are additional compartments for bacteria as well as higher-order predators including myctophid fish and penguins. Nonliving dissolved organic matter and organic detritus compartments complete the system of carbon exchanges. Some obvious exchanges are disallowed (e.g., protozoans eating krill or diatoms consuming particles); otherwise all biologically possible trophic exchanges (e.g., detritovory by microzooplankton) are allowed, and the solution procedure determines their magnitudes based on the specified constraints, the required daily rations and mass balance. A detailed list of constraints can be found in Daniels et al. (2006).

Table 4 provides a summary of observations defining trophic structure and exchange during the phytoplankton blooms in the WAP and southern Ross Sea. Note that while phytoplankton properties are relatively well constrained by observation, exchanges between phytoplankton and grazers, and among the heterotrophs and detrital pools are not. The principal contrasts between the two regions are the dominance of colonial *Phaeocystis* in the Ross Sea and the great dominance of krill ($>2000\,\mathrm{mmol\,C\,m^{-2}}$) in the WAP. There are surprisingly few documented observations for mesozooplankton and krill biomass in the southern Ross Sea. Note also the greater accumulation of plankton biomass in the WAP. In 1999, a year with lower PP (see above and Daniels et al., 2006) the phytoplankton stocks in the WAP were comparable to the Ross Sea observations (Fig. 8). The goal of the model is obtaining an objective and complete description of the full system of trophic exchanges, consistent with these observations and specified biological constraints.

The inverse approach recovers from incomplete observations (Table 3) a complete description of foodweb structure as defined by a network of trophic exchanges among prescribed compartments, from which we can make further structural and functional analyses. Fig. 9 shows the resulting flow networks from the spring/summer blooms in the WAP in 1996 and the southern Ross Sea in 1997. In the WAP, the system is dominated (as expected) by krill grazing of large phytoplankton (diatoms) and by export of krill fecal pellets. Overall in the WAP, the fates or destinations for phytoplankton production are spread evenly across the foodweb, with no single process accounting for more than 60% of the total production (Fig. 10B). Trophic exchanges in the Ross Sea are characterized by large flows through the detrital compartment as a consequence of non-grazing mortality of *P. antarctica* in its unicellular flagellated and colonial forms. Over 80% of the total PP and almost 100% of the PP by *Phaeocystis* enter the detrital pool (Fig. 10A). Only small amounts of the PP are exuded as DOC in either system. An additional pair of large flows in the Ross Sea was unanticipated: heavy ingestion of detritus by microbial grazers (Fig. 9). Mesozooplankton-controlled flows were minor, as required by the low standing stock. In general the dominance of *Phaeocystis*, unpalatable to most grazers (see Section 4) strongly influences the contrasts between these two systems.

4. Discussion

4.1. Interannual variability

The Palmer LTER was established in 1990 within the framing hypothesis that the annual advance and retreat of sea ice is the major physical determinant of spatial and temporal changes in the structure and function of the Antarctic marine ecosystem (Ross et al., 1996). Sea-ice

Table 2
Regression statistics for interannual anomalies of ice and biogeochemical properties

	Ice extent	Ice area	Open water	Ice retreat	Ice advance	Ice-free days	Krill N shelf	Salp N shelf	PP inshore (annual)	PP offshore (January)
PAL PP	ns	ns	0.33 0.06 (14)	ns	ns	ns	ns	ns	—	0.455 0.032 (9)
Grid PP	ns	ns	0.50 0.007 (11)	ns	ns	ns	ns	ns	0.46 0.032 (9)	—
Sedimentation	ns	ns	ns	ns	ns	ns	0.52 0.012 (11)	ns	ns	ns
Sed % PP	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Krill	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Salp		0.36 0.05 (11)		0.37 0.05 (11)		0.35 0.06 (11)				0.46 0.05 (9)

The first row for each entry gives r^2 for the significant least-squares regressions. The significance level and number of samples (parentheses) are also given. ns, not significant.

Table 3
Multiple regression results among annual anomalies (1992–2004) for sea-ice indices, primary production, sedimentation and zooplankton abundance

Dependent variable	Equation[a]	r^2	Significance (*n*)
Offshore PP	1.15(area)−2.47(open)−0.06	0.85	0.004 (9)
Offshore PP	3.12(area)−2.81(open)−7.1(retr) +0.18	0.94	0.008 (9)
Salps	−8.12(retr)−1.12(offPP)−0.26	0.65	0.04 (9)
Sedimentation	0.015(salp)−0.33(krill)+0.02	0.52	0.05 (11)

[a] Area—ice area in grid; Open—area of open water in grid; Retr—day of ice retreat from trap location; OffPP—offshore PP (January); Salp—abundance of salps in northern shelf area of grid; Krill—abundance of krill in northern shelf area of grid.

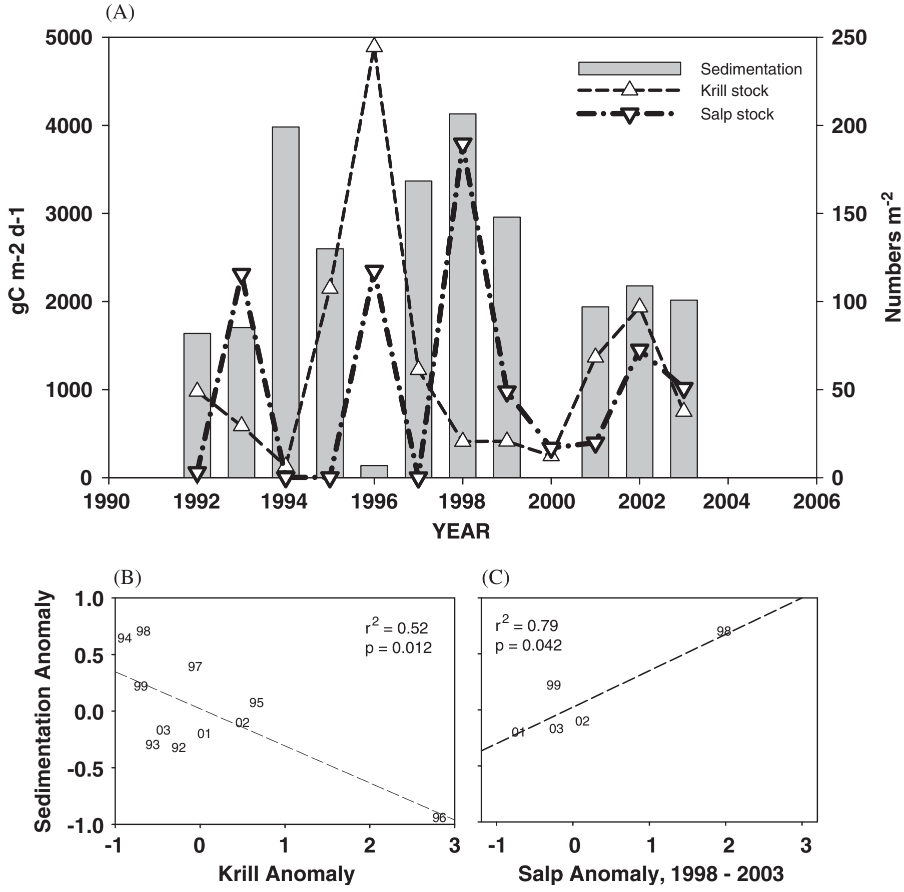

Fig. 7. (A) Sedimentation rate, krill and salp abundance over the northern continental shelf (500 and 600 lines of Fig. 1), 1992–2004. (B, C) Relationships between interannual anomalies of krill or salp abundance with sedimentation anomaly.

variability along the WAP is driven by a global teleconnection to the Southern Oscillation (Smith et al., 1996b; Stammerjohn and Smith, 1996, 1997; Yuan and Martinson, 2000) (Fig. 3) and varies by up to 20–25% interannually. A longer-term declining trend overlies the interannual variability in the WAP region. (Smith et al., 2003). Sea-ice extent in the LTER grid has declined by about 30% since the inception of remote microwave observations in 1979. A major goal of Palmer LTER is discerning and understanding the responses of the Antarctic marine ecosystem to climate change, driven primarily by declining sea ice and regional warming.

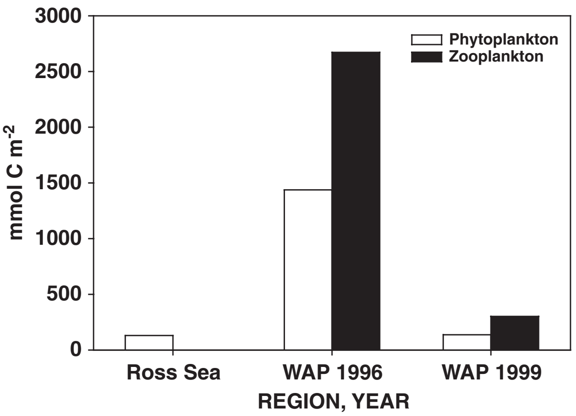

Fig. 8. Observations of phytoplankton and mesozooplankton stocks in the Ross Sea and WAP.

The overarching LTER hypothesis is founded on a conceptual model linking phytoplankton blooms and subsequent trophodynamic processes to ice retreat and stratification by meltwater (Smith and Nelson, 1985; Ackley and Sullivan, 1994). Sinking particle fluxes in marginal ice zones also correspond to this model, with large sedimentation pulses following the ice retreat (Wefer et al., 1988). The Palmer LTER sediment trap mooring provides a decade-long record of sedimentation in the marginal ice zone of the WAP with an annual pulse of sedimentation following the ice retreat in each year (Fig. 4). Fig. 11 shows the sequence of events in the contrasting years of 1995–96, and 1996–97. Ice extent was 5% greater than average in 1995–96 and it retreated past the trap site around day 335 (Table 1), about 25 days later than average. Chlorophyll at Palmer Station E began to bloom in response to the ice retreat, and reached 39 $\mu g\,l^{-1}$ in mid-January (Fig. 11A). There were no winter chlorophyll samples during 1995. Sedimentation was typically low throughout the Austral winter, 1995 and also began to increase following ice retreat. The annual sedimentation in 1996 following the 1995–96 bloom was 28% greater than average (Table 1). In contrast, the following year, ice advanced late and retreated early (Fig. 11B), receding from the trap site on day 305, 5 days earlier than average (Table 1). Chlorophyll was consistently $<10\,\mu g\,l^{-1}$, and the sedimentation was the lowest observed (Figs. 4, 11B) at 0.14 gC $m^{-2}\,yr^{-1}$, 90% below average (Table 1). These two years show how ±5–10% variations in ice extent and retreat modulate large (±30–80%) variations in biogeochemical processes such as sedimentation.

What we lack is a better process-level understanding of the relationship between variations in ice cover, phytoplankton dynamics, and sedimentation. In the classic model, spring blooms track the receding ice edge as phytoplankton become exposed to increasing solar irradiance in a water column stabilized by meltwater (Smith and Nelson, 1985). Arrigo et al. (1998a) suggest that the interaction between ice recession, wind and stratification may determine the size and intensity of the bloom in a given year. In their model, when ice recedes early and if winds are still high, phytoplankton are mixed into deeper water or transported into less favorable areas for growth, and blooms are small. Conversely, in years when ice recedes later when winds are lower, phytoplankton can grow in more stable regimes, fostering larger blooms.

Multiyear observations in the LTER study region along the WAP tend to support this hypothesis. In this paper, our analysis is limited to the time series of climatological mean values for selected sea-ice indices and ecological variables (PP, zooplankton abundance, sedimentation). This data set is still too brief (~10 years) to encompass longer-term variations. However, by extending the analysis to the spatial domain, further insight can be gained regarding relationships among processes. For example, when comparisons are made station by station within the sampling grid (a matrix of >40 stations per year over 13 years), empirical orthogonal function (EOF) analysis shows, for example, that PP is strongly correlated with spatial and temporal patterns of ice extent, retreat and duration, as are distributions and interannual variations in the abundance of different zooplankton groups. Our analysis was limited because sedimentation is measured at only one single location within the study area, and firmer conclusions must await a longer time series, or more trap moorings in other parts of the region.

It is surprising that sedimentation is inversely related to krill abundance. Krill produce large, rapidly sinking fecal pellets, but it may be that heavier sedimentation occurs when krill grazing is lower and more of the phytoplankton stock sinks as ungrazed diatoms, analogous to the prevailing condition in the Ross Sea. It is also possible that krill fragment sinking particles, slowing sedimentation velocities and allowing more time for decomposition during transport (Turner, 2002). Antarctic microbial communities can rapidly decompose fecal pellets (Povero et al., 2003). The direct relationship

Table 4
Input data for inverse foodweb model solutions. Stocks mmol Cm^{-2}; rates mmol $Cm^{-2}\ d^{-1}$

	Total phytoplank production	Small phytoplank production	Large phytoplank production	Diatom production	Colonial phaeocystis production	Phototrophic nanoplank biomass	Phytoplankton biomass	Diatom biomass	Colonial phaeocystis biomass	Bacterial productivity
Ross Sea: November– December 1997										
AVG	95	44	51	8.5	43	33	131	16	82	4.8
St Dev	53	24	29	4.8	24	22	—	14	160	3.7
Min	41	19	22	3.7	19	11	—	—	—	1.1
Max	148	68	80	13.3	66	56	—	—	—	8.5
WAP January 1996										
AVG	255	85	170	na	na	na	1438	na	na	—
St Dev	166	55	111	na	na	na	1008	na	na	—
Min	88	29	59	na	na	na	—	na	na	0
Max	421	140	281	na	na	na	—	na	na	50% of PP
	Bacterial biomass	Heterotroph nanoplank (<20 μm) biomass	Microzoop grazing	Microzoop (20–200 μm) Biomass	Mesozoop grazing	Mesozoop biomass	Export	Adelie grazing	Myctoph grazing	Myctoph biomass
Ross Sea: November– December 1997										
AVG	145	21	0.0	34	—	13.5	—	—	—	—
St Dev	73	12	0.0	21	—	—	—	—	—	—
Min	—	8.6	25% PP	13	0.2	9	13	—	—	—
Max	—	34	75% PP	54	0.5	18	23	—	—	—
WAP January 1996										
AVG	10.09	—	—	—	—	2672	12	0.07	—	0.73
St Dev	5.70	—	—	—	—	—	—	—	—	—
Min	—	—	0	—	37	—	6.0	0.03	0.06	—
Max	—	—	75% PP	—	400	—	—	—	—	—

— not available; na, not applicable.

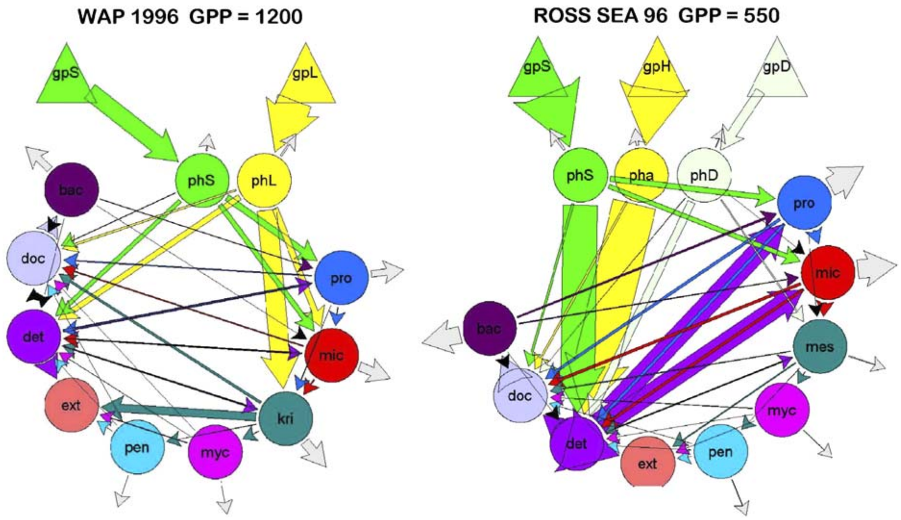

Fig. 9. Foodwebs for the Ross Sea (November 1997) and West Antarctic Peninsula (January 1996) determined from inverse solutions to observations. See text for details. phS, small phytoplankton (nanoflagellates); phL, large phytoplankton (diatoms); pha, colonial *Phaeocystis*; phD, diatoms; pro, protozoan grazers; mic, microzooplankton grazers; mes, mesozooplankton grazers (krill); myc, Myctophid fish; pen, Adèlie penguins; ext, export to external environment; det, particulate detritus and fecal pellets; doc, dissolved organic carbon; bac, bacterioplankton.

between sedimentation and salp abundance is supported in the literature, which abundantly documents the large size and rapid sinking rates of salp pellets (Perissinotto and Pakhomov, 1998). Although the interannual variability in krill abundance was not related in a simple way to sea-ice variability, there was some evidence that salp variations were inversely related to ice retreat—that is, when ice retreated earlier, there were more salps. This finding is consistent with a more through analysis that examined spatial and temporal variability of zooplankton groups in the WAP region, and found that salp abundance was inversely related to ice retreat and the duration of ice cover. Earlier studies (Loeb et al., 1997) established the concept of apparent alternation of salp vs. krill dominance in the Antarctic marine foodweb, also tied to sea-ice variations. Since it now appears that zooplankton exert a direct influence on interannual variations in sedimentation, our model of sedimentation, ice and phytoplankton blooms (Fig. 11) may be too simple. But we caution that the data record is still rather short (11 years) for firm conclusions to be drawn.

Direct relationships between PP and sedimentation have been established at the interbasin to global scale (Suess, 1980). Direct relationships between total PP and sedimentation at the within-region, between-year scale are more difficult to resolve (Pace et al., 1987) and are obscured by interannual variations in the *f*-ratio relating new and total PP. New production is the fraction of the PP supported by external nutrient supplies (e.g., NO_3^-) and it is related over larger scales to the amount of the PP available for export (Eppley and Peterson, 1979; Eppley et al., 1983). In a region experiencing rapid climate change, possible regime shifts in the climate and ecosystem may make these relationships ever harder to resolve. Nonetheless, the annual sedimentation appears to be related to interannual variations in the standing stocks of zooplankton near the mooring site (Fig. 7).

4.2. Foodweb structure

There may be strong contrasts in ecosystem structure and dynamics of different regions in the sea ice zone. We compared two of the most productive Antarctic coastal regions governed by sea-ice dynamics, the Ross Sea and WAP. Arrigo et al. (1998b) estimated that the areal PP rates in the marginal ice zones of the two regions were broadly similar, ranging from 0.66 to 1.69 $\mathrm{gC\,m^{-2}\,d^{-1}}$ and 0.77 to 1.39 $\mathrm{gC\,m^{-2}\,d^{-1}}$ between November and February in the Ross and WAP, respectively. They also estimated that the peak rates of production occurred during November–December in the Ross

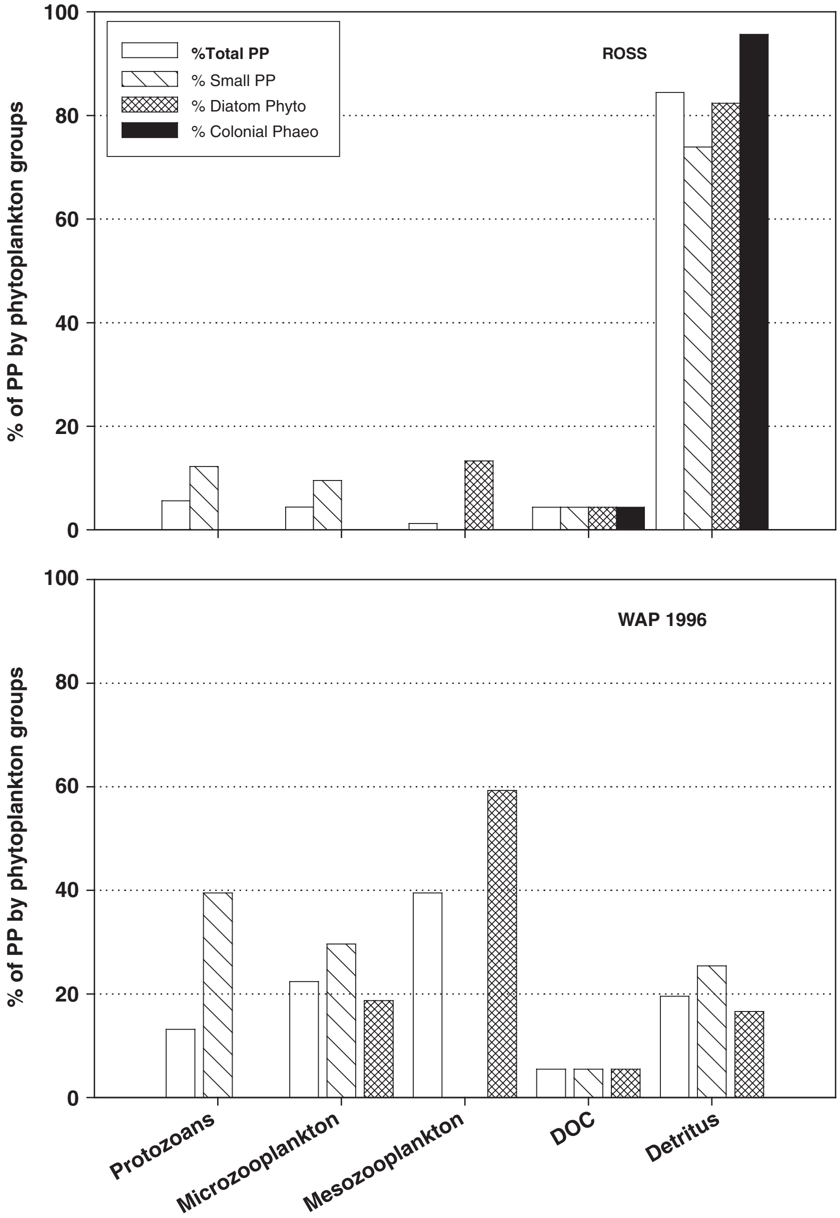

Fig. 10. Fates of primary production size fractions in the Ross Sea and WAP foodweb models.

Sea, and January in the WAP, supporting our decision to compare the two regions during those particular time periods. In the years we compared, PP in WAP was about twice as great as in the Ross Sea (Table 4). Our choice of years was constrained by data availability for the Ross Sea. The disparity in PP did not affect our results, as will be explained below.

We address plankton foodweb structure through construction and analysis of patterns of elemental flows between foodweb compartments (Vézina and Platt, 1988; Ducklow et al., 1989; Daniels et al., 2006). In the case for carbon flows, values of coefficients (or ranges of values for them, see Section 2) for biomass-specific maintenance respiration are applied by the model to prescribed standing stocks (Table 2) for each compartment. This gives the amount of food needed by each group to sustain the observed stocks. The problem then is to determine the food supply for all compartments

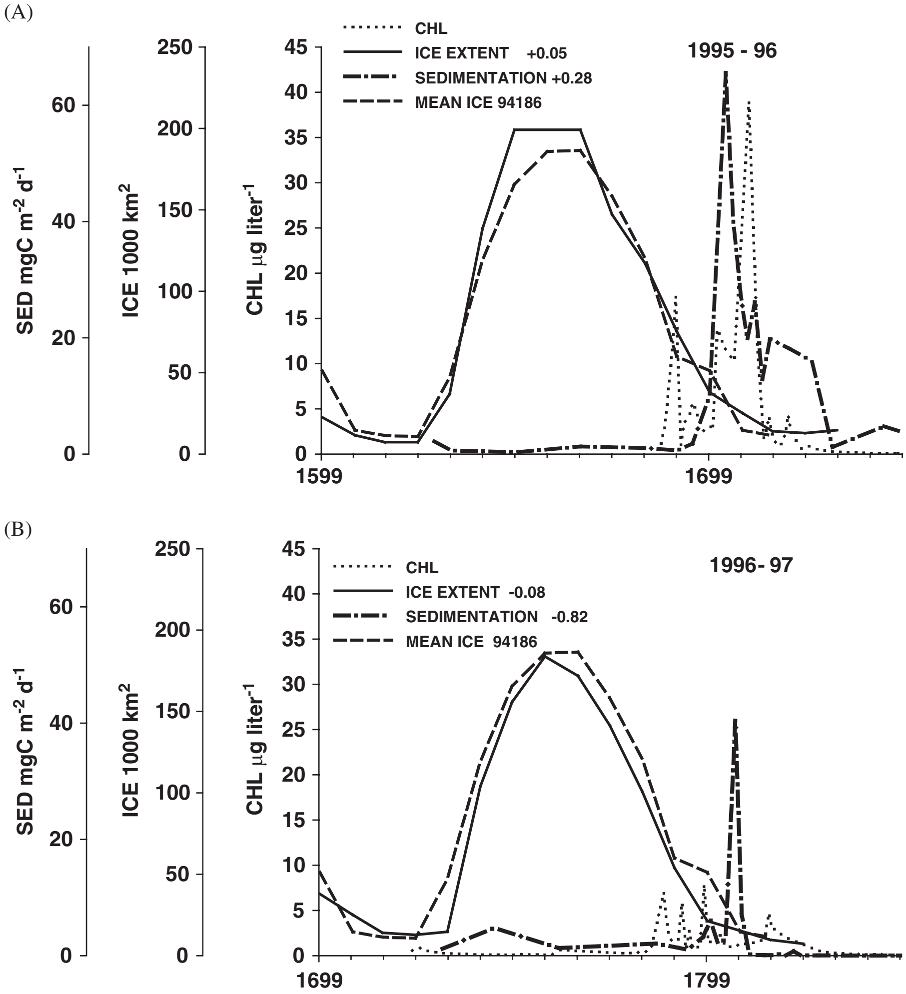

Fig. 11. Observations of sea-ice extent, chlorophyll-*a* and sedimentation in the LTER study region in (A) 1995–96 and (B) 1996–97. Ice extent is the monthly mean in the study region. Chl-*a* measured at Palmer Station. There were no winter observations of Chl-*a* at Palmer Station in 1995.

that satisfies the matrix of energy requirements and grazer rules (who eats what) for the foodweb. Ingested food is apportioned among different fates within organisms according to physiological parameters such as assimilation and growth efficiencies. This procedure sometimes leads to surprising results. For example, the relatively high detrital ingestion rates by the nano- and microzooplankton (Fig. 8) are a consequence of the input biomass (Table 2). They are forced to ingest detritus because the production of small phytoplankton alone is not sufficient to meet their needs.

The primary determinants of the resulting foodweb structures are the observed (or imposed) size composition of the PP and the grazer stocks. In both regions the PP is dominated by large phytoplankton, which minimizes rates of herbivory by microzooplankton, compared to lower latitude foodwebs (Daniels et al., 2006). In the WAP the phytoplankton community is dominated by diatoms (Garibotti et al., 2003) whereas in the Ross Sea the colonial Prymnesiophyte *P. antarctica* is the dominant bloom former (Arrigo et al., 1999). For the two foodwebs we considered, the overall pattern of flows was largely determined by the mesozooplankton biomass, which contrasted greatly between the two areas. Krill biomass is very well constrained in the WAP (Ross et al., 1996b; Loeb et al., 1997) but there are few reports of krill stocks in the Ross Sea interior. The sparse data available suggest krill stocks are lower than in the Bellingshausen—Peninsula sector (Atkinson et al., 2004). In the

WAP in 1996 krill stocks were very high, about double the phytoplankton stocks (Table 4) and about 3 times the average for 1992–2004 in this area. Atkinson et al. (2004) show an abundance of 2–4 individuals per m^2 for the Ross Sea ($\sim$9–18 mmol C m^{-2}) or about 10% of the phytoplankton stock, and this remains the largest uncertainty in our description of the Ross Sea foodweb. The mean for the WAP is about 60 individuals m^{-2}. In spite of the low krill stocks and implied low flows to upper levels of the foodchain (myctophids, Adèlie penguins), these higher predators received enough carbon to sustain observed stocks. We derived Ross Sea penguin stocks from the colony census data and foraging ranges given in Ainley et al. (2003) and used the results from a model of Adèlie penguin growth (Salihoglu et al., 2001) to specify their energy requirements. Penguin respiration is a very small term in the overall carbon budget (Fig. 10), in contrast to earlier hypotheses that upper level predators were an important 'leak' of metabolic CO_2 from the marine ecosystem to the atmosphere (Huntley et al., 1992; and see also Banse, 1995).

As a consequence of contrasting grazer stocks and ingestion rates, our model gave strongly differing patterns of carbon flow for the two regions, as exemplified in the fates of the primary producers (Figs. 9 and 10). The WAP has a foodweb dominated by herbivorous flows from large phytoplankton (diatoms) to krill, and export from the krill via fecal pellet production (Fig. 10B), whereas in the Ross Sea, mesozooplankton grazing is a small removal term (5–15% of large phytoplankton production; Fig. 10A). The reason for this result is that we prescribed that mesozooplankton could not consume colonial *Phaeocystis*. Therefore grazing by mesozooplankton (with a small standing stock) was limited to removal of diatoms, which comprised just 9% of the total PP (Table 4). The fate of ungrazed colonial *Phaeocystis* was mortality and conversion to detritus, followed by export (Figs. 9 and 10).

The literature on *Phaeocystis* is contradictory regarding the role of zooplankton as a removal mechanism. Joiris et al. (1982) observed that grazing was largely absent during the spring bloom dominated by *P. pouchetti* in the Belgian coastal zone, and Verity et al. (1988) subsequently concluded that grazing was not responsible for terminating *P. pouchetti* blooms. They also dismissed sedimentation as a removal process, but Wassmann et al. (1990) observed mass sedimentation of a *P. pouchetti* bloom in the Barents Sea, possibly indicating differences in the dynamics of *Phaeocystis* blooms at mid- and high latitudes. The principal fate for *P. pouchetti* in the North Sea appears to be lysis and decomposition by the microbial foodweb (van Boekel et al., 1992). In contrast to these reports, the dominant copepods in the Greenland Sea ingested *P. pouchetti* (Estep et al., 1990). In the Ross Sea in spring (November–December) mortality of *P. antarctica* is correlated with the ratio of flagellated unicellular forms to colonies and removal of both life stages by grazers of all sizes and feeding modes was low (Smith et al., 2003). We assumed that grazing on *P. antarctica* by krill and mesozooplankton was nonexistent. Increasing the grazing removal by small amounts ($\sim$10%) does not affect the overall conclusions of our modeling study.

To assess contrasting foodweb structure at higher levels of system integration, we used our complete descriptions of trophic exchanges as input to the descriptive foodweb scheme of Legendre and Rassoulzadegan (1996). They postulated three principal fates for PP: (i) decomposition and remineralization within the euphotic zone, (ii) ingestion and transfer up the foodweb, and (iii) sinking of ungrazed cells. In most cases there are only insufficient observations for fully constraining these three processes in any given time and place. Legendre and Rassoulzadegan used indices of foodweb structure, like the ratio of large to small phytoplankton and the matching of production and grazing, as proxies for actual flows in a model of foodweb structure designed to allocate the production among the three fates. Using data from the literature, they were able to quantitatively separate five distinct foodweb types based on the relative importance of the three fates just identified (Table 5). The foodweb types span a gradient from complete sinking of ungrazed phytoplankton (no foodweb processing) through various degrees of microbial and metazoan grazing to full decomposition and incorporation into the microbial loop of dissolved organic matter (no grazing nor sinking). We used our complete descriptions of foodweb processes to examine the two Antarctic sea ice zone ecosystems within this scheme (Table 5).

In Legendre and Rassoulzadegan's idealized scheme based on a family of linear balance equations, the five foodweb types fit evenly along the "everything sinks" to "everything decomposes" continuum (Table 5, top). In our data-based foodwebs (as reconstructed by the inverse modeling

Table 5
Biogenic carbon pathways in plankton foodwebs (Legendre and Rassoulzadegan, 1996)

	P_L/P_T	R_T/P_T	F_T/P_T	D_T/P_T
(1) Sinking of ungrazed cells	1.00	0.00	0.00	1.00
(2) Herbivorous food web	0.80	0.30	0.60	0.10
(3) Multivorous food web	0.35	0.60	0.30	0.10
(4) Microbial food web	0.10	0.80	0.20	0.00
(5) Microbial loop	0.00	1.00	0.00	0.00
Inverse model results[a]				
Ross Sea November 1997	0.54	0.47	0.02	0.50
WAP January 1996	0.67	0.69	0.19	0.11
WAP January 1999	0.67	0.68	0.22	0.10
North Atlantic May 1989	0.50	0.78	0.04	0.18

P_L/P_T is the ratio of large phytoplankton to the total phytoplankton production. R_T/P_T is the ratio of recycled carbon to the net primary production. F_T/P_T is the ratio of carbon passed up the foodweb and exported out of the surface ocean to the net primary production. D_T/P_T is the ratio of sinking phytoplankton to net primary production.

[a] Inverse model values were calculated from the model results. F_T/P_T and D_T/P_T were calculated directly from the model results and R_T/P_T is $1-(F_T/P_T+D_T/P_T)$.

approach) it is less straightforward to place the foodwebs into a single category. In both the Ross Sea and WAP, greater than 50% of the PP was by large phytoplankton (Table 5, bottom), which, if these systems followed the theoretical scheme, would indicate herbivorous to multivorous foodwebs (cf. Table 5, top). However, foodweb transfer was relatively low in both systems ($F_T/P_T{\sim}0.2$). This is because much of the ingested production was remineralized or dissipated as respiration within the foodweb before it could exit from the upper level consumers. Accordingly, recycling was high in both systems ($R_T/P_T{\sim}0.5-0.7$). The one process by which these two systems can be differentiated is sinking of ungrazed phytoplankton, which was high (0.5) in the Ross Sea but low (0.1) in the WAP. We include in Table 5 both the WAP high production season of January 1996 and the low production season of January 1999. In spite of a 3-fold difference in total production, these functional characteristics of the foodweb are identical, suggesting the foodweb is robust over a wide range of total throughput. We also include for comparison results from the North Atlantic bloom in 1989 (Ducklow and Harris, 1993) during which the total PP and its size distribution were similar to the other sites. This mid-latitude (47° North) system was broadly similar to the polar systems with somewhat more intense recycling and low foodweb transfer. Overall, all three systems most resemble multivorous foodwebs. The high degree of recycling and low foodweb transfer indicates surprisingly a strong microbial component in all three cases. This result suggests that old generalizations about the structure and functioning of Antarctic foodwebs dominated by simple linear diatom-krill-predator foodchains and possibly with decoupled (Bird and Karl, 1999) microbial foodwebs are no longer tenable. Furthermore, we demonstrate that foodwebs retain similar functionality across years characterized by contrasting forcing by sea ice and regimes differing in the dominant producers and consumers. Finally we emphasize the strong influence of both phytoplankton (Fig. 9) and zooplankton (Fig. 7) community composition on Antarctic foodweb structure and functioning.

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