

**Water column processes**

**in the West Antarctic Peninsula and the Ross Sea:  
interannual variations and foodweb structure.**

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## INTRODUCTION.

Antarctic coastal waters exhibit high rates of primary production (over  $2 \text{ gC m}^{-2} \text{ d}^{-1}$  and  $100\text{--}200 \text{ gC m}^{-2} \text{ y}^{-1}$ ) during a limited growing season of about 150-180 days (Smith et al. 1996; Smith Jr. et al. 1997; Arrigo et al. 1998; Smith et al. 1998). 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. 1996; Smith et al. 1998). Sea ice retreat triggers an annual spring phytoplankton bloom typically dominated by diatoms, but by *Phaeocystis antarctica* in the Ross Sea (Smith Jr. et al. 1997; Arrigo et al. 1999). This primary production supports large standing stocks of top predators (whales, seals and seabirds; Valiela 1995) and a rich and diverse benthic fauna (REFS to EASIZ 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)(Craig Smith this volume. The plankton foodweb is traditionally thought to be characterized by short food chains leading from diatoms to krill to top predators (REF—Knox book?) although more recently the importance of microbial foodwebs and detritus-based trophic exchanges have been recognized (Hewes 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 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 Jr. et al. 2000), the ROAVERRS Program in the Ross Sea (Arrigo et al. 1998), Southern Ocean Global Ecosystem Dynamics (Hofmann et al. 2001) and the Palmer Long-Term Ecological Research (PAL-LTER) Program (Ross et al. 1996). 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 connections among interannual variability in sea ice, primary production 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.

## 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.who.edu/jg/dir/jgofs/>) and LTER ([http://pal.lternet.edu/datausepolicy\\_03pal.html](http://pal.lternet.edu/datausepolicy_03pal.html)) websites and in cited papers. Southern Ocean Oscillation data were obtained at <http://www.bom.gov.au/climate/current/soihtml1.shtml>. The data used here were taken from these websites.

*West Antarctic Peninsula:* The Palmer Long-Term Ecological Research (PAL-LTER) project has been making routine observations of local and regional ice extent, primary production 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

(Smith et al. 1998; Stammerjohn et al. 2003). Sea ice extent is defined as the ocean area enclosed by the 15% sea ice concentration contour (Smith et al. 1998) as determined in the microwave imagery. This region includes areas with < 15% sea ice cover occurring at subpixel resolution. Sea ice area is the ocean area covered only by ice of >15% concentration. 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 is the date of last occurrence of >15% ice concentration from a given pixel in the ice imagery.

Inshore primary production rates were measured approximately twice per week at Stations B and E in Arthur Harbor near Palmer Station (lat. 64.7 S.; 64.0 W.). These rates were integrated through a 180 day growing season (October 15 to April 15) to obtain total annual production. Offshore primary production rates were determined on annual January cruises in the LTER sampling grid (**Figure 1**). These rates are expressed as the daily means averaged over all grid stations. 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 to mid-January) at 170 meters depth (lat 64.48 S; long 66.04W) in 350 meters depth over the midshelf (Figure 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 (Figure 4), this integration splits each annual peak between two years. Integration from July to July would place each annual peak within one 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 ( $r^2=0.98$ ,  $p<0.001$ ;  $n=7$ ).

Sea ice data were extracted from the Palmer LTER website ([http://pal.lternet.edu/projects/si\\_wap/](http://pal.lternet.edu/projects/si_wap/)). Interannual variability in sea ice and ecological properties was characterized using the standardized anomaly,  $S$ :

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

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 the decade 1991-2002).

*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. (2004). For the WAP, data were taken from January 1996, a year with high primary production relative to the long-term mean (see Daniels et al. 2004 for discussion). Data were selected from LTER grid stations within the foraging radius of Adélie penguins nesting near Palmer Station in that year, as estimated from satellite transmitters mounted on individual penguins (W. R. Fraser, *personal communication*). For the Ross Sea, data were taken from the November, 1997 cruise (NBP97-8; [http://usjgofs.who.edu/jg/dir/jgofs/southern/nbp97\\_8/](http://usjgofs.who.edu/jg/dir/jgofs/southern/nbp97_8/)) because this period was deemed to be most analogous to the January period in the WAP (Daniels et al. 2004). The data used in our models are presented below.

*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 advance and 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 the ice year (see Discussion). Thus the annual sedimentation in 1993 corresponds to the ice extent and retreat for

1992 and so on. Finally, the primary production season is initiated by the spring bloom following ice retreat around day 300 and the full year's integral of primary production extends from October to April. Thus the primary production (PP) year corresponding to the ice and sedimentation years just mentioned would be the 1992-93 season. These designations are listed in Table 1. Graphs are plotted by ice years.

## RESULTS.

### Sea Ice, primary production and sedimentation in the WAP, 1991-2002.

Sea ice extent, primary production and sedimentation all exhibited substantial interannual variations during the decade of LTER observations. The annual sea ice extent in the 200,000 km<sup>2</sup> observation grid (**Figure 1**) averaged 92,234 km<sup>2</sup> 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 up to 25 days earlier or later (Table 1). The local primary production at Palmer Station averaged 172 gC season<sup>-1</sup> (**Figure 2**;  $0.96 \pm 0.60$  gC m<sup>-2</sup> d<sup>-1</sup>). Both PP and 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 (Ropelewski et al. 1987) (**Figure 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<sup>-2</sup> d<sup>-1</sup> in most years (**Figure 4**). Sedimentation at 170 m averaged 2.29 gC m<sup>-2</sup> yr<sup>-1</sup> or 1.4% of the primary production at Palmer Station (Table 1).

Interannual anomalies for ice-related properties were generally somewhat lower than the anomalies for biogeochemical processes of primary production and sedimentation (**Figure 5**). Anomalies for ice extent, area and open water (Smith et al. 1998) ranged from -0.25 to +0.25. The ice extent was above average for 1991-95, then generally below average for 1996-2001, mirroring a declining trend in sea ice coverage over the decade (Table 1). The day of ice retreat near the trap mooring varied less, with no trend. Primary production and sedimentation varied from -0.5 to +0.71 and -0.83 to +0.47, respectively.

*Relationships.* Ice area covaried strongly (in most years) with the date of ice retreat from the sediment trap site (**Figure 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. There is a tendency for the mean January primary production in the LTER study region to be greater in years when the sea ice retreats later from the trap site (**Figure 7A**;  $p=0.07$ ,  $n=8$ ). The annual primary production at Palmer Station and annual sedimentation were not directly related, with no consistent pattern of correspondence between positive and negative anomalies for the two processes (Figure 7B). However both data sets show ENSO-like cycles and the record for sedimentation is incomplete. There was also no relationship between the mean primary production over the LTER Grid and sedimentation (Figure 7B). However there was better correspondence between sedimentation and ice retreat with negative sedimentation anomalies generally matching years of early ice retreat and vice-versa (Figure 7C). One exception is sedimentation year 1999 following the 1998-99 spring bloom (and 1998 ice). In this year sedimentation was almost 7% of the annual PP, about 4 times the average ratio while PP was the

lowest observed in the decade of observations at Palmer Station. 1998-99 was also a year in which the zooplankton community was dominated by salps, which perhaps explains the high export efficiency (Daniels et al. 2004). In general we expect that in high ice years, the ice retreat is late, triggering large phytoplankton blooms and high sedimentation. In years of lower ice extent, ice retreats early, before optimal conditions for the spring bloom, and sedimentation tends to be lower.

### **Foodweb structure in the WAP and Ross Sea.**

*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  $\mu\text{m}$ ) and large (>5  $\mu\text{m}$ ) phytoplankton and three size classes of grazers including protozoans, microzooplankton and mesozooplankton. The small and large phytoplankton 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.

**Table 2** provides a relatively complete, if condensed 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  $\text{mmol C m}^{-2}$ ) 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 primary production (see above and Daniels and Ducklow, 2004) the phytoplankton stocks in the WAP were comparable to the Ross Sea observations (**Figure 8**). The problem for the model is obtaining an objective and complete description of the full system of trophic exchanges, consistent with these observations.

The inverse approach recovers from incomplete observations (Table 2) 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. **Figure 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 (**Figure 10B**). Trophic exchanges in the Ross Sea are characterized by large flows through the detrital compartment as a consequence of non-grazing mortality of *Phaeocystis antarctica* in its unicellular flagellated and colonial forms. Over 80% of the total PP and almost 100% of the PP by *Phaeocystis* enters the detrital pool (Figure 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 (Figure 9). Mesozooplankton-controlled flows were minor, as required by

the low standing stock. In general the dominance of *Phaeocystis*, unpalatable to most grazers (see Discussion) strongly influences the contrasts between these two systems.

## DISCUSSION.

*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 variability along the West Antarctic Peninsula is driven by a global teleconnection to the Southern Oscillation (Smith et al. 1996; Stammerjohn et al. 1996; Stammerjohn et al. 1997; Yuan et al. 2000) (Figure 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.

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 Jr. et al. 1985; Ackley et al. 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 West Antarctic Peninsula with an annual pulse of sedimentation following the ice retreat in each year (Figure 4). **Figure 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  $39 \mu\text{g l}^{-1}$  in mid-January (Figure 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 95-96 bloom was 28% greater than average (Table 1). In contrast, the following year, ice advanced late and retreated early (Figure 11B), receding from the trap site on day 305, 5 days earlier than average (Table 1). Chlorophyll was consistently  $< 10 \mu\text{g l}^{-1}$  and the sedimentation was the lowest observed (Figures 4, 11B) at  $0.45 \text{ gC m}^{-2} \text{ y}^{-1}$ , 82% below average (Table 1). These two years show how  $\pm 5\text{-}10\%$  variations in ice extent and retreat modulate large ( $\pm 30\text{-}80\%$ ) variations in biogeochemical processes like 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 (**REFS- ???**). Arrigo et al. (1998) suggest that the interaction between ice recession, wind and stratification may determine the size and intensity of the bloom in a given year. When ice recedes early and 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 and winds are lower, phytoplankton can grow in more stable regimes, fostering larger blooms. Multiyear observations in the LTER study region along the West Antarctic Peninsula tend to support this hypothesis (Figure 7A).

Direct relationships between primary production and sedimentation have been established at the interbasin to global scale (Suess, Betzer refs). Direct relationships between total primary production and sedimentation at the within-region, between-year scale are more difficult to resolve (Pace ref) and are obscured by interannual variations in the f-ratio relating new and total primary production. New production is the fraction of the primary production supported by external nutrient supplies (e.g.,  $\text{NO}_3^-$ ) and it is related over larger scales to the amount of the primary production available for export (Eppley et al. 1979; Eppley et al. 1983). New production has not been measured directly in the WAP but the sediment trap observations suggest the long term e- (export) ratio varies by an order of magnitude (Table 1). For example, in a year with PP half as great as in a preceding year, if the export ratio is greater, any relationship between primary production and export will be obscured (e.g., 1996-97 and 97-98 in Table 1). Longer records seem required for better understanding. However 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 data of ice retreat from our mooring site (Figure 7C).

*Foodweb structure.* There may be strong contrasts in ecosystem structure and dynamics of different regions in the sea ice zone. We compared the two most productive Antarctic coastal regions governed by sea ice dynamics, the Ross Sea and WAP. **Need to discuss remote sensing observations on phyto stocks in 2 areas – Arrigo, Smith et al, Longhurst** Arrigo et al (1998) estimated that the areal primary production rates in the marginal ice zones of the two regions were broadly similar, ranging from 0.66 to 1.69  $\text{gC m}^{-2} \text{d}^{-1}$  and 0.77 to 1.39  $\text{gC m}^{-2} \text{d}^{-1}$  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 Sea, and January in the WAP, supporting our decision to compare the two regions during those particular time periods. In the years we compared, primary production in WAP was about twice as great as in the Ross Sea (Table 3). Our choice of years was constrained by data availability for the Ross Sea. The disparity in primary production 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 et al. 1988; Ducklow et al. 1989; Daniels et al. 2004). In the case for carbon flows, values of coefficients (or ranges of values for them, see Methods) 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 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 (Figure 9) are a consequence of the input biomass (Table 2). They are forced to ingest detritus because the available small phytoplankton production 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 primary production and the grazer stocks. In both regions the primary production is dominated by large phytoplankton, which minimizes rates of herbivory by microzooplankton, compared to lower latitude foodwebs (Daniels et al. 2004). In the WAP the phytoplankton community is dominated by diatoms (Garibotti et al. 2003) whereas in the Ross Sea the colonial Prymnesiophyte *Phaeocystis 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 West Antarctic Peninsula (Ross et al. 1996; 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 2) but about average for the 1991-2000 decade in this area (data not shown). Atkinson et al (2004) show an abundance of 2-4 individuals per m<sup>2</sup> for the Ross Sea (~9-18 mmol C m<sup>-2</sup>) or about 10% of the phytoplankton stock and this remains the largest uncertainty in our description of the Ross Sea foodweb. 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 (Figure 9), in contrast to earlier hypotheses that upper level predators were an important ‘leak’ of metabolic CO<sub>2</sub> from the marine ecosystem to the atmosphere (Huntley et al. 1992; and see also Banse 1995).

In consequence of contrasting grazer stocks and their estimated ingestion rates, our model gave strongly differing patterns of carbon flow for the two regions, as exemplified in the fates of the primary producers (Figures 9, 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 (Figure 10B), whereas in the Ross Sea, mesozooplankton grazing is a small removal term (5-15% of large phytoplankton production; Figure 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 2). The fate of ungrazed colonial *Phaeocystis* was mortality and conversion to detritus, followed by export (Figures, 9, 10).

The literature on *Phaeocystis* is still conflicting as regards firm conclusions about 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 Wassman 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 *Phaeocystis 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 Jr. et al. 2003). We assumed that grazing on *P. Antarctica* by krill and mesozooplankton was nonexistent. Increasing the grazing removal by small amounts (~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 Rassoulzedegan (1996). They postulated three principal fates for primary production: decomposition and remineralization within the euphotic zone, ingestion and transfer up the foodweb and 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 Rassoulzedegan 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 3). 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 3).

In Legendre and Rassoulzedegan'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 3, top). In our data-based foodwebs (as reconstructed by the inverse modeling 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 primary production was by large phytoplankton (Table 3, bottom), which, if these systems followed the theoretical scheme, would indicate herbivorous to multivorous foodwebs (cf. Table 3, 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 3 both the WAP high production season of January, 1996 (Figure 7A) and the low production season of January 1999 (Figure 7A). In spite of a three-fold difference in total production the structural 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 et al. 1993) during which the total primary production 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 indicate surprisingly a strong microbial component in all 3

cases. This result suggests that old generalizations about the structure and functioning of Antarctic foodwebs dominated by simple linear diatom-krill-predator foodchains (REF) and possibly with attenuated or malfunctioning microbial foodwebs (Karl ref?) are no longer tenable. Furthermore, we demonstrate that foodwebs retain similar structure across years characterized by contrasting forcing by sea ice and regimes differing in the dominant producers and consumers.

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**Table 1.** Sea ice extent, day of ice retreat, primary production and sedimentation near Palmer Station, Antarctica. Note staggering of years for ice, PP and sedimentation data (see text for explanation). Primary production is integrated over 180 days, 15 Oct to 15 April. Ice and sedimentation are calculated over calendar years.

Pri. Prod. Season	Ice year	Sedimentation year	Sea ice extent kilometers	Sea ice retreat* day of year	Primary Prod. gC m <sup>-2</sup>	Sedimentation gC m <sup>-2</sup> y <sup>-1</sup> (% of PP)
1991-92	1991	1992	107753	na	250	na
1992-93	1992	1993	106750	295	120	2.52 (2.1)
1993-94	1993	1994	96733	320	60	1.09 (1.8)
1994-95	1994	1995	103164	330	177	3.47 (2.0)
1995-96	1995	1996	96765	335	351	3.20 (0.9)
1996-97	1996	1997	84627	305	212	0.45 (0.2)
1997-98	1997	1998	99872	330	106	3.13 (3.0)
1998-99	1998	1999	74213	285	47	3.11 (6.7)
1999-00	1999	2000	79780	320	63	na
2000-01	2000	2001	78005	305	293	na
2001-02	2001	2002	69932	305	212	1.76 (0.8)
2002-03	2002	2003	110298	na	176	1.77 (na)
2003-04	2003	2004	na	na	na	na
Mean	--	--	92324	310	172	2.29 (1.4)

\*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.

**Table 2.** Input data for inverse foodweb model solutions. – not available. na, not applicable.

	<b>Total Phytoplank Production</b>	<b>Small Phytoplank Production</b>	<b>Large Phytoplank Production</b>	<b>Diatom Production</b>	<b>Colonial Phaeocystis Production</b>	<b>Phototrophic Nanoplank Biomass</b>	<b>Phytoplankton Biomass</b>	<b>Diatom Biomass</b>	<b>Colonial Phaeocystis Biomass</b>	<b>Bacterial Productivity</b>
<b>Ross Sea: Nov -Dec 1997</b>										
<b>AVG</b>	95	44	51	8.5	43	33	131	16	82	4.8
<b>St Dev</b>	53	24	29	4.8	24	22	–	14	160	3.7
<b>Min</b>	41	19	22	3.7	19	11	–	–	–	1.1
<b>Max</b>	148	68	80	13.3	66	56	–	–	–	8.5
<b>Change</b>	0	0	0			0	–	–	–	0
<b>Model Output</b>	46	19	27	8.0	19	–	–	–	–	1.1
<b>WAP January 1996</b>										
<b>AVG</b>	255	85	170	na	na	na	1438	na	na	–
<b>St Dev</b>	166	55	111	na	na	na	1008	na	na	–
<b>Min</b>	88	29	59	na	na	na	–	na	na	0
<b>Max</b>	421	140	281	na	na	na	–	na	na	50 % of PP

**Table 2.** Input data for inverse foodweb model solutions (continued).

	<b>Bacterial biomass</b>	<b>Heterotroph Nanoplank (&lt; 20 um) Biomass</b>	<b>Microzoop Grazing</b>	<b>Microzoop (20-200um) Biomass</b>	<b>Mesozoop Grazing</b>	<b>Mesozoop Biomass<sup>1</sup></b>	<b>Export</b>	<b>Adelie Grazing</b>	<b>Myctoph Grazing</b>	<b>Myctoph Biomass</b>
<b>Ross Sea: Nov -Dec 1997</b>										
<b>AVG</b>	145	21	0.0	34	–	13.5	–	–	–	–
<b>St Dev</b>	73	12	0.0	21	–	–	–	–	–	–
<b>Min</b>	–	8.6	25% PP	13	0.2	9	13	–	–	–
<b>Max</b>	–	34	75% PP	54	0.5	18	23	–	–	–
<b>Change</b>	0	0	0	0	–	0	0	–	–	–
<b>Model Output</b>	–	–	57% PP	–	0.4	–	13	–	–	–
<b>WAP January 1996</b>										
<b>AVG</b>	10.09	–	–	–	–	2672	12	0.07	–	0.73
<b>St Dev</b>	5.70	–	–	–	–	–	–	–	–	–
<b>Min</b>	–	–	0	–	37	–	6.0	0.03	0.06	–
<b>Max</b>	–	–	75 % PP	–	400	–	–	–	–	–

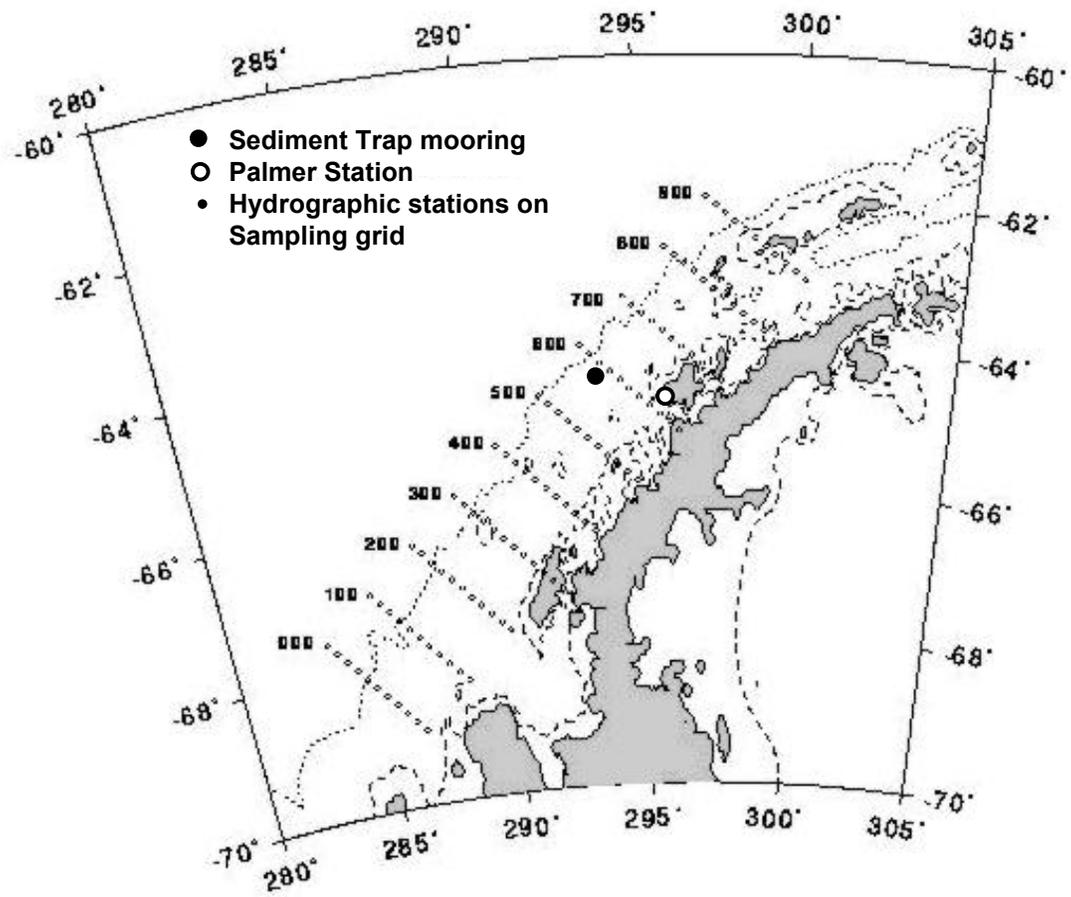
**Table 3.** Biogenic carbon pathways in plankton foodwebs (Legendre & Rassoulzadegan, 1996).  $P_L/P_T$  is the ratio of large phytoplankton to the total net phytoplankton production.  $M$  is the degree of matching between phytoplankton production and zooplankton grazing.  $R_T/P_T$  is the ratio of recycled carbon to the net primary production.  $F_T/P_T$  is the ratio of carbon passed up the food web 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.

	$P_L/P_T$	$M$	$R_T/P_T$	$F_T/P_T$	$D_T/P_T$
(1) Sinking of ungrazed cells	1.00	0.00	0.00	0.00	1.00
(2) Herbivorous food web	0.80	0.55	0.30	0.60	0.10
(3) Multivorous food web	0.35	0.65	0.60	0.30	0.10
(4) Microbial food web	0.10	0.25 or 0.75	0.80	0.20	0.00
(5) Microbial loop	0.00	0 or 1	1.00	0.00	0.00
<b>Inverse Model results<sup>1</sup></b>					
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

<sup>1</sup> 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  $1 - (F_T/P_T + D_T/P_T)$ . The matching coefficient  $M$  was not expressed for the inverse model results because this was an arbitrary value chosen by Legendre & Rassoulzadegan for the 5 different food web types.

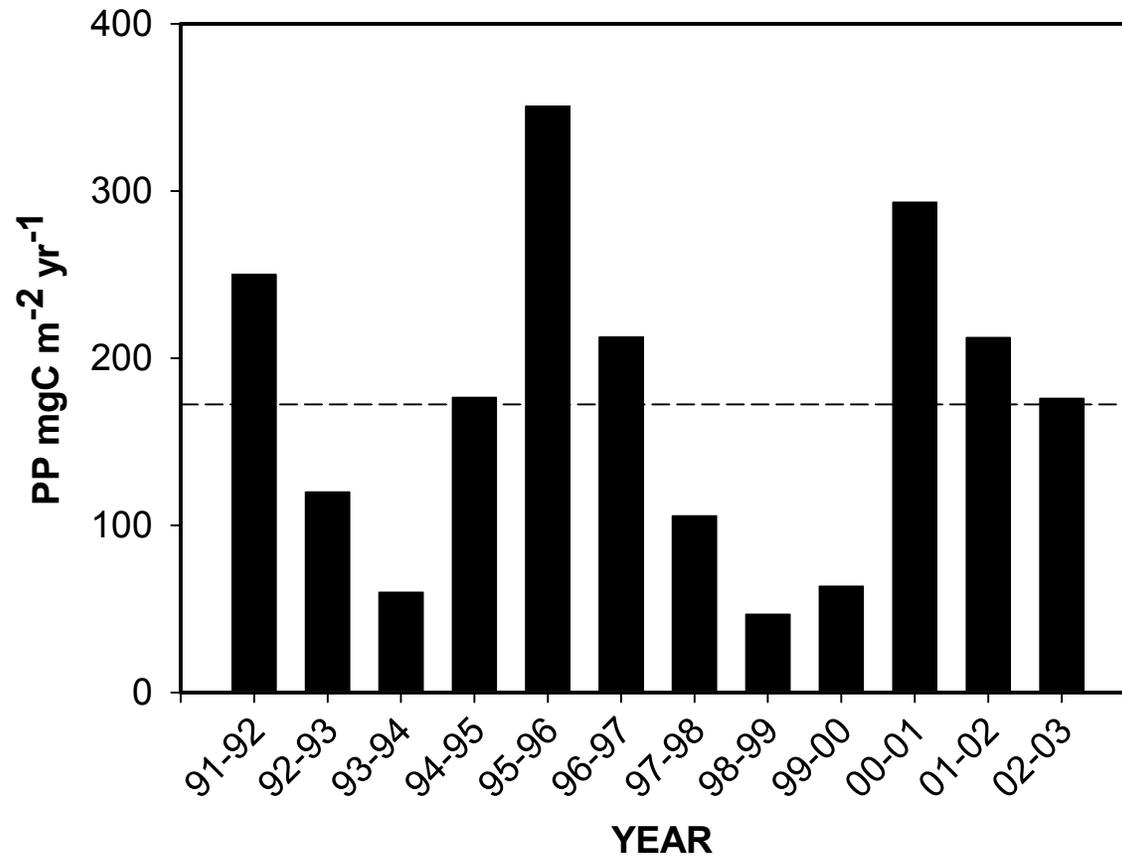
## Figure legends

- Figure 1.** Palmer Long-Term Ecological Research sampling region. The 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 locations of Palmer Station, site of semiweekly local sampling and the sediment trap mooring are also depicted.
- Figure 2.** Multiyear record of annual primary production (October-April) at Palmer Station.
- Figure 3.** Relationship between Southern Oscillation Index and ice extent within the LTER study area.
- Figure 4.** Multiyear record of annual sedimentation within the LTER study area.
- Figure 5.** Interannual anomalies for ice and ecological properties within the LTER study area.
- Figure 6.** Multiyear record of relationships between ice area in the LTER study region and retreat from the sediment trap mooring site.
- Figure 7.** A. relationship between mean regional primary production in January in the study region and ice retreat from the sediment trap mooring site. B. relationship between local and regional primary production and sedimentation in the LTER study region. C. relationship between ice retreat and sedimentation.
- Figure 8.** Observations of phytoplankton and mesozooplankton stocks in the Ross Sea and WAP.
- Figure 9.** Foodwebs for the Ross Sea (Nov. 1997) and West Antarctic Peninsula (Jan. 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.
- Figure 10.** Fates of primary production size fractions in the Ross Sea and WAP foodweb models.
- Figure 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 annual 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.

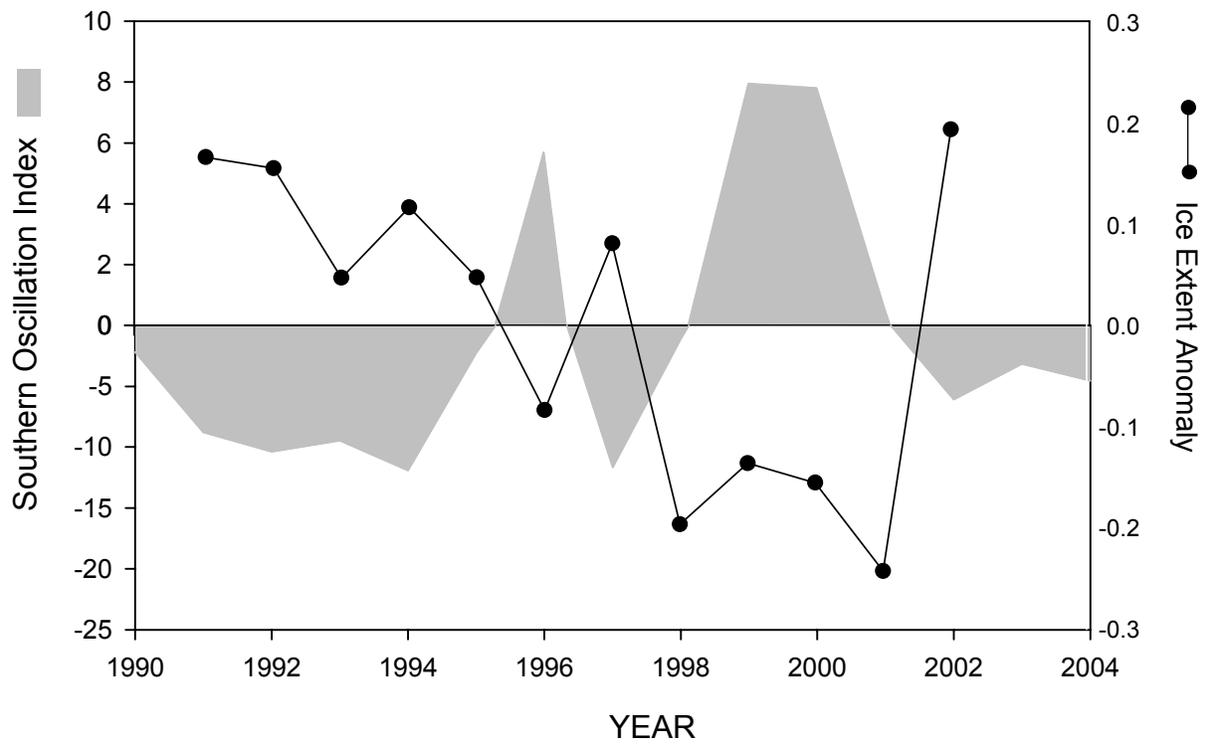


**Figure 1.** Ducklow and Daniels EASIZ volume

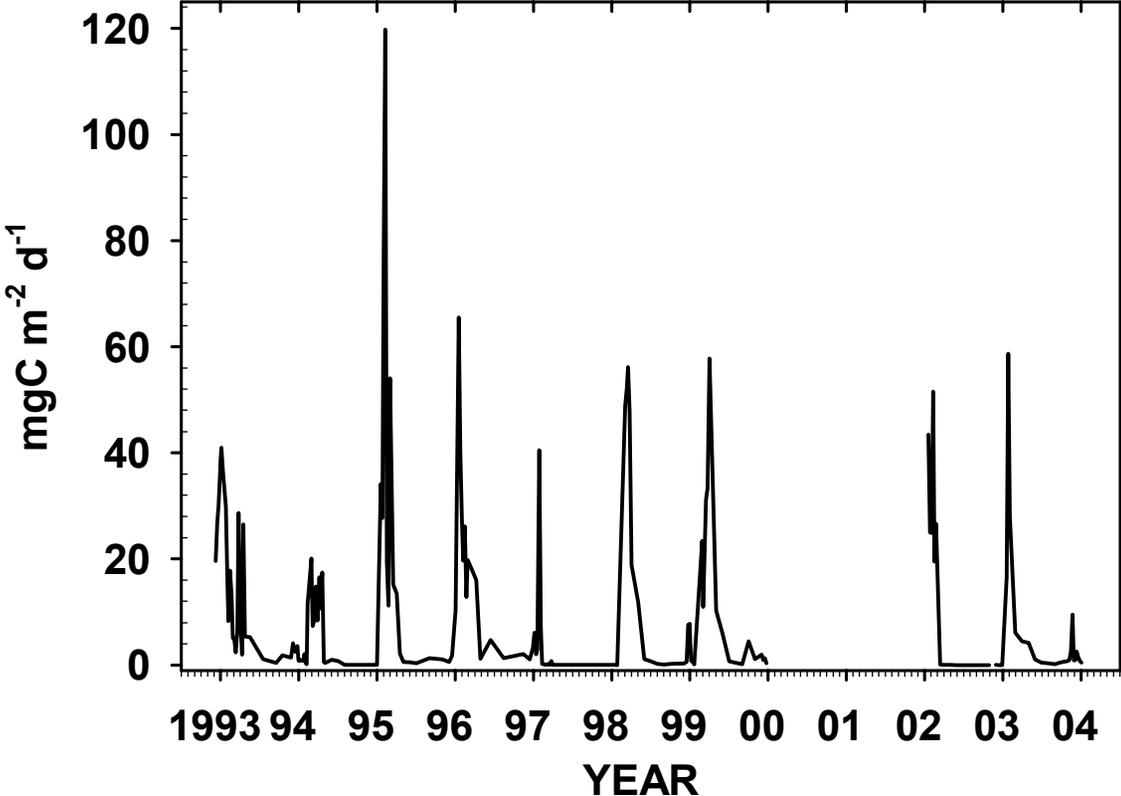
**Figure 2.** Ducklow & Daniels EASIZ volume.



**Figure 3.** Ducklow and Daniels EASIZ



**Figure 4.** Ducklow and Daniels EASIZ volume.



**Figure 5.** Ducklow & Daniels EASIZ Volume.

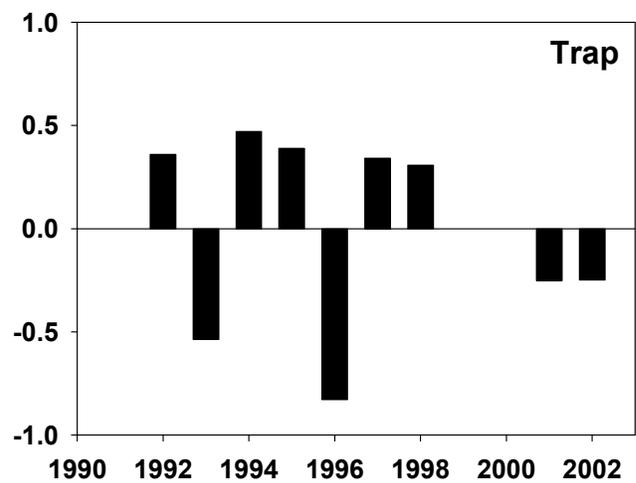
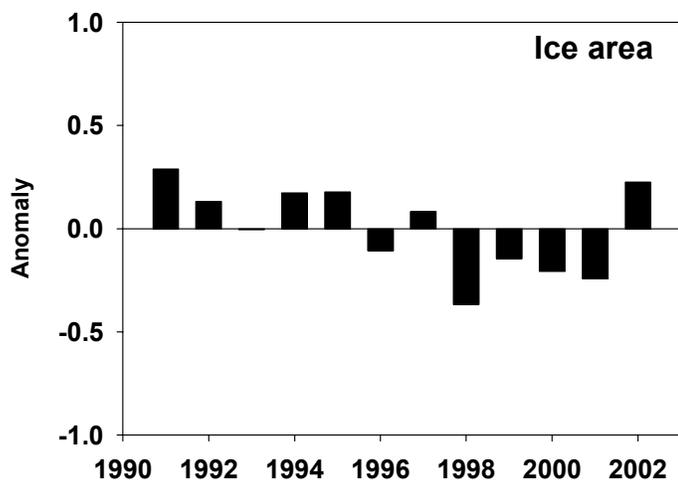
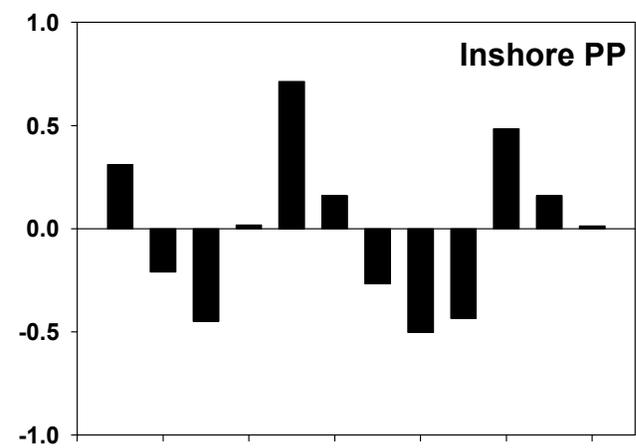
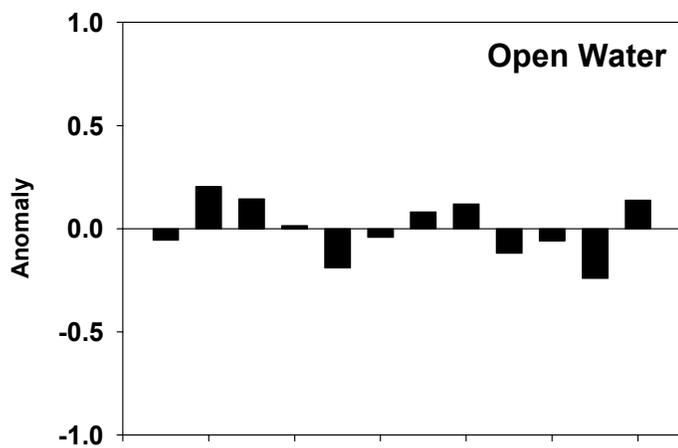
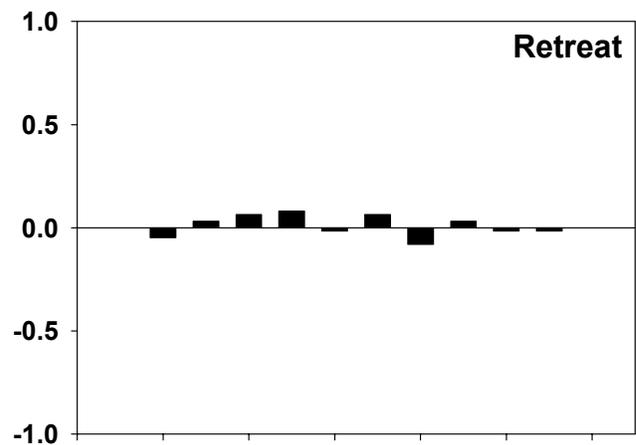
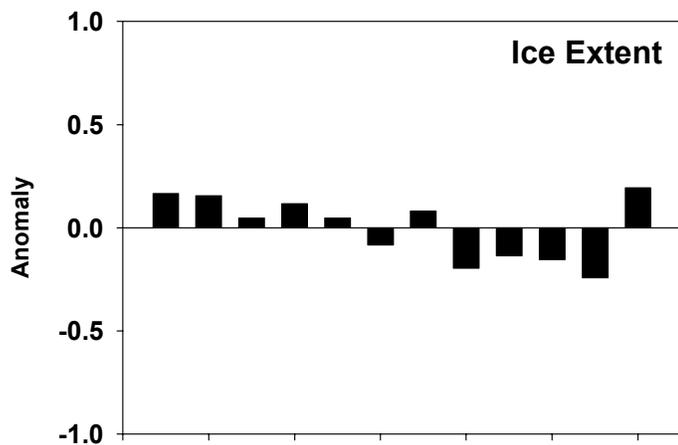


Figure 6. Ducklow & Daniels EASIZ volume.

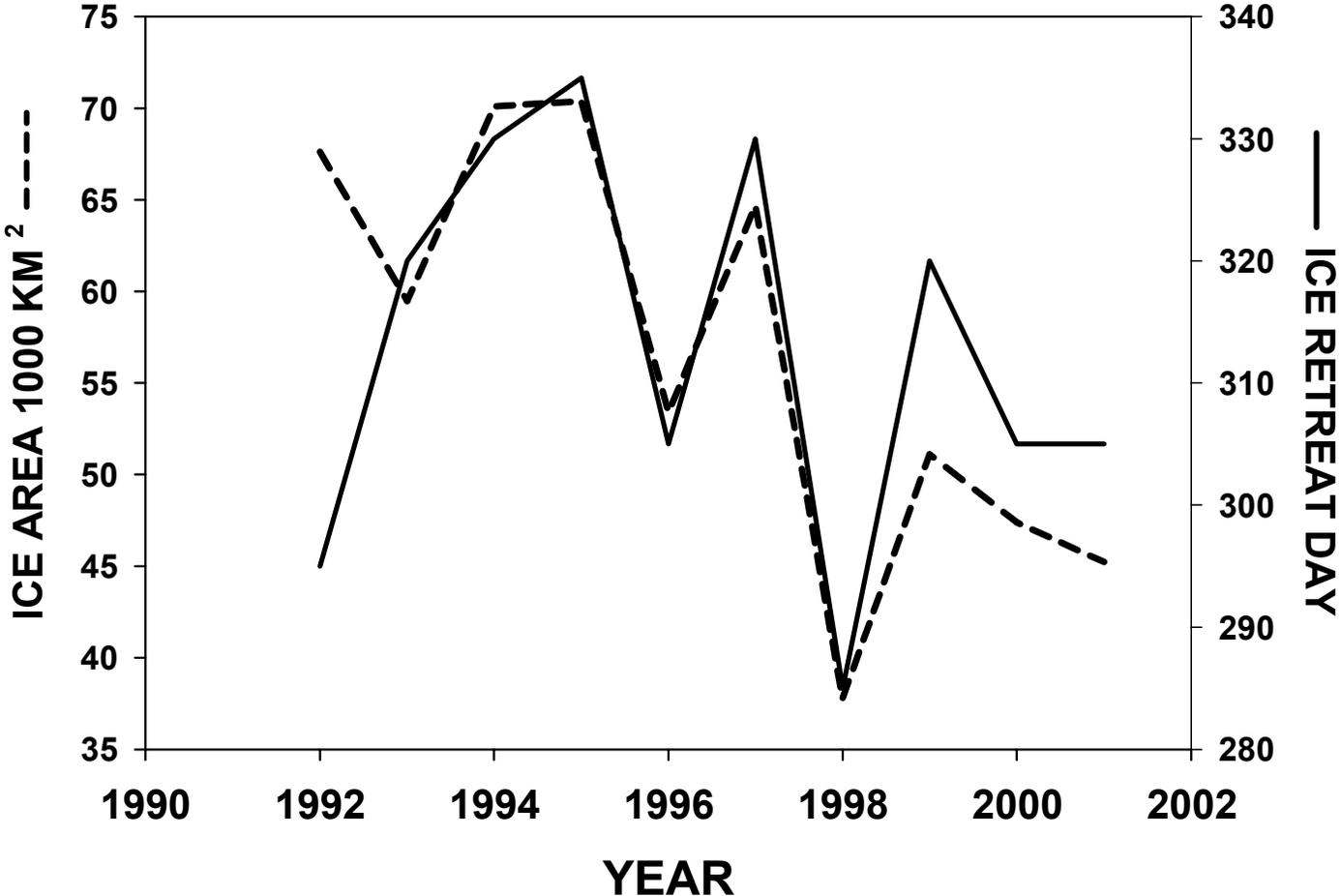
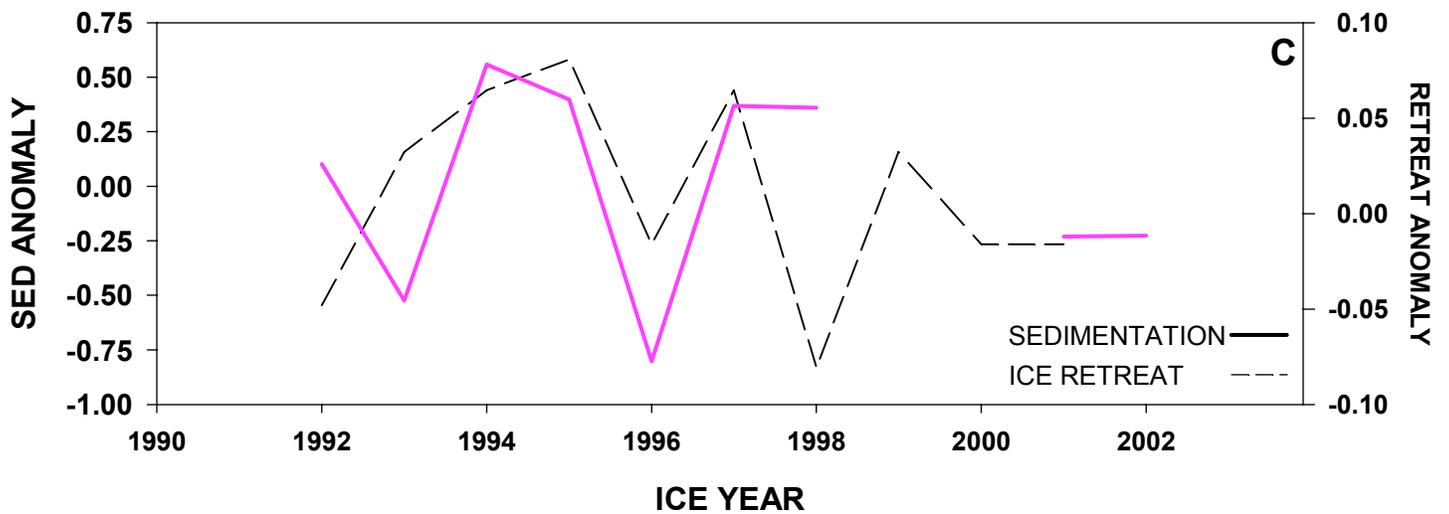
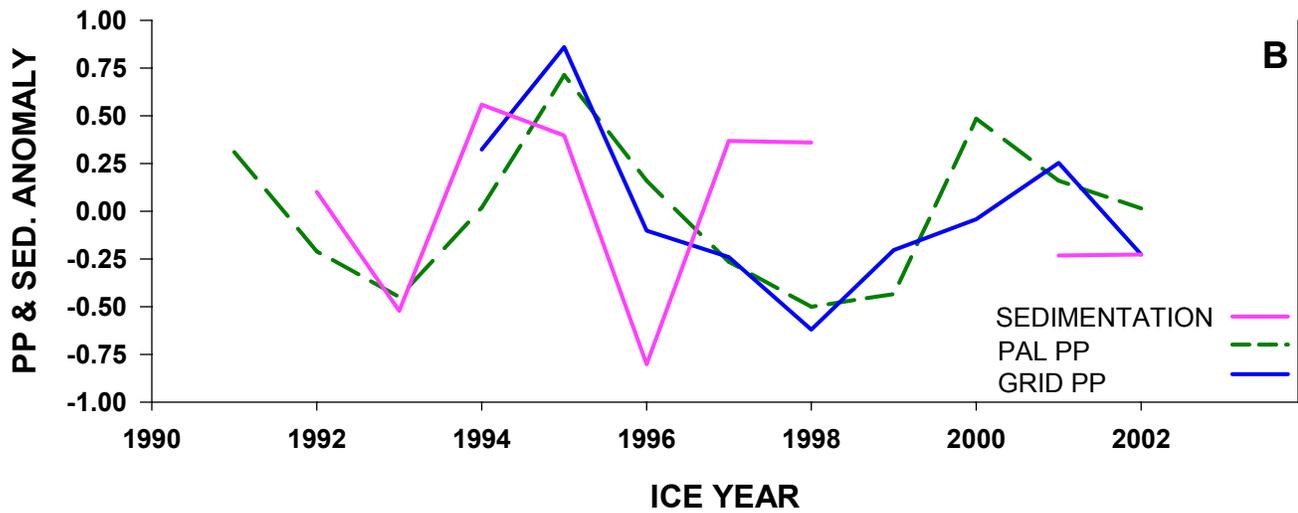
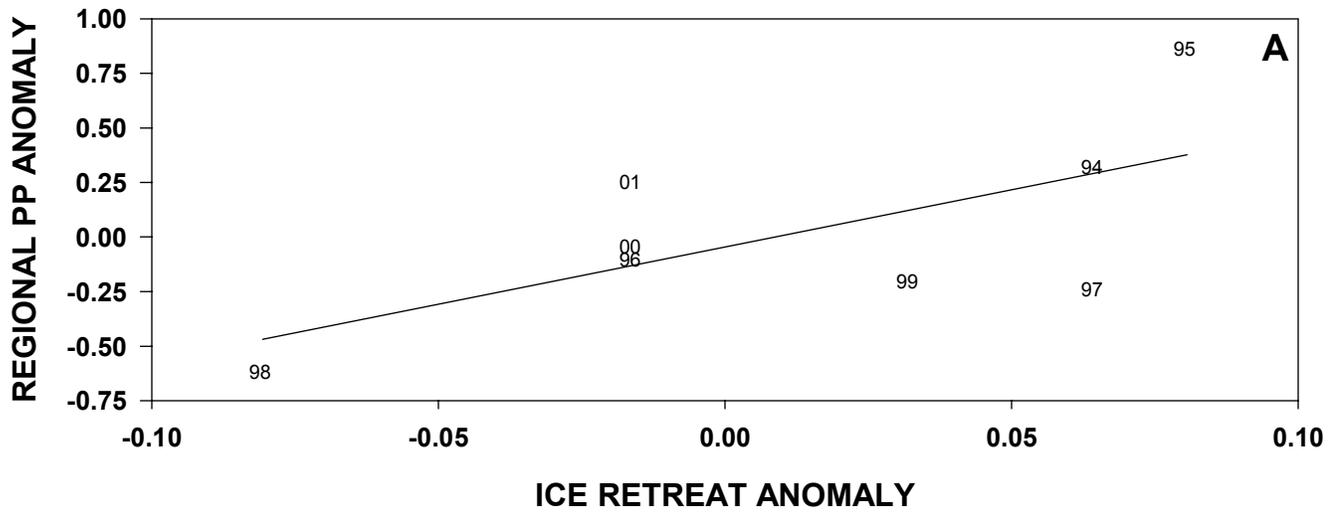
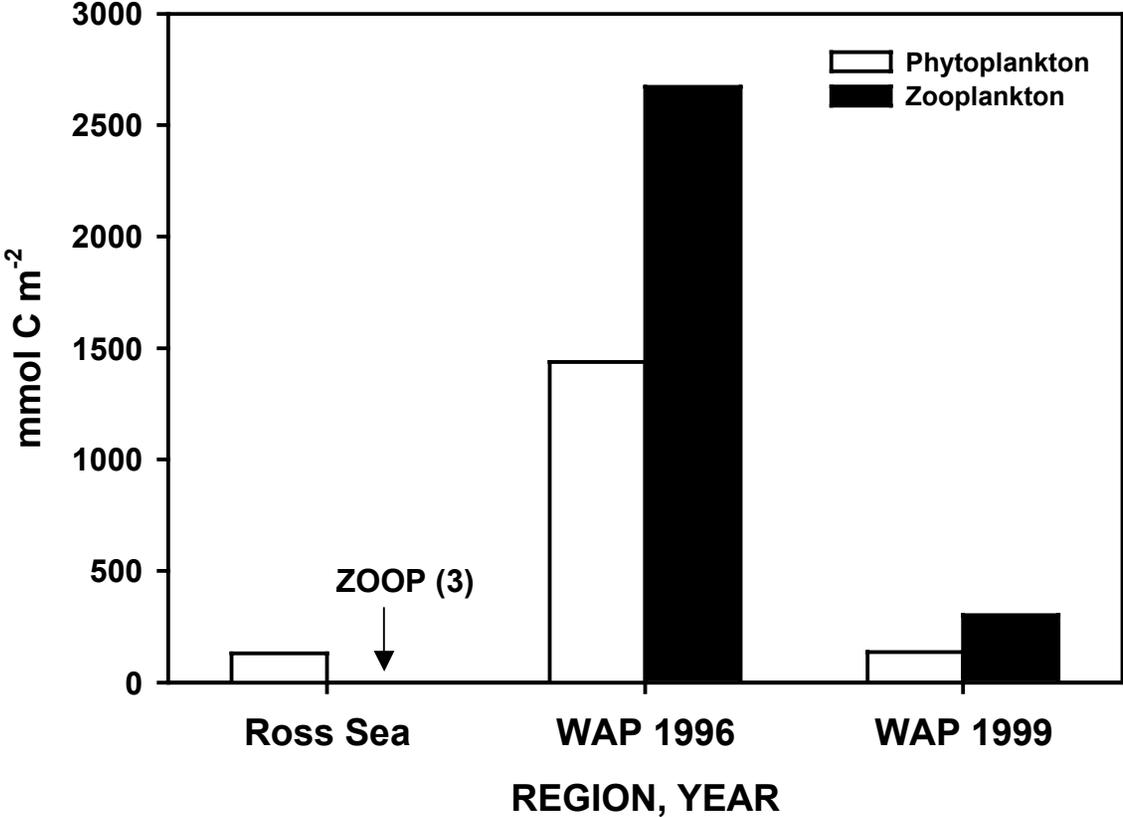


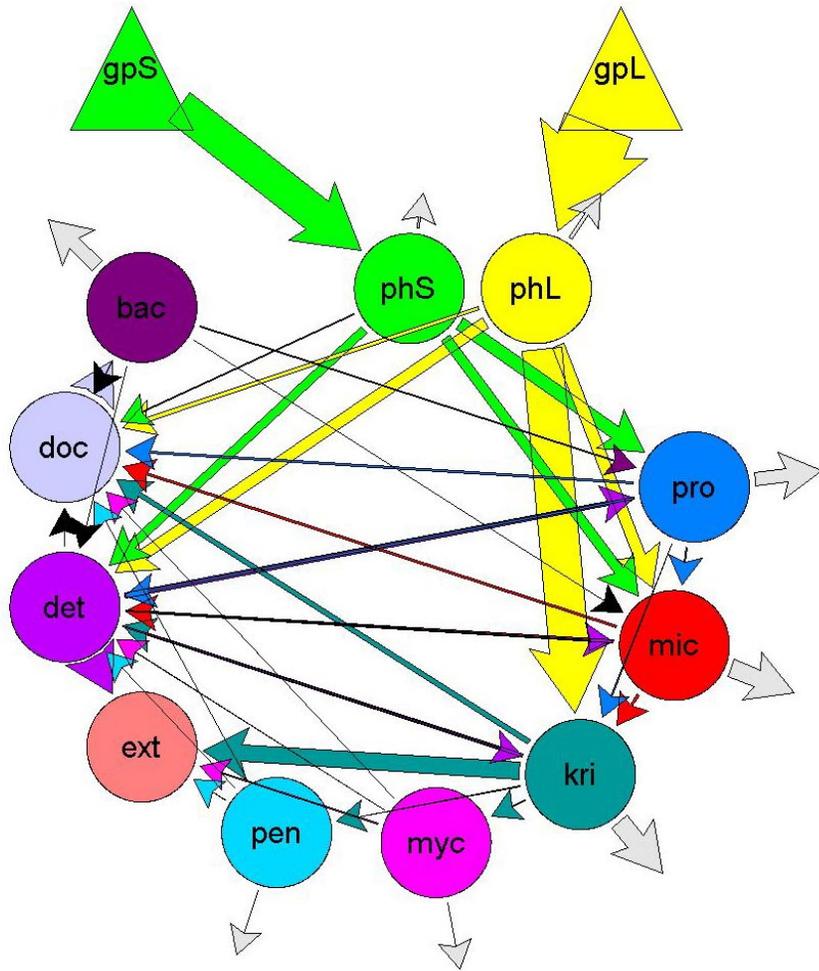
Figure 7. Ducklow & Daniels EASIZ volume.



**Figure 8.** Ducklow & Daniels, EASIZ article



WAP 1996 GPP = 1200



ROSS SEA 96 GPP = 550

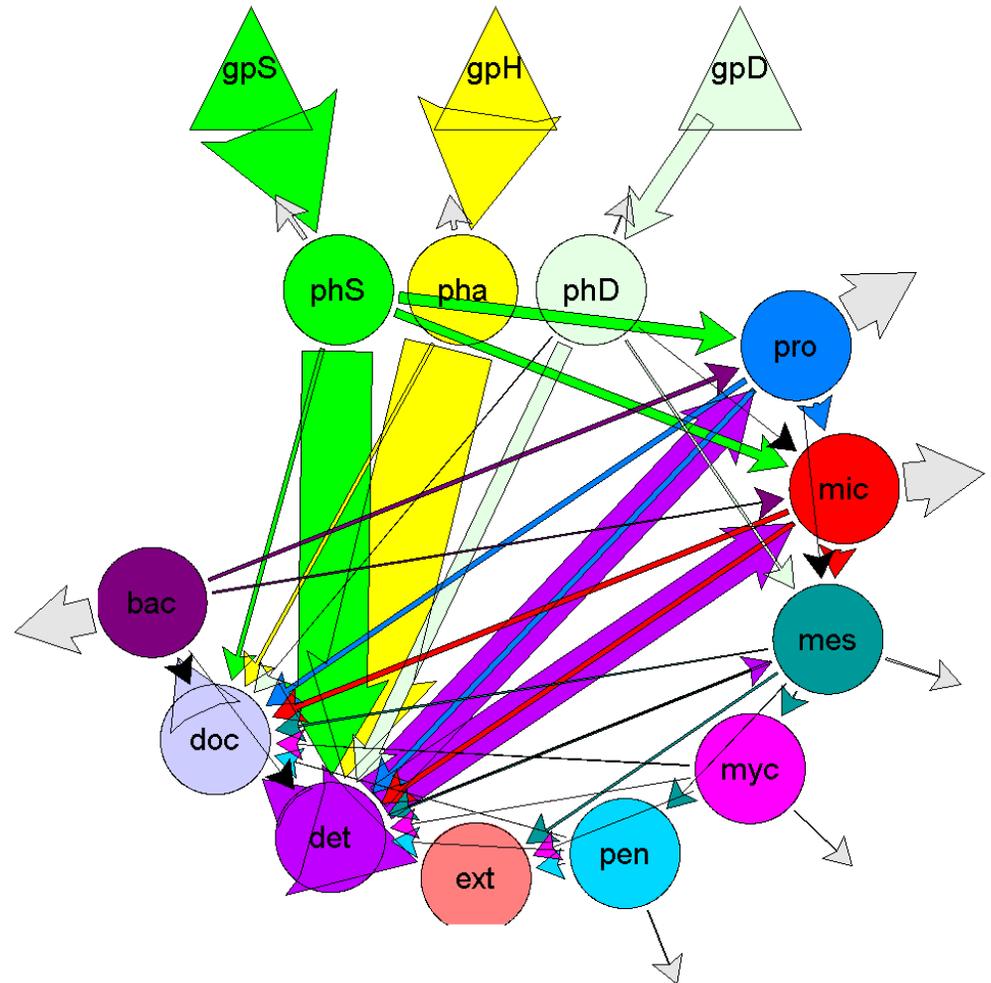


Figure 9 Ducklow and Daniels EASIZ article

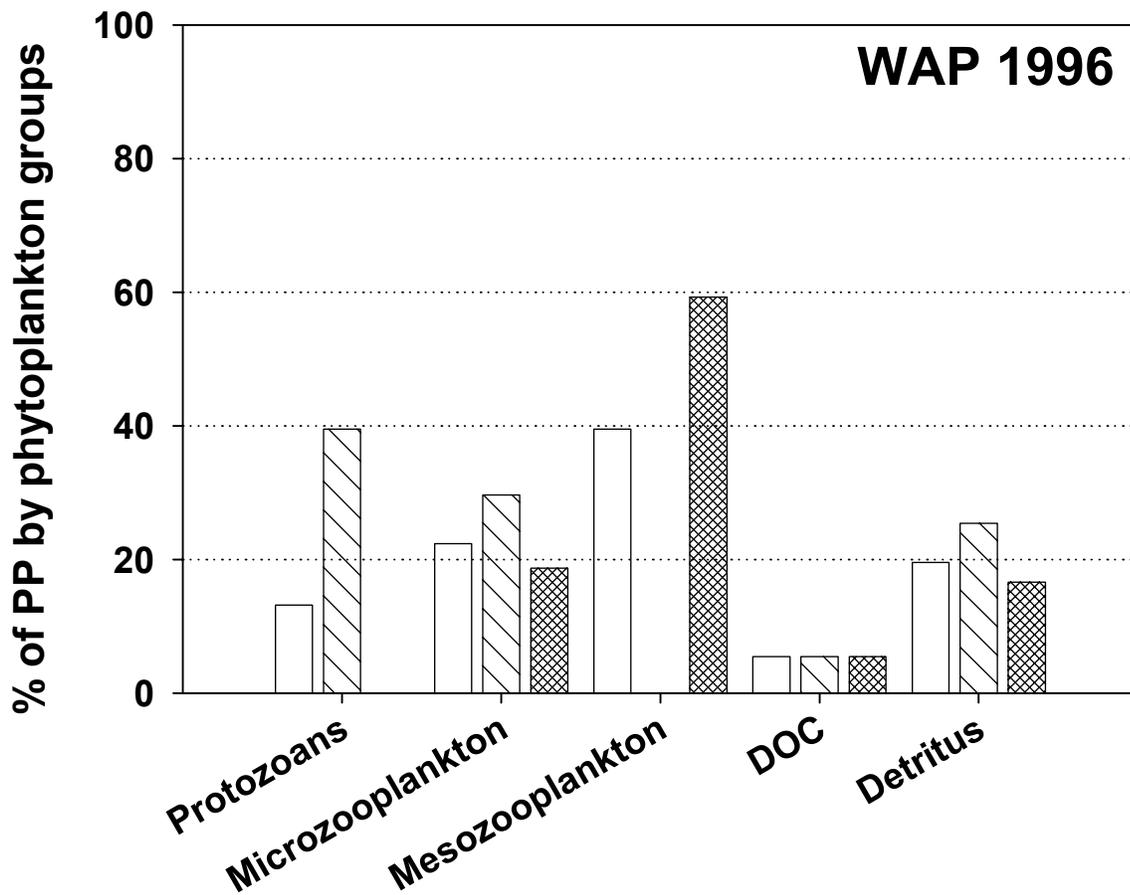
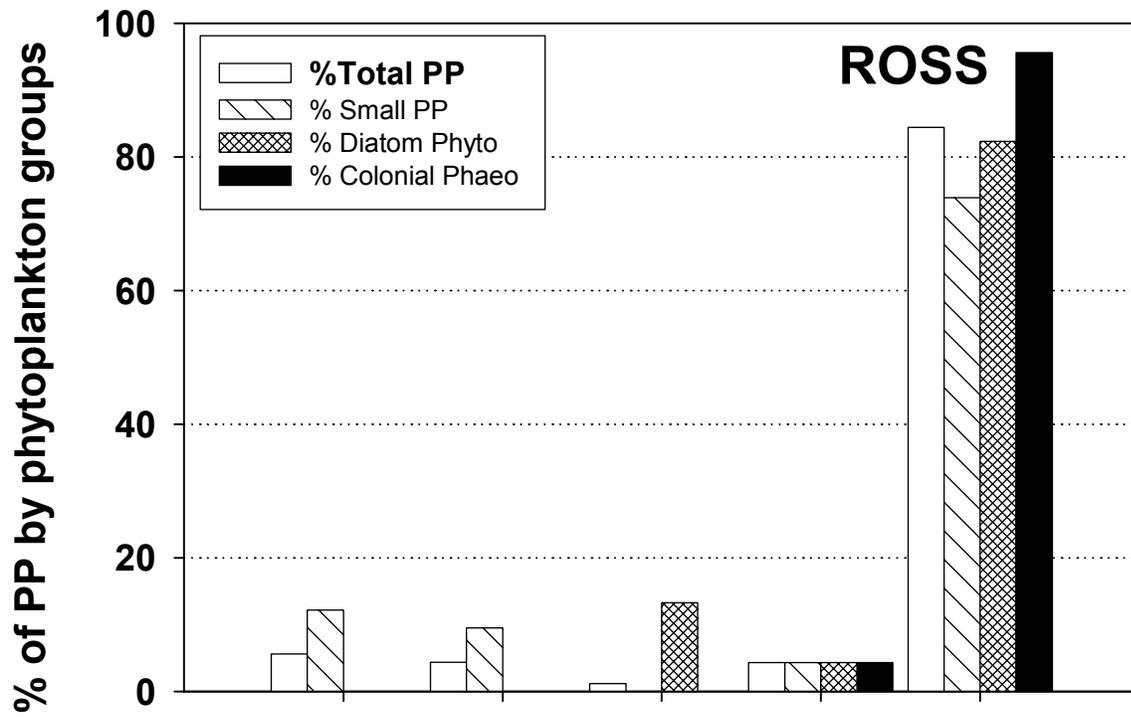


Figure 10. Ducklow & Daniels, EASIZ Volume

