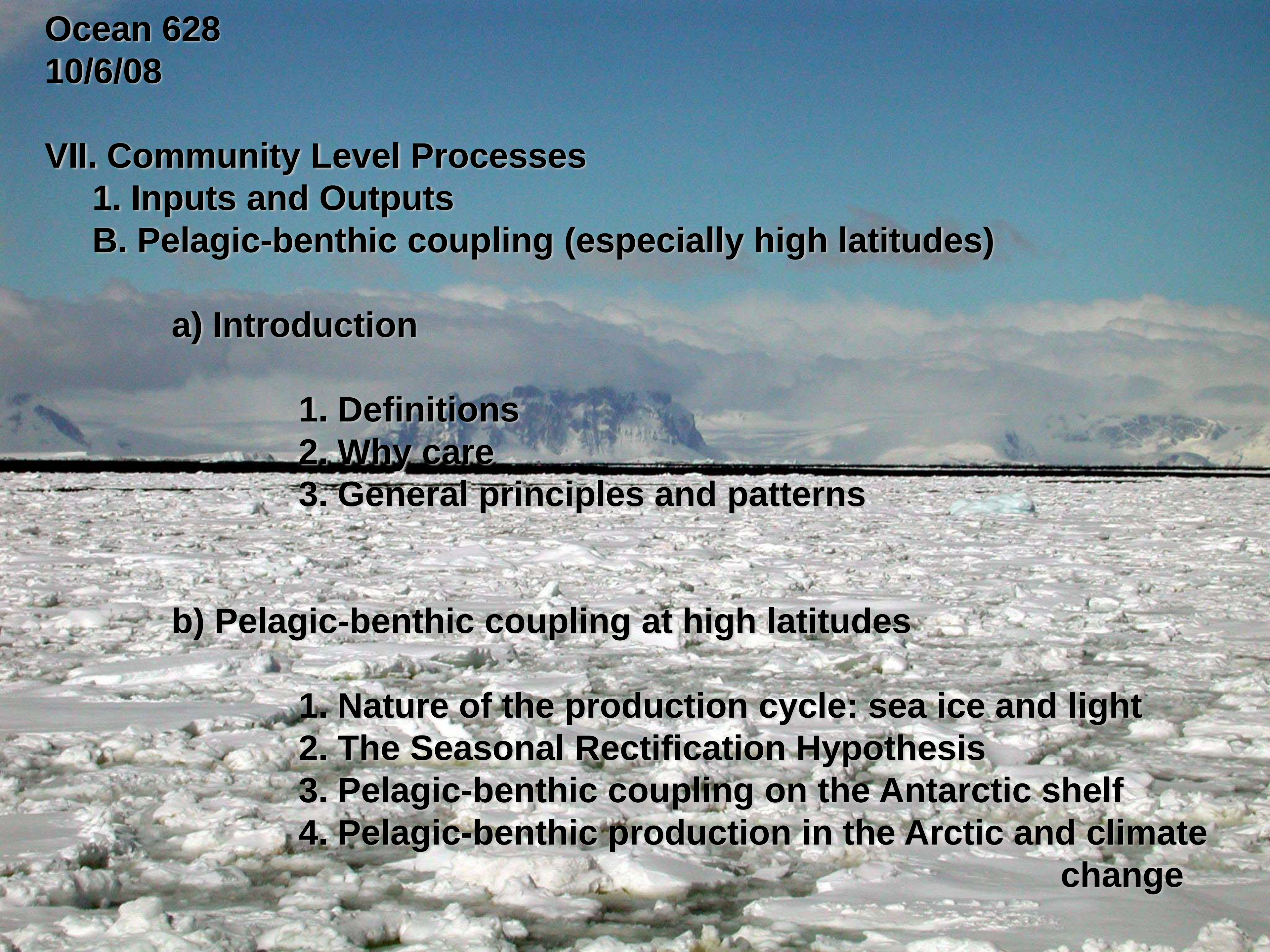

Ocean 628
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VII. Community Level Processes

1. Inputs and Outputs

B. Pelagic-benthic coupling (especially high latitudes)

a) Introduction

1. Definitions
2. Why care
3. General principles and patterns

b) Pelagic-benthic coupling at high latitudes

1. Nature of the production cycle: sea ice and light
2. The Seasonal Rectification Hypothesis
3. Pelagic-benthic coupling on the Antarctic shelf
4. Pelagic-benthic production in the Arctic and climate change

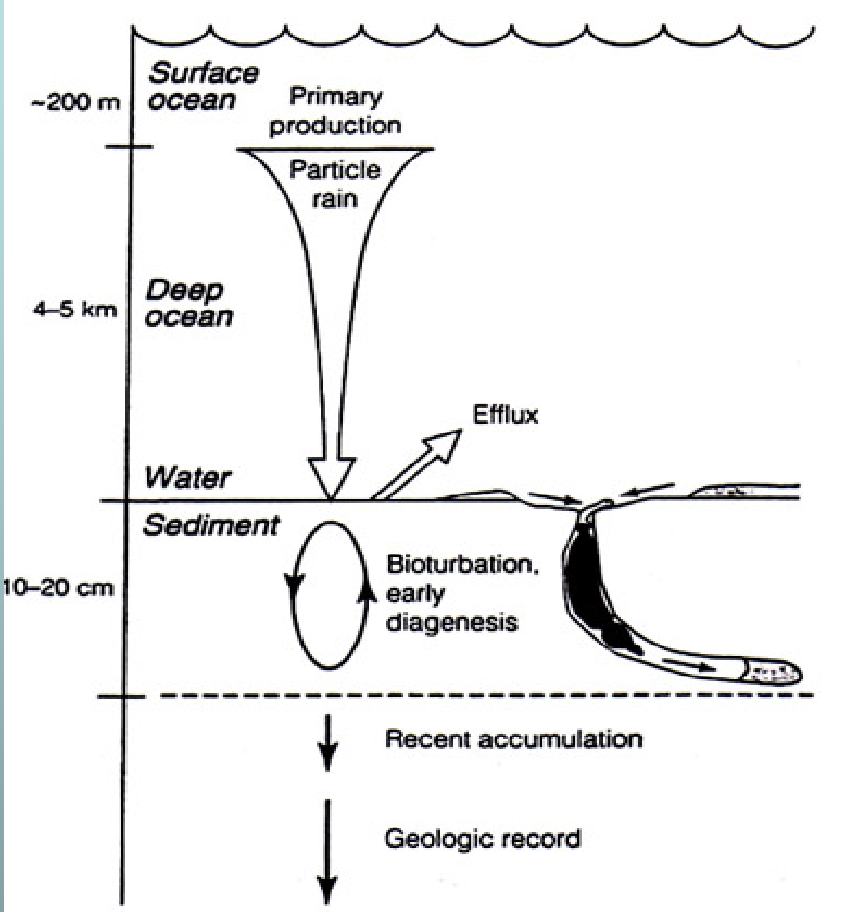
1) Definition:

Pelagic-benthic coupling =

"A causal relationship between water-column and benthic processes"

***Pelagic-to-benthic example*:**

The amount of primary production in the overlying water column determines SCOC and biomass at the seafloor.



Smith et al. 1997

2) Why is benthic-pelagic coupling important (why care)?

a. In shelf regions, as much as 6 – 60% of net primary production can sink to the seafloor, and the seafloor can be a major source of nutrients to the water column.

b. 40% of global fisheries yield, and much of coastal ecosystem biomass (e.g., suspension feeders, fishes, marine mammals feeding on seafloor), is comprised of species dependent on BPC.

c. Below euphotic zone (i.e. in the deep-sea), virtually all of benthic production, and the structure and dynamics of benthic communities, depend on organic flux from the pelagos.

d. Seafloor ecosystems provide an integrated view of production processes in the overlying water column.

3. General principles and patterns

Seuss, 1980

$$C_{flux(z)} = \frac{C_{prod}}{0.0238\, z} + 0.212$$

$$r^2 = 0.78$$

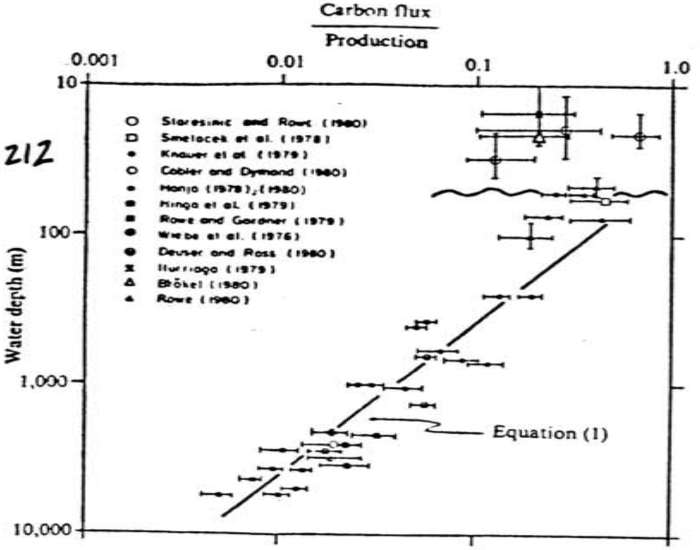


Fig. 1 Organic carbon fluxes with depth in the water column normalized to mean annual primary production rates at the sites of sediment trap deployment. The undulating line indicates the base of the euphotic zone; the horizontal error bars reflect variations in mean annual productivity as well as in replicate flux measurements during the same season or over several seasons; vertical error bars are depth ranges of several sediment trap deployments and uncertainties in the exact depth location. The data points by Rowe (1980) represent selected averages of 2–5 single sites at ~10 m above the bottom, where resuspension was assumed to be minimal.

Martin et al, 1987
(D-SR 34:267-285)

Data from the oceanic Pacific.

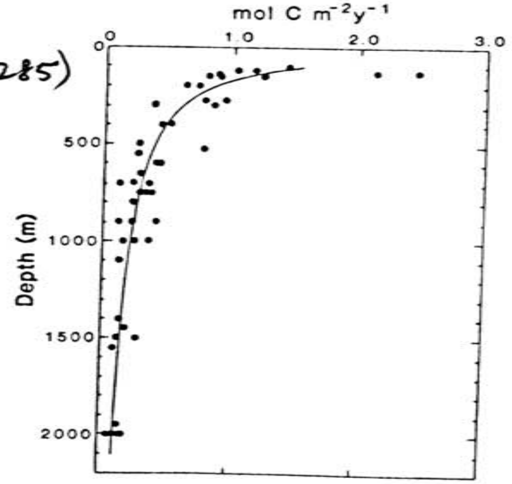


Fig. 5. Open ocean composite (OOC) fluxes for C using the means of replicates at various depths from Stas 2, 4, 5, II, III and NPEC: $F = 1.53(z/100)^{0.858}$; $r^2 = 0.81$; $n = 48$.

Jumars & Gallagher, 1982

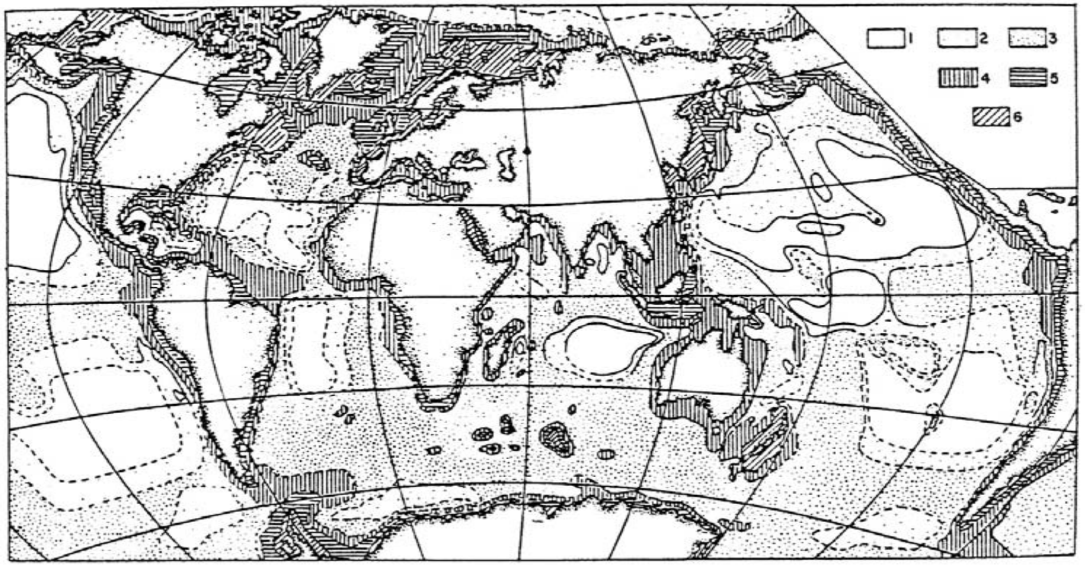
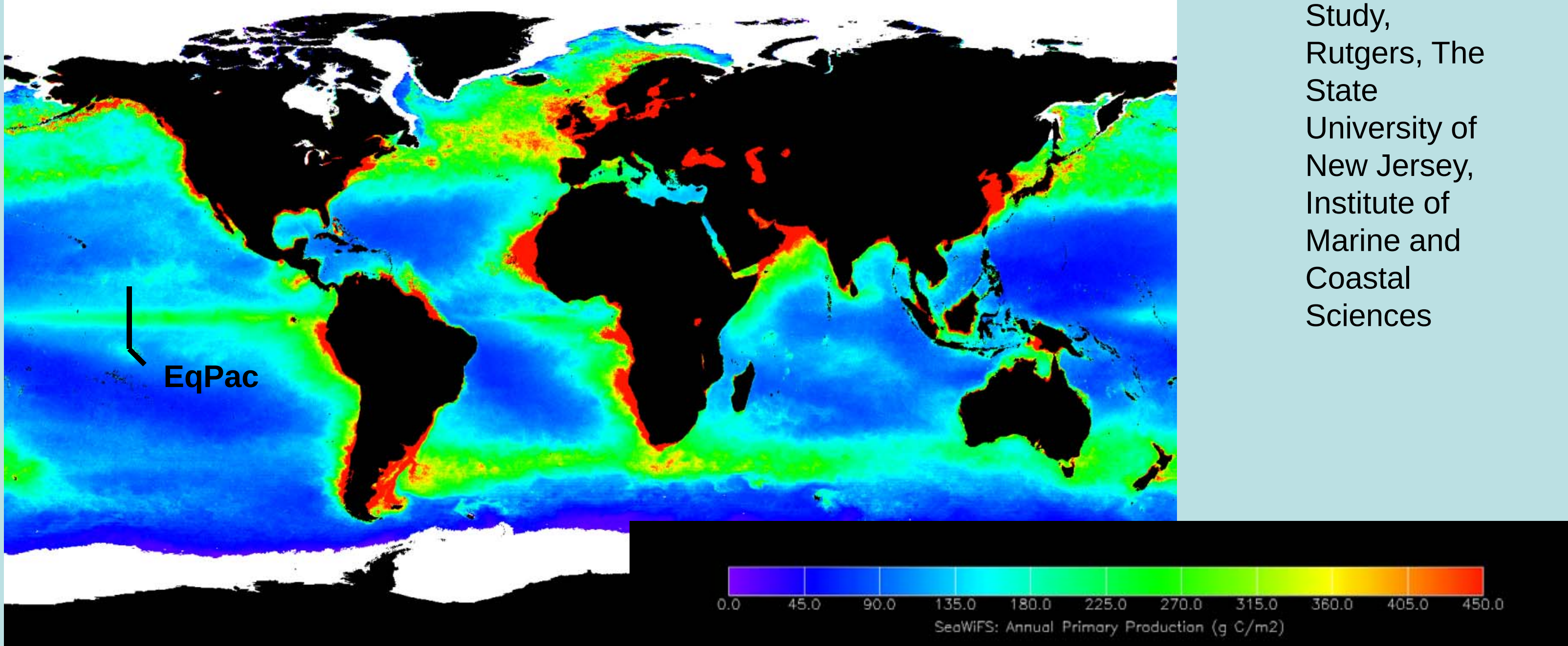


Fig. 10-2. Biomass (wet weight) of infauna from Okean grab samples (Belyayev *et al.*, 1973). Symbols (all in g m^{-2}): 1, <0.05; 2, 0.05–0.1; 3, 0.1–1.0; 4, 1.0–10.0; 5, 10.0–50.0; 6, 50.0– >1000.0 With permission, from Hessler and Jumars, 1977, Fig. 2.



SeaWIFS primary production - September 1998 - August 1999

Ocean Primary Productivity Study, Rutgers, The State University of New Jersey, Institute of Marine and Coastal Sciences

SeasonalpPhytodetritus pulses in deep-sea are common following blooms:

E.g.

Phytodetrital Pulse following spring bloom – 4025 m, NE Atlantic, 47 N, 20 W (Lampitt, 1985, DSR 32: 885-898) - ~40% of annual POC flux arrives phytodetritus pulse.

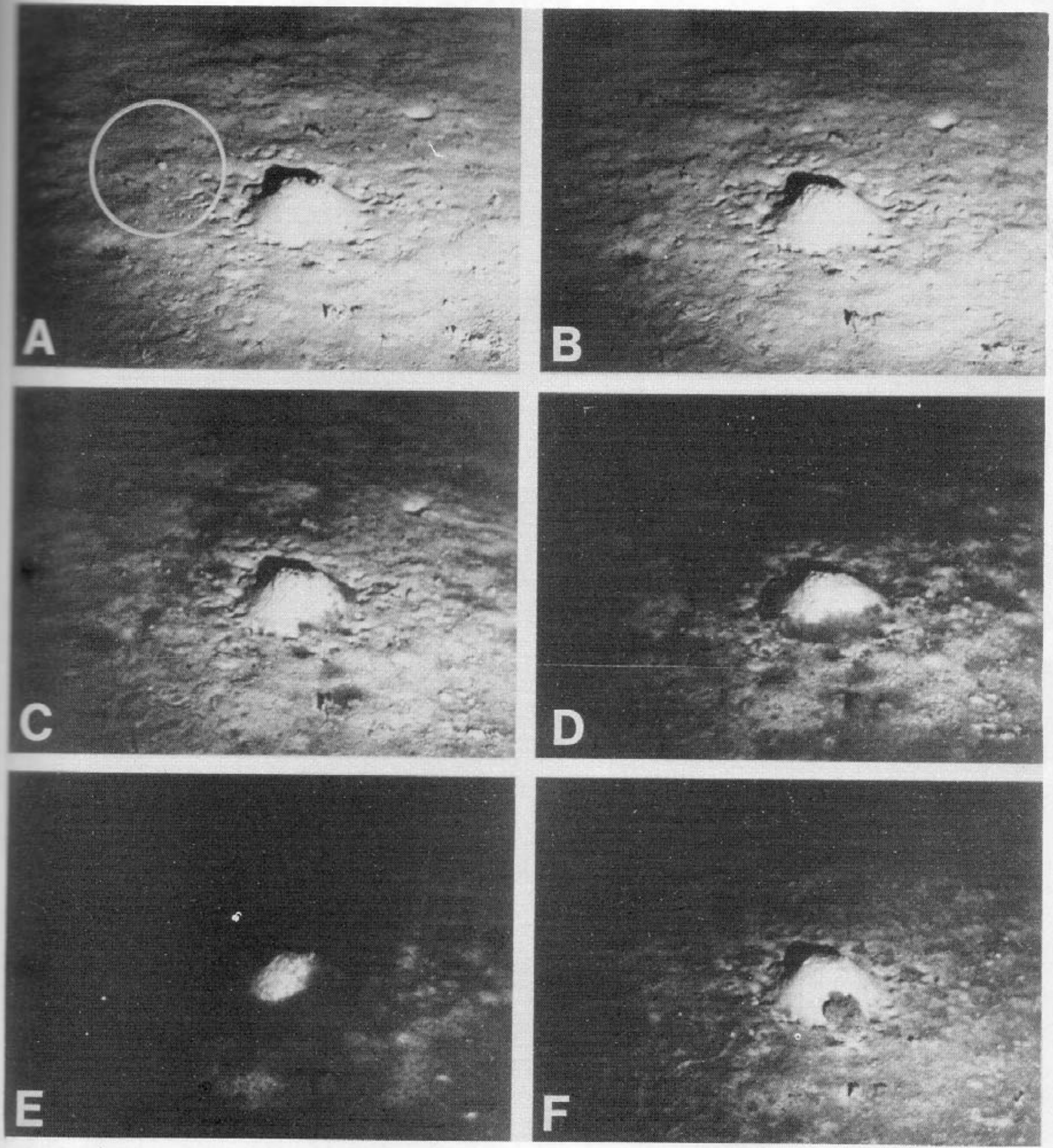


Fig. 1. Examples of photographs of the sea bed taken on Sta. 51720 (4025 m) during 1983. (A) 1 May, (B) 15 June, (C) 22 June, (D) 29 June, (E) 14 July, (F) 13 August. The circle in (A) is that area of the frame, the density of which was used to give a measure of the quantity of phytodetritus present on the sea bed (see Fig. 2).

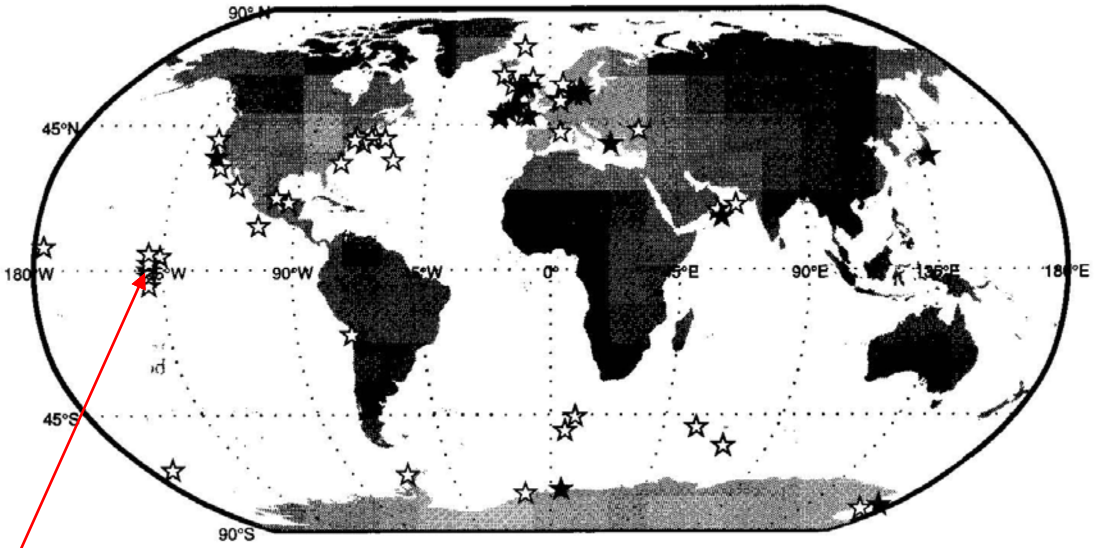
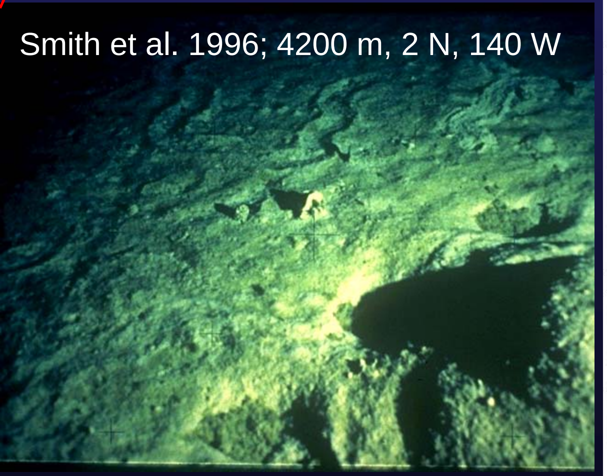
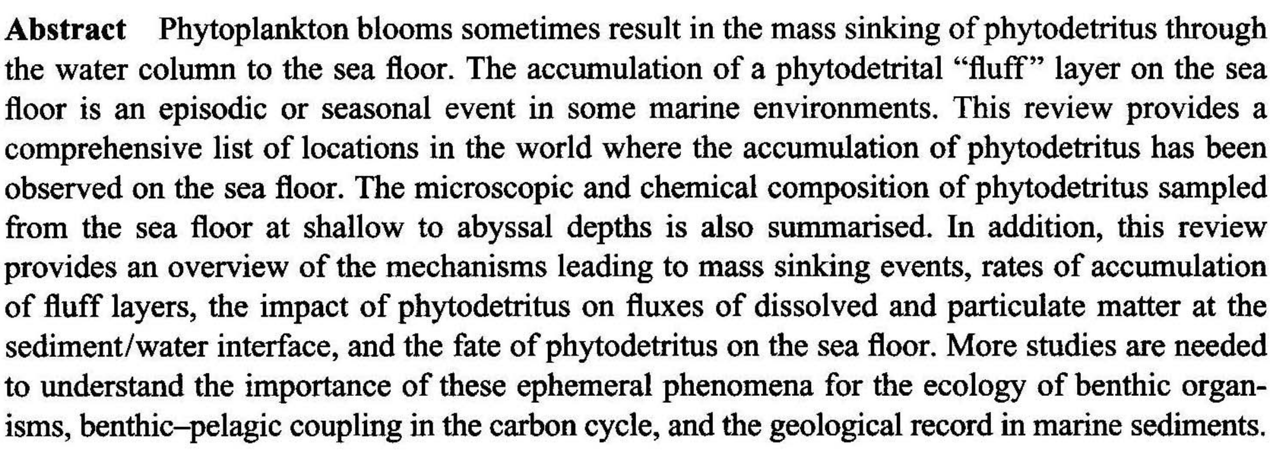


Figure 1 Sites (listed in Table 1) where the accumulation of phytodetritus was observed on the sea floor. For those studies with multiple stations, a single site is plotted except for endpoints of the studies by Mackensen et al. (1993), Riaux-Gobin et al. (1997), de Wilde et al. (1998), and E. Escobar-Briones (pers. comm.), sites B and C of the BENBO study, the north and west sites of the BIGSET Arabian Sea study, and five sites for the JGOFS equatorial Pacific study. Filled symbols indicate sites with seasonal accumulation of phytodetritus (listed in Table 2, with the addition of four shallow-water sites). Update of Fig. 5 in C. Smith (1994).

Beaulieu, S. E. 2002. Accumulation and fate of phytodetritus on the sea floo
Oceanogr. Mar. Biol. Annu. Rev. **40:** 171–232.


Smith et al. 1996; 4200 m, 2 N, 140 W


Abstract Phytoplankton blooms sometimes result in the mass sinking of phytodetritus through the water column to the sea floor. The accumulation of a phytodetrital "fluff" layer on the sea floor is an episodic or seasonal event in some marine environments. This review provides a comprehensive list of locations in the world where the accumulation of phytodetritus has been observed on the sea floor. The microscopic and chemical composition of phytodetritus sampled from the sea floor at shallow to abyssal depths is also summarised. In addition, this review provides an overview of the mechanisms leading to mass sinking events, rates of accumulation of fluff layers, the impact of phytodetritus on fluxes of dissolved and particulate matter at the sediment/water interface, and the fate of phytodetritus on the sea floor. More studies are needed to understand the importance of these ephemeral phenomena for the ecology of benthic organisms, benthic–pelagic coupling in the carbon cycle, and the geological record in marine sediments.

Temporal patterns in BPC: blooms → pulsed POC flux → varying SCOC

Station M, 4000 m California Margin

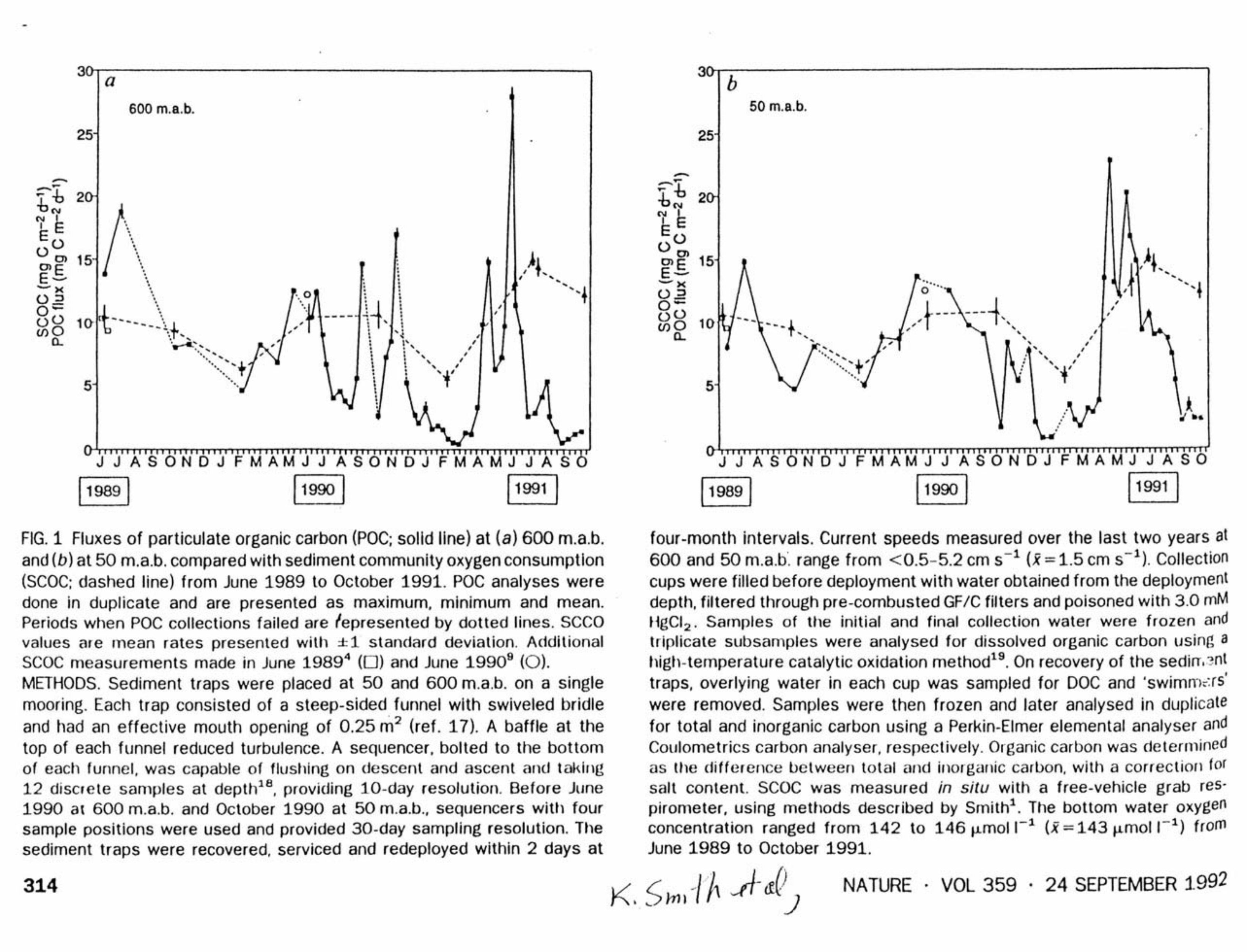


FIG. 1 Fluxes of particulate organic carbon (POC; solid line) at (*a*) 600 m.a.b. and (*b*) at 50 m.a.b. compared with sediment community oxygen consumption (SCOC; dashed line) from June 1989 to October 1991. POC analyses were done in duplicate and are presented as maximum, minimum and mean. Periods when POC collections failed are represented by dotted lines. SCCO values are mean rates presented with ±1 standard deviation. Additional SCOC measurements made in June 1989[4] (□) and June 1990[9] (○).

METHODS. Sediment traps were placed at 50 and 600 m.a.b. on a single mooring. Each trap consisted of a steep-sided funnel with swiveled bridle and had an effective mouth opening of 0.25 m^2 (ref. 17). A baffle at the top of each funnel reduced turbulence. A sequencer, bolted to the bottom of each funnel, was capable of flushing on descent and ascent and taking 12 discrete samples at depth[18], providing 10-day resolution. Before June 1990 at 600 m.a.b. and October 1990 at 50 m.a.b., sequencers with four sample positions were used and provided 30-day sampling resolution. The sediment traps were recovered, serviced and redeployed within 2 days at four-month intervals. Current speeds measured over the last two years at 600 and 50 m.a.b. range from <0.5–5.2 cm s^{-1} ($\bar{x}$ = 1.5 cm s^{-1}). Collection cups were filled before deployment with water obtained from the deployment depth, filtered through pre-combusted GF/C filters and poisoned with 3.0 mM HgCl$_2$. Samples of the initial and final collection water were frozen and triplicate subsamples were analysed for dissolved organic carbon using a high-temperature catalytic oxidation method[19]. On recovery of the sediment traps, overlying water in each cup was sampled for DOC and 'swimmers' were removed. Samples were then frozen and later analysed in duplicate for total and inorganic carbon using a Perkin-Elmer elemental analyser and Coulometrics carbon analyser, respectively. Organic carbon was determined as the difference between total and inorganic carbon, with a correction for salt content. SCOC was measured *in situ* with a free-vehicle grab respirometer, using methods described by Smith[1]. The bottom water oxygen concentration ranged from 142 to 146 µmol l^{-1} ($\bar{x}$ = 143 µmol l^{-1}) from June 1989 to October 1991.

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K. Smith et al,

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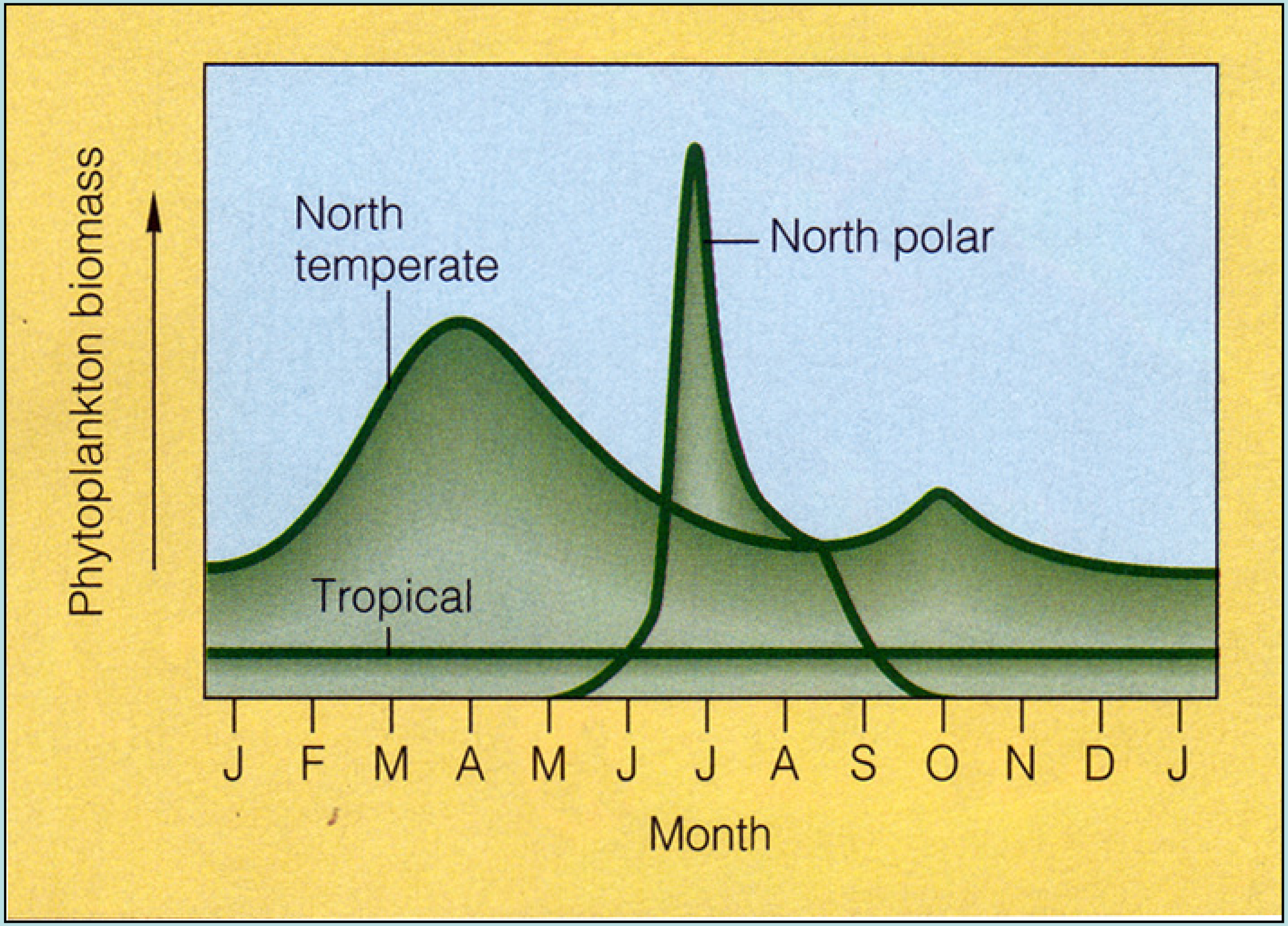
Pelagic-benthic coupling at high latitudes:

Polar regions – extreme seasonality in phytoplankton biomass and primary production



Oct-Nov (Late Spring)

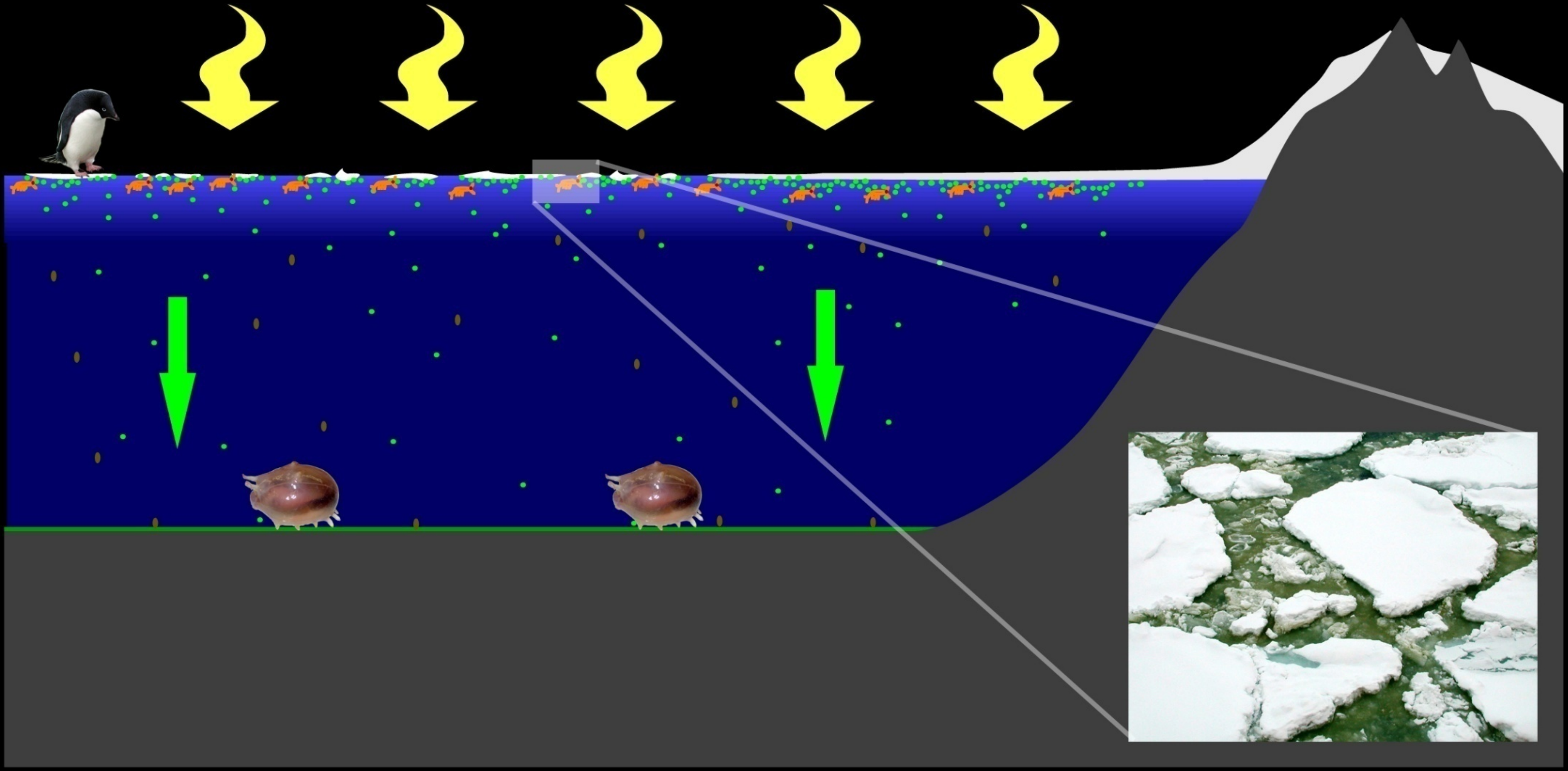
Antarctica

Based on west Antarctic Peninsula at 63-68 S

-Sea-ice cover breaking up; nearing 24 hr daylight

-Ice-algae released by melting ice

-Melt water-induced stratification of the water column begins

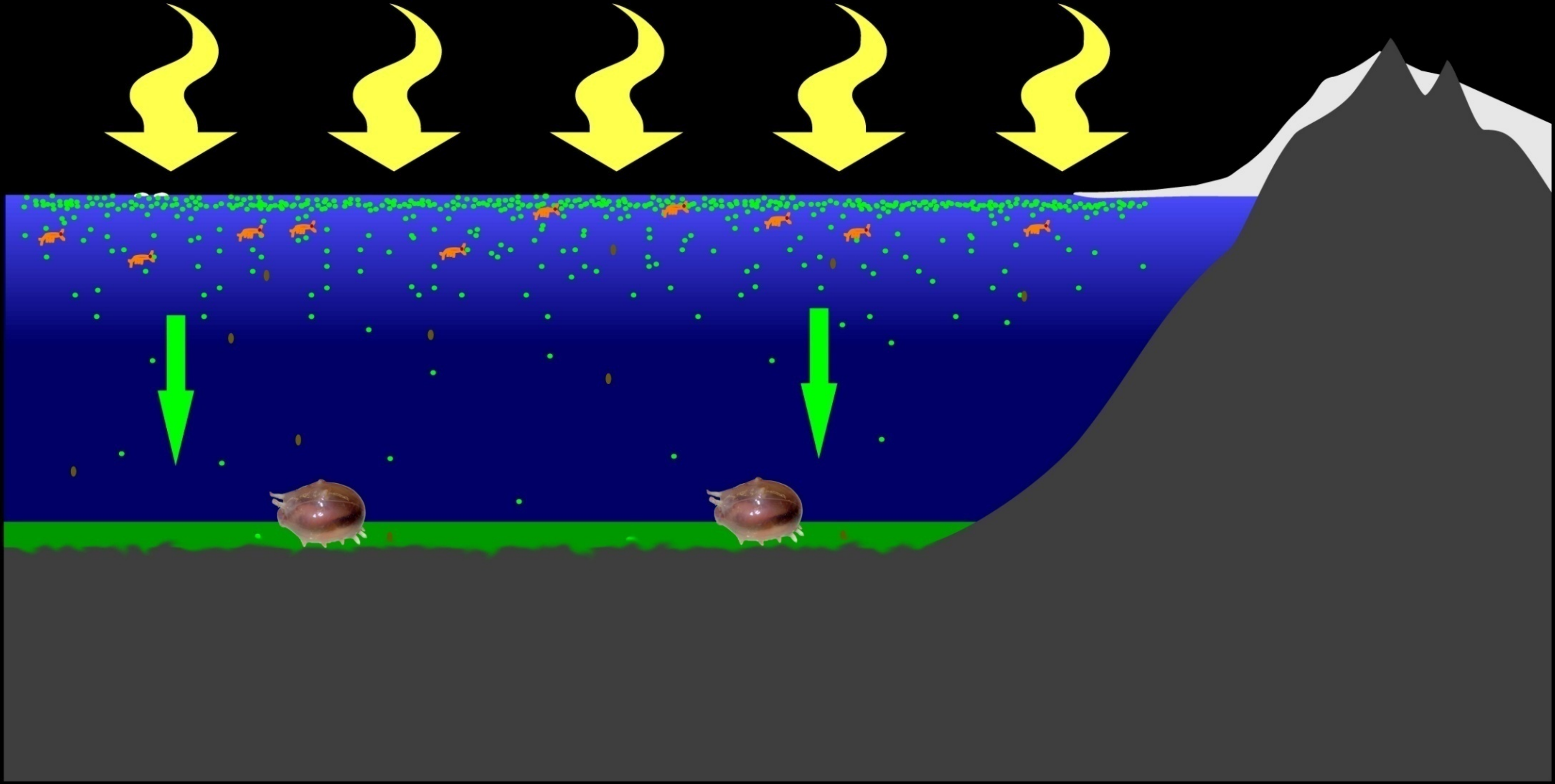


Jan-March (Austral Summer)

Antarctica

-Sea-ice cover receded

-Phytoplankton bloom fully developed; sedimentation of organic material can produce thick phytodetrital carpet

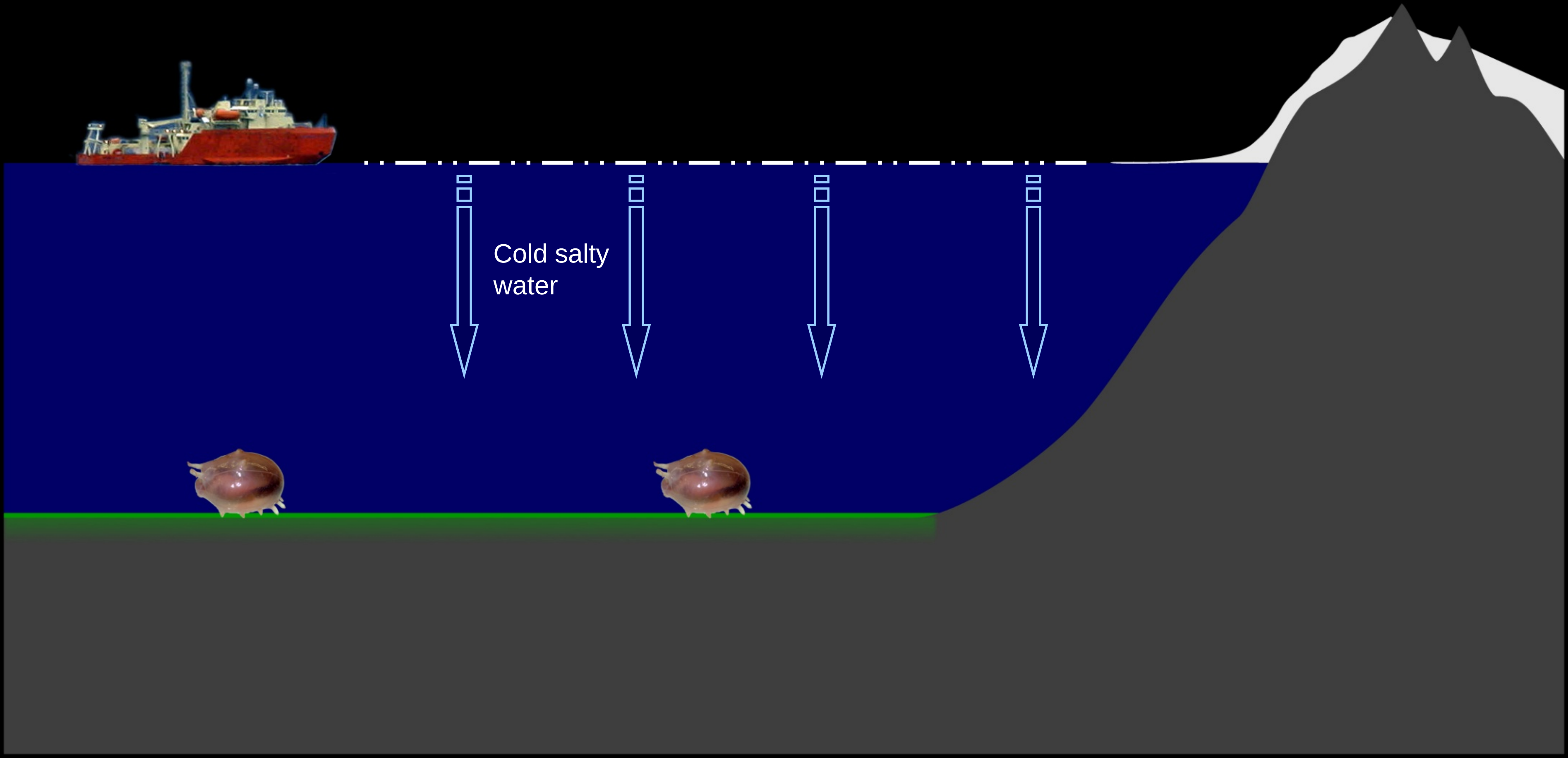


Antarctica

May-July (Late Fall-Winter)

-Nearly 24 hr darkness, sea-ice forms

-Very low phytoplankton biomass

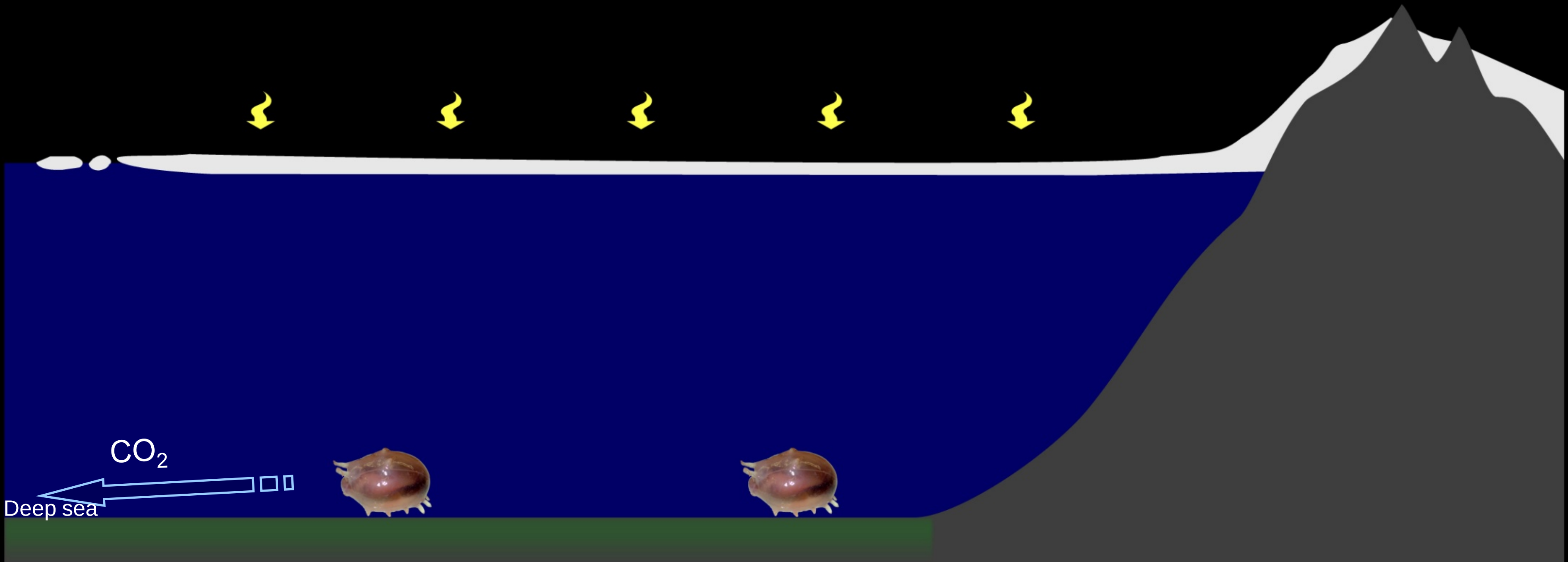


Antarctica

Aug-Sept (Late Winter - Early Spring)

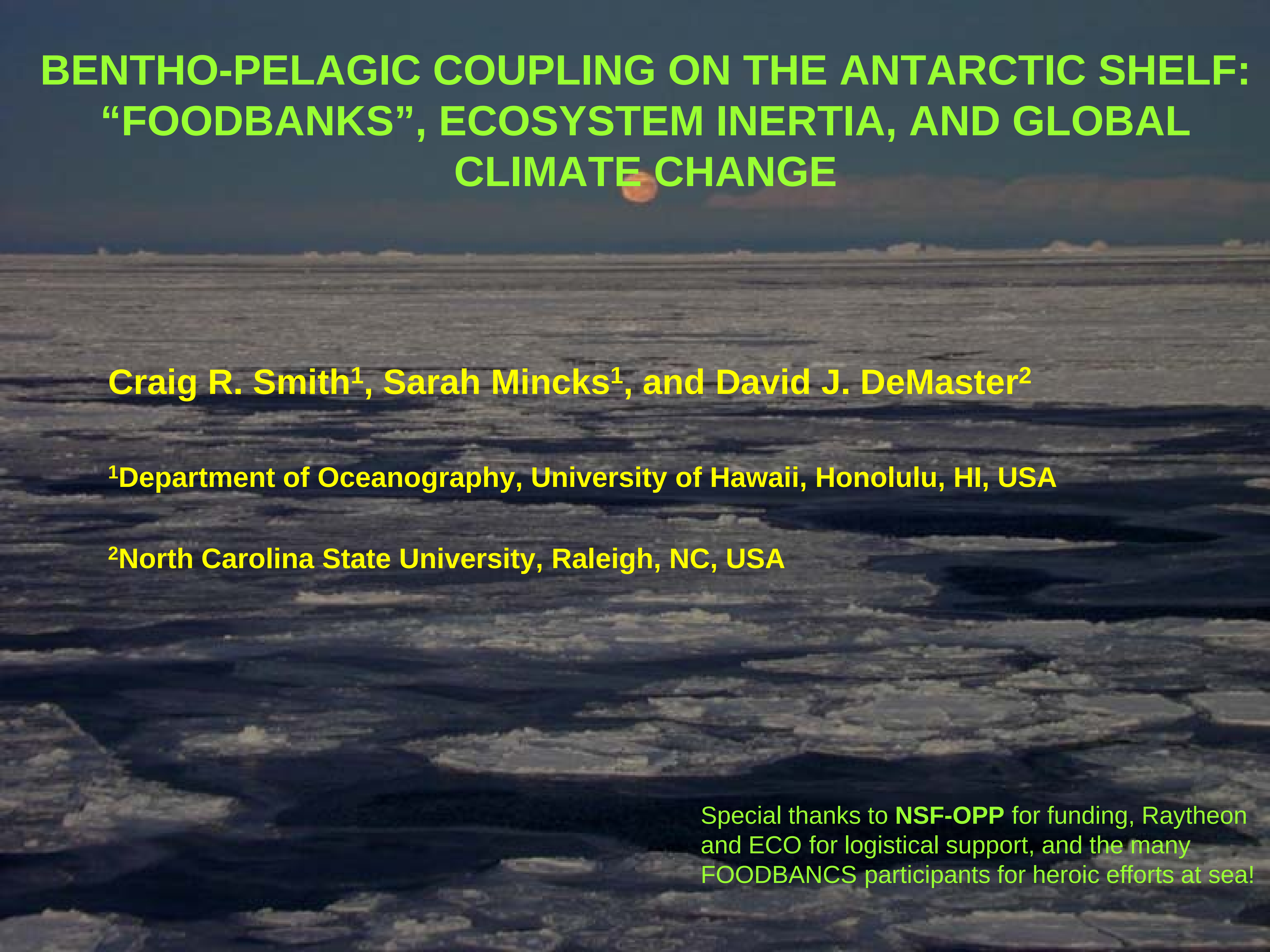
-Period of maximum sea-ice coverage, short but lengthening daylight hours

-Relatively austere water column



If much of summer primary production sinks to seafloor and is respired in winter under sea ice “cap”, resultant CO_2 may be advected into deep-sea → <u>Seasonal Rectification Hypothesis</u>

(Yager et al., 1995)



BENTHO-PELAGIC COUPLING ON THE ANTARCTIC SHELF: “FOODBANKS”, ECOSYSTEM INERTIA, AND GLOBAL CLIMATE CHANGE

Craig R. Smith[1], Sarah Mincks[1], and David J. DeMaster[2]

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[2]North Carolina State University, Raleigh, NC, USA

Special thanks to **NSF-OPP** for funding, Raytheon and ECO for logistical support, and the many FOODBANCS participants for heroic efforts at sea!

Outline:

A) Antarctic shelf generalizations

B) Address 4 major BPC questions:

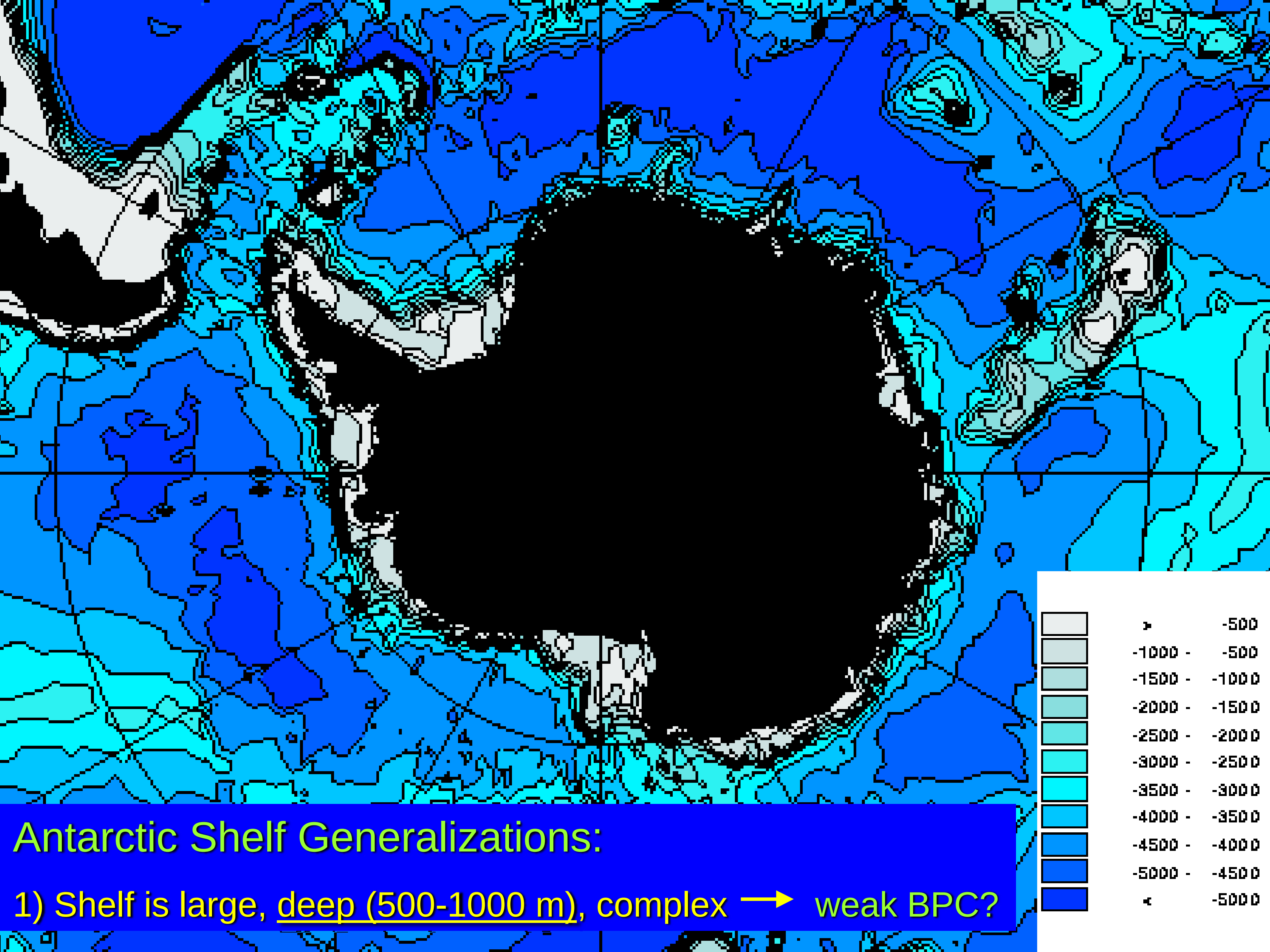
1) Are water column production signals rapidly transmitted to the seafloor?

2) Do benthic parameters match <u>regional</u> variations in sea-ice cover and water-column production?

3) Do benthic processes vary in phase with seasonal primary production and flux?

4) Will patterns of BPC in Antarctica be altered by climate change?

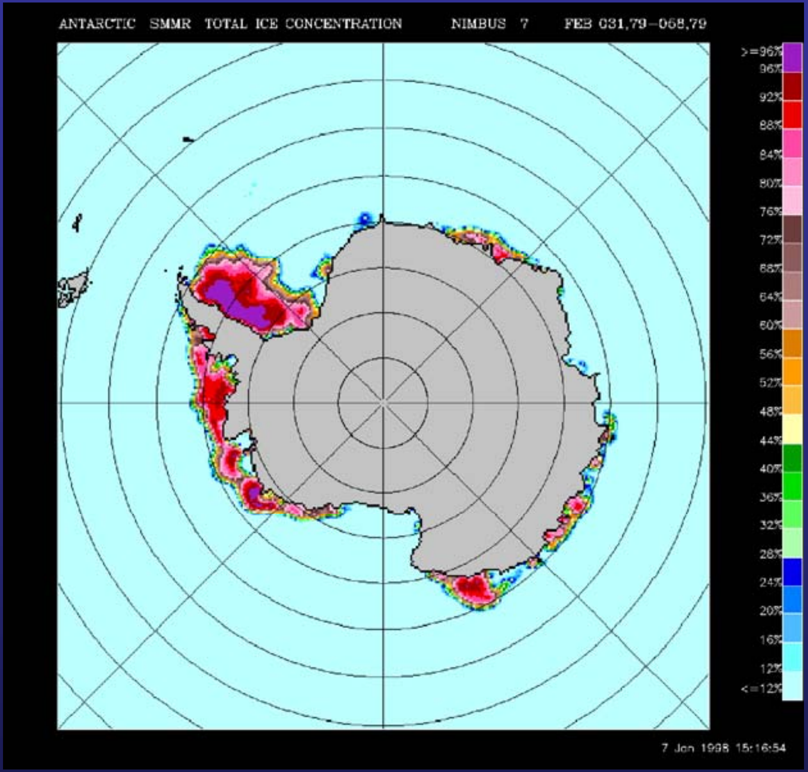
C) Conclusions about BPC on Antarctic shelf



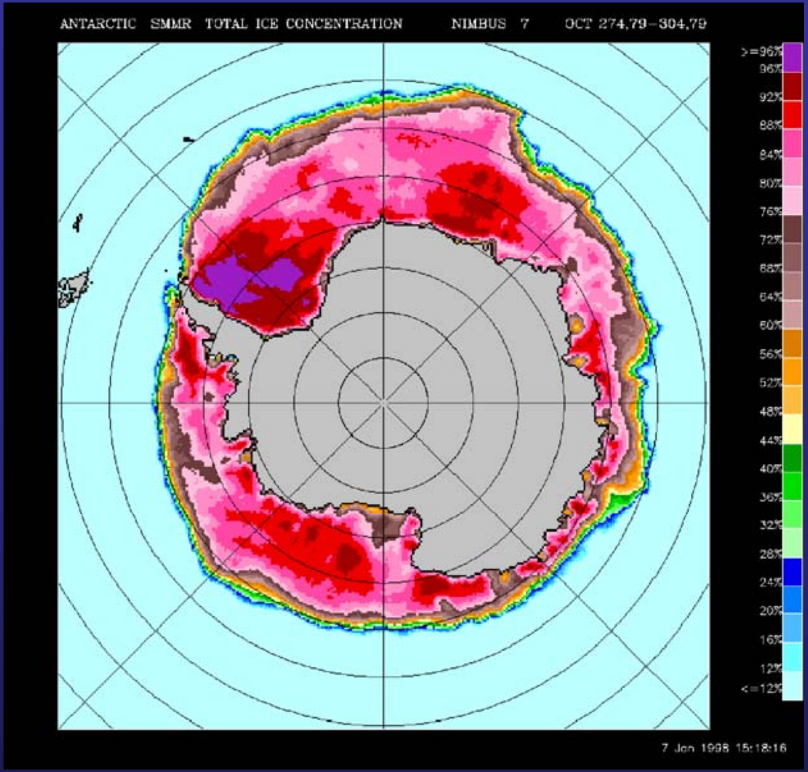
Antarctic Shelf Generalizations:

1) Shelf is large, deep (500-1000 m), complex → weak BPC?

2) Oceanic end member in seasonal/annual variability in water-column production (driven by summer/winter contrasts in light, sea ice, stratification, etc.)



Sea-ice extent – February 1979

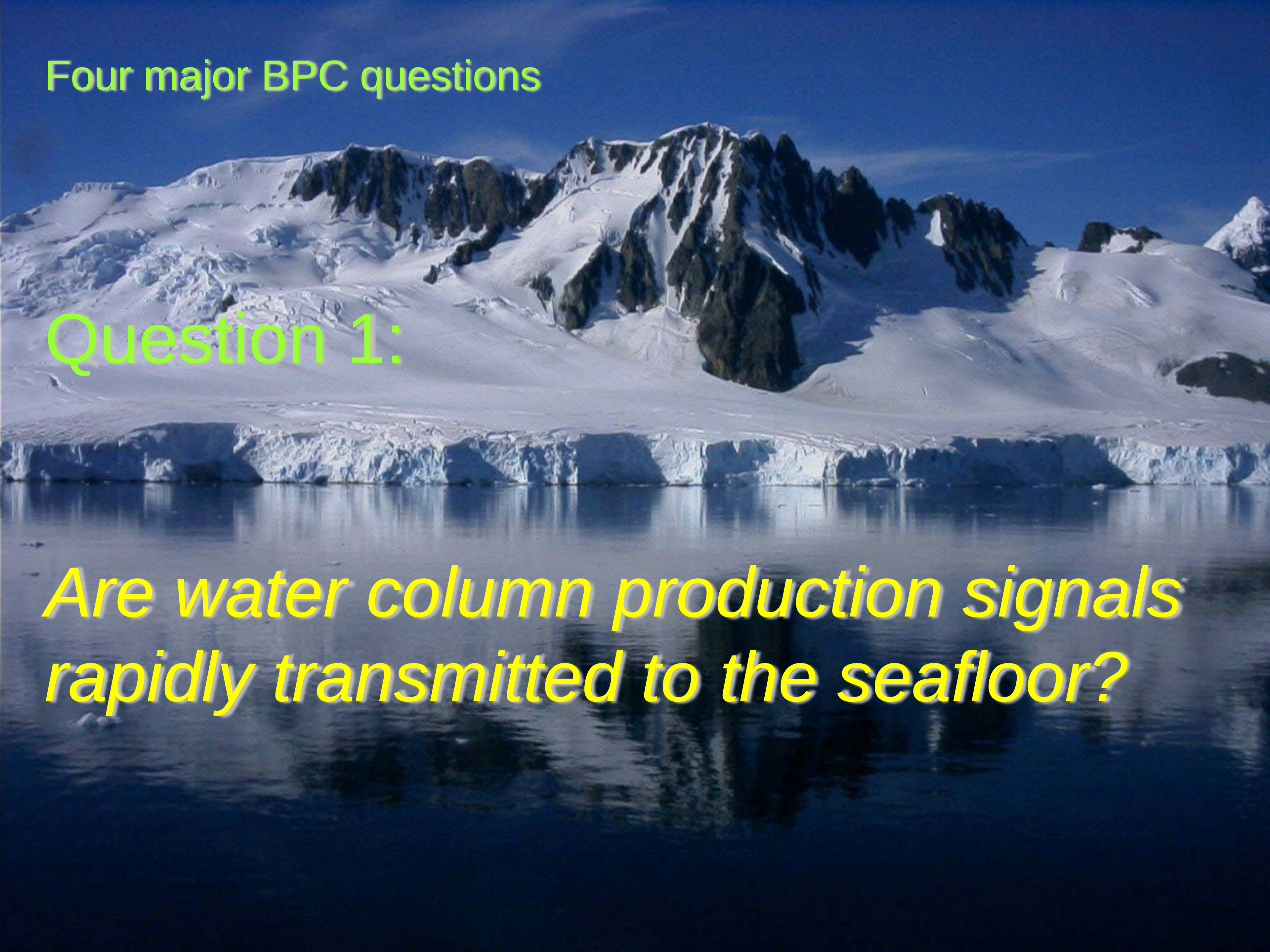


Sea-ice extent – October 1979

3) Can have short pelagic food webs (diatoms → krill → fecal pellets)

4) Relatively high benthic biomass on the shelf

→ Strong BPC?



Four major BPC questions

Question 1:

Are water column production signals rapidly transmitted to the seafloor?

Deep sediment-trap studies → intense summer pulses of POC flux to shelf floor -

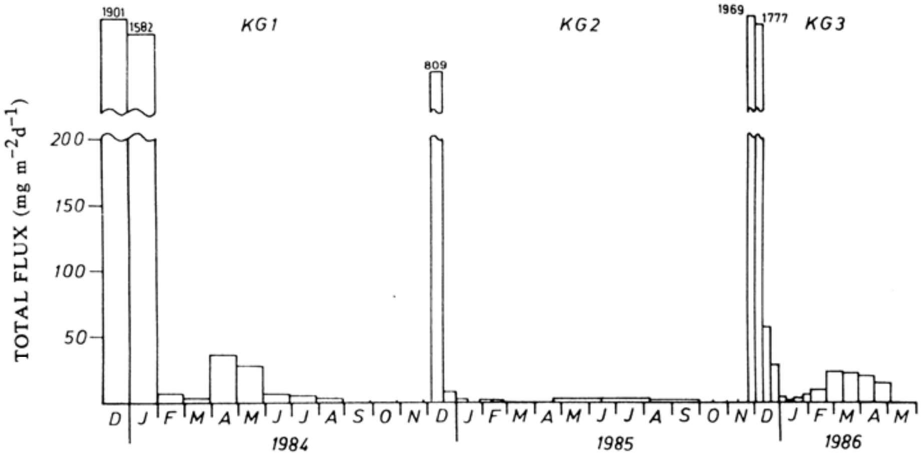
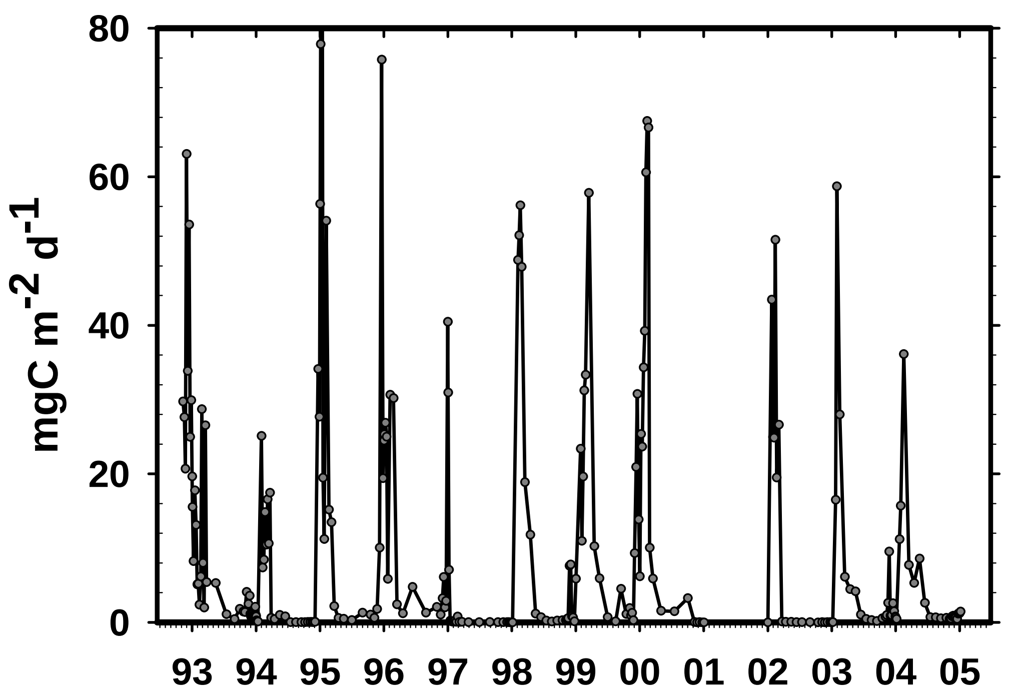


Fig. 6—30-month record of particle flux from the Bransfield Strait (from Wefer et al. 1988, and unpublished da

Bransfield Strait;
trap depth = 494 m
(Wefer et al., 1988
& unpublished)

Palmer LTER
region, Antarctic
Peninsula shelf;
trap depth = 150 m
(Ducklow et al.
2006)



Flux pulses not always coupled to ice disappearance or plankton blooms -

E.g., Collier et al. (2000) in Ross Sea →
(another e.g., Dunbar et al., 1998)

Time lags due to:

- complex bloom/current structure
- wind vs. melting-induced sea-ice removal
- development times of grazer assemblages

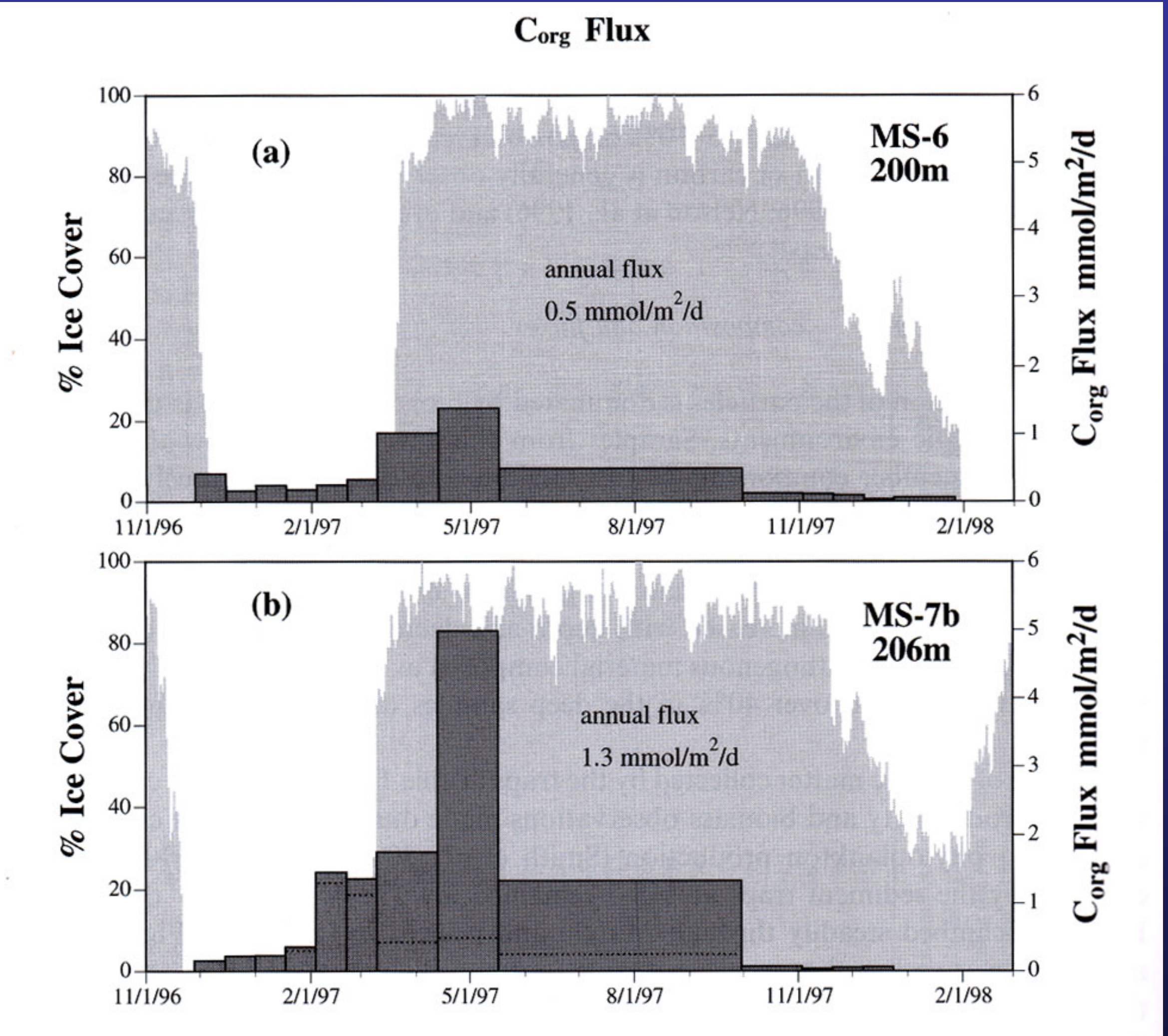
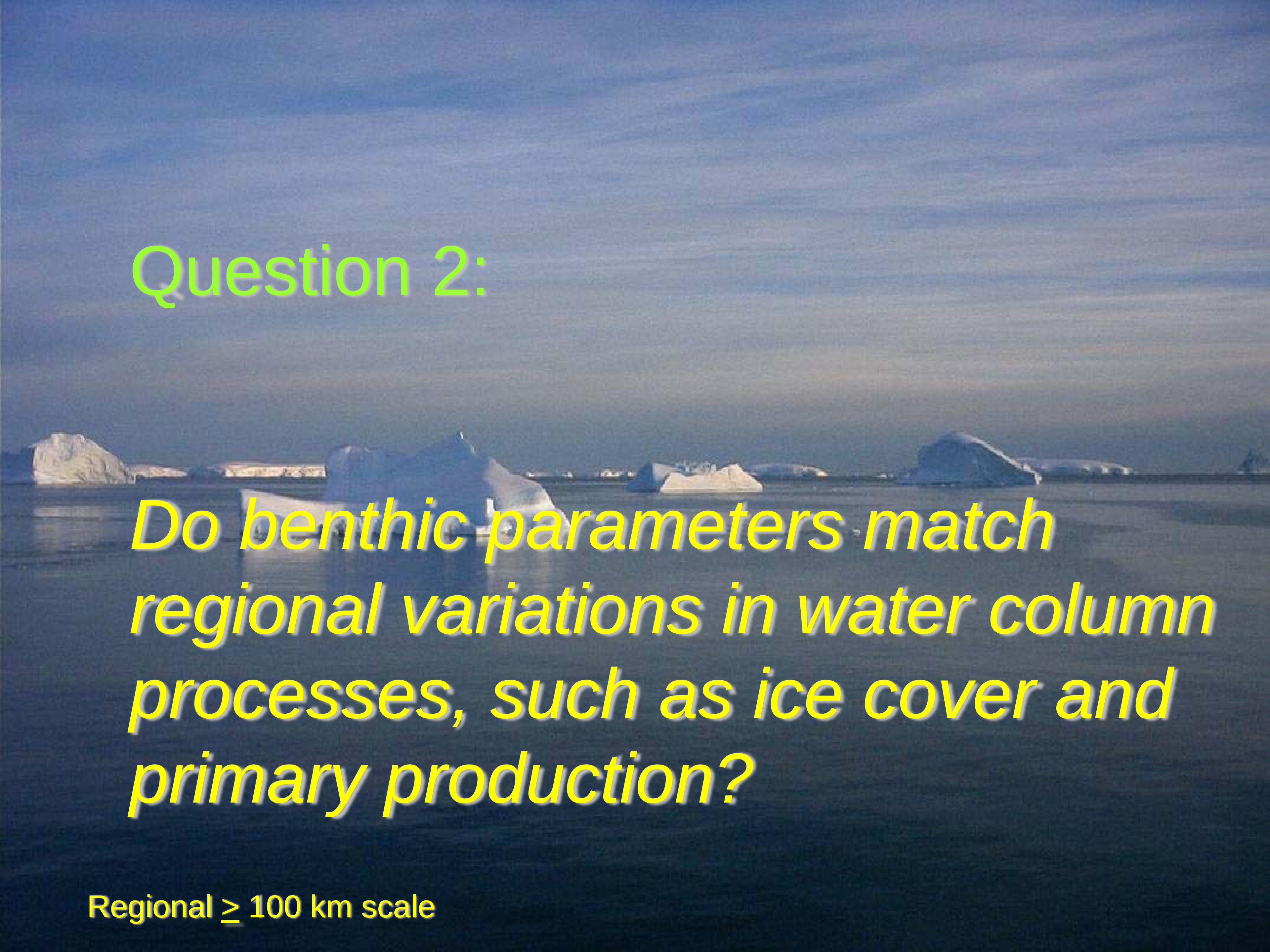


Fig. 3. Time series of organic carbon fluxes (C_{org}, mmol m^{-2} d^{-1}) to the upper traps at MS-6 (a) and MS-7 (b). Ice coverages from Fig. 2 are shown for reference. The annual fluxes were averaged over a single "season", not the full deployment, beginning with the first cup (November 28, 1996) through cup 11 (November 20, 1997). The dotted lines on the fluxes for MS-7b (b) represent the estimated organic carbon flux after removing a component potentially associated with pteropods (see discussion in text).

Conclusion for Question 1:

Intense production pulses are transmitted to seafloor, but these are not always tied tightly (in space and time) to local ice/bloom conditions overhead.



Question 2:

Do benthic parameters match regional variations in water column processes, such as ice cover and primary production?

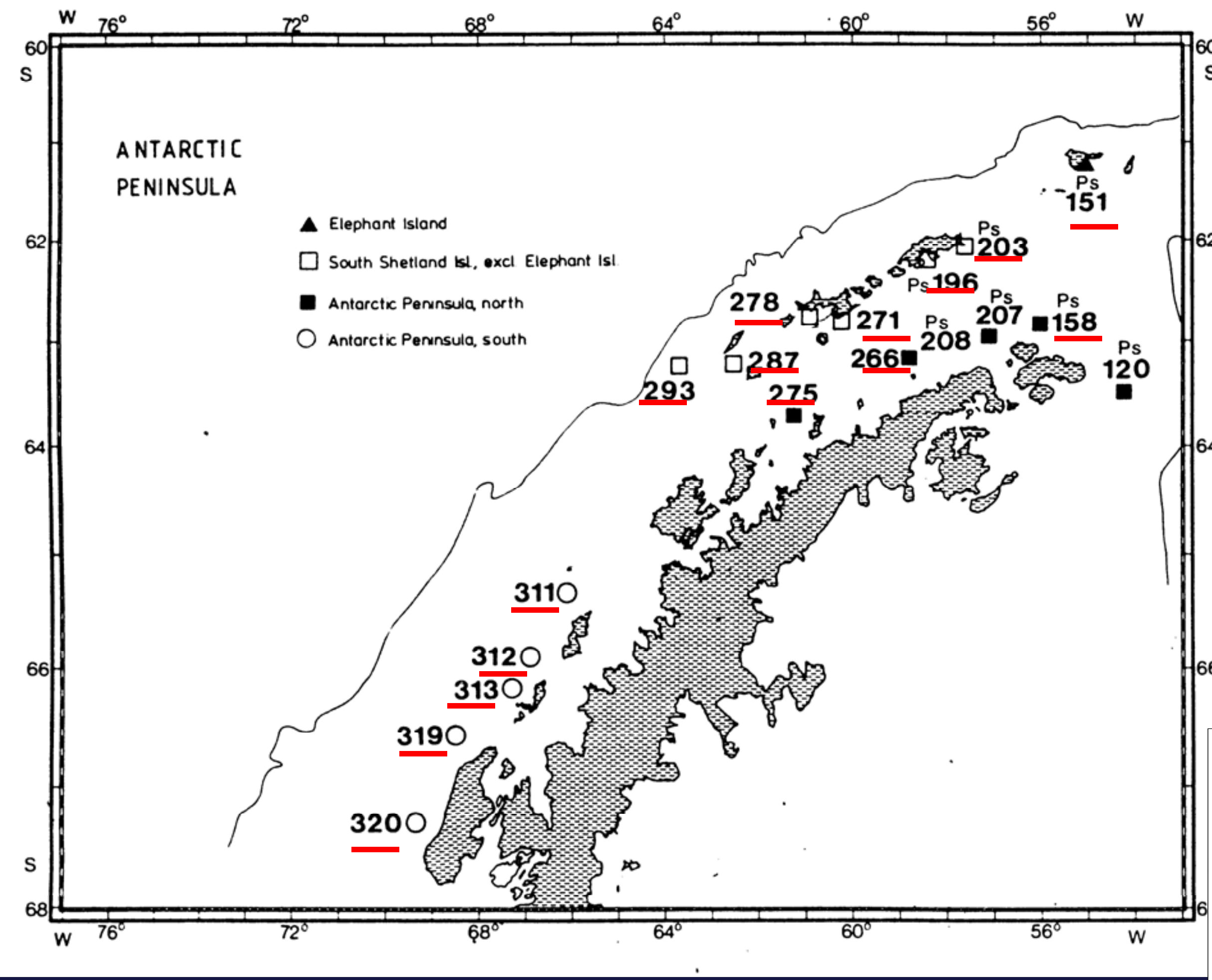
Regional ≥ 100 km scale

Restrict analysis to a single habitat type, e.g., to

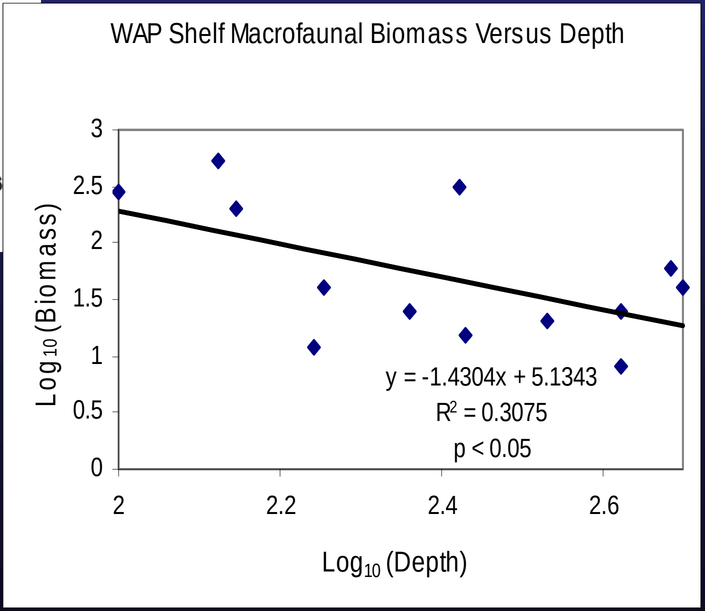
Muddy Sediments

which characterizes much of the deep Antarctic shelf?

Required meta-analysis of soft-sediment biomass data versus water-column parameters

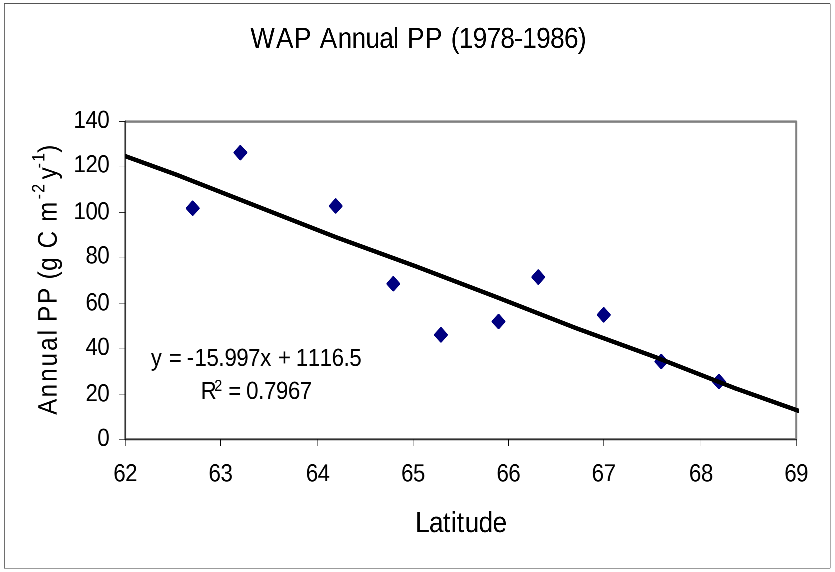


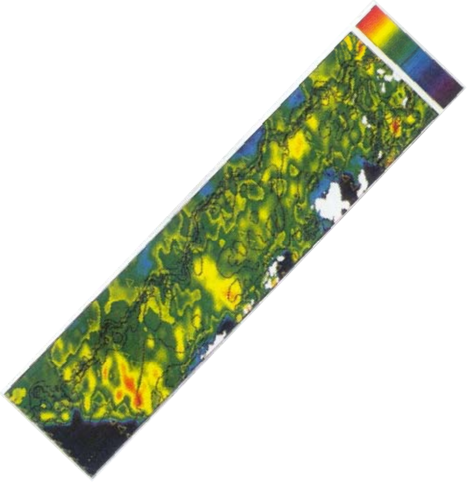
1) Macrofaunal biomass data from Muhlenhardt-Seigel (1988) for 15 WAP stations at 100-500 m depths.



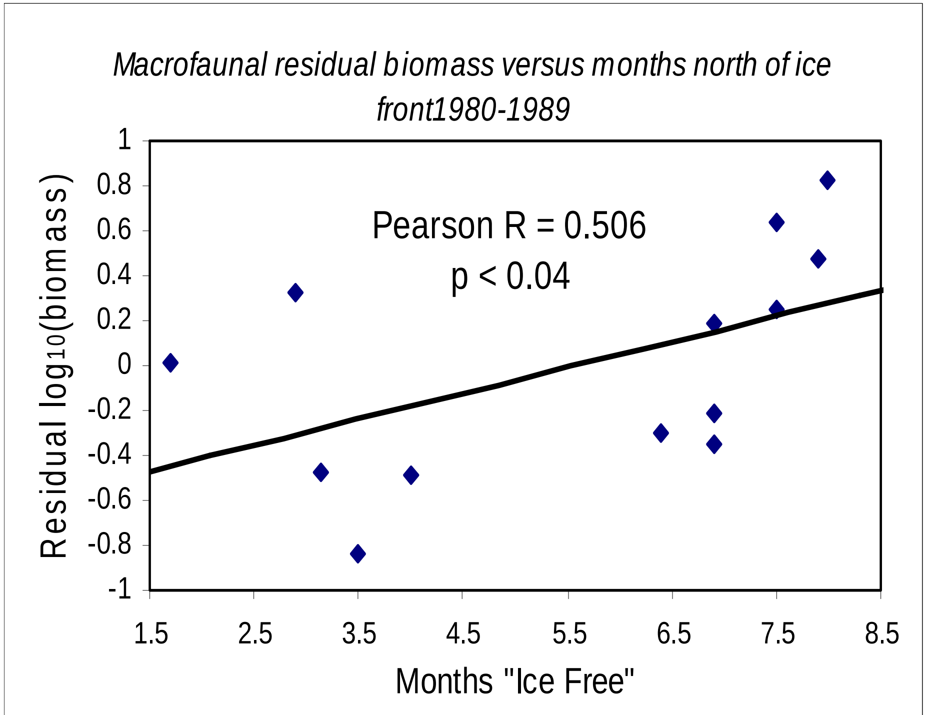
2) Removed effects of depth with regression analysis.

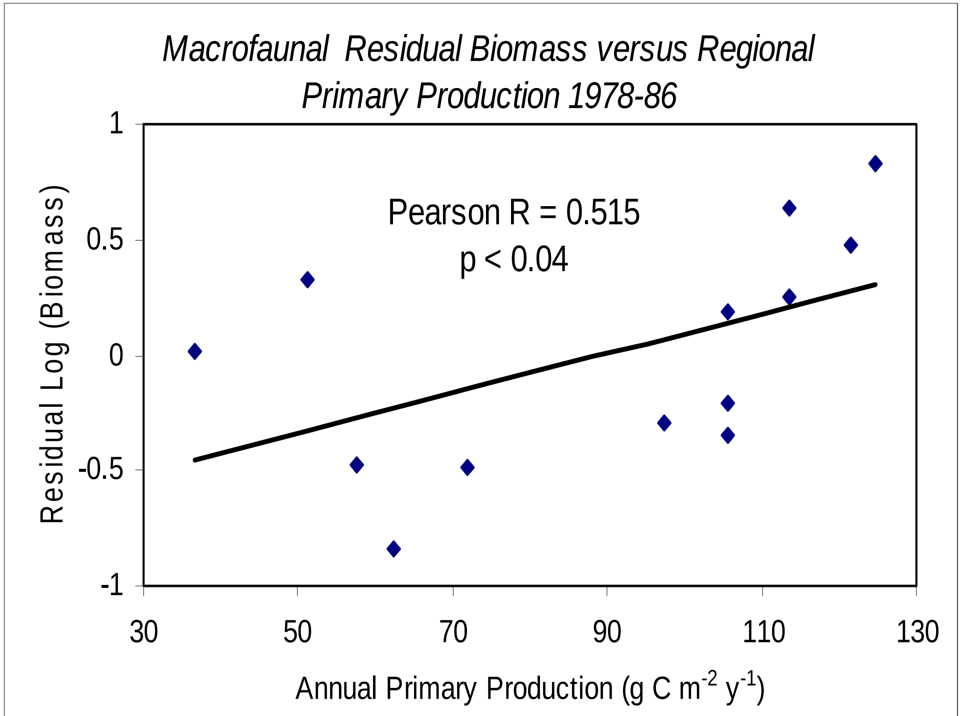
4) Estimated regional primary production around stations, from R. Smith et al. (1998) model of CZCS data.





5) Compared macrobenthic biomass to sea-ice duration and annual primary production (after removal of depth effects).



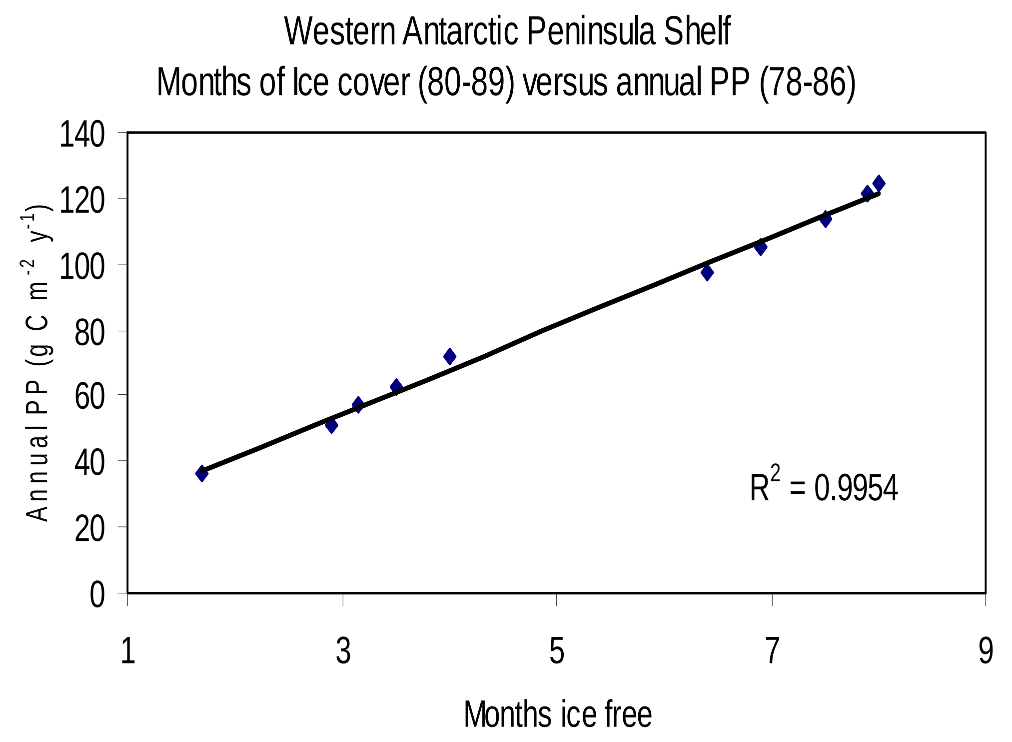


CONCLUSION FROM META-ANALYSIS

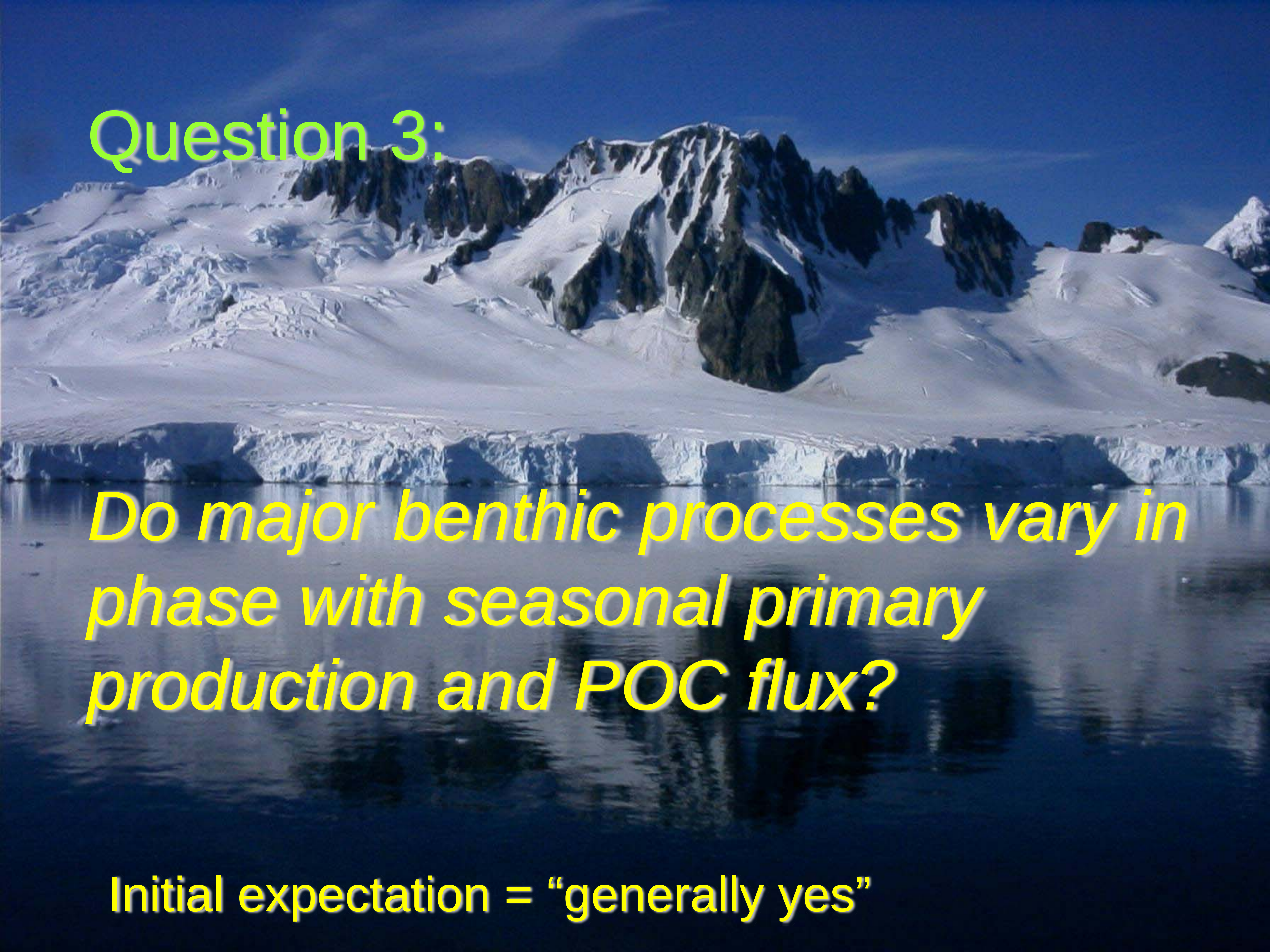
Within *muddy shelf habitats*, macrofaunal biomass is coupled to:

- *length of ice-free period*

- *annual primary production*.



Similarity of coupling not surprising – PP and IFP are highly correlated!



Question 3:

Do major benthic processes vary in phase with seasonal primary production and POC flux?

Initial expectation = “generally yes”

Sediment Community Oxygen Consumption?

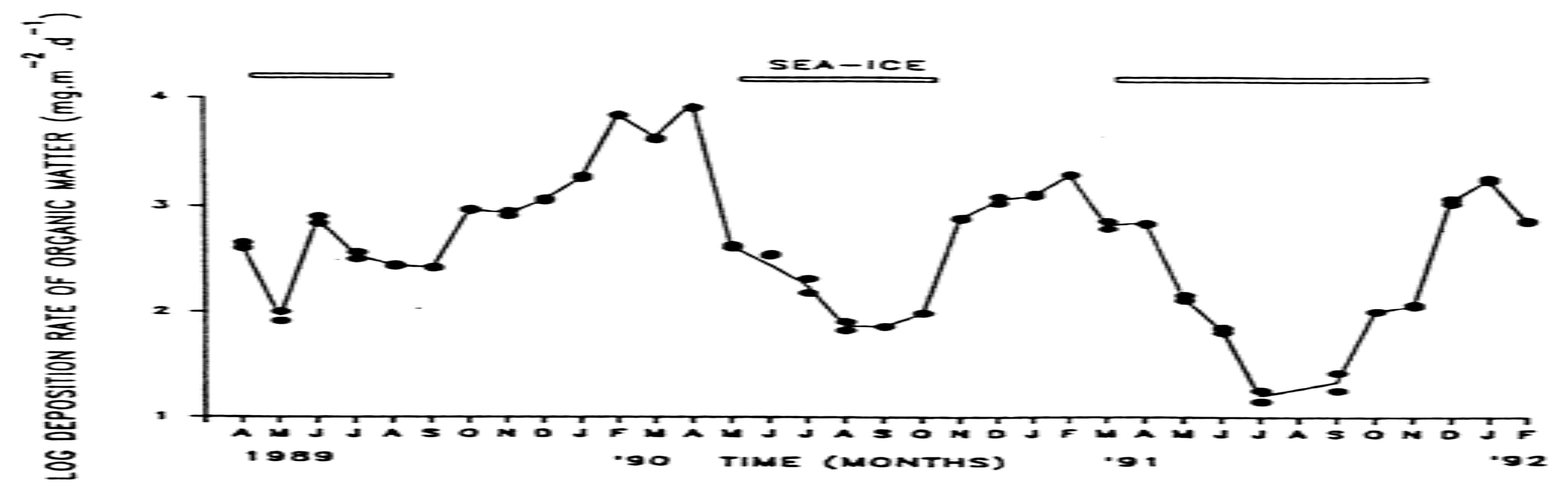


FIG. 4. Settlement rates of organic matter in the water column. Duplicate traps were used.

E.g., Nedwell et al. (1993), Signy Island –

Weak seasonal coupling with strong interannual variability.

Baldwin & Smith (2003), Deception Is. – similar pattern.

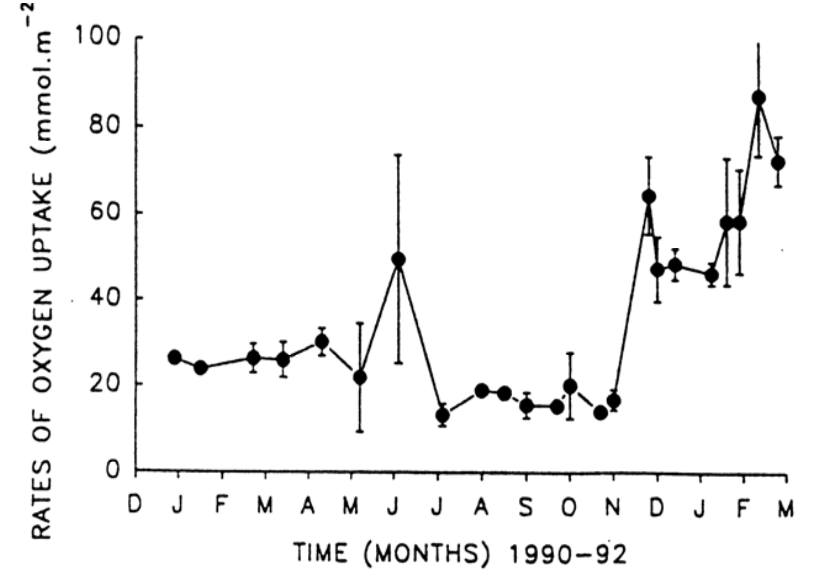


FIG. 1. Rates of O_2 uptake by bottom sediments in Factory Cove, Signy Island. Bars indicate standard errors; *n* = 3.

Seasonality in suspension feeding?

High seasonality expected due to large seasonal variations in chlorophyll-a concentrations (from large phytoplankton).

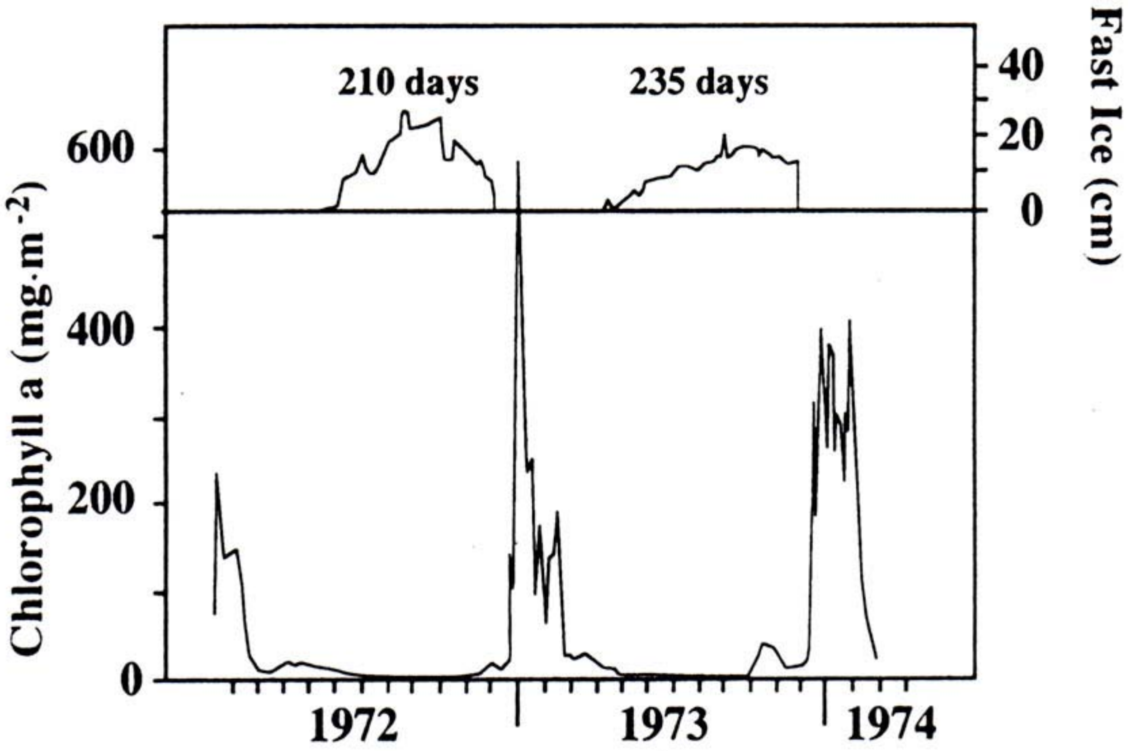


Figure 5 Annual cycle of chlorophyll *a* biomass and fast ice thickness in Borge Bay, Signy Island, South Orkney Islands. (Redrawn from Clarke 1988 after Whitaker 1982).

Barnes and Clarke, (1995), Signy Island

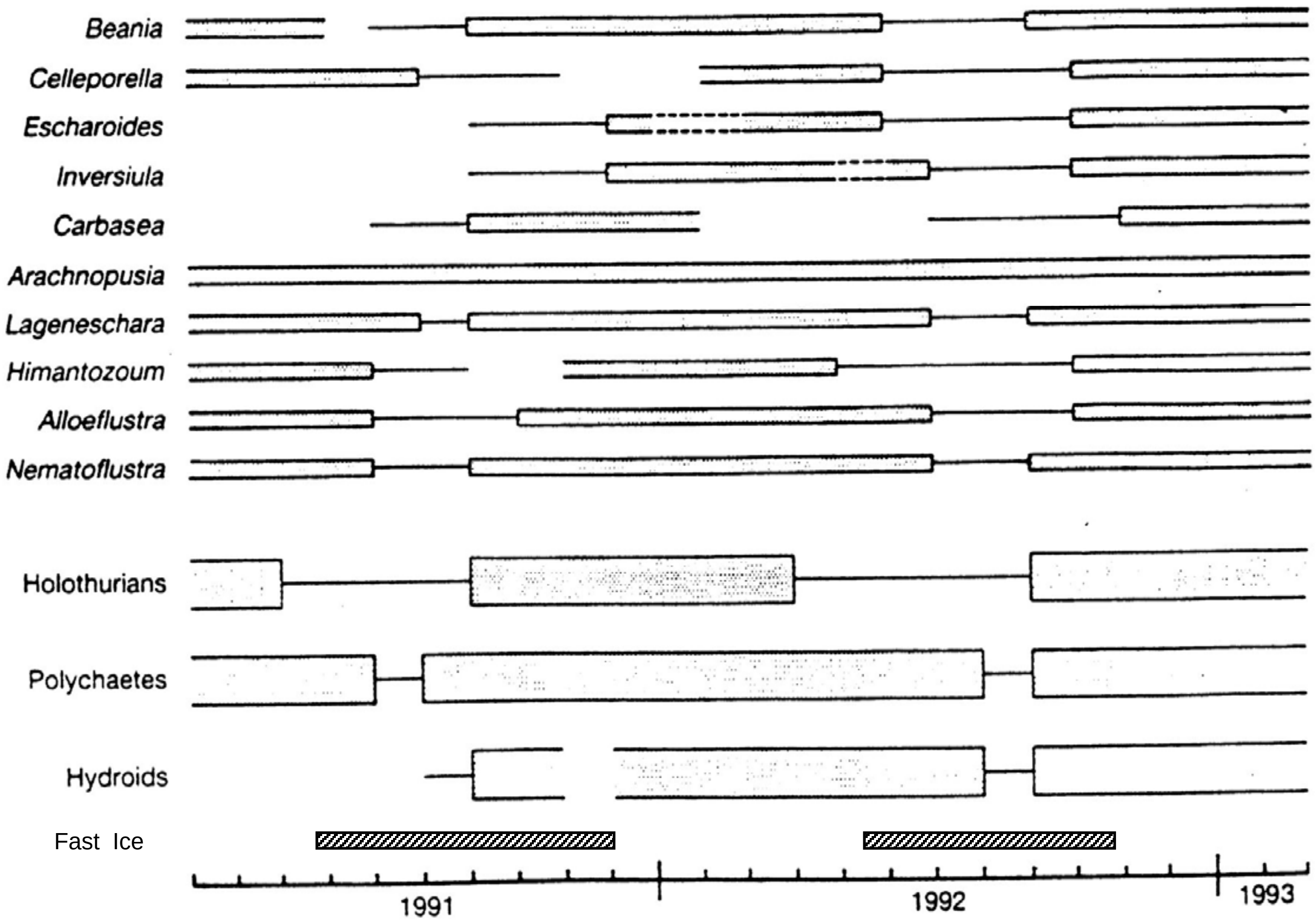
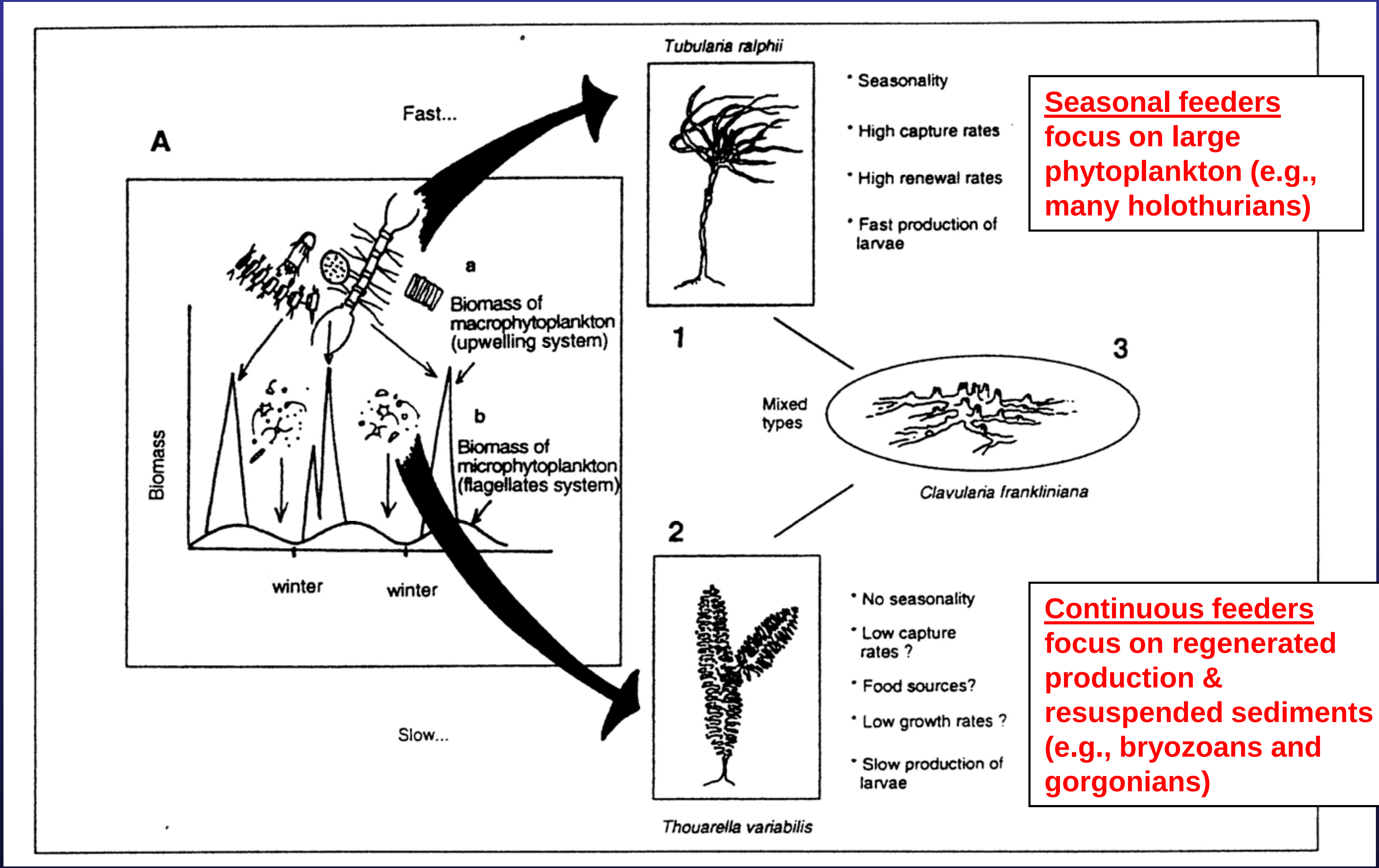


Fig. 2 Feeding activity (*shaded blocks*) and inactivity (*lines*) of various benthic suspension feeders with month of year, for 1991–1993. Results are meaned between sites. *Dotted lines* in *Escharoides* and *Inversiula* mark periods of likely feeding although actual data suggested inactivity (probably because of high currents)

Many species do stop feeding, but often for < 2 - 3 months even though fast ice and low-chlorophyll concentrations last for 5 - 6 months!

Orejas et al. (2000) – Two end-member Antarctic Suspension Feeding Strategies



<u>Seasonal feeders</u> focus on large phytoplankton (e.g., many holothurians)

<u>Continuous feeders</u> focus on regenerated production & resuspended sediments (e.g., bryozoans and gorgonians)

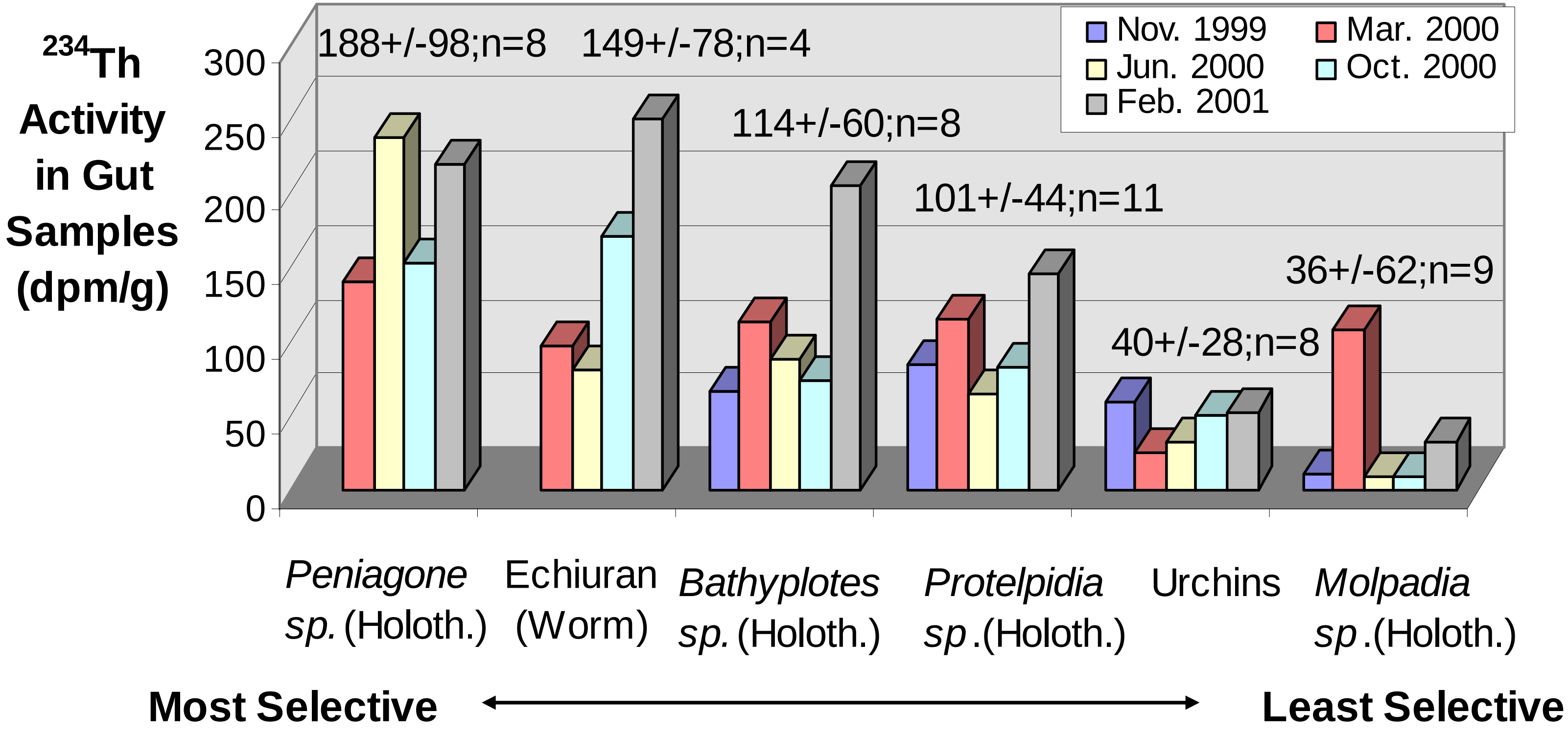
I.e., *<u>strong</u>* or *<u>weak</u>* BPC for suspension feeders, depending on feeding strategy.

Contrasts with FOODBANCS studies – deep shelf near Palmer Station (64° S)

Sea ice for ~ 4 mo


Bathyplotes

^{234}Th Activities in Animal Gut Samples Collected from the Antarctic Shelf



DeMaster et al., in manuscript

All species contain high quality material in gut in summer and winter

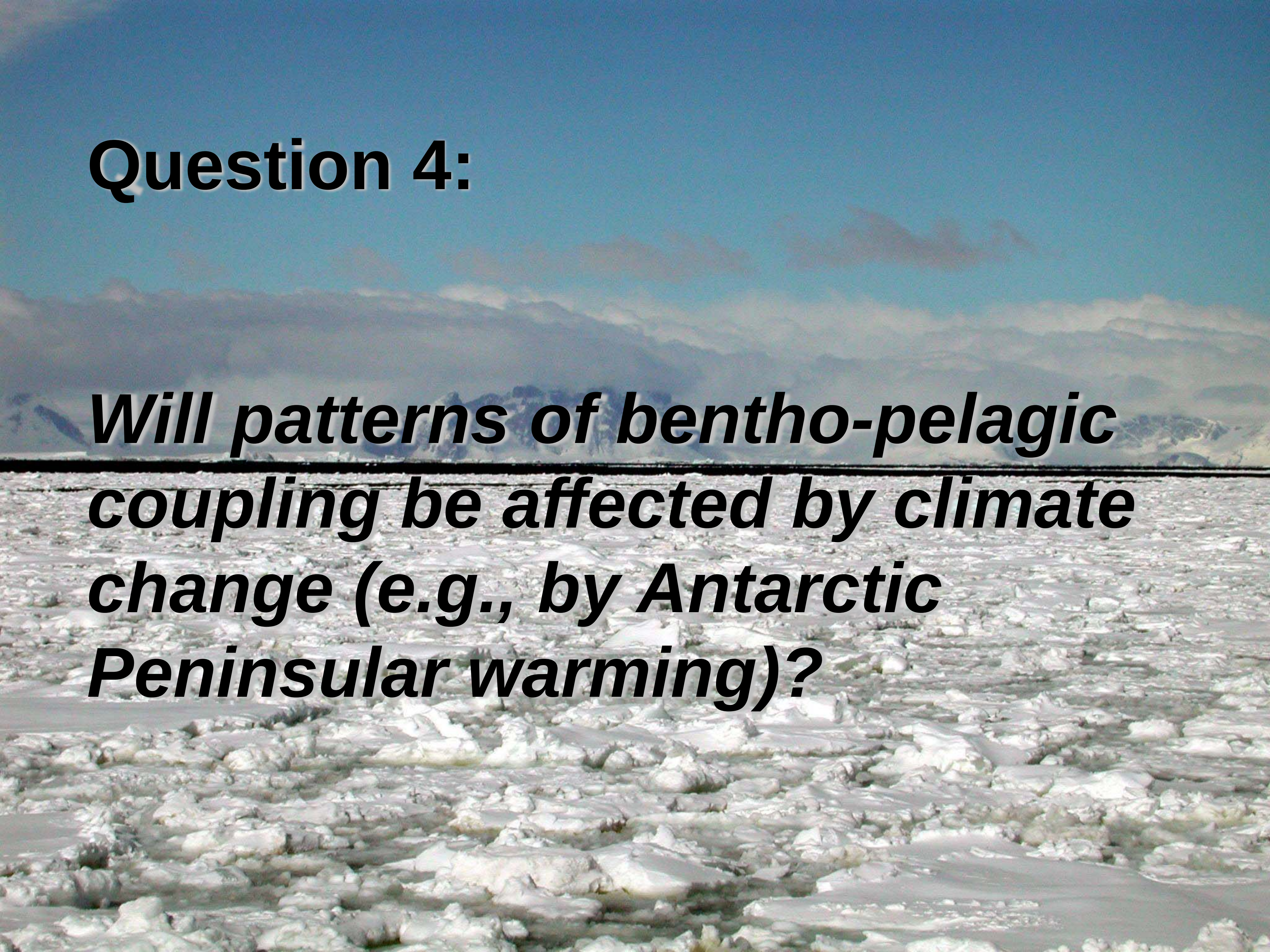
Conclusions regarding phasing of benthic processes with seasonal primary production (Question 3):

Most benthic processes initially expected to vary in phase with boom/bust water-column production cycle.

In fact, many processes (including SCOC, feeding and reproduction) often are poorly coupled.

WHY??

Best insights likely obtained from integrative, time-series study of benthic ecosystem response to seasonal/interannual production patterns.

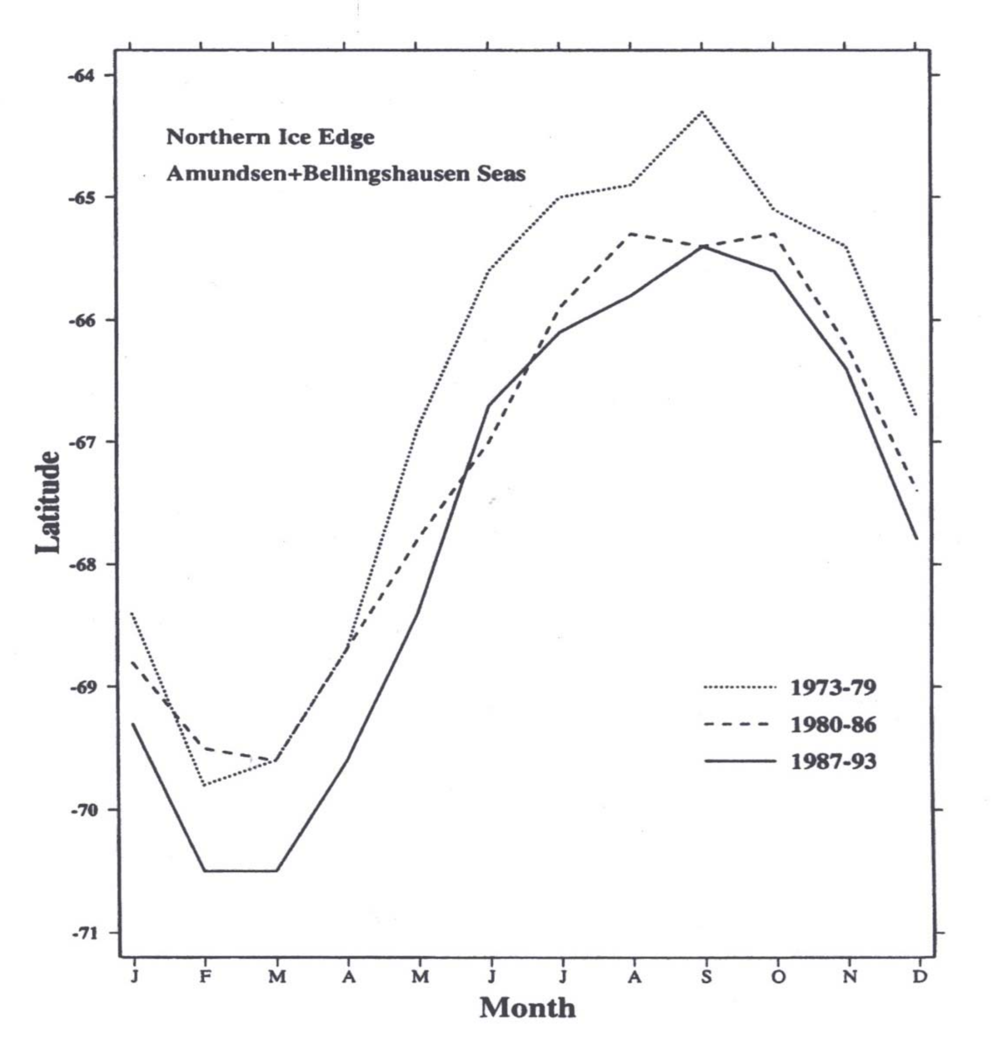


Question 4:

Will patterns of bentho-pelagic coupling be affected by climate change (e.g., by Antarctic Peninsular warming)?

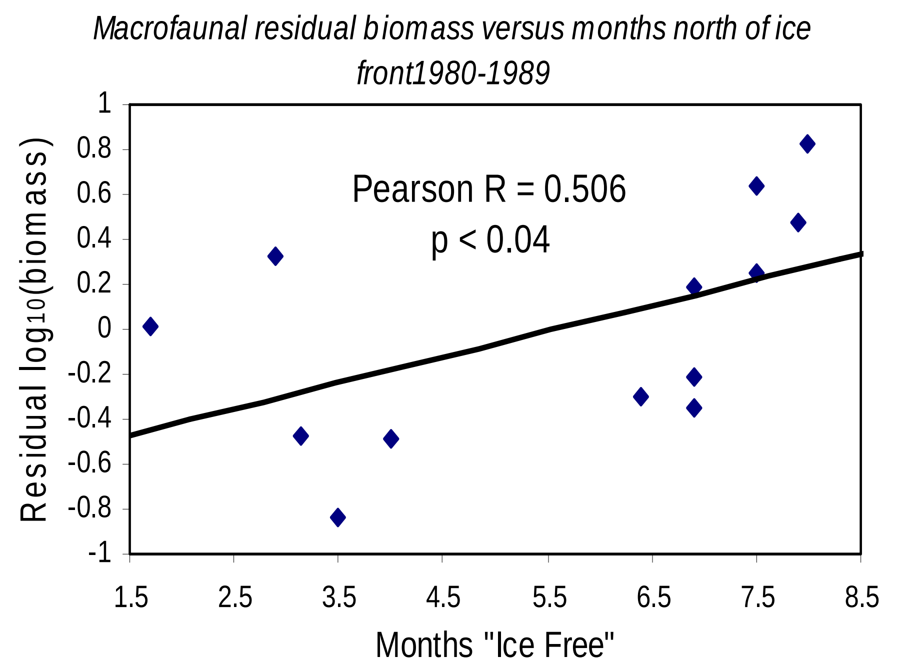
Very likely YES! For example:

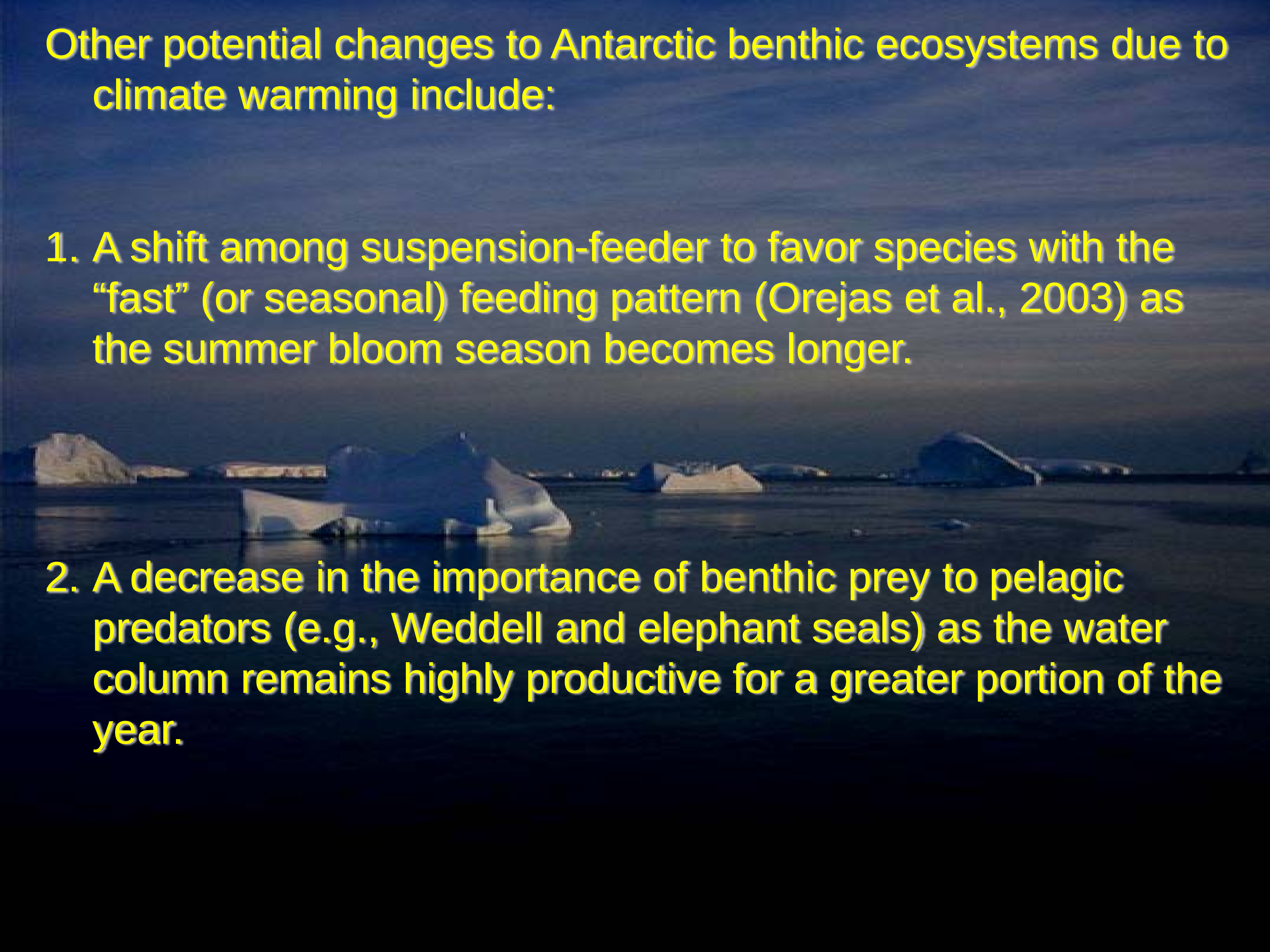
Warming is yielding reduction in duration of sea-ice cover -



Jacobs and Comiso, 1997

And duration of sea-ice is correlated with shelf macrofaunal biomass -





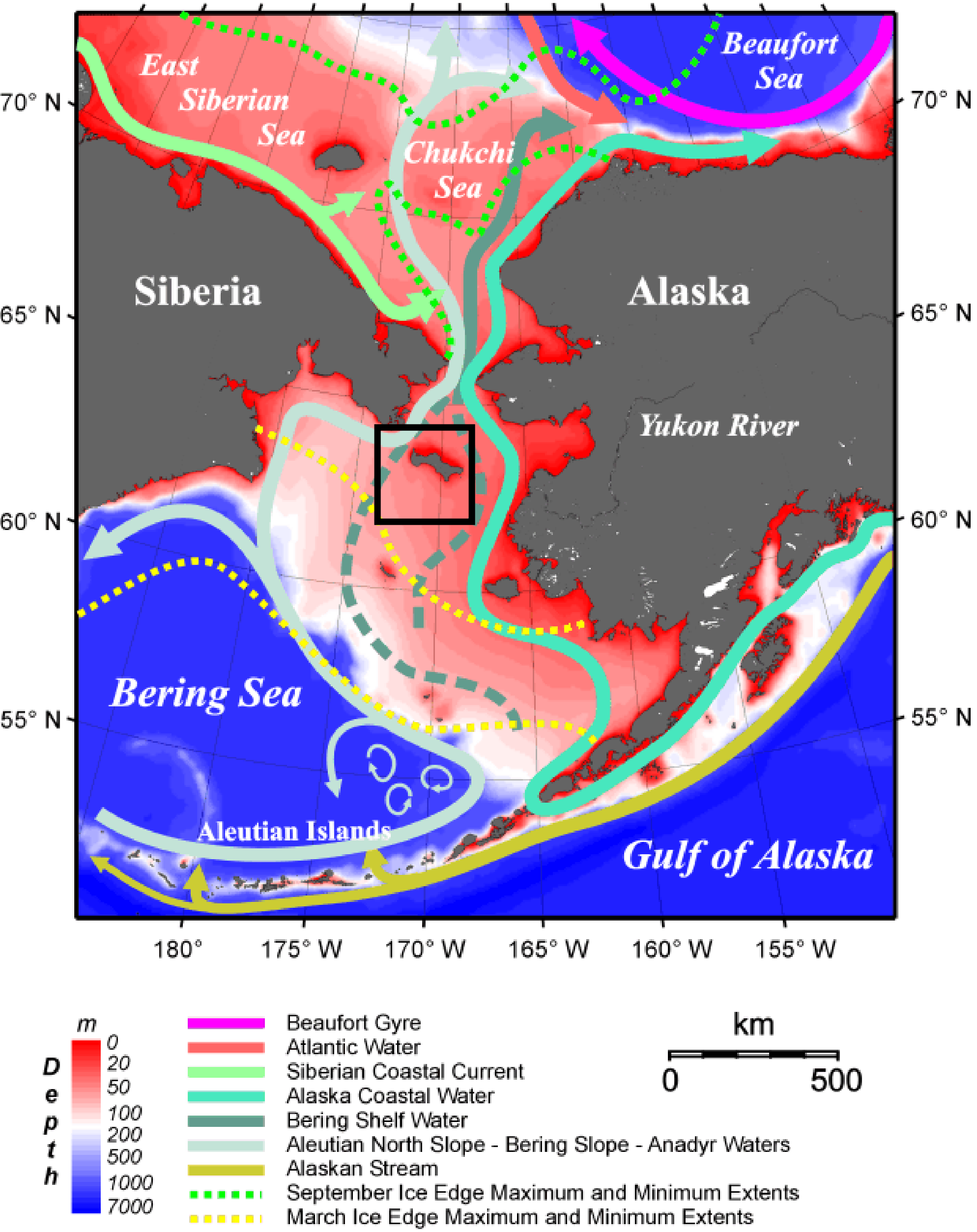
Other potential changes to Antarctic benthic ecosystems due to climate warming include:

1. A shift among suspension-feeder to favor species with the “fast” (or seasonal) feeding pattern (Orejas et al., 2003) as the summer bloom season becomes longer.
2. A decrease in the importance of benthic prey to pelagic predators (e.g., Weddell and elephant seals) as the water column remains highly productive for a greater portion of the year.

Many other impacts of warming on bentho-pelagic coupling also extremely likely –

Especially because the structure and export production of Antarctic pelagic ecosystems is heavily modulated by sea ice.

High-Latitude Arctic Shelf System



[courtesy Tom Weingartner]

- Shallow and highly productive under Pacific water influence
- Sea ice important, influences seawater temperature
- Timing of annual production critical for water column production, carbon cycling, and pelagic-benthic coupling
- Short food chains ⟶ lower trophic levels can efficiently support higher trophic organisms
- Climate change may have broad implications for ecosystem structure

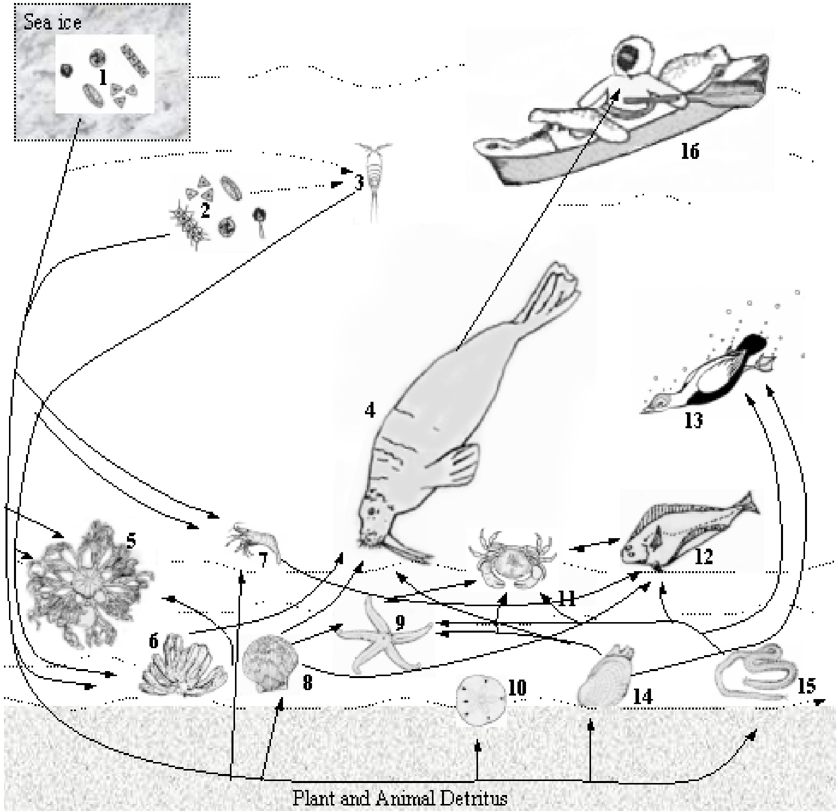
Grebmeier et al. 2006 and other papers

Walrus herd in the Chukchi Sea– June 2002

[M. Webber-USFWS]

Clam food in walrus stomachs →

[photos courtesy G. Sheffield



← Schematic of pre-warming foodweb in the northern Bering and Chukchi Seas

[Grebmeier and Dunton 2000]

Many Arctic “pelagic” vertebrates (ducks, walruses, gray whales) feed on relatively shallow, high-biomass benthos.

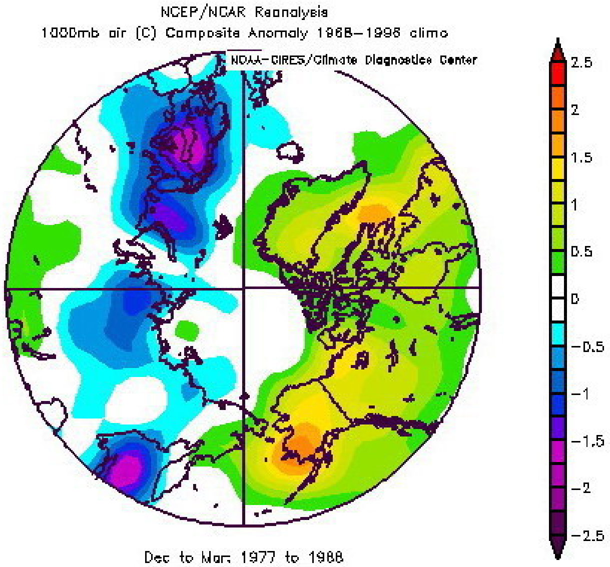
[photos by J. Lovvorn]

Spectacled Eider and benthic food supply (dominated by bivalves: *Nuculana radiata, Nucula belloti, Macoma calcarea*)

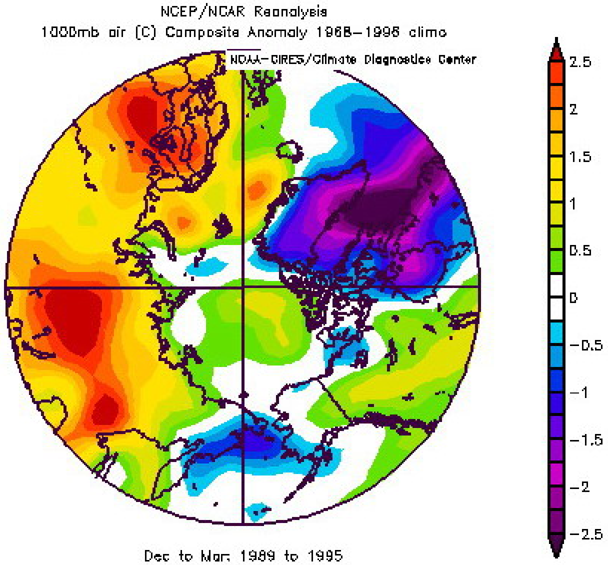
J. Grebmeier et al.

Arctic Climate Patterns

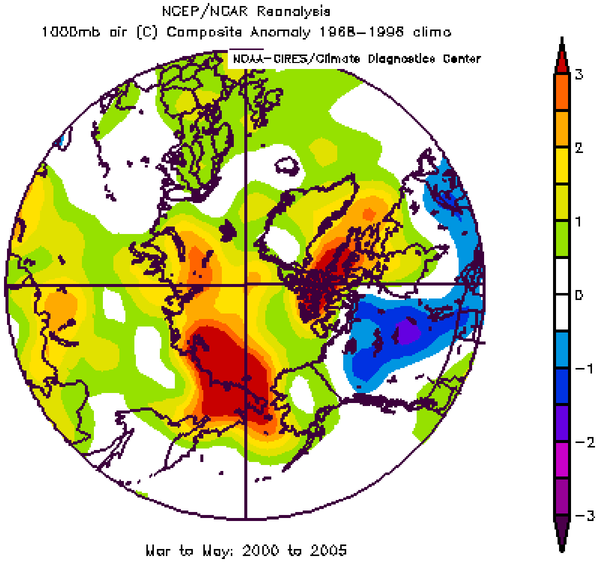
Temperature Anomalies



1977-1988 (PNA+)
Pacific North American



1989-1995 (AO+)
Arctic Oscillation



2000-2005 (Arctic Warm)

Northern Bering Sea Ice Concentration (April 2000-2004; A) and St. Lawrence Temperature Changes (B)

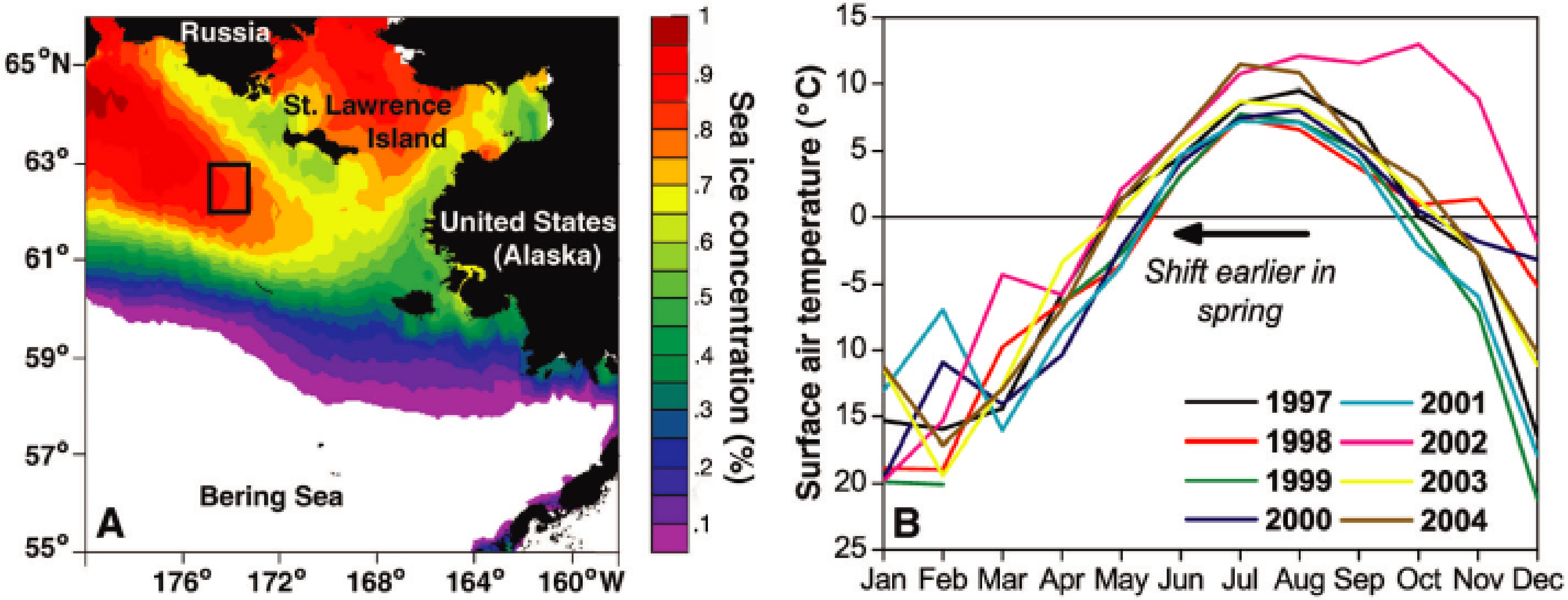
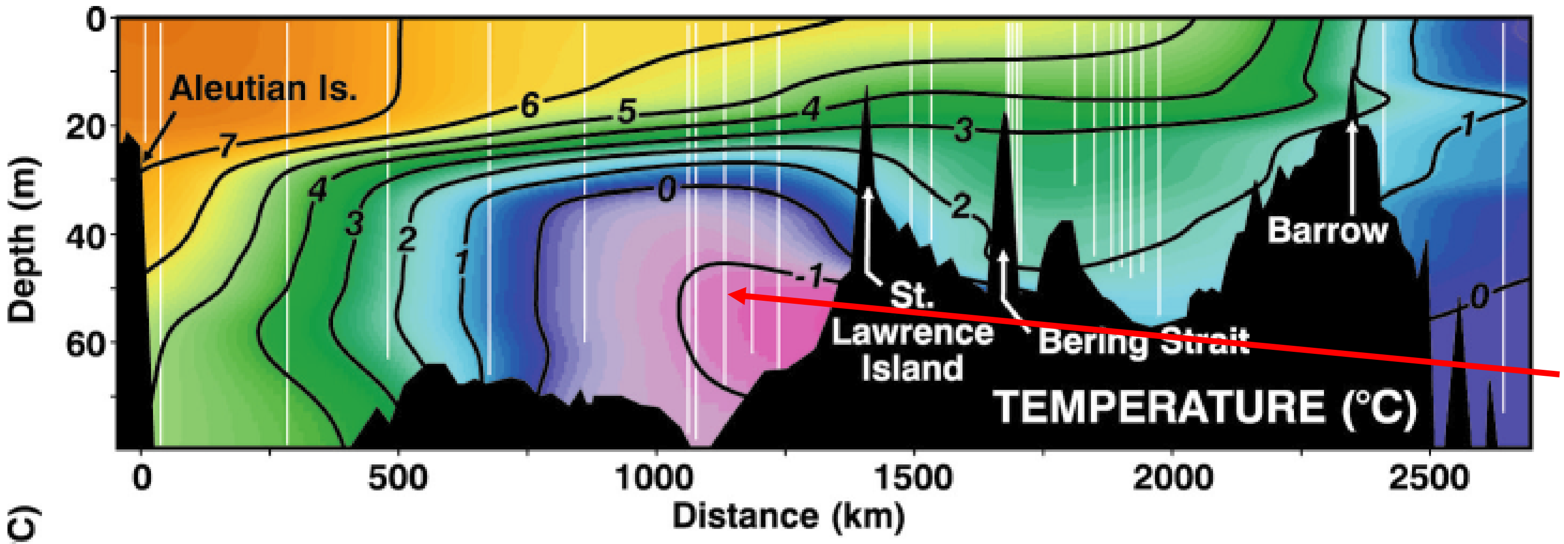


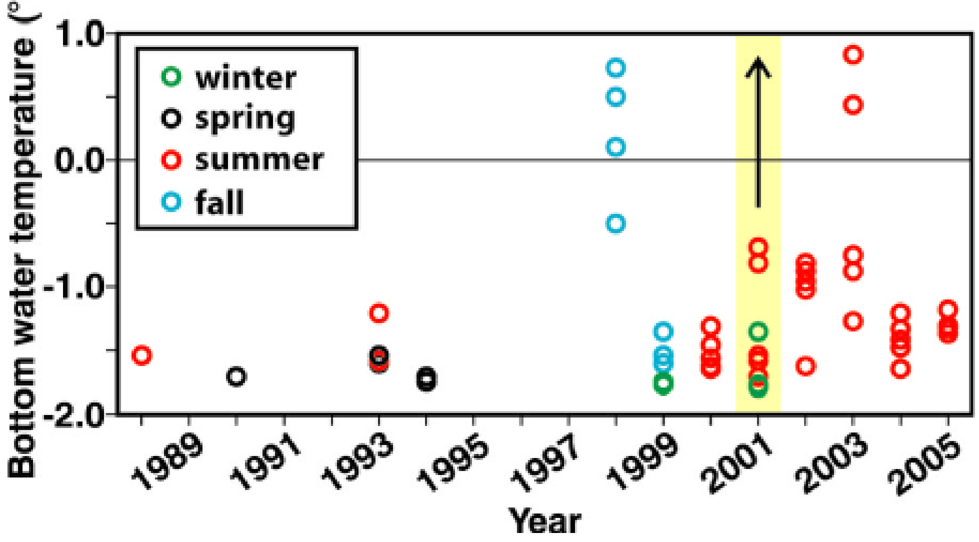
Fig. 1. (A) Location map (box indicates location of time-series biological sites) and average April sea ice concentration (1 corresponds to 100%, and 0.1 corresponds to 10%) in the northern Bering Sea from 2000 to 2004. Ice concentrations are based on microwave satellite instruments, Defense Meteorological Satellites Program SSM/I (12, 16). (B) Monthly averaged surface air temperature measured at Savoonga (63.68-N, 170.5-W) on St. Lawrence Island over the years 1997 to 2004. Note the interannual variability in the timing of melt onset (È3 weeks) based on date air temperature rises above 0-C (13).

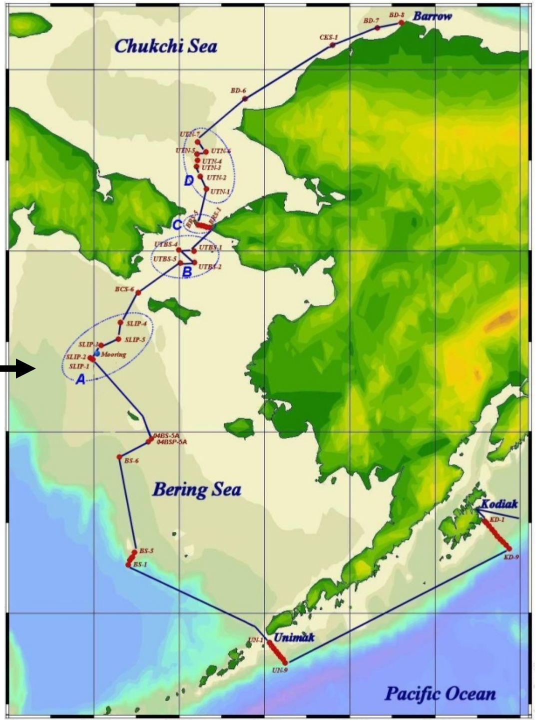
[Grebmeier et al. Science, 2006]



[Grebmeier et al. Science, 2006]

Temp. barrier to subarctic demersal fish

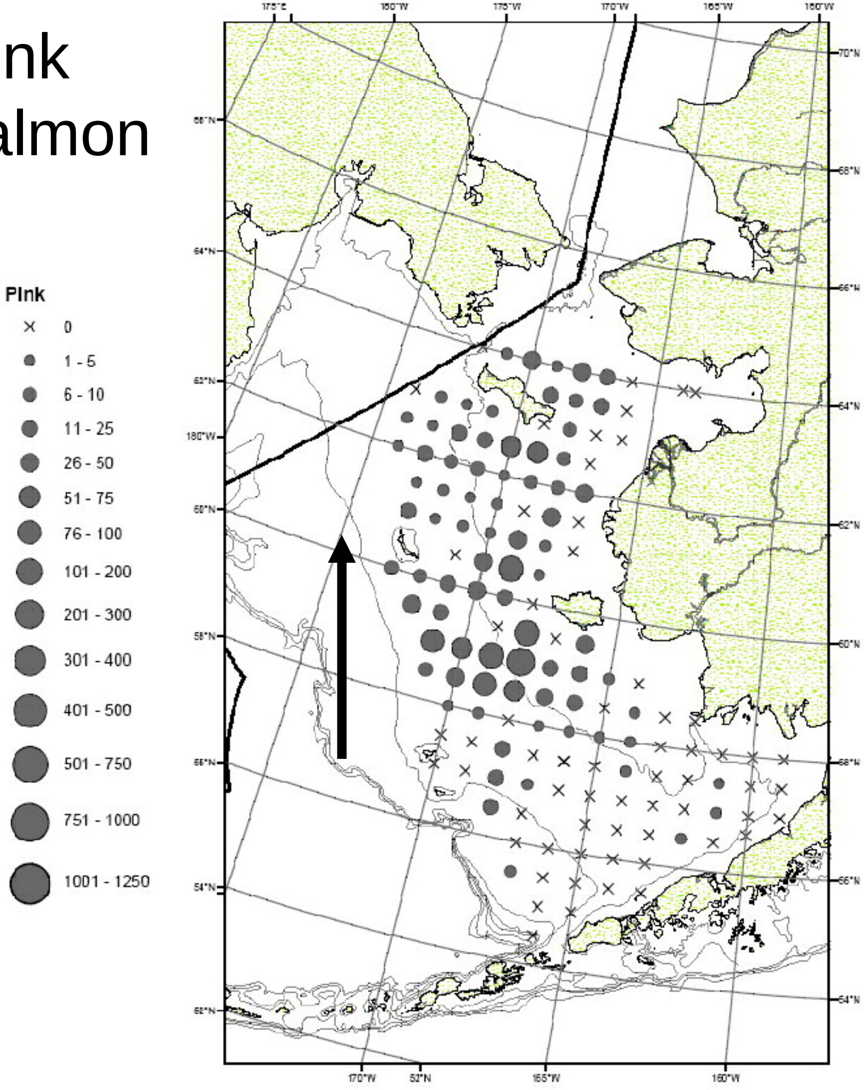




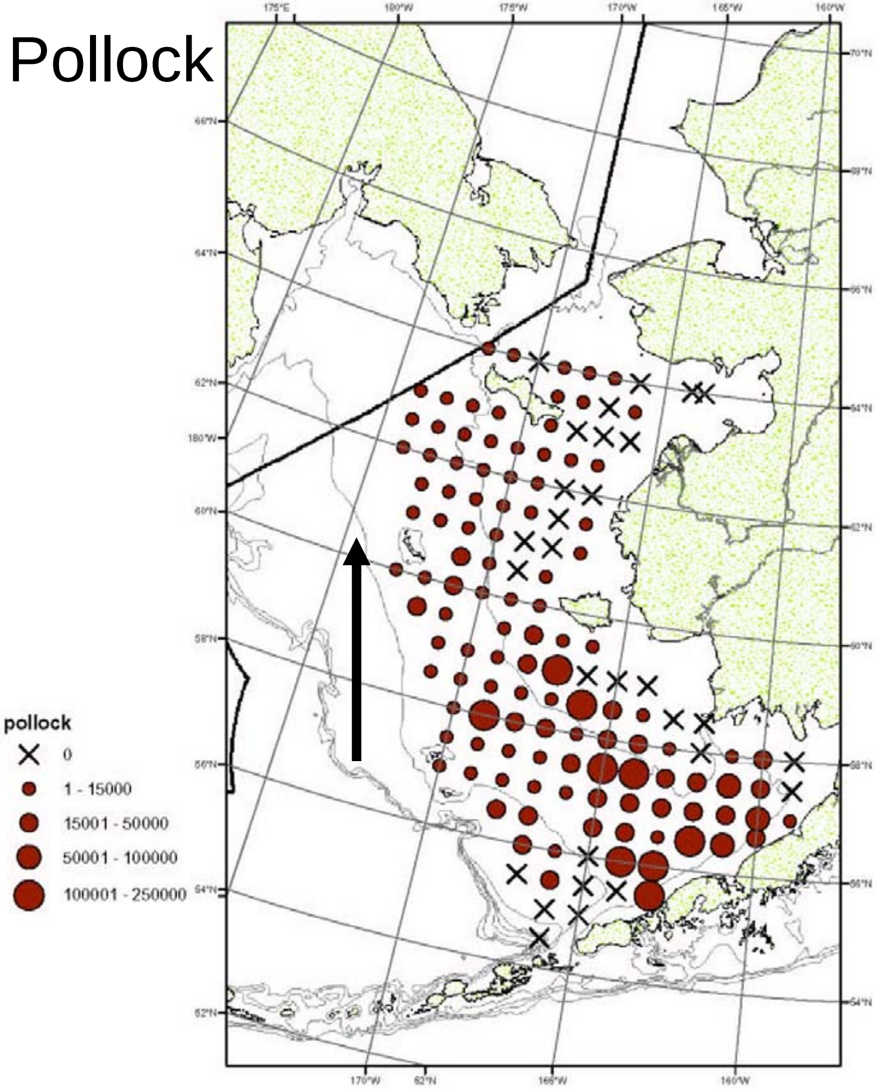
Seawater temperature extending from the Aleutian Islands, Alaska (top left) to Barrow, Alaska (top right) in July 2001 from the CCGS *Sir Wilfrid Laurier*. Bottom panel is time series of bottom water temperatures (<0°C) in cold pool SW of St. Lawrence Island.

Annual July cruises on CCGS *Sir Wilfrid Laurier*

Pink salmon

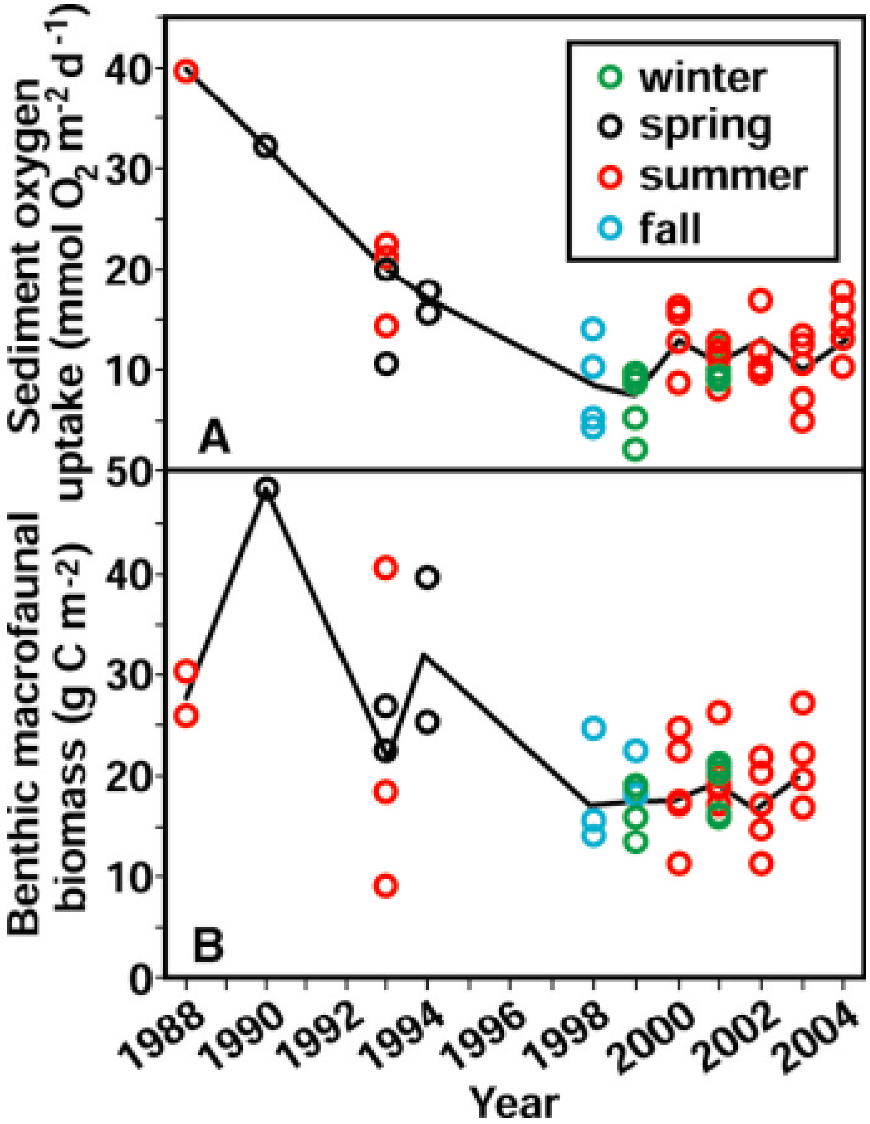


Pollock



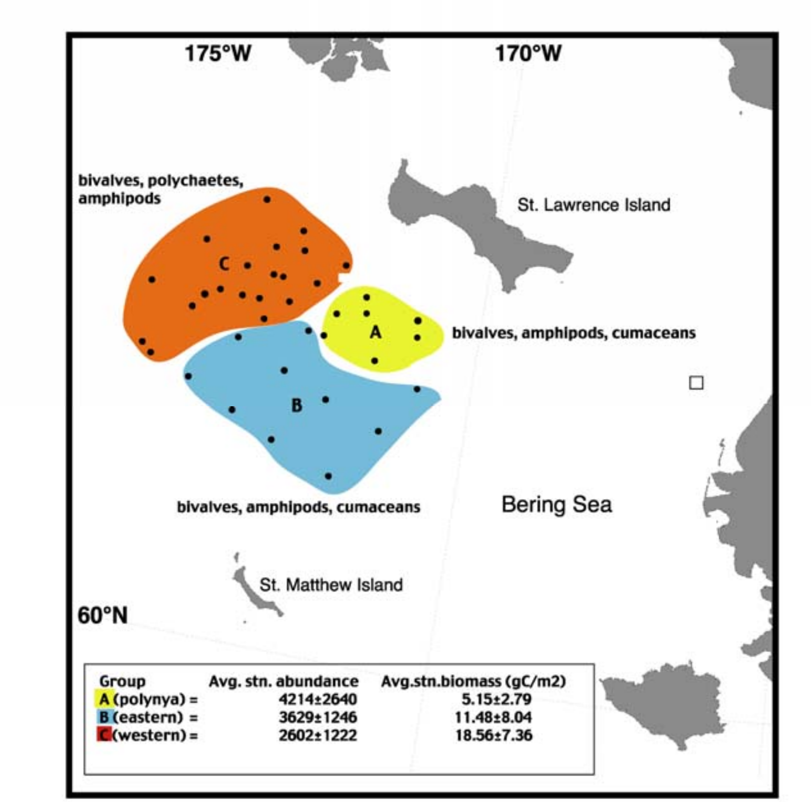
10 Million new Salmon in the N. Bering Sea in 2004; coincident with increased northward movement of pollock - [Jack Helle]

Change in sediment oxygen uptake (indicator of carbon supply to benthos) and benthic macrofaunal biomass SW of St. Lawrence Island; trend lines through station means of values

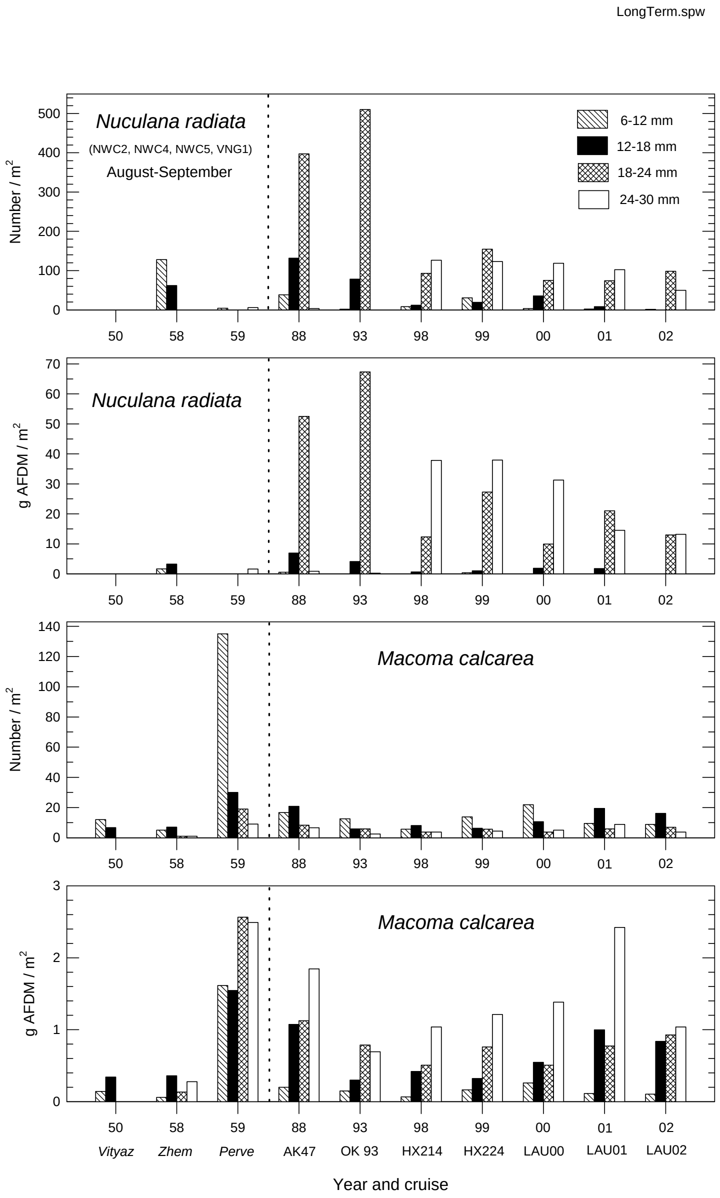


[Grebmeier et al. Science, 2006]

BSEO-S sites embedded in Group C, orange



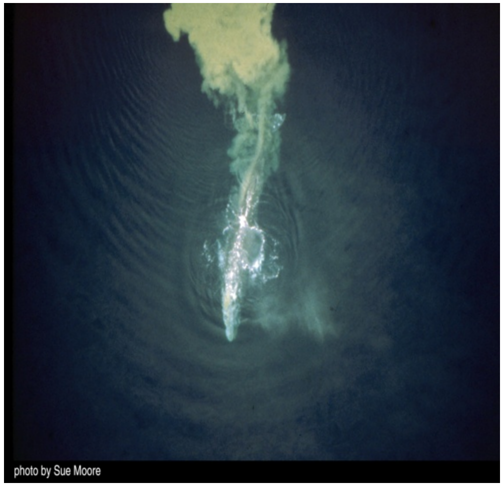
Group	Avg. stn. abundance	Avg.stn.biomass (gC/m2)
A (polynya) =	4214±2640	5.15±2.79
B (eastern) =	3629±1246	11.48±8.04
C (western) =	2602±1222	18.56±7.36



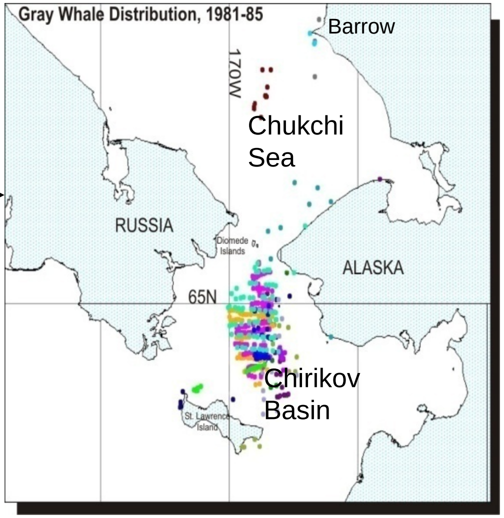
- retrospective study indicates changes in dominant bivalve from *Macoma calcarea* to *Nuculana radiata,* results in lower bivalve prey caloric content

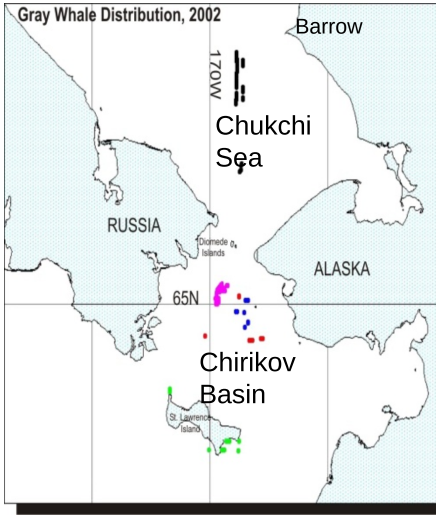
[Lovvorn et al. 2003; Grebmeier et al., in prep.]

Gray Whales as Ecosystem Sentinels? ‘Weight of Evidence’



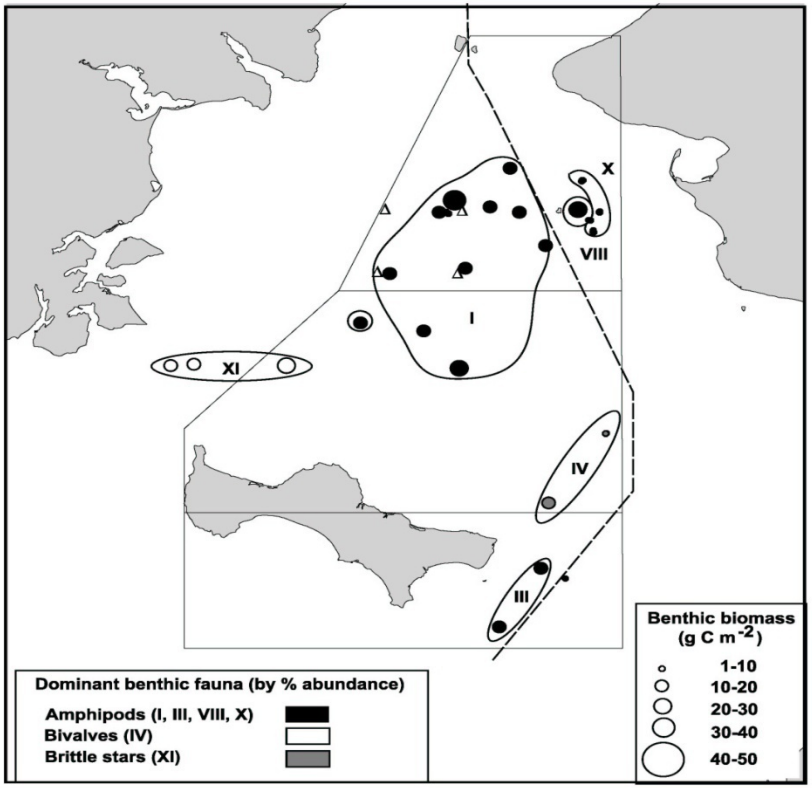
- One-week delay in southbound migration timing, coincident with NPAC regime shift **(Rugh et al. 2001)**
- Calving rates positively correlated with ice-free Chirikov Basin **(Perryman et al. 2002)**
- Absence of feeding GW in Chirikov Basin, coincident with decline in benthic infauna **(Moore et al. 2003)**
- Feeding whales year-round near Kodiak (Moore et al.*)
- Calls detected year-round near Barrow (Stafford et al.*)

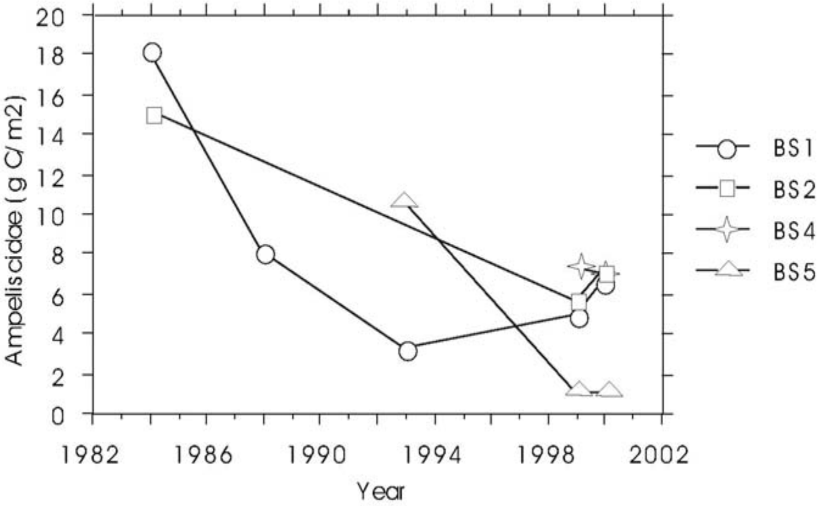




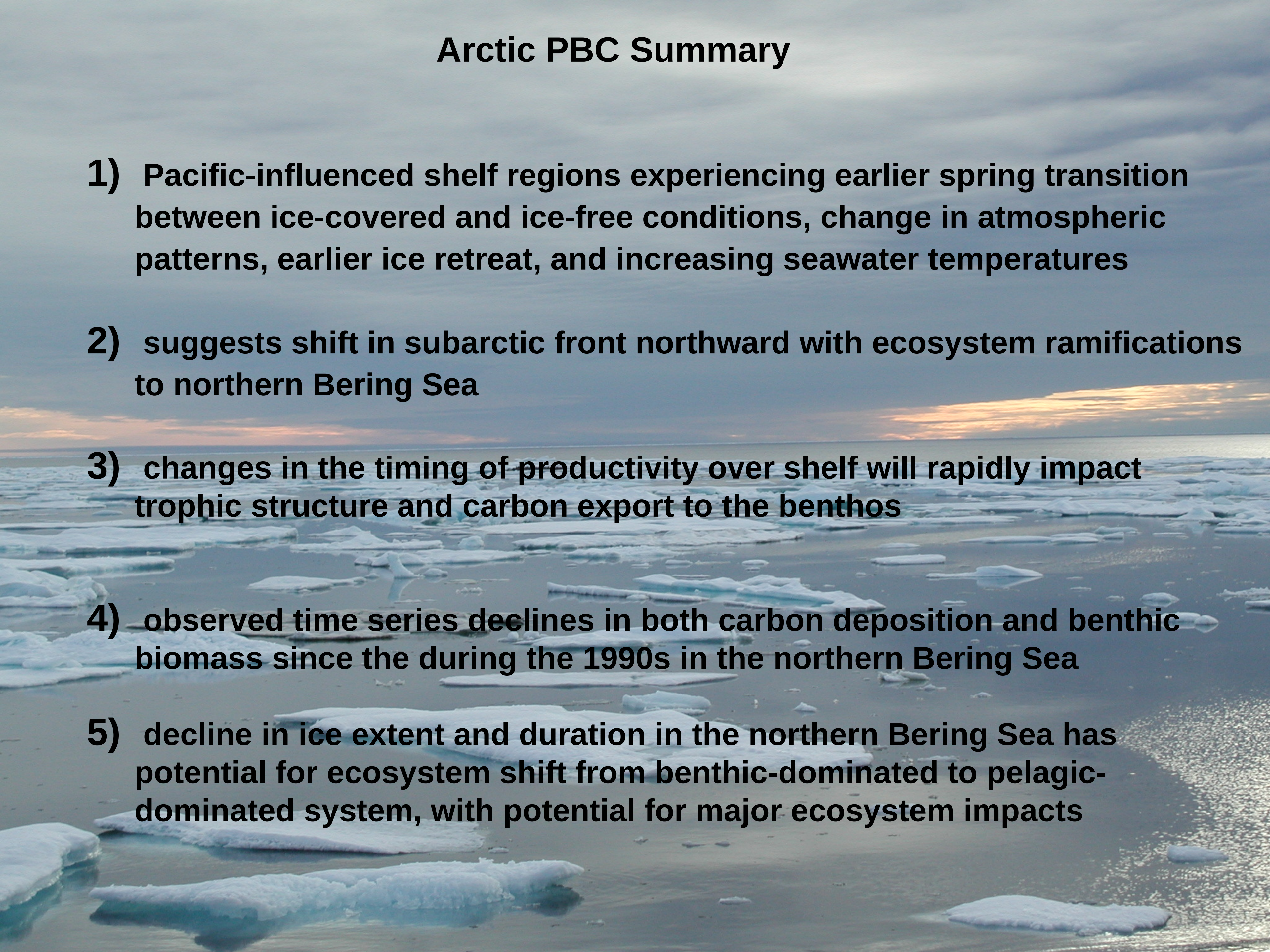
Co-incident with Decline in Infaunal Benthic Prey

BSEO Benthic Time Series





[Moore et al. 2003]



Arctic PBC Summary

1) Pacific-influenced shelf regions experiencing earlier spring transition between ice-covered and ice-free conditions, change in atmospheric patterns, earlier ice retreat, and increasing seawater temperatures

2) suggests shift in subarctic front northward with ecosystem ramifications to northern Bering Sea

3) changes in the timing of productivity over shelf will rapidly impact trophic structure and carbon export to the benthos

4) observed time series declines in both carbon deposition and benthic biomass since the during the 1990s in the northern Bering Sea

5) decline in ice extent and duration in the northern Bering Sea has potential for ecosystem shift from benthic-dominated to pelagic-dominated system, with potential for major ecosystem impacts

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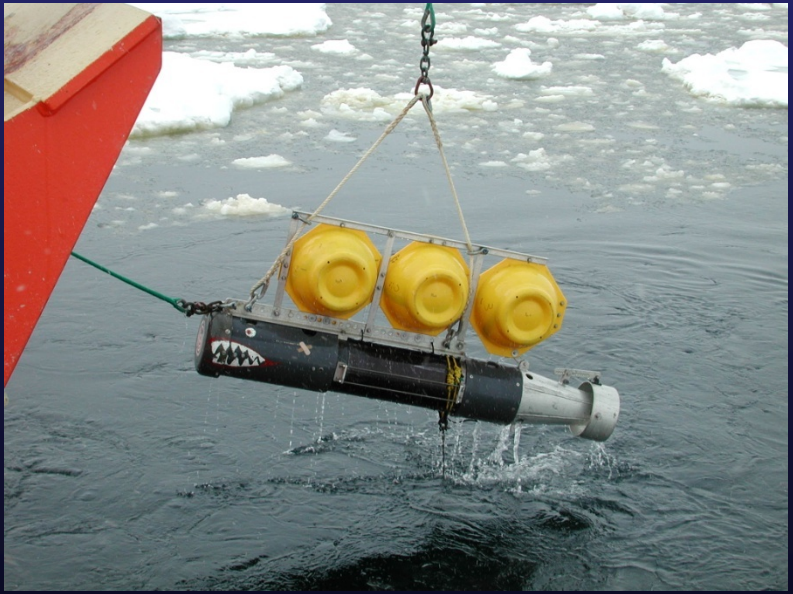
Broad range of parameters sampled ≥ 5x over 15 months (Nov 99 – Mar 01):

- *Sediment traps* - moored ~150 mab at Sta. B
- *Seafloor video surveys* – all stations
- *Time-lapse photography* – picture every 12 h of 2 m^2 of seafloor at Sta. B
- *Megacore samples* – microbes–macrofauna, sediment geochemistry and radiochemistry
- *Respirometry* - whole core incubations
- *Otter trawls* - megafauna

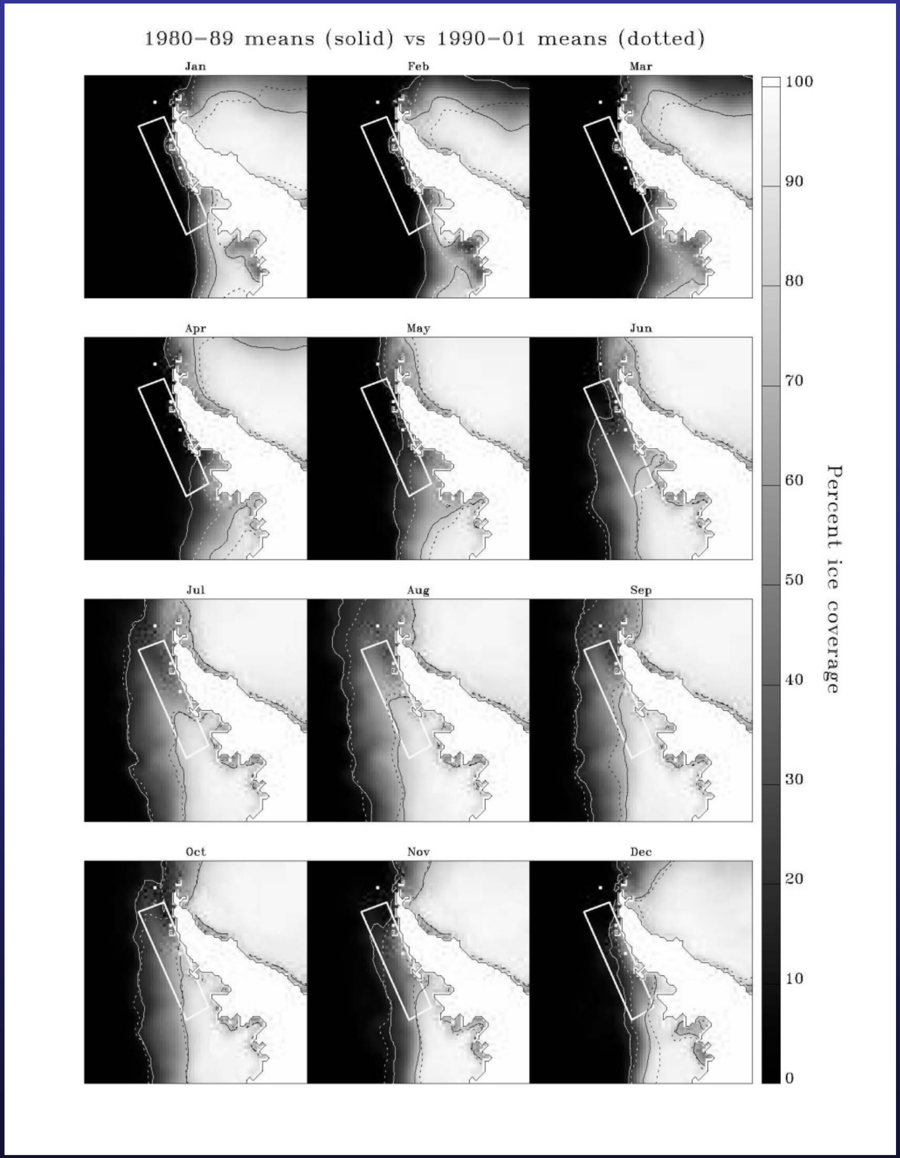
SEDIMENT TRAP RECOVERY

MEGACORE

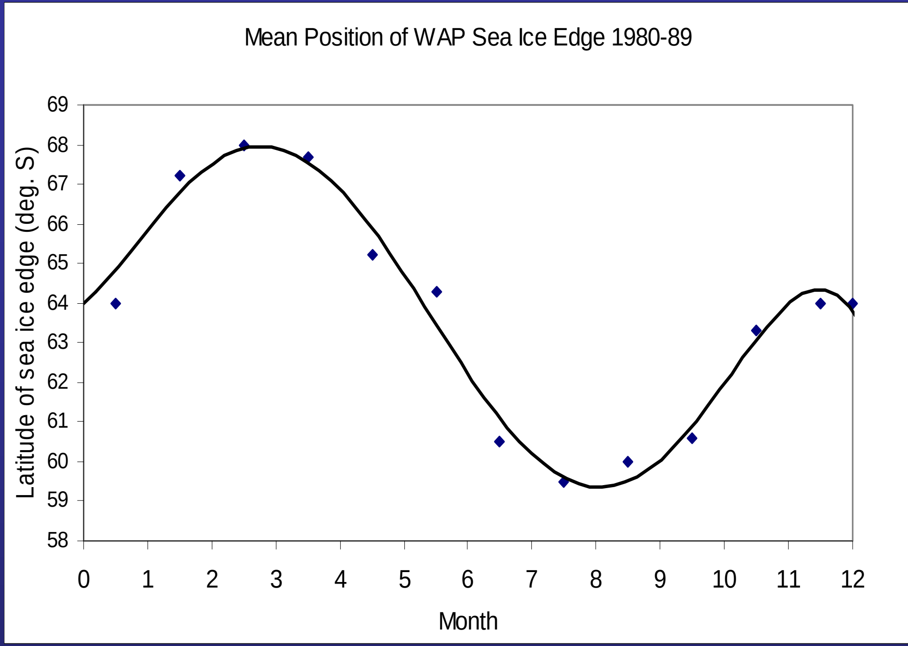
TOWED SEAFLOOR VIDEO SURVEY SYSTEM



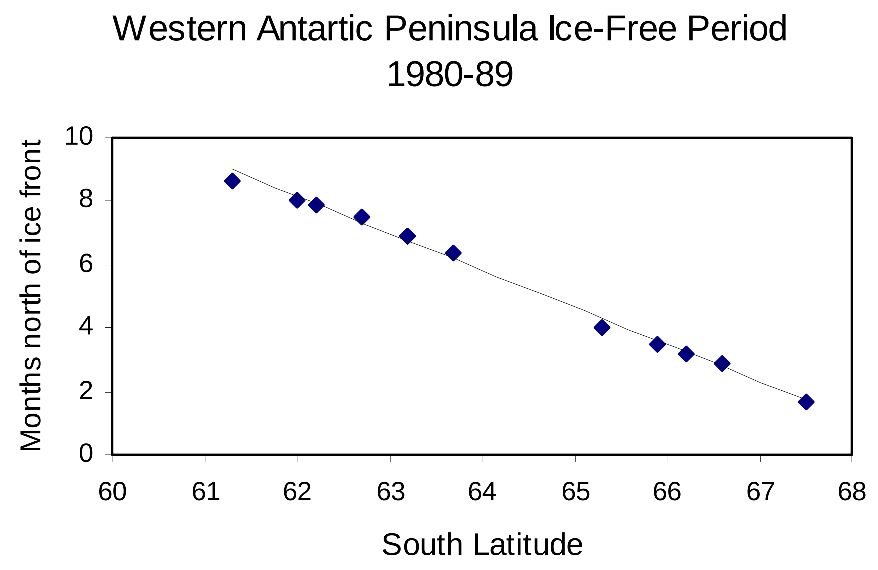
3) Estimate Ice free period for each station (as a function of latitude).



1980–89 means (solid) vs 1990–01 means (dotted)



Mean Position of WAP Sea Ice Edge 1980-89



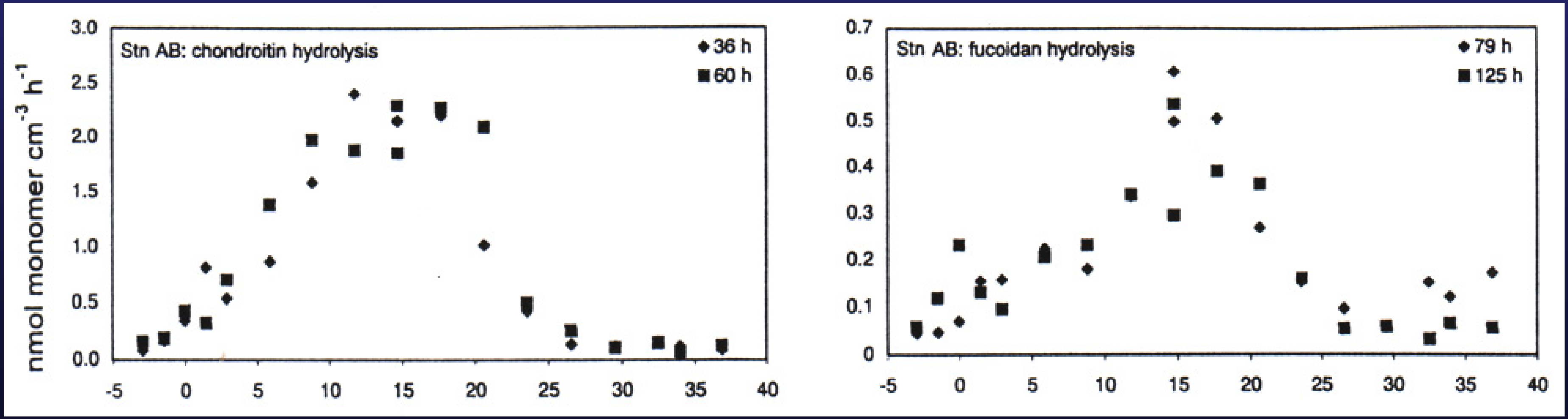
Western Antartic Peninsula Ice-Free Period 1980-89

Temperature Responses of Enzymes

- Declining temperatures (below 15°C) yield declines in microbial hydrolytic enzyme efficiency.

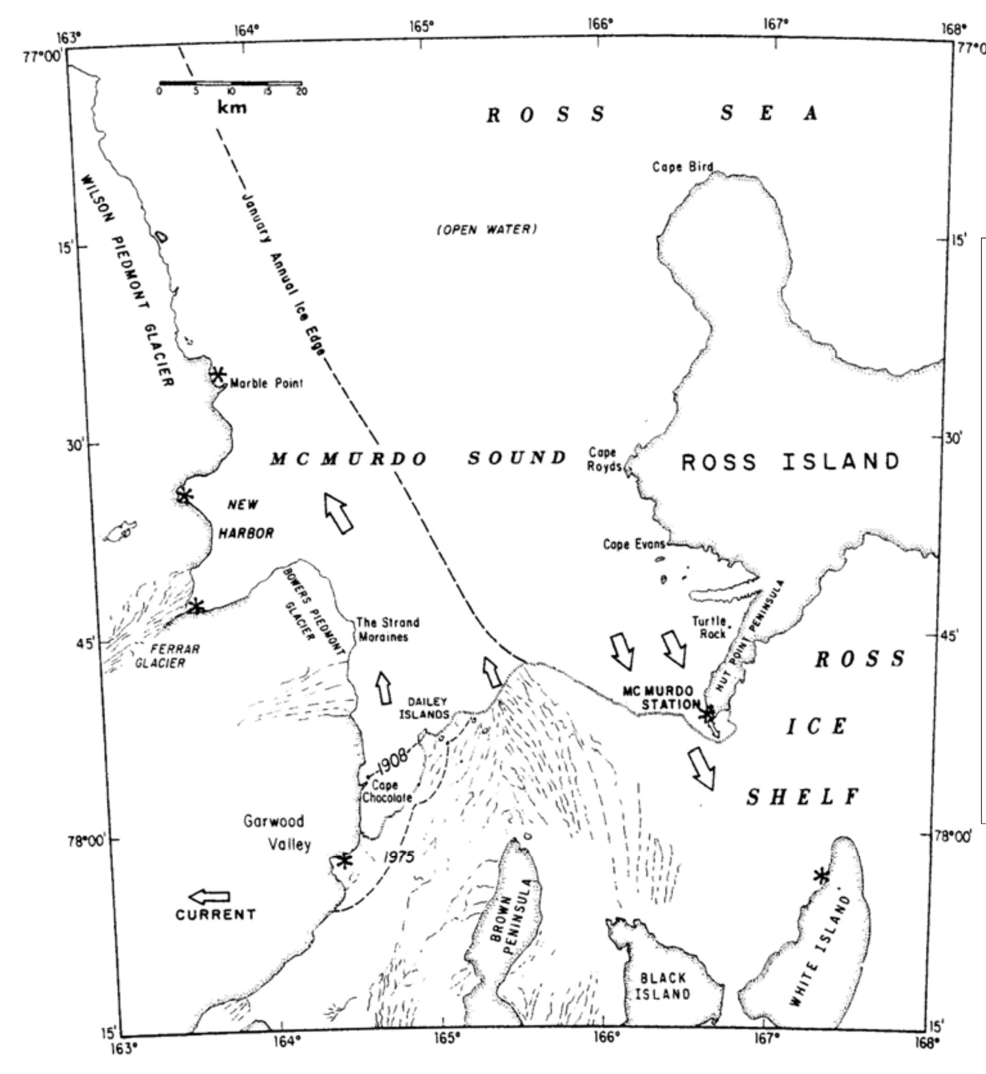
- To maintain a given level microbial of community metabolism higher substrate concentrations are required at lower temperatures.

- Thus, concentrations of labile organic matter build up to higher levels build up to relatively high levels in Antarctic sediments.

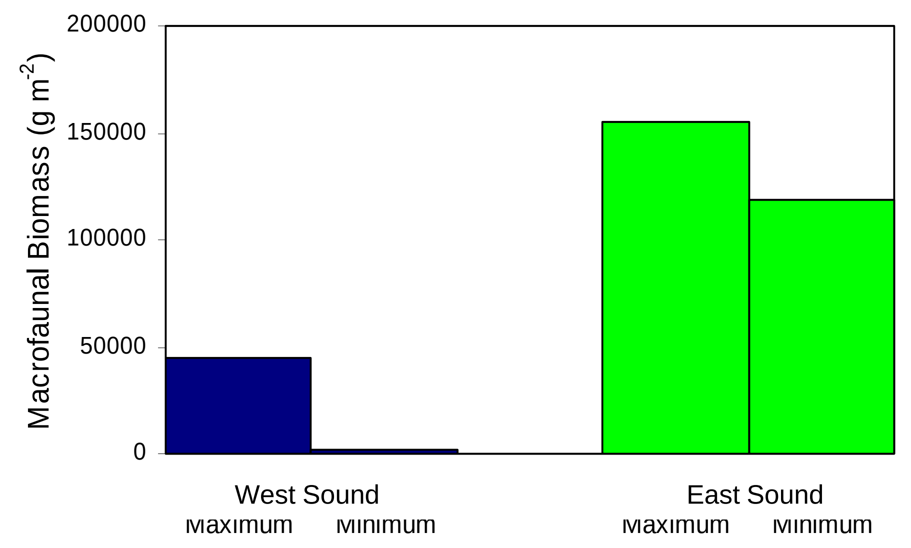


Arnosti & Jorgensen (2003)

At extremes, yes, e.g. -



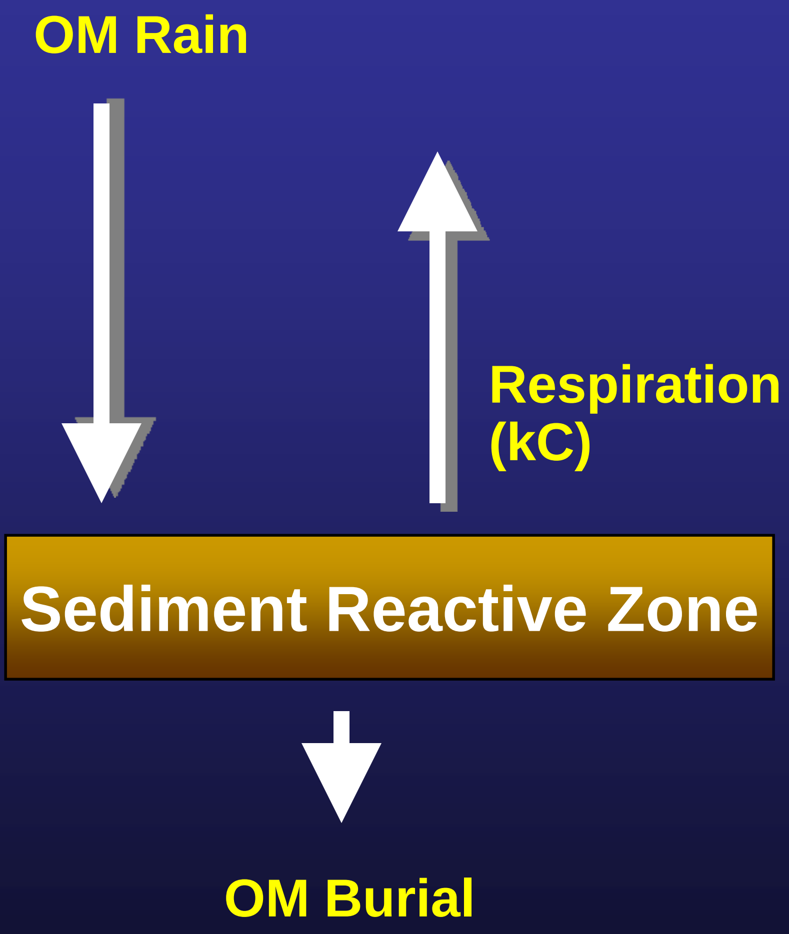
Dayton and Oliver, 1977



Macrofaunal biomass

Mean directions of surface currents (arrows)

Temperature-Substrate Limitation Hypothesis

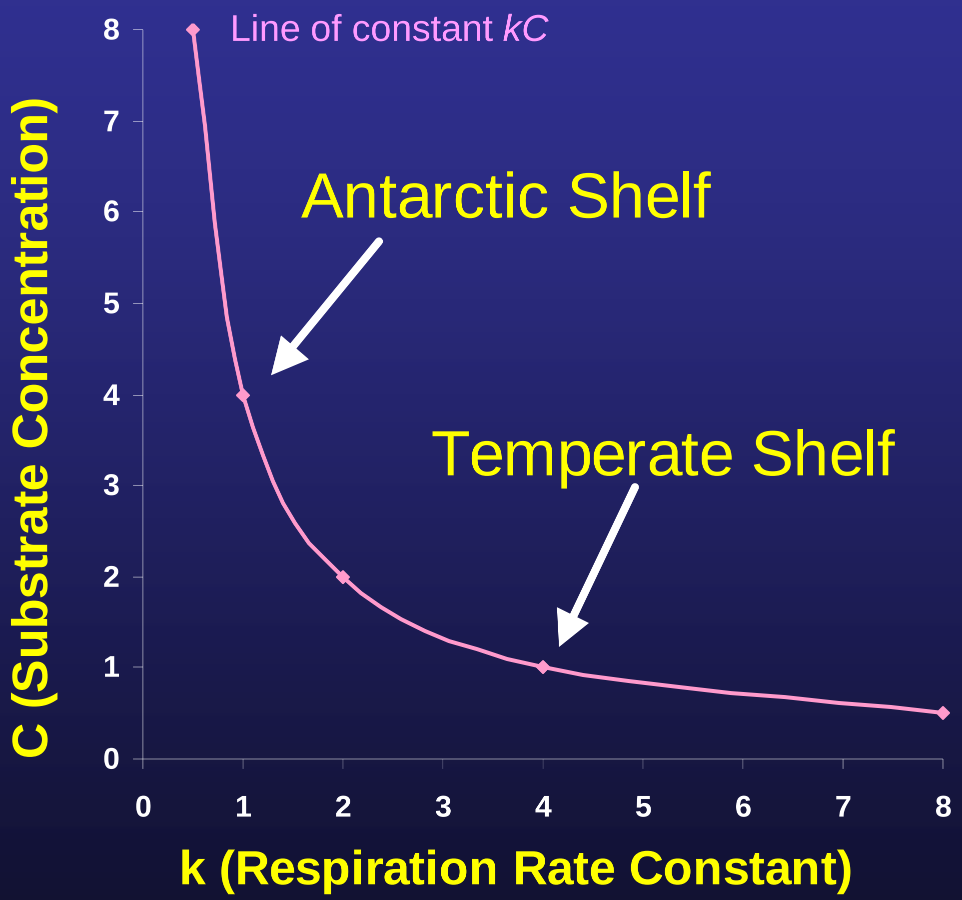


OM Rain

Respiration (kC)

Sediment Reactive Zone

OM Burial



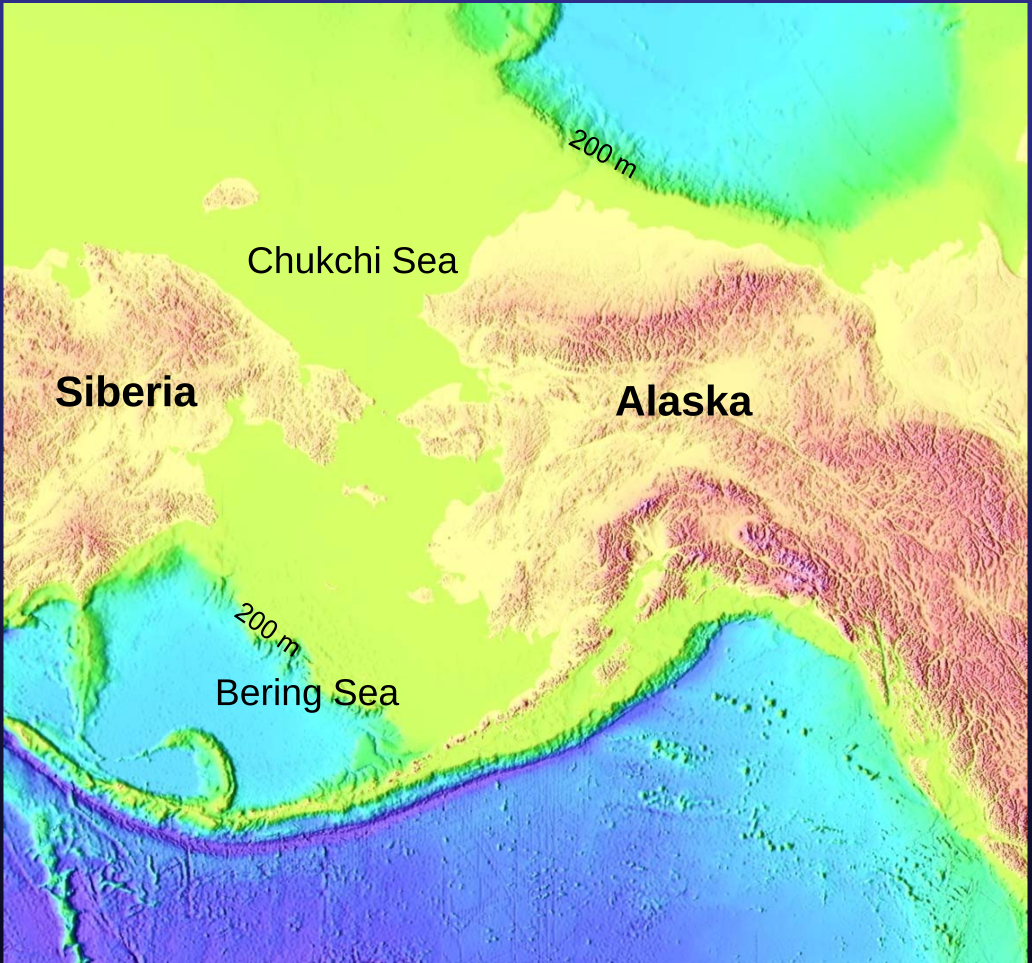
At SS, rain = respiration + burial

Winter

Summer

For discussion of Antarctic versus Arctic BPC and climate change, consider the following:

1) The Antarctic shelf is generally 500 -1000 m deep, while the Arctic shelf is >200 m deep (often much less!).



OVERALL CONCLUSIONS REGARDING BENTHO-PELAGIC COUPLING ON THE ANTARCTIC SHELF

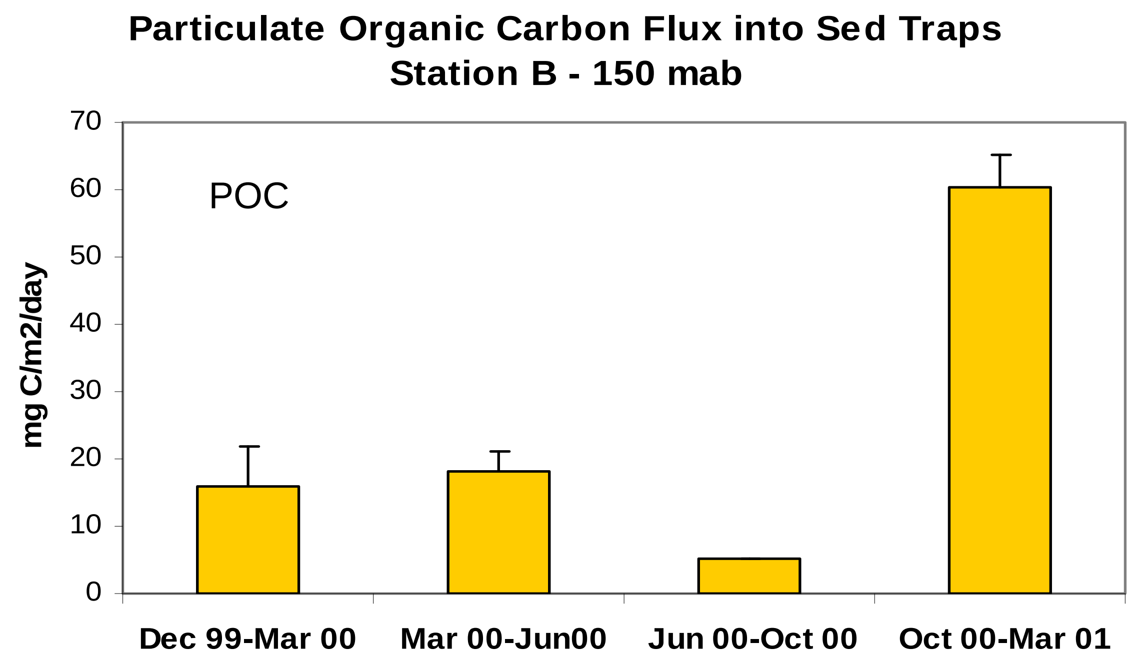
1) POC flux to the Antarctic shelf floor is dominated by large summer pulses – these pulses often are offset in time or space from overlying plankton blooms.

2) Across all benthic habitat types, regional patterns of primary production are only weakly imprinted on the shelf floor - however, on the *muddy shelf*, macrofaunal biomass does reflect large-scale patterns of sea-ice duration and primary production.

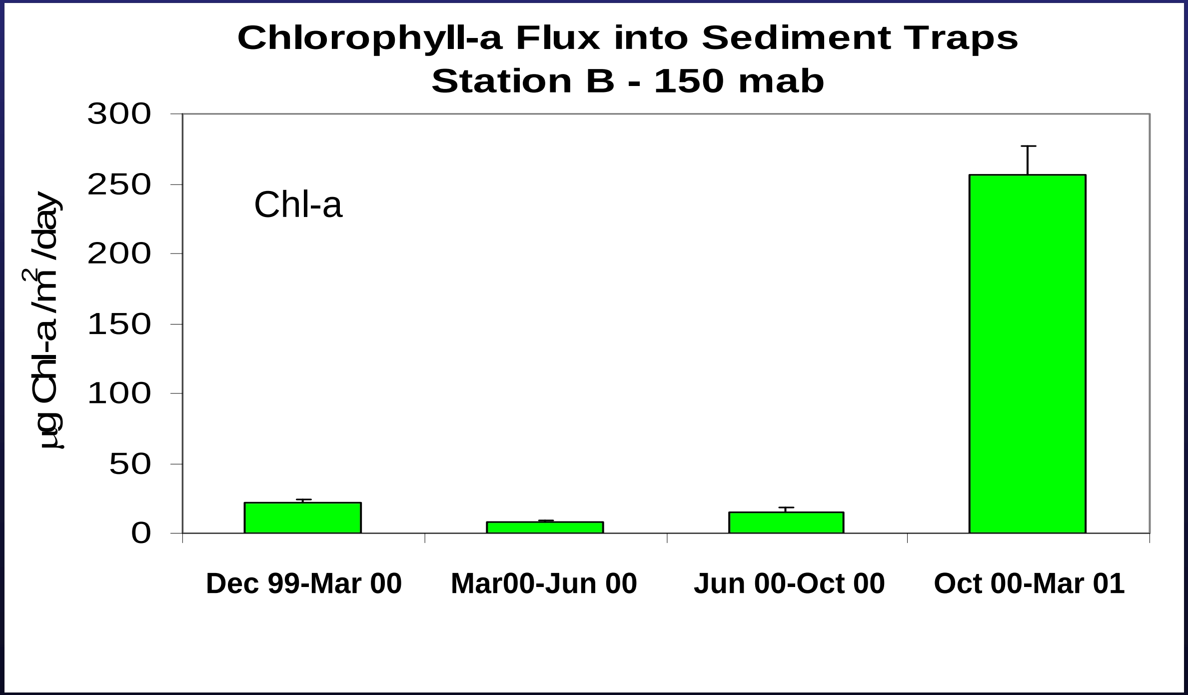
3) Despite initial expectations, many benthic processes (e.g., SCOC, suspension feeding, deposit feeding) are weakly phased to seasonal patterns of water-column production, exhibiting substantial "*inertia*" (due to presence of food banks).

4) Because of this "*inertia*", benthic processes may act as low pass filters and be useful indicators of long-term trends in Antarctic ecosystem function.

5) To predict the effects of climate warming on the Antarctic shelf ecosystem, studies of benthic-pelagic coupling along existing latitudinal sea-ice gradients are urgently needed.

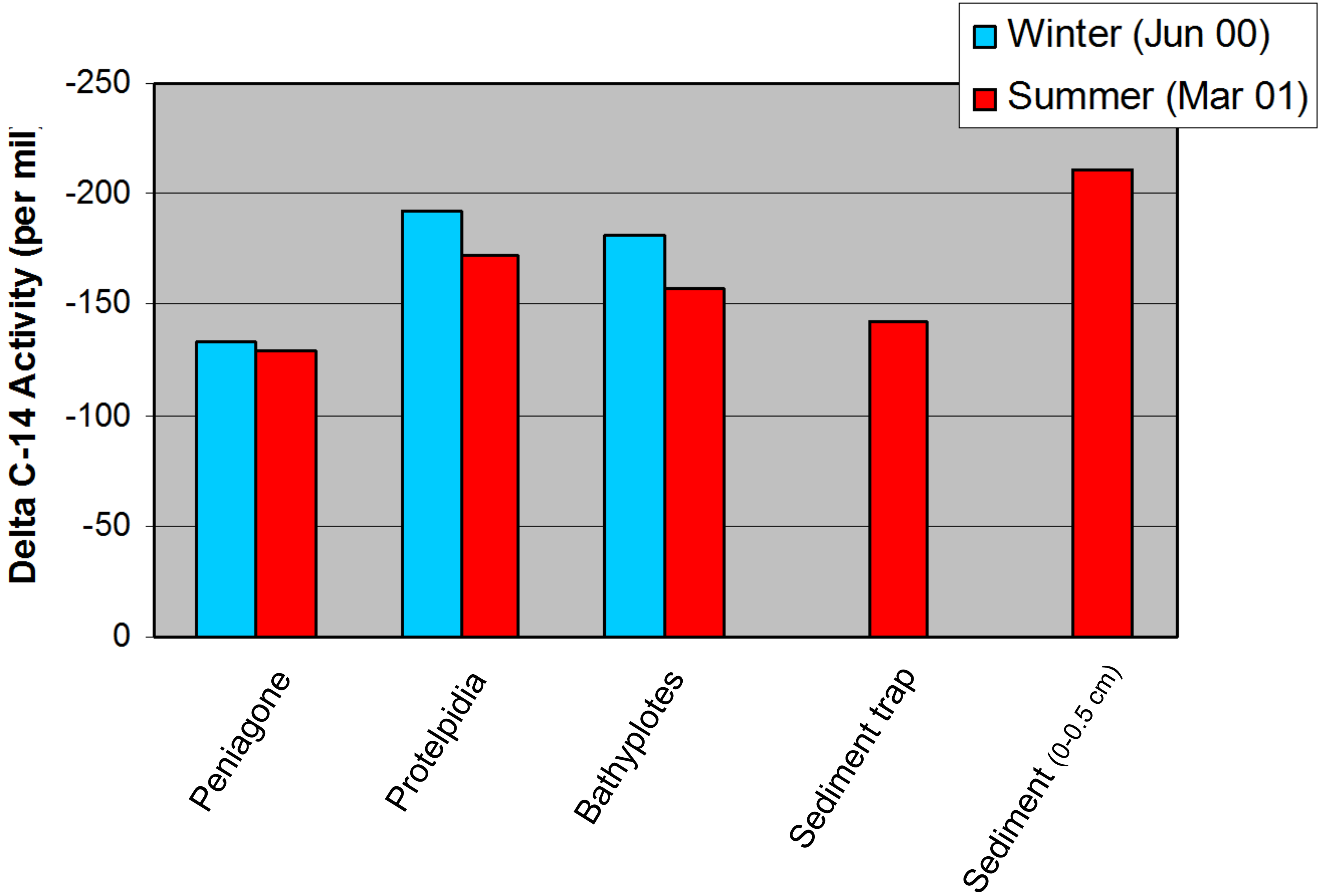


Particulate Organic Carbon Flux into Sed Traps
Station B - 150 mab



Chlorophyll-a Flux into Sediment Traps
Station B - 150 mab

“Young” $^{14}C_{org}$ is present in deposit feeder guts in summer and winter – also suggests high quality food available over winter months



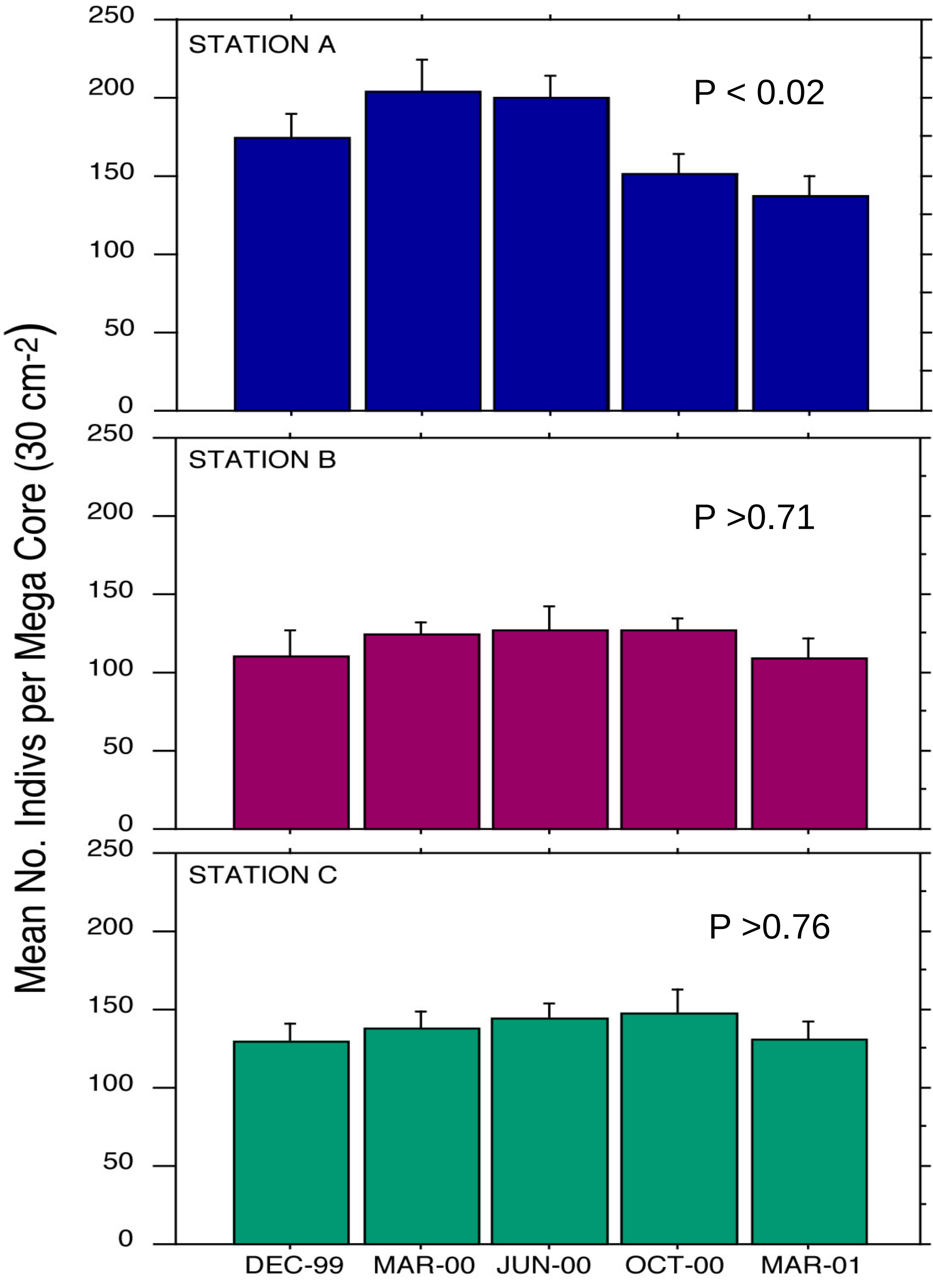
Macrofaunal community abundance:

-High (15,000 – 25,000 m^{-2})

-Dominated by small deposit feeders (spionids, paraonids, ampharetids)

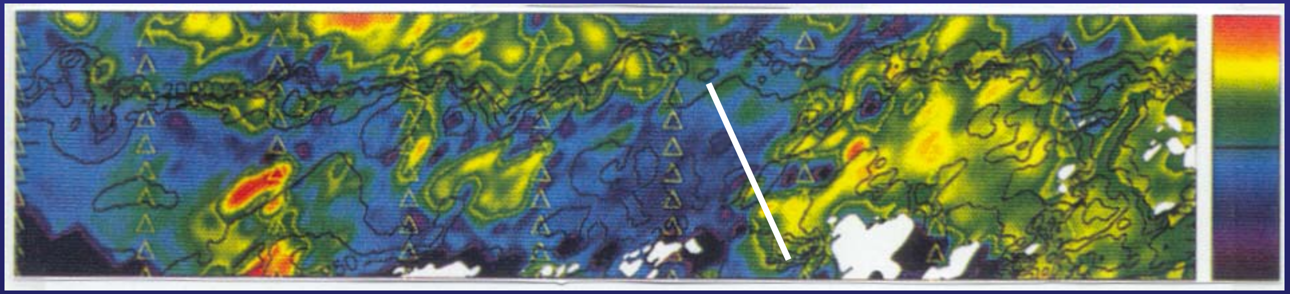
-Relatively constant at all sampling times (especially Stations B & C)

- Little evidence of seasonal recruitment pulse

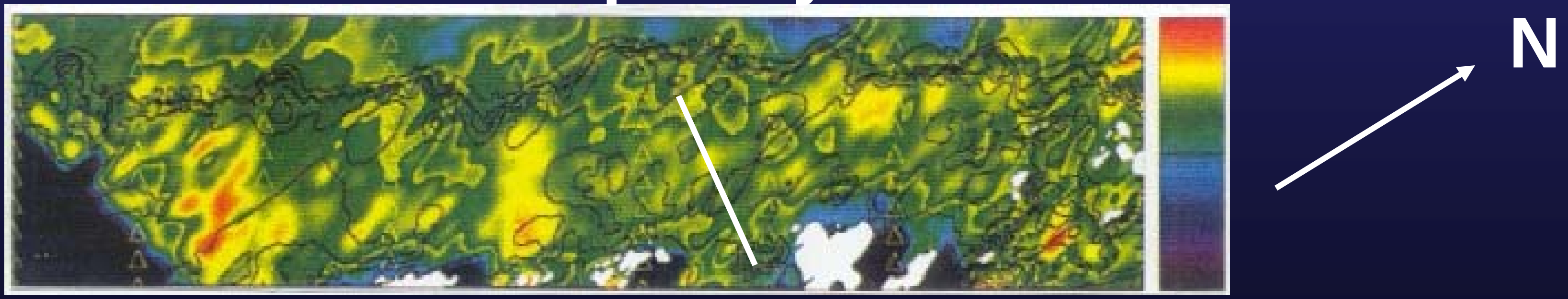


Sep Oct Nov

Dec Jan Feb



Mar Apr May

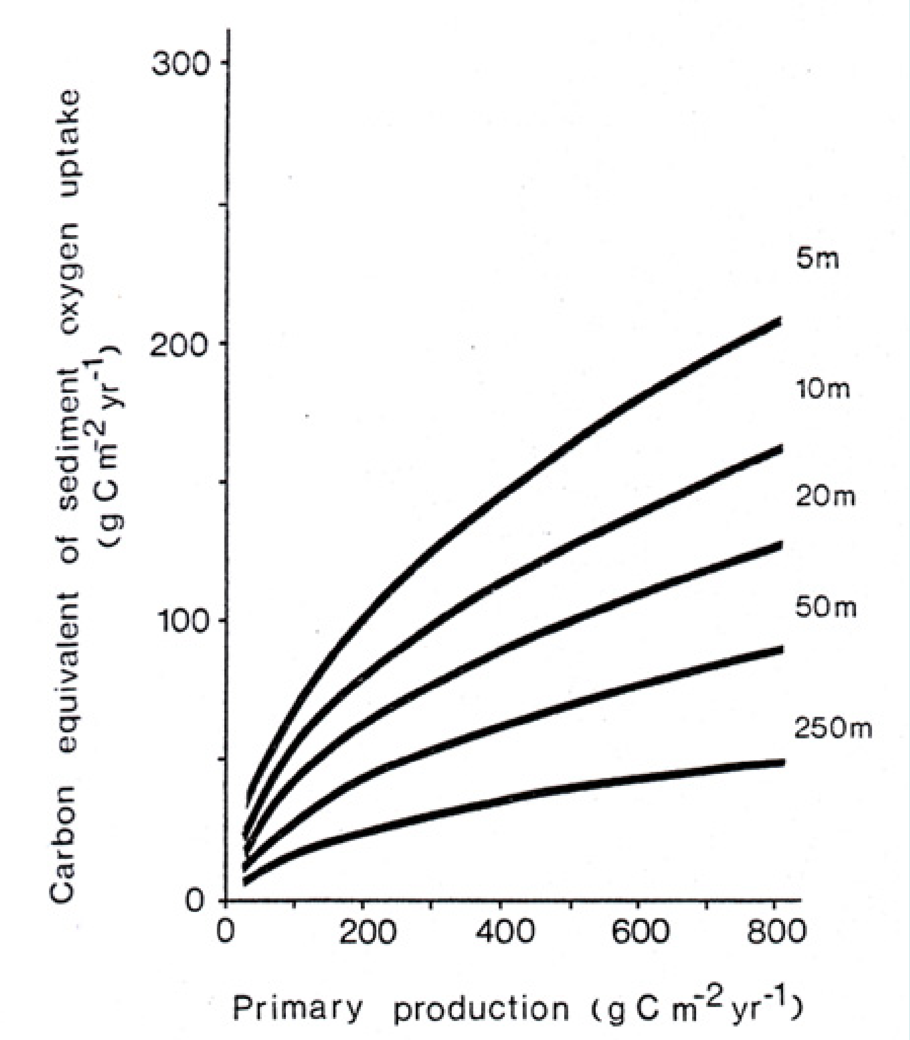


Primary production in FOODBANCS area is highly seasonal (R.C. Smith *et al.*, 1996)

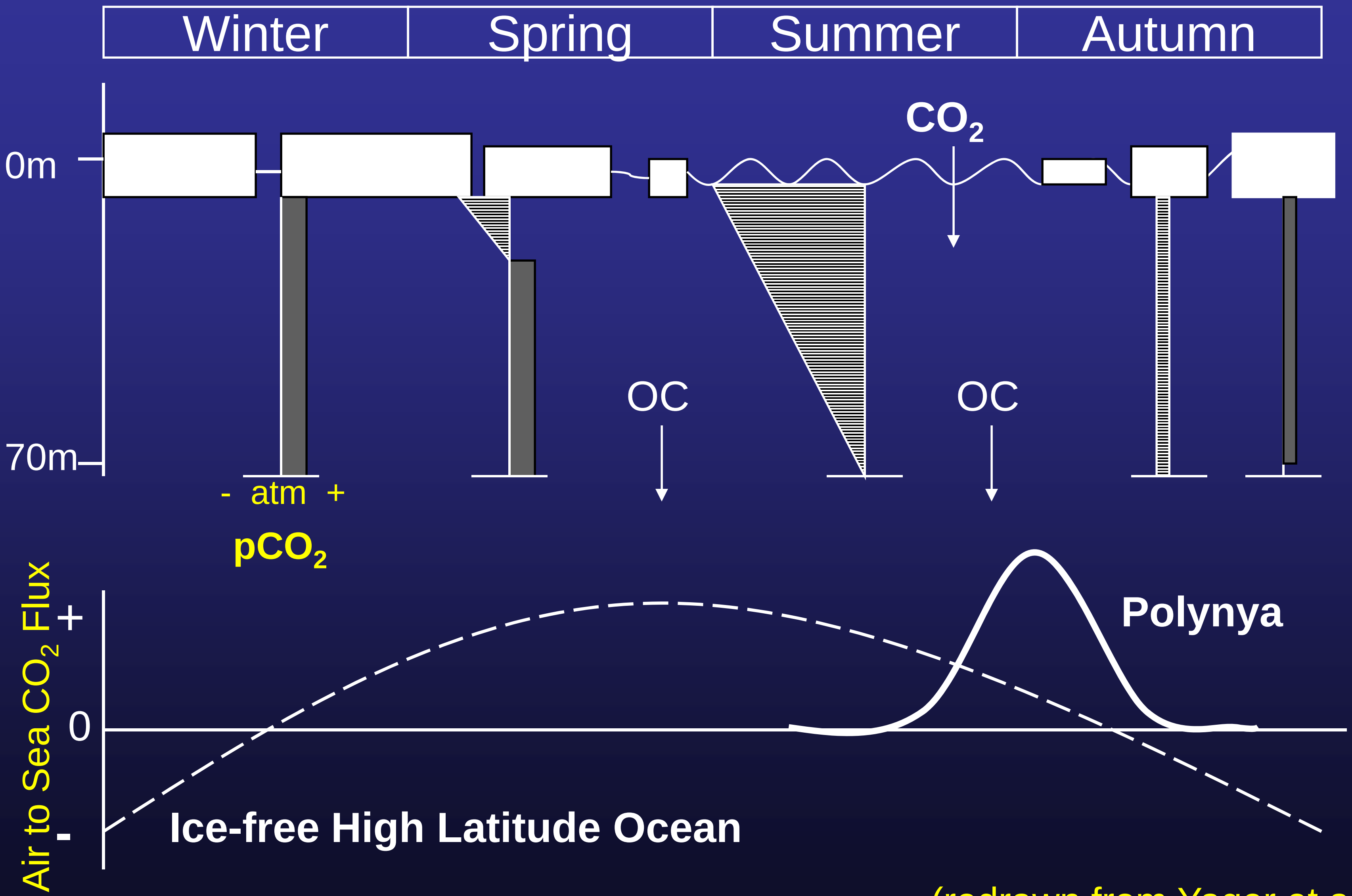
Early Studies

Hargrave (1973)

- One of the first studies to demonstrate a relationship between energy flow in benthic communities and pelagic primary production.
- Oxygen uptake by sediments modeled as a function of primary production and mixed layer depth.

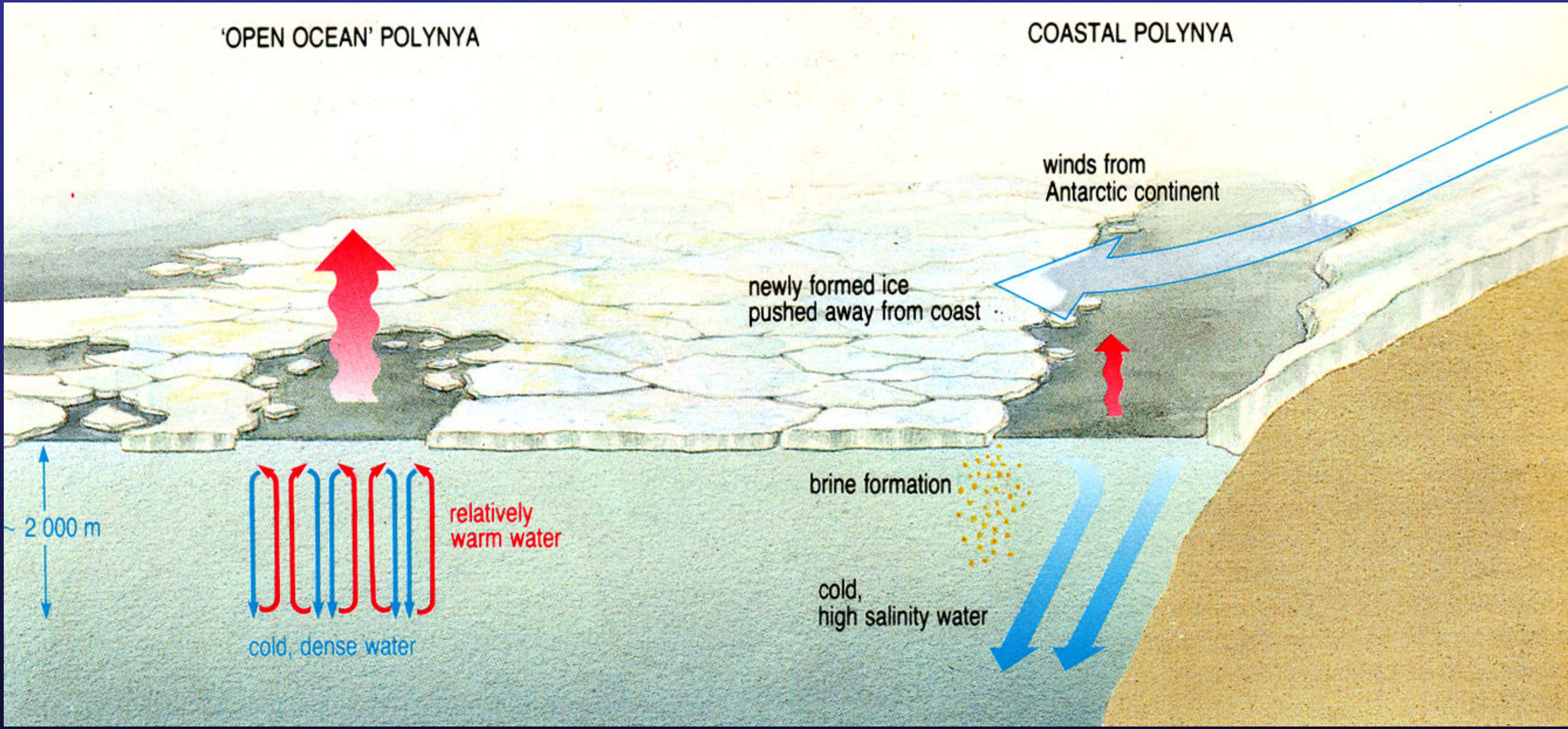


Seasonal Rectification Hypothesis

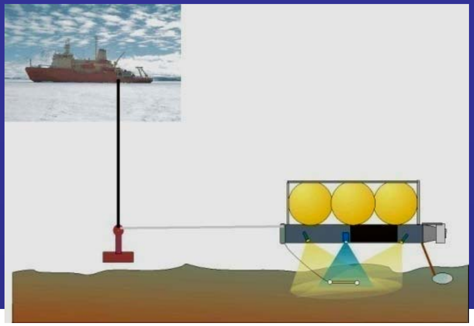


(redrawn from Yager et al., 1995)

Primary production in polynyas provides another way to advect CO^2 into deep-sea (Yager et al., 1995)



Regional correlations between water column production and benthic parameters often difficult to detect (esp. across benthic habitat types) –



E.g., Barry et al. (2003) –

Surveyed megafauna at ~60 stations in Ross Sea

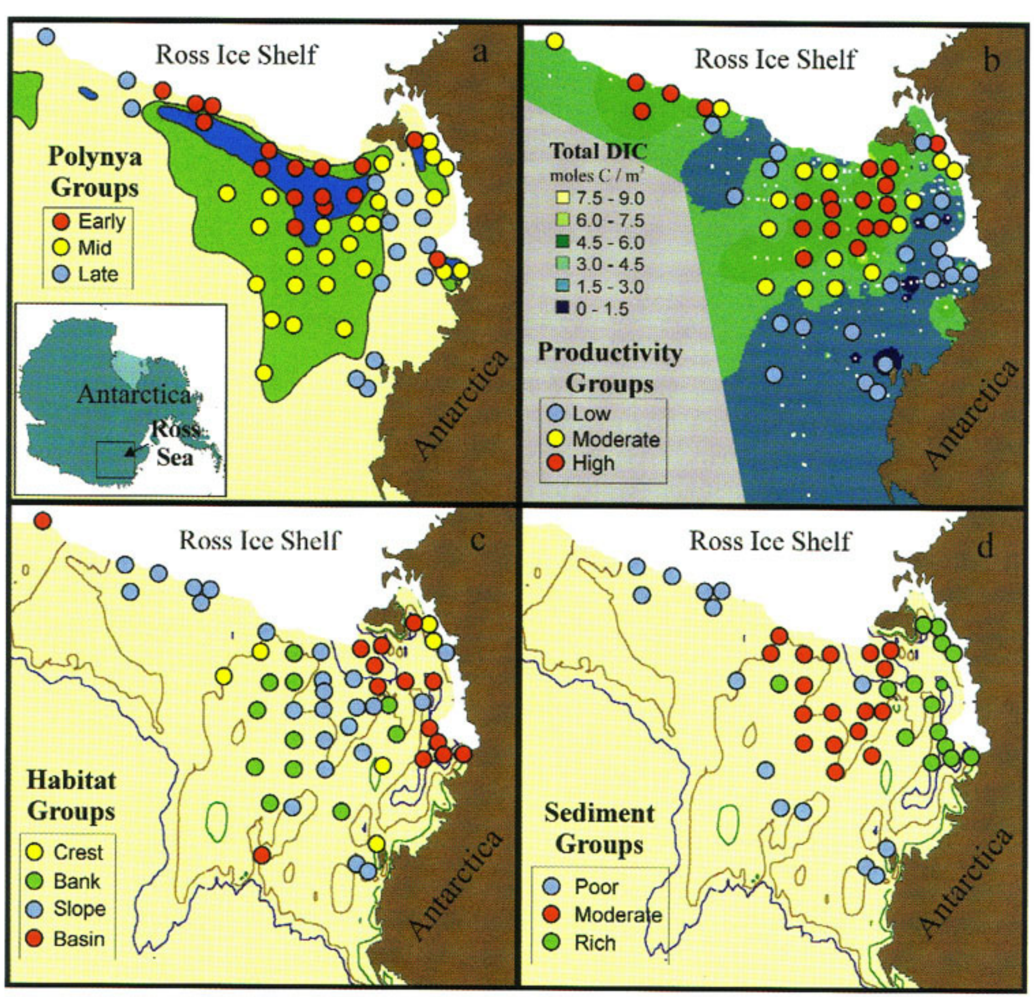
- Classified stations by

Water column forcing

- sea-ice duration (“polynya groups”)
- primary productivity

Benthic forcing

- topographic location (“habitat groups”)
- sediment type (benthic forcing)



In summary: Despite highly pulsed flux, labile organic matter accumulates in WAP sediments yielding a predictable *"food bank"* for deposit feeders during low-productivity winter periods.

NB: Large "Food Bank" may result from high substrate requirements for sediment bacteria at very low (< 1 C) temperatures (see Mincks et al. 2005)

Only habitat type (i.e., topography) was strongly correlated with megafaunal abundance and species richness -

Barry et al. (2003)

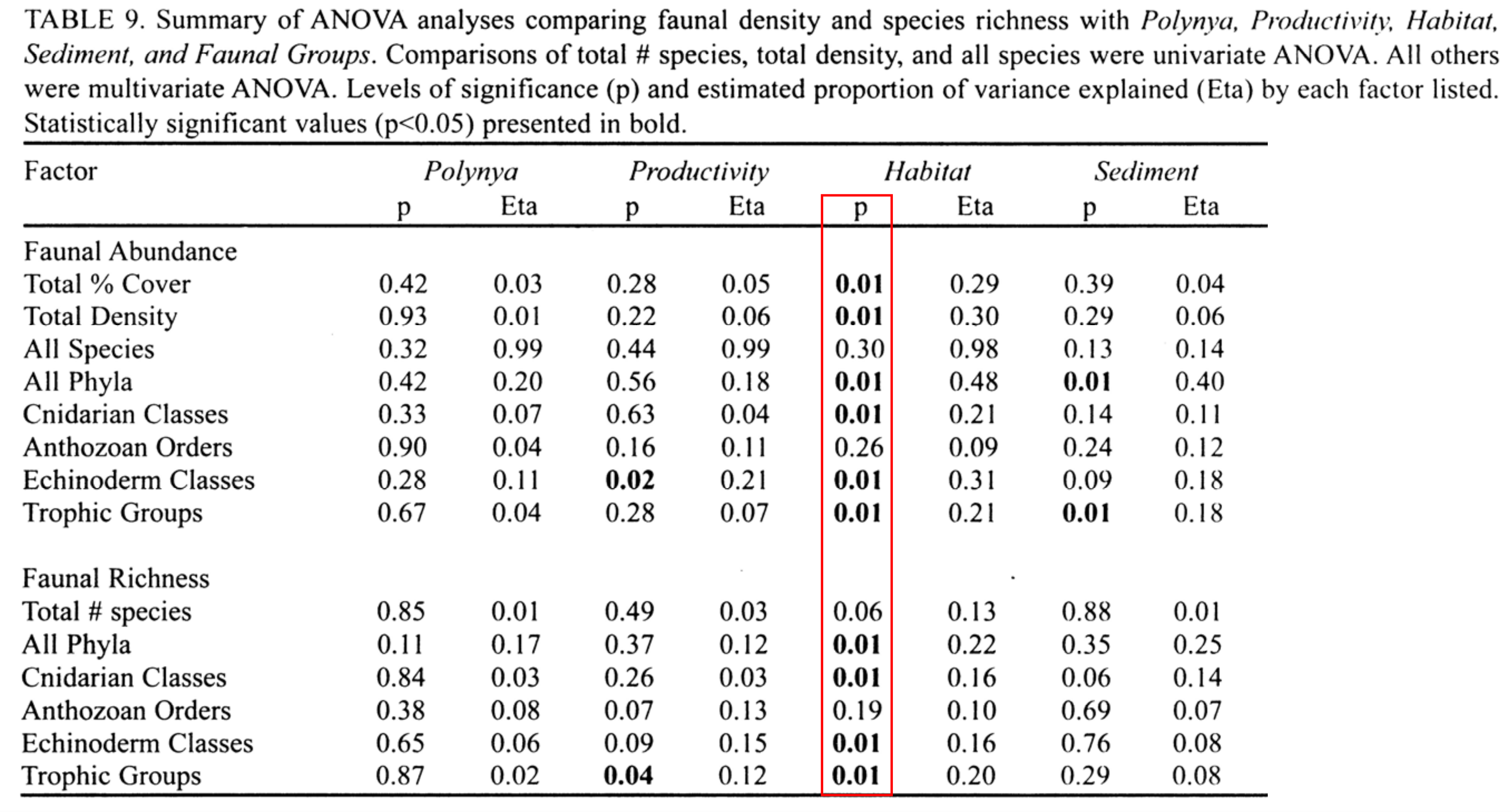


TABLE 9. Summary of ANOVA analyses comparing faunal density and species richness with *Polynya, Productivity, Habitat, Sediment, and Faunal Groups*. Comparisons of total # species, total density, and all species were univariate ANOVA. All others were multivariate ANOVA. Levels of significance (p) and estimated proportion of variance explained (Eta) by each factor listed. Statistically significant values (p<0.05) presented in bold.

Factor	*Polynya*		*Productivity*		*Habitat*		*Sediment*	
	p	Eta	p	Eta	p	Eta	p	Eta
Faunal Abundance								
Total % Cover	0.42	0.03	0.28	0.05	**0.01**	0.29	0.39	0.04
Total Density	0.93	0.01	0.22	0.06	**0.01**	0.30	0.29	0.06
All Species	0.32	0.99	0.44	0.99	0.30	0.98	0.13	0.14
All Phyla	0.42	0.20	0.56	0.18	**0.01**	0.48	**0.01**	0.40
Cnidarian Classes	0.33	0.07	0.63	0.04	**0.01**	0.21	0.14	0.11
Anthozoan Orders	0.90	0.04	0.16	0.11	0.26	0.09	0.24	0.12
Echinoderm Classes	0.28	0.11	**0.02**	0.21	**0.01**	0.31	0.09	0.18
Trophic Groups	0.67	0.04	0.28	0.07	**0.01**	0.21	**0.01**	0.18
Faunal Richness								
Total # species	0.85	0.01	0.49	0.03	0.06	0.13	0.88	0.01
All Phyla	0.11	0.17	0.37	0.12	**0.01**	0.22	0.35	0.25
Cnidarian Classes	0.84	0.03	0.26	0.03	**0.01**	0.16	0.06	0.14
Anthozoan Orders	0.38	0.08	0.07	0.13	0.19	0.10	0.69	0.07
Echinoderm Classes	0.65	0.06	0.09	0.15	**0.01**	0.16	0.76	0.08
Trophic Groups	0.87	0.02	**0.04**	0.12	**0.01**	0.20	0.29	0.08

Similar habitat-dominated patterns for megafauna described by –

- *Starmans et al. (1999) – Weddell, Bellinhausen-Amundsen Seas*
- *Gutt (2000 review) – Weddell Sea*

Seasonality in deposit feeding? Few studies

Best = Brockington et al. (2001) for *Sterechinus neumayeri,* at Rothera (relatlvely high latitude – 68^{o} S).

S. neumayeri

Sterechinus feeding = highly seasonal

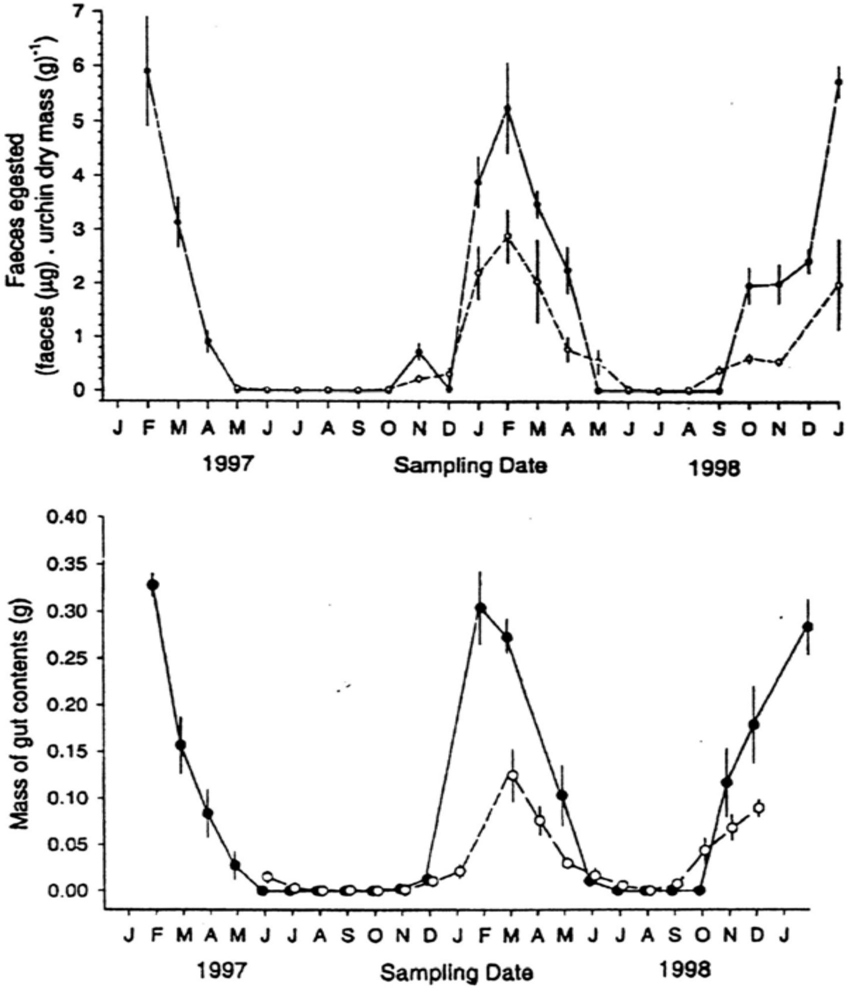
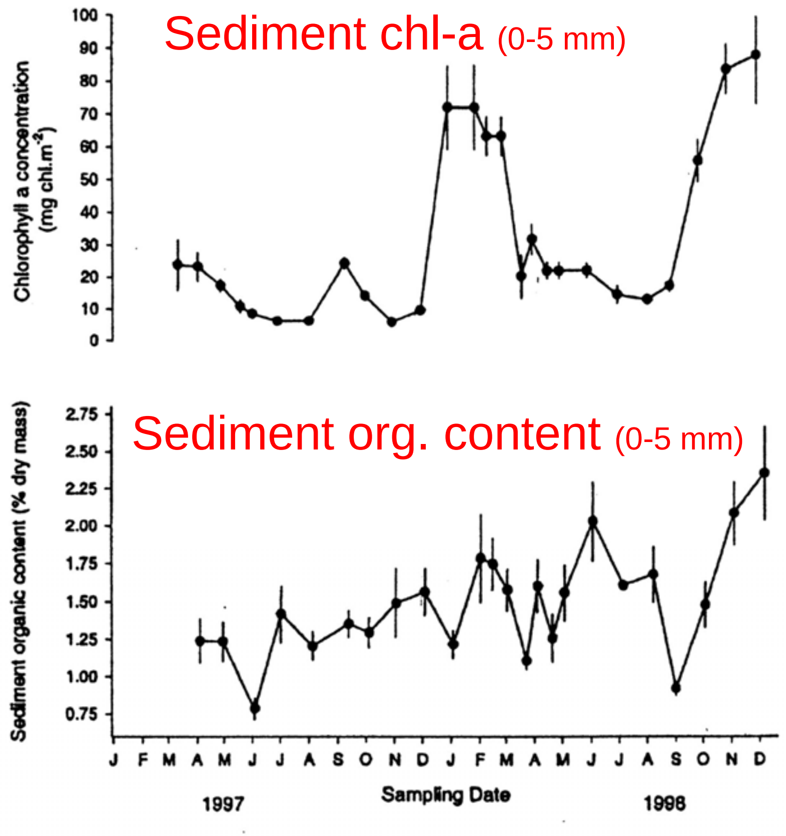


Fig. 4A, B *Sterechinus neumayeri.* **A** Seasonal variation in feeding (as measured by faecal egestion) from both North (●) and South Cove (○) at Rothera Point. Each point represents a mean of four

Sediment chl-a (0-5 mm)

Sediment org. content (0-5 mm)



Seasonality in life histories?

- Most macrofauna have direct or lecithotrophic development (i.e., larvae rely in *benthic* food resources)

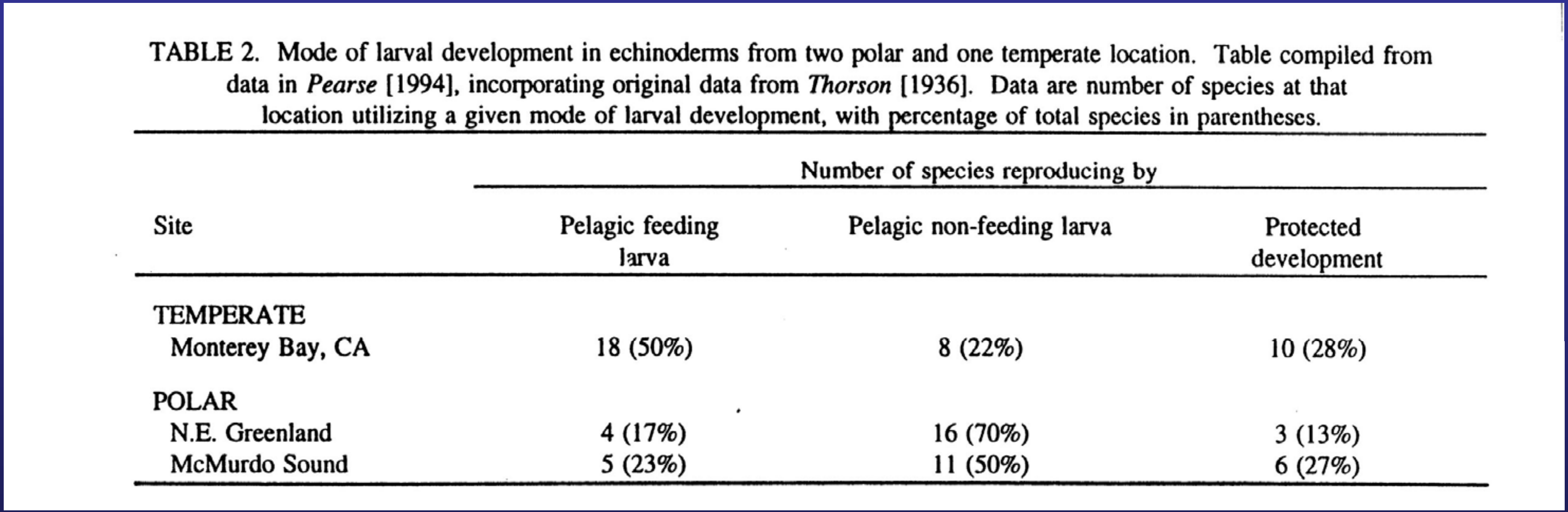


TABLE 2. Mode of larval development in echinoderms from two polar and one temperate location. Table compiled from data in *Pearse* [1994], incorporating original data from *Thorson* [1936]. Data are number of species at that location utilizing a given mode of larval development, with percentage of total species in parentheses.

Site	Number of species reproducing by: Pelagic feeding larva	Pelagic non-feeding larva	Protected development
TEMPERATE			
Monterey Bay, CA	18 (50%)	8 (22%)	10 (28%)
POLAR			
N.E. Greenland	4 (17%)	16 (70%)	3 (13%)
McMurdo Sound	5 (23%)	11 (50%)	6 (27%)

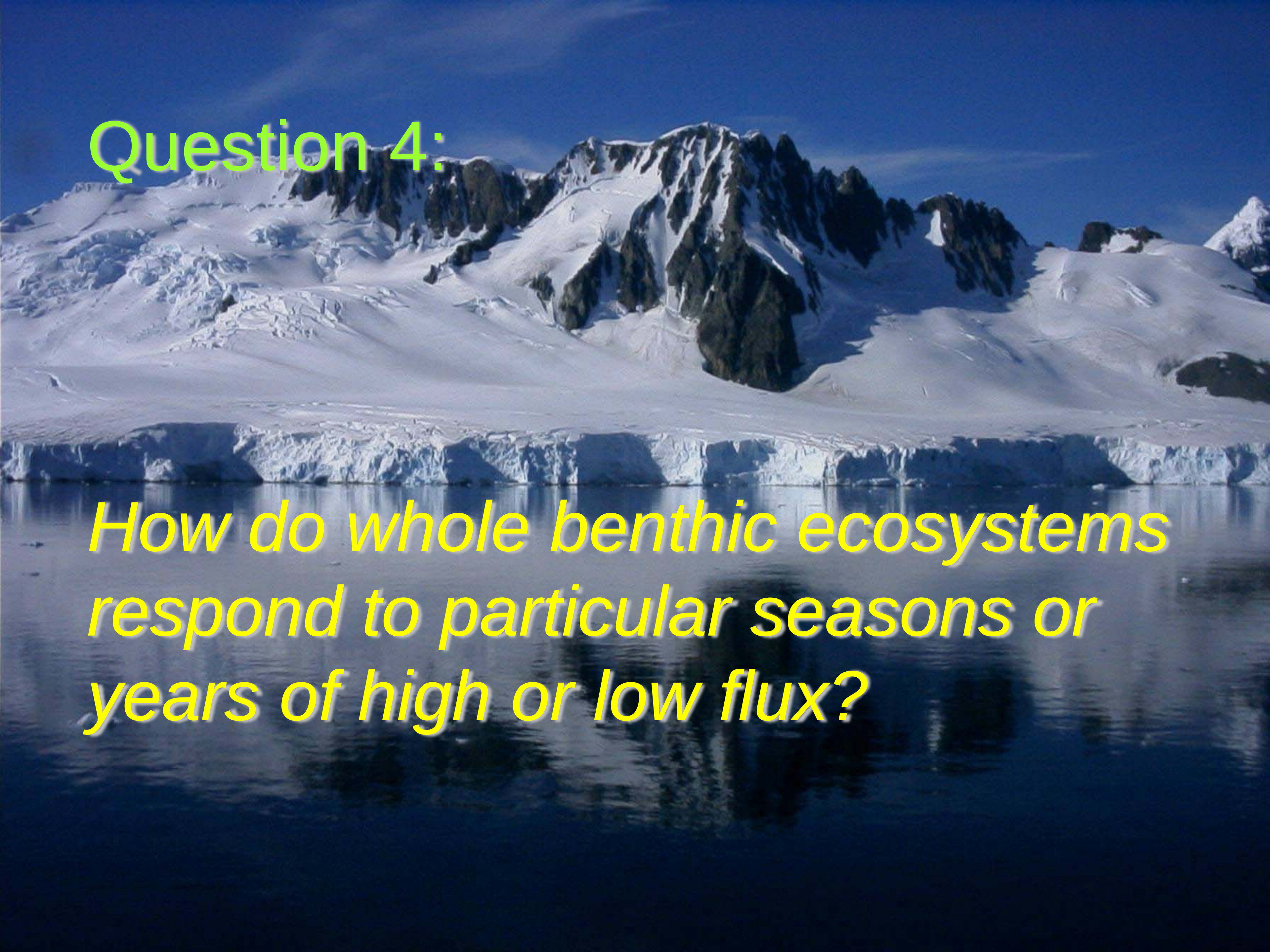
Clarke, 1996

- 70% of echinoids in Antarctic are brooders, versus 28% in Monterey Bay, CA (Smith et al., 2006).

- Spawning, larval presence and recruitment often occur in non-summer months (e.g., Stanwell-Smith et al., 1998; Galley, 2003; Bowden, 2005; Mincks, 2005)

In other words:

Life histories often surprisingly weakly coupled to summer primary production in the water column (weaker than in temperate zone! – Bowden, 2005)



Question 4:

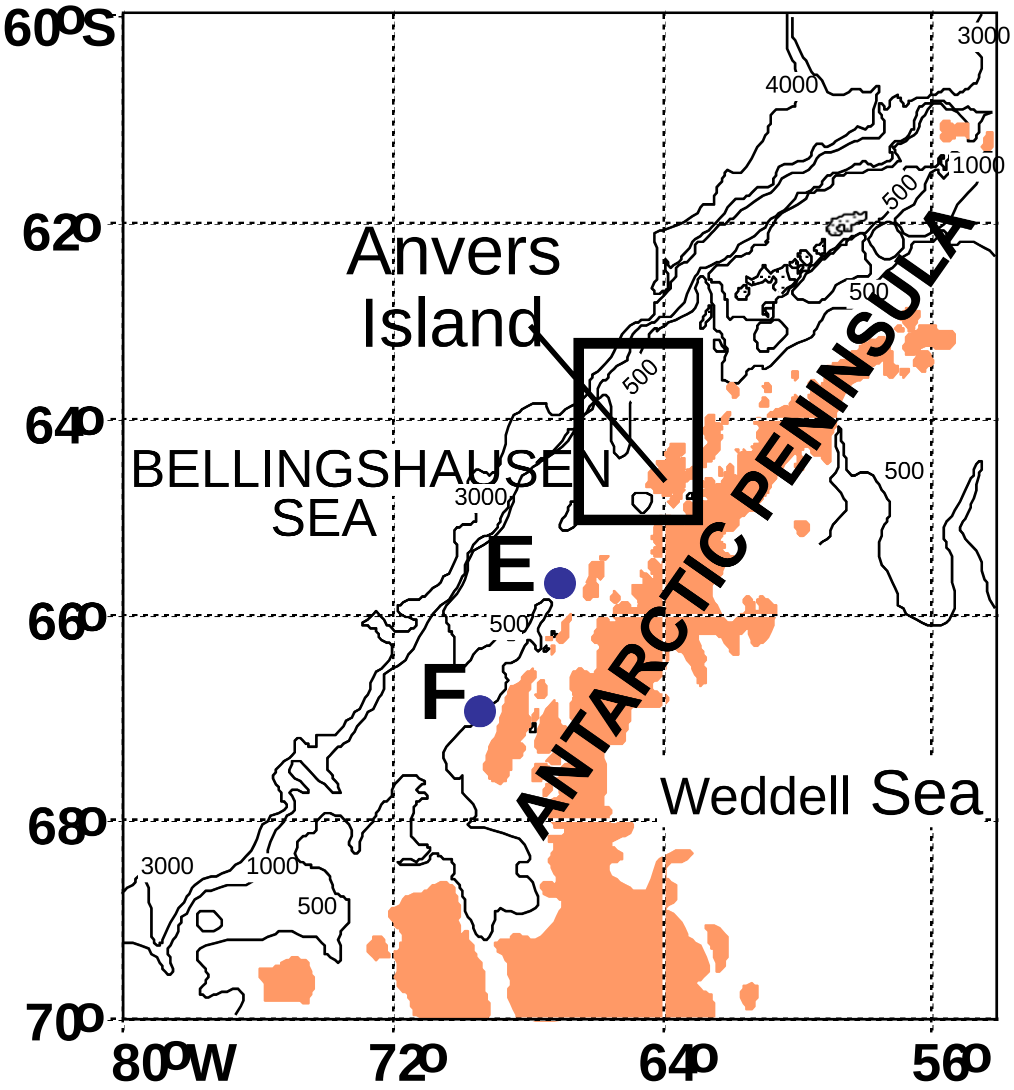
How do whole benthic ecosystems respond to particular seasons or years of high or low flux?

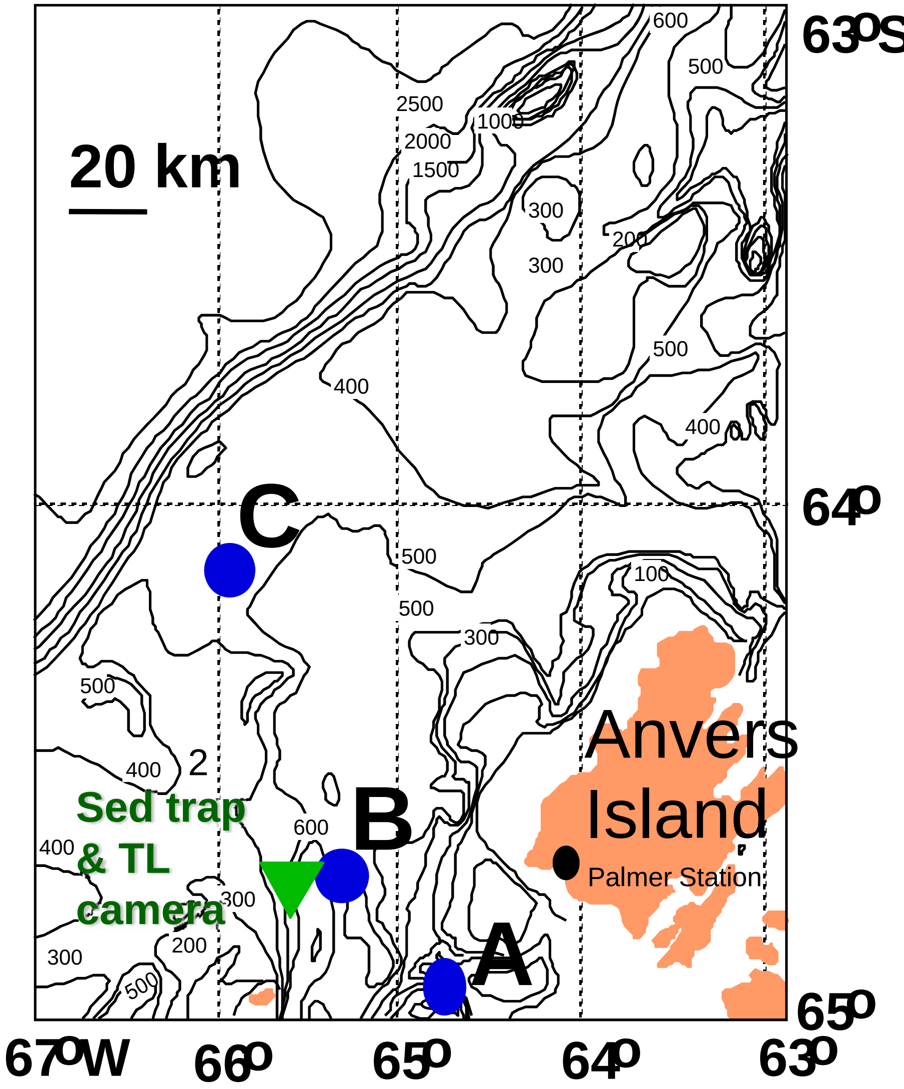
“Food Bank” Hypothesis

- Large amounts of summer bloom detritus are rapidly deposited on the WAP shelf floor
- Because of slow decomposition at low AA water temperatures, the phytodetritus provides a “food bank” for benthic detritivores during lean winter months

FOODBANCS Study – Nov 99 – Mar 01

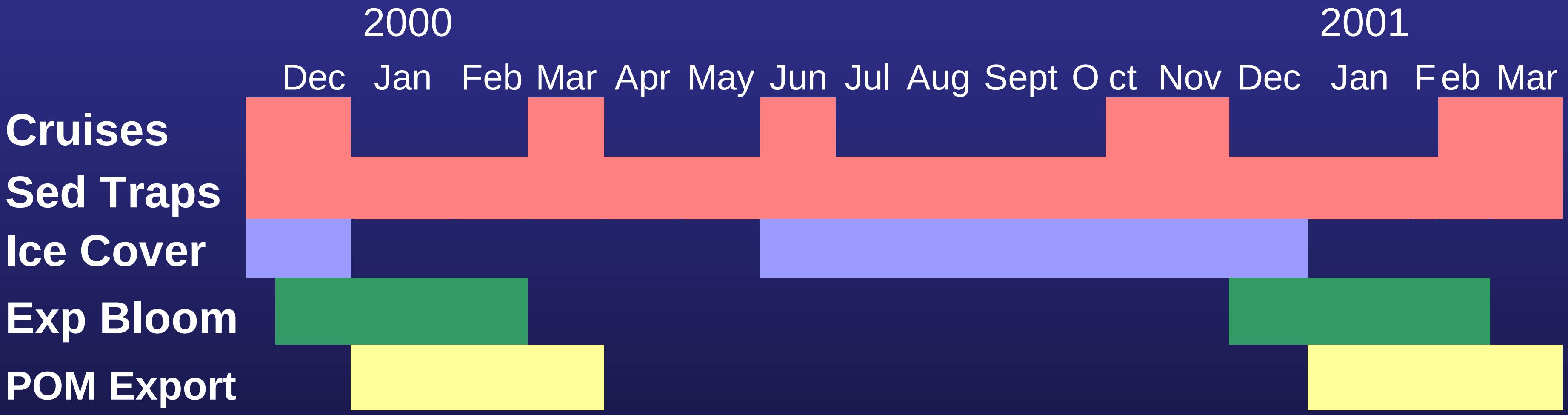
(Food for Benthos on the Antarctic Continental Shelf)





Smith, DeMaster and many others

Sampling Time-line



Phytodetritus obvious in FOODBANCS video surveys during March 2001

DEC 1999

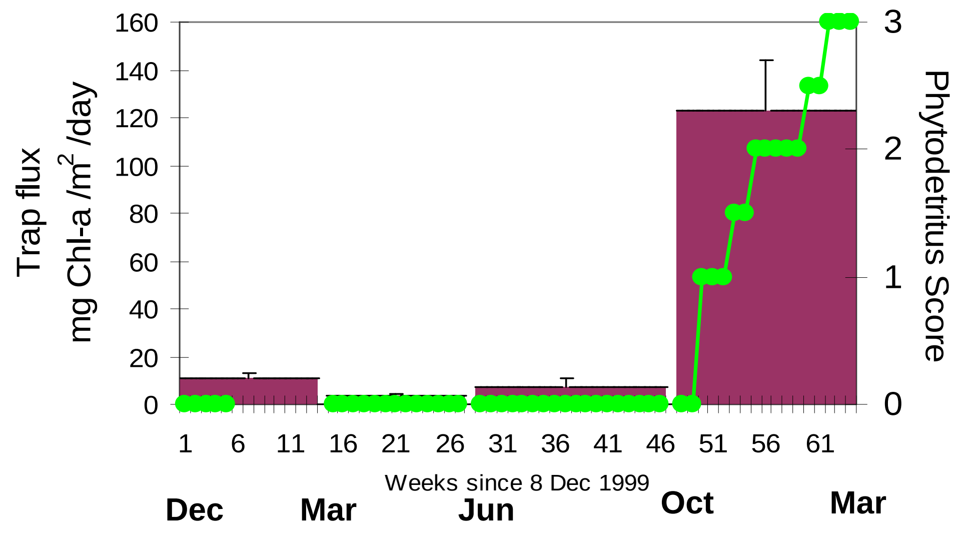
MAR 2000

JUN 2000

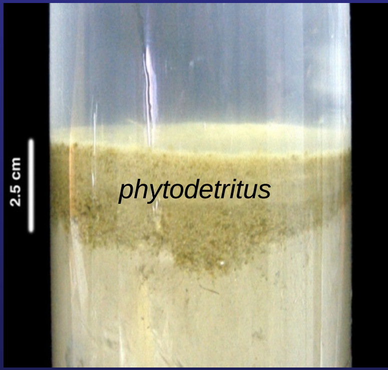
OCT 2000

MAR 2001

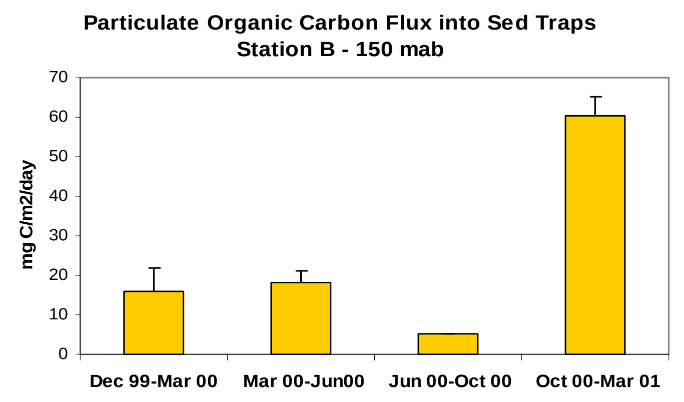
Laser dots are separated by 10 cm



Chlorophyll-a Flux into Sediment Traps (150 mab)
& Seafloor Phytodetritus Score

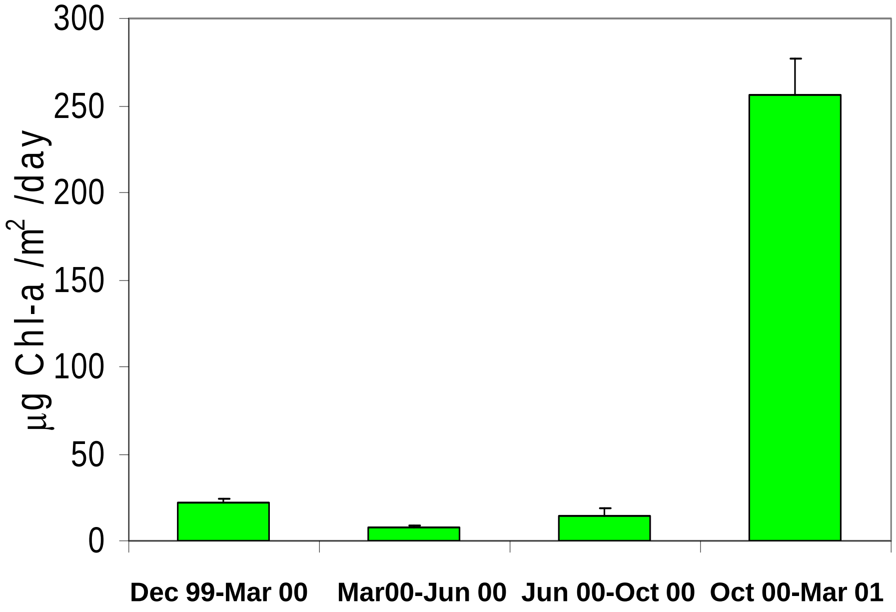


Megacore sample



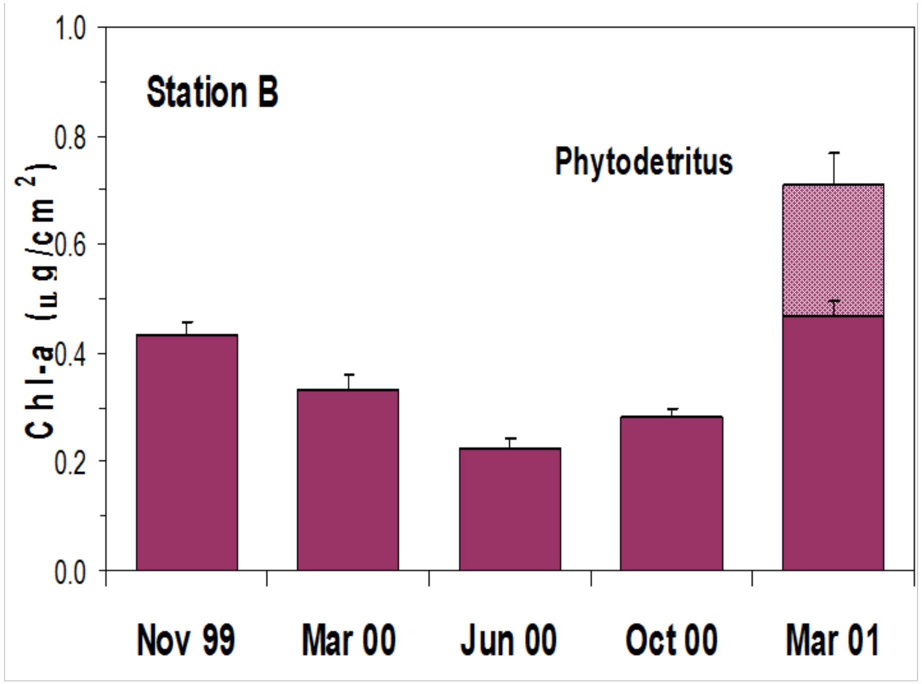
Benthic response is muted compared to water column variability

Chlorophyll-a Flux into Sediment Traps



Interannual variability = <u>11.5 X</u>

Chlorophyll a inventory in sediments (0 – 10 cm)

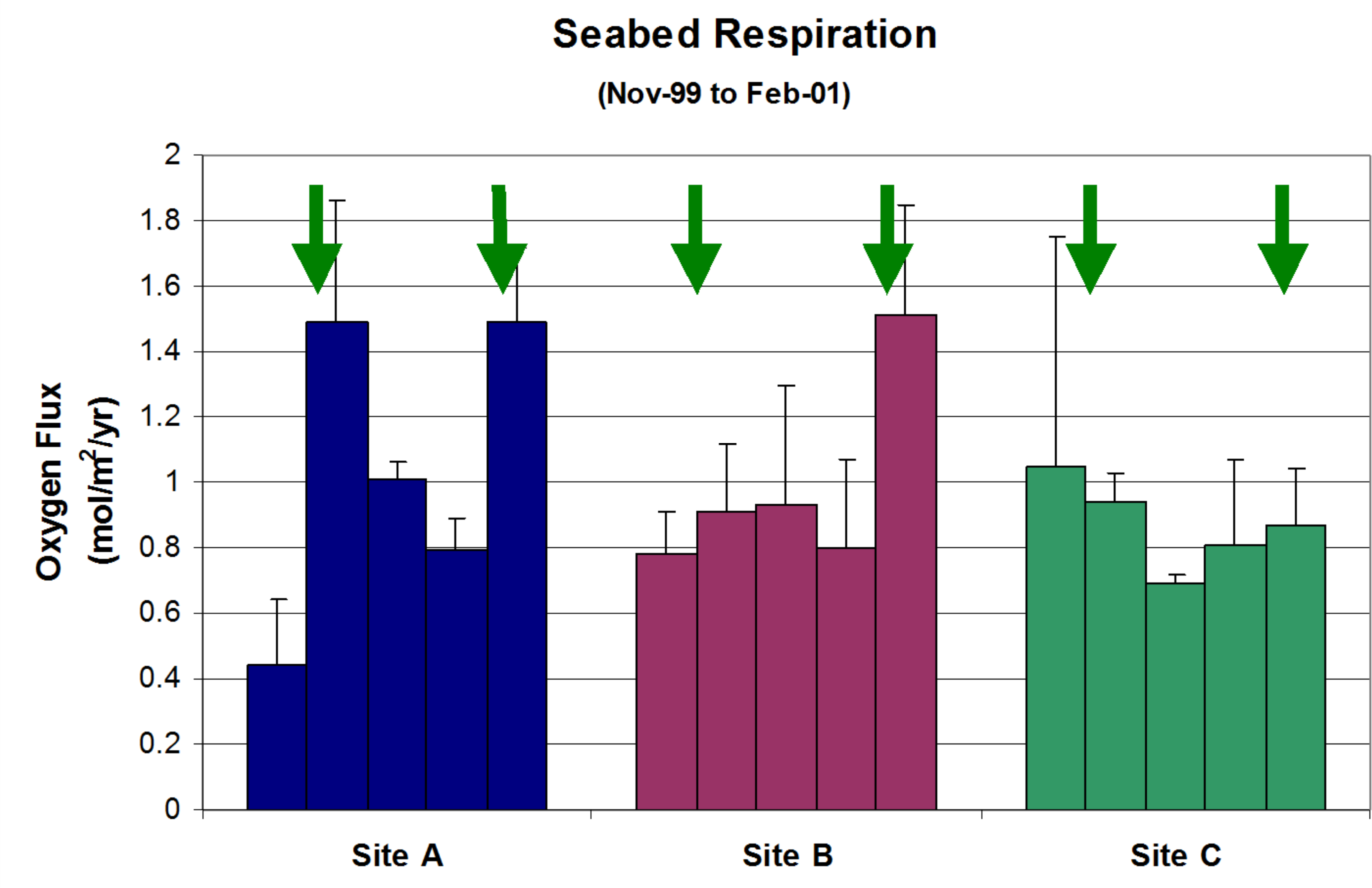


Interannual variability ~ <u>3 X</u>

Half life of Chl-a inventory in the top 10 cm of sediment ~ **50 - 400 d** -

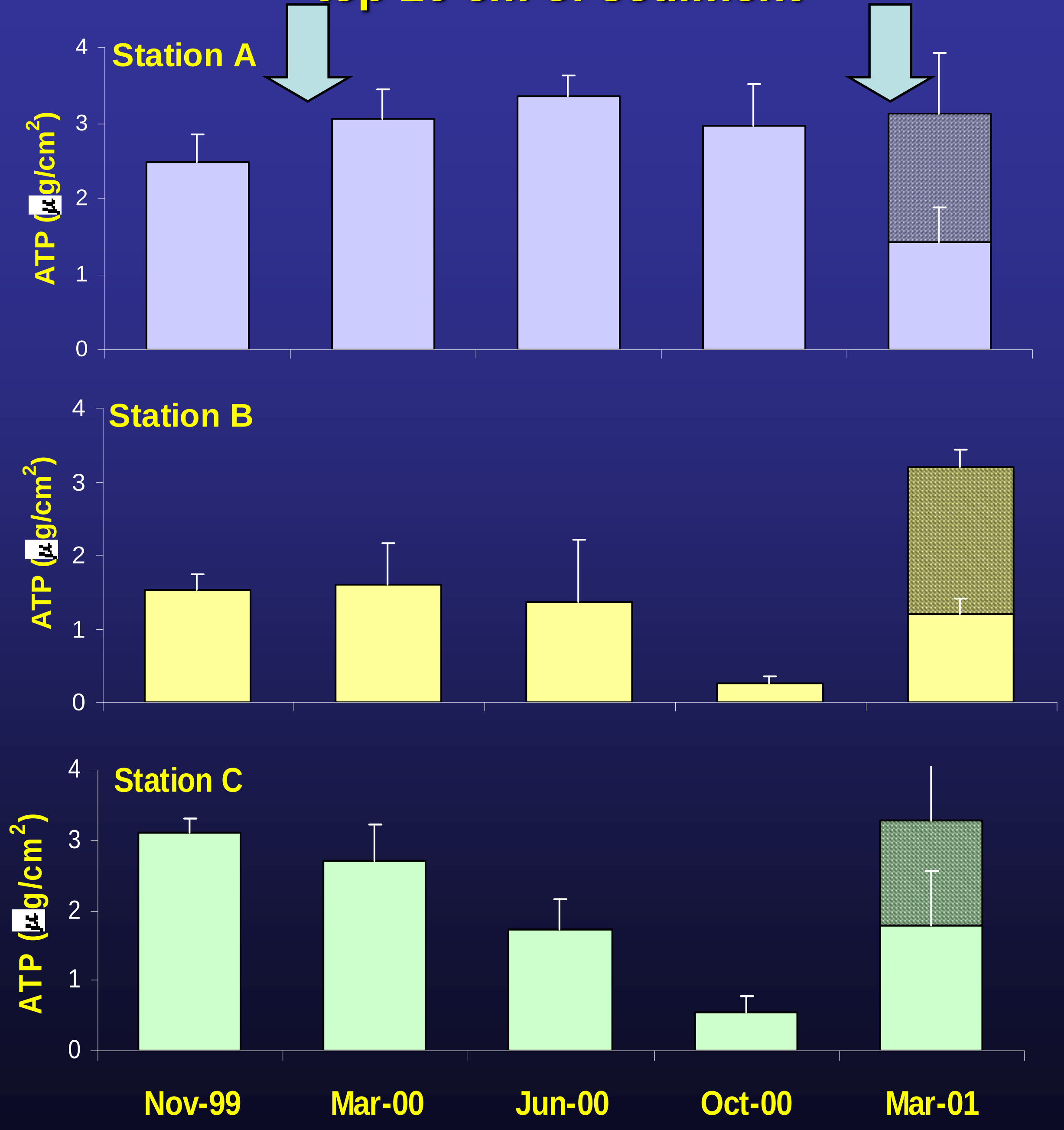
i.e., there is persistent labile organic material in sediments.

Mincks et al., 2005

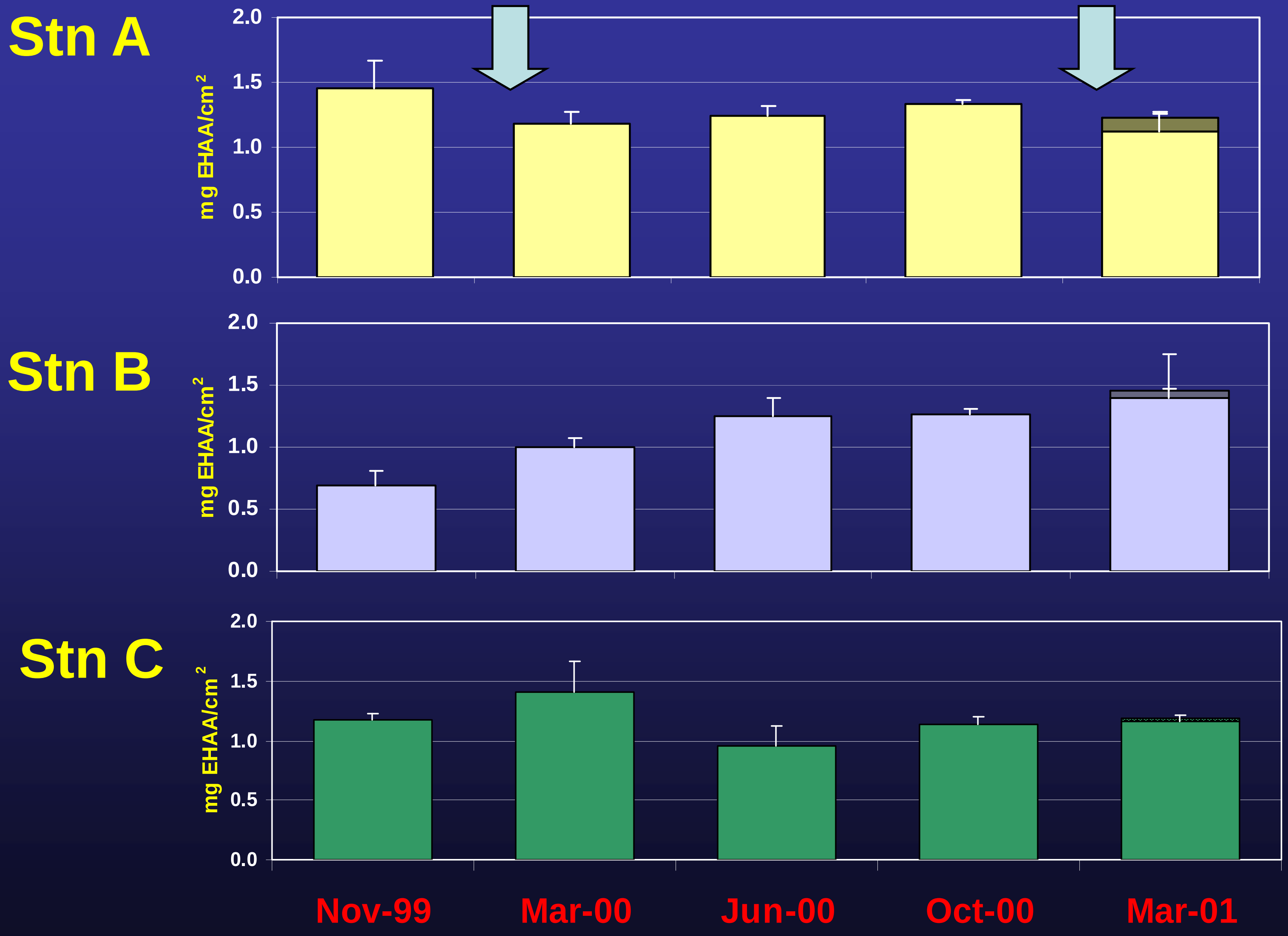


Respiration rates vary 1.3 – 2 fold at Stations B and C (versus >4-fold variability for sediment trap POC flux at Sta. B)

Sediment ATP Inventories – Measure of microbial biomass in top 10 cm of sediment



Sediment EHAA Inventories (DF'er food)



Similarly muted benthic ecosystem responses seen by others, eg.:

Nedwell et al. (1993) – Signy Island, 9 m depth

POM flux varies >>100X (note log scale)

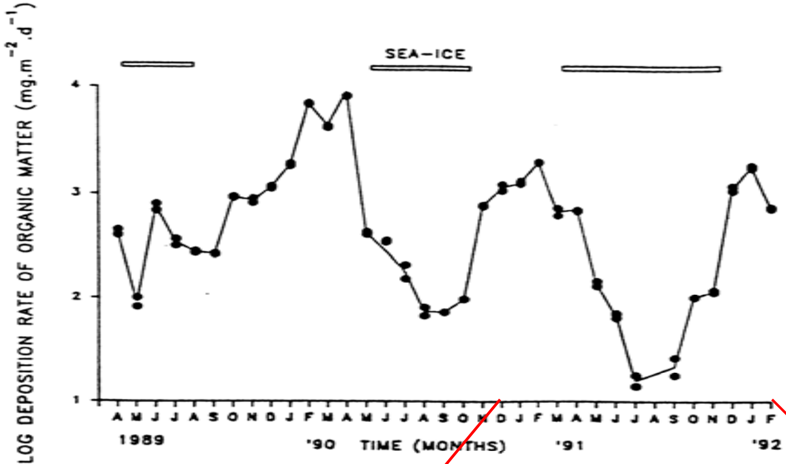


FIG. 4. Settlement rates of organic matter in the water column. Duplicate traps were used.

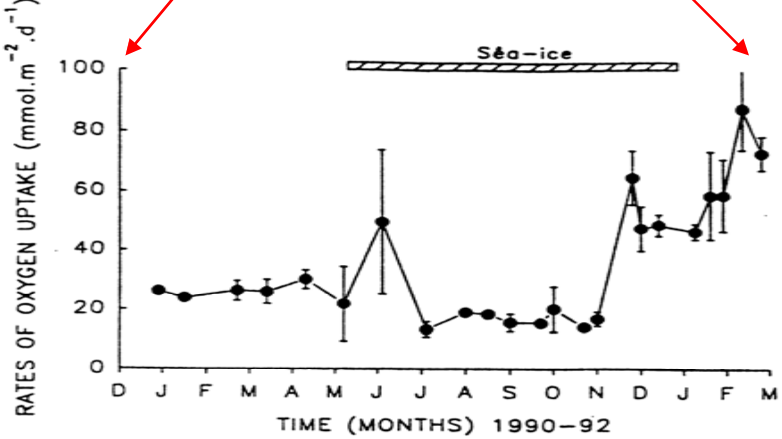


FIG. 1. Rates of O_2 uptake by bottom sediments in Factory Cove, Signy Island. Bars indicate standard errors; n = 3.

SCOC varies ~6X (mostly inter-annually)

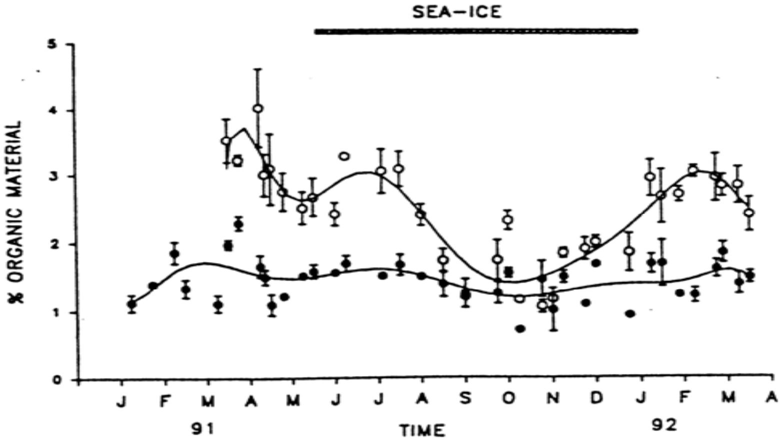


FIG. 3. Sedimentary organic content (AFDW) in the 0- to 0.5-cm (○) and 1- to 2-cm (●) depth horizons. Bars indicate standard errors; n = 3.

POM inventory in top 5 mm sediment varies ~ 2X

Conclusions regarding Question 4:

Benthic ecosystem response to summer flux pulses has substantial *inertia* (in part due to presence of sediment “food bank”).

Many benthic processes may act as “low-pass filters” – primarily recording longer-term (e.g., inter-annual) trends in water-column processes.

OVERALL CONCLUSIONS REGARDING PELAGIC-BENTHIC COUPLING ON THE ANTARCTIC SHELF

1) **POC flux to the Antarctic shelf floor is dominated by large summer pulses – BUT pulses often are offset in time or space from overlying plankton blooms.**

2) **Across all benthic habitat types, regional patterns of primary production are only weakly imprinted on the shelf floor - however, on the *muddy shelf*, macrofaunal biomass does reflect large-scale patterns of sea-ice duration and primary production.**

3) **Despite initial expectations, many benthic processes (including SCOC, suspension feeding, and deposit feeding) are only weakly phased to seasonal patterns of water-column production, exhibiting substantial "*inertia*" (due to presence of *food banks*).**

4) **Because of this "*inertia*", benthic processes may act as low pass filters and be useful indicators of long-term trends in Antarctic ecosystem function.**