

The influence of oceanographic processes on pelagic–benthic coupling in polar regions: A benthic perspective

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ABSTRACT

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Benthic community abundance and biomass in polar marine systems is directly influenced by food supply from the overlying water column. Variability in hydrographic regimes, ice coverage, light, water column temperature and pelagic food web structure limit the amount of organic carbon reaching the benthos. Data from the high Arctic and Antarctic indicate that a large percentage of surface-produced organic matter is consumed by both macro- and micro-zooplankton as well as recycled in the water column via the microbial loop. This results in food-limited regimes for the underlying benthos. The few exceptions are nearshore continental shelf systems, such as in the Bering and Chukchi Seas in the western Arctic and portions of the Canadian Archipelago and Barents Sea in the eastern Arctic, where high benthic abundance and biomass occurs due to a tight coupling between water column primary production and benthic secondary production. A major difference between the Antarctic and Arctic is that the nearshore deep Antarctic is characterized by relatively high benthic abundance and biomass despite low water column production, suggesting that stability, low disturbance levels and cold temperatures enable benthic organisms to grow larger than in the Arctic. Both physical and biological disturbance levels are high in the marginal seas of the Arctic and may directly influence benthic productivity. The relationship between primary production and sedimentation of organic material to the benthos is nonlinear due to its dependence on the role of the pelagic food web. Therefore, in this review we will only discuss the pelagic system with respect to how it impacts the net food supply reaching the benthos. A major objective of this review paper is to demonstrate the influence of oceanographic processes on pelagic–benthic coupling in polar regions from a “bottom-up” perspective, using benthic studies from various regions in both the Arctic and Antarctic. Similarities and differences in oceanographic processes, benthic abundance and biomass, and benthic carbon cycling within these polar marine systems are discussed and areas for further research identified.

Introduction

High to low values of benthic faunal abundance and biomass occur in both shallow and deep habitats of polar marine systems and are directly influenced by food supply from the overlying water column. Polar environments are characterized by seasonal or permanent ice coverage, cold temperatures, variable salinities nearshore (Arctic), variable incident light levels, dynamic hydrographic and circulation patterns, and variable levels of organic carbon input or benthic

primary production. In addition, pelagic food webs have a direct impact on the amount of organic matter reaching the benthos, particularly where variable zooplankton and bacterial population levels intercept fluxes between high water column primary productivity and the benthos. A major distinguishing feature between Arctic and Antarctic polar ecosystems is that the Arctic is an ocean surrounded by continental land masses with shallow (< 200 m) shelves and freshwater inflow, while the Antarctic is a continental land mass surrounded by a deep shelf (average 500 m) and is

ice-covered. Thus, no freshwater dilution occurs at its margins. This disparity in physical features leads to contrasting biological patterns and dynamics both within the water column and in the benthos. Our objective in this review is to discuss the current knowledge on the influence of oceanographic processes on pelagic-benthic coupling in polar regions from a "bottom-up" perspective, using studies from both the Arctic and Antarctic, and to identify data gaps for future studies.

General environment of the Arctic and Antarctic

Physical oceanography

The Arctic Ocean, bounded nearly entirely by land masses, is characterized by shallow and wide continental shelves, and has a limited connection with the Pacific Ocean through Bering Strait (50–

60 m) and the Atlantic Ocean through Fram Strait (440 m; Fig. 1, Table 1). Currents are dominated by a transpolar flow of cold, low salinity surface water from east Siberian waters to the Greenland Sea. A high cover of pack ice occurs during most of the year, particularly in the central Arctic and in western Fram Strait and the Barents Sea (Aagaard, 1989). Ice export is primarily through Fram Strait where a majority of the present-day water exchange occurs (Aagaard, 1989). River runoff and sea-ice melting contribute large volumes of freshwater into the Arctic Ocean, resulting in pronounced water column stratification and vertical stability during spring and summer. Mud and clay sediments suspended in riverine water are transported and deposited in the marginal seas and central Arctic basin, with variable content of silt, sand, and boulders near the coastline and in the straits.

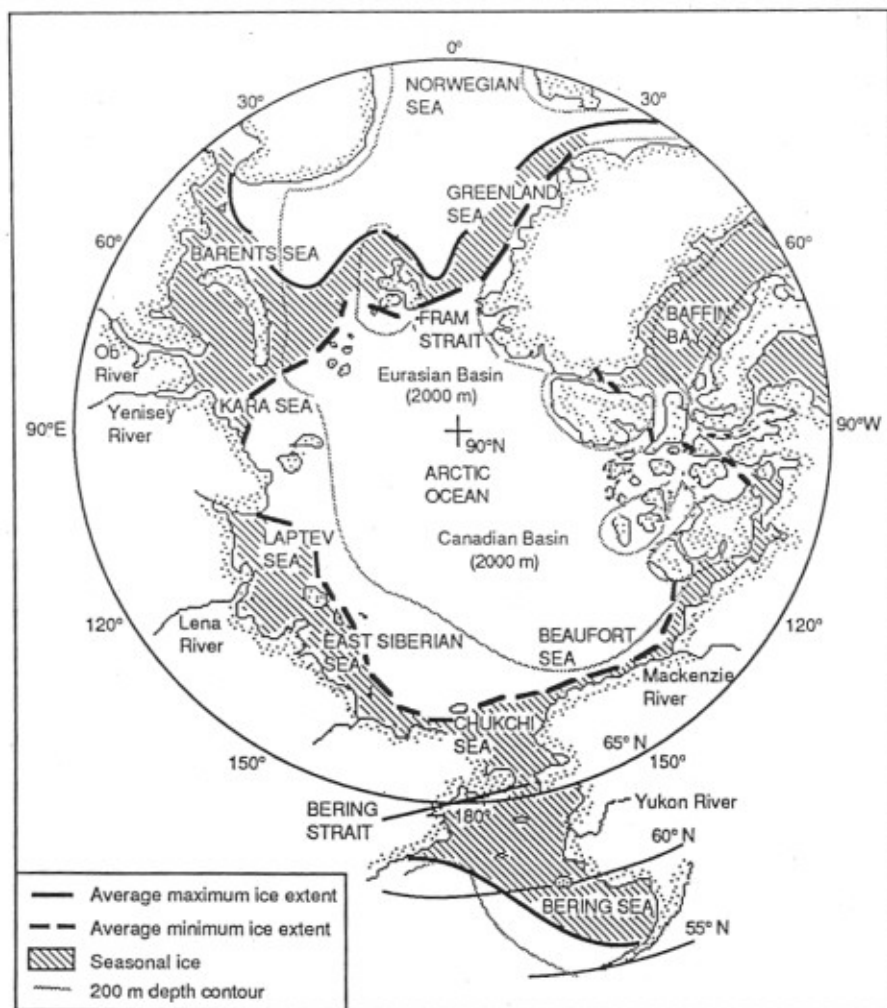


Fig. 1. The Arctic Ocean and its shallow marginal seas.

TABLE 1

Comparison of the marine environment of the Antarctic and Arctic [modified from Knox and Lowry (1977), Hempel (1985) and Dayton (1990)]

Antarctic	Arctic
1. Land mass surrounded by ocean; oceanic area normally studied between 50–70°S	Ocean surrounded by land; oceanic area normally studied between 70–80°N
2. Free connection with Atlantic, Pacific and Indian Ocean	Limited connection with Pacific (Bering Strait: 60 m); maximum with Atlantic (Fram Strait: 440 m)
3. Circumpolar circulation of surface waters (West Wind Drift; also eddies: Weddell, Ross Sea)	Surface water transport transpolar from Bering Strait to Fram Strait; Beaufort Gyre
4. Permanent ice shelf, with variable pack ice in summer	Large amount pack ice on ocean
5. Little/no dilution by river runoff on shelves	High dilution by river runoff on shelves
6. Little stratification or vertical stability; sinking of high salinity (> 34.5‰), low temperature (< 0.5°C) water near continent; upwelling high salinity (34.7‰), high temperature (1–2°C) water at Antarctic Divergence	Pronounced stratification and high vertical stability. High salinity in central Arctic (variable on shallow shelves). Low salinity (30–32‰), low temperature (–1.6°C) surface water (100–150 m); high salinity (34.8‰), high temperature (0–1.8°C) Atlantic Water (600 m); high salinity (34.8‰), low temperature (–1.0 to 0.5°C) bottom water (600–800 m)
7. High nutrient levels (20–30 µM) in euphotic zone year round	Variable nutrient levels seasonally in euphotic zone, e.g. high (20–30 µM) in Bering/Chukchi Seas to low (1 µM) in Beaufort, Kara, parts of Barents Seas
8. High levels of primary productivity nearshore; moderate offshore	Variable (low to high) levels of primary productivity
9. Mosaic of glacial marine sediments: muds, fine sands to boulders	Large input mud and clay from rivers flowing into Arctic Basin; variable silt, sand to boulders near coastline and in the straits
10. High degree climatic stability over last 200 years	Evidence of climatic temperature rise over last few decades

By comparison, the Antarctic is a land mass bounded entirely by water (Fig. 2, Table 1), including an ocean encompassed by the West Wind Drift (Antarctic Circumpolar Current) and oceans south of South America, Australia and Africa. The Antarctic is physically very different from the Arctic. The Antarctic continental shelf is deep (mean = ~ 500 m) due to isostatic depression and scouring by large glaciers. The continental slope descends 3000 to 5000 m to the abyssal plain. Unlike the Arctic, there are no rivers to discharge large volumes of freshwater into adjacent seas. In the water column, the mixed layer extends to ca. 150 m and encompasses most or all of the euphotic zone. Like the Arctic, salinity is the major factor controlling density and seasonal stratification usually is generated by the addition of meltwater from sea ice to the surface waters over large areas and to limited glacial input along coastal regions. Unlike the Arctic, the system is more constant and

homogeneous, with narrower seasonal fluctuations in salinity, temperature and dissolved gases.

Nutrients and primary production

Nutrients are overall high by the end of winter in the Arctic Ocean. When light returns to the Arctic in the spring, the ice retreats partially or completely from the marginal seas as well as thinning in the high Arctic, allowing the onset of phytoplankton production. Nitrate levels normally become limiting for production by summer in the marginal seas. Low concentrations occur in the Beaufort, Kara and parts of the Barents Sea (< 1 µM), although high nutrient concentrations are maintained in the western portions of the Bering and Chukchi Seas (20–30 µM; Walsh et al., 1989). Primary production ranges from < 5 gC m⁻² y⁻¹ in the ice pack of the high Arctic (English, 1961)

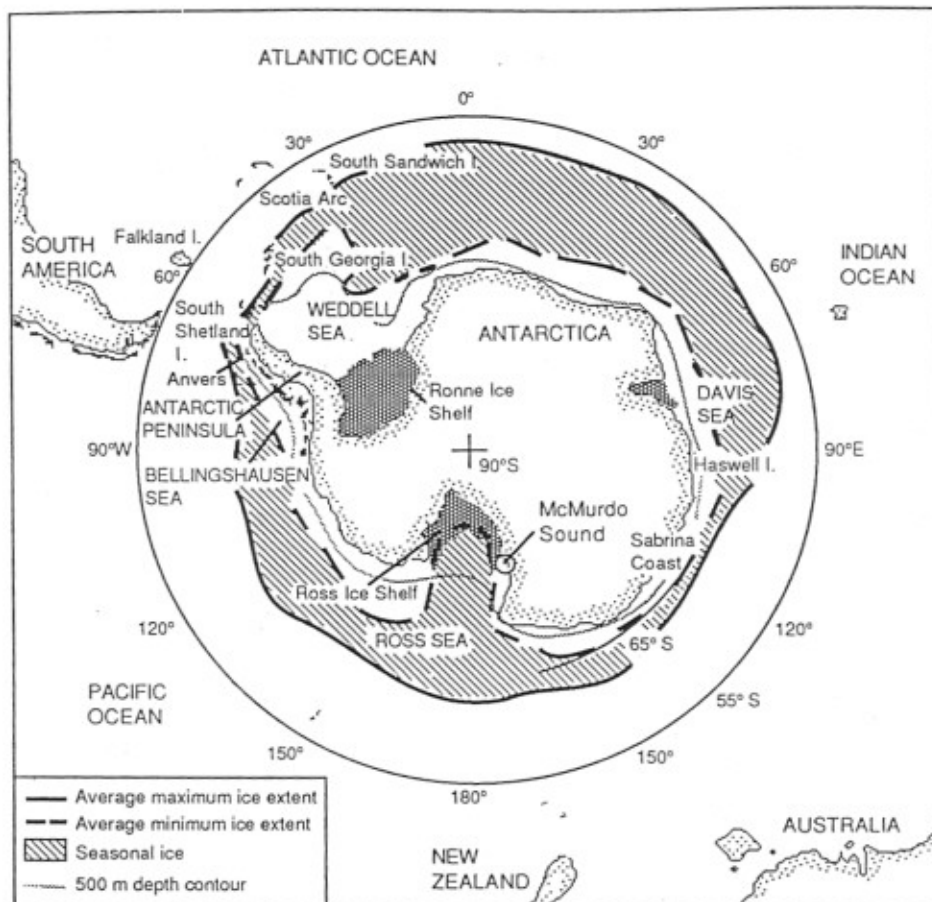


Fig. 2. Antarctica and its surrounding seas.

up to $40\text{--}80 \text{ gC m}^{-2} \text{ y}^{-1}$ in most of the Arctic marginal seas (Zenkevitch, 1963; Subba Rao and Platt, 1984; Anderson and Dyrssen, 1989). Maximum primary production is as high as $300 \text{ gC m}^{-2} \text{ y}^{-1}$ in the northern Bering and southern Chukchi Seas due to the upwelling of deep Bering Sea water onto the shelf via the Anadyr Stream (Walsh et al., 1989).

Nutrient concentrations generally are higher in the Antarctic than the Arctic, with values in upwelled water along the Antarctic Divergence ranging from $27\text{--}40 \mu\text{M}$ nitrate, $1.0 \mu\text{M}$ ammonium and $2\text{--}2.4 \mu\text{M}$ phosphate. In some areas, ammonia plays a major role in nutrient cycling and constitutes 50–80% of the nitrogen taken up by phytoplankton (Holm-Hansen, 1985). Antarctic nanoplankton ($< 20 \mu\text{m}$) apparently utilize ammonia at a higher rate than nitrate, compared to microplankton ($> 20 \mu\text{m}$, e.g. diatoms). Identifying the source that sustains this high ammonia flux is an important area of research. Holm-Han-

sen (1985) concluded that only 2% results from zooplankton ($> 200 \mu\text{m}$) excretion and $> 90\%$ of ammonium is contributed by bacterioplankton and microzooplankton ($< 20 \mu\text{m}$). The high rate of grazing and ammonium production in the euphotic zone indicates that grazing rates are high and that much of the production is regenerated, thereby restricting the potential for export of organic carbon to benthic communities.

Although nutrients typically are high in the water column ($20\text{--}40 \mu\text{M}$ nitrate), primary production over vast waters surrounding Antarctica is surprisingly low ($16\text{--}100 \text{ gC m}^{-2} \text{ yr}^{-1}$), limited by the deep mixed layer, with water column stability being the major factor controlling phytoplankton growth and accumulation (Ryther, 1969; El-Sayed, 1978; Smith and Nelson, 1985, 1986). In some regions, however, particularly nearshore habitats and upwelling regions, primary production is seasonally very high ($> 2 \text{ gC m}^{-2} \text{ d}^{-1}$; Heywood and Whitaker, 1984; Barry, 1988). In addition, high

densities and primary production values (41 gC m^{-2}) of microalgae in bottom sea ice indicate they may be an important source of carbon to the water column (Gross et al., 1987). Recent studies estimate about 10–76% of primary production in nearshore and open waters of the Antarctic is cycled through a bacterial loop in the water column (Cota et al., 1990; Sullivan et al., 1990), resulting in variable organic carbon input to the underlying benthos.

Benthic fauna

The Arctic has a relatively high number of endemic benthic species which evolved from Pacific ancestors, although its present day fauna are dominated by Atlantic species that have immigrated into the Arctic basin with Atlantic water intrusion in the eastern Arctic (Golikov and Scarlato, 1989; Golikov et al., 1990). Many dominant invertebrate species of the polar benthos reproduce primarily by brooding and do not have pelagic larval stages. This reduces dispersal and promotes the isolation of these communities (White, 1984). However, there are some species of invertebrates which produce planktonic larvae, such as bivalves and echinoderms, along with fishes, that have successfully penetrated further north in the Arctic (Golikov and Scarlato, 1989). The highest diversity of species occurs in the Norwegian and Barents Sea due to immigration through the north Atlantic. Species richness decreases northward and eastward into the eastern Barents, Kara and Laptev Seas; the latter two seas are influenced greatly by the large Siberian rivers flowing into the Arctic Ocean. Pacific-boreal species become more important in the East Siberian and Chukchi Seas.

Low temperature in itself is not a limiting condition for benthic fauna in polar regions and slow growth rates are more a reflection of severe seasonal food limitation than biological limitations due to temperature (Clarke, 1983). Most polar invertebrates confine their growth and reproduction to seasons with adequate food availability. Polar invertebrates generally have lower metabolic rates, such that for a given amount of food consumed, a relatively greater percentage of energy is

directed to growth and reproduction and less is used for maintenance, enabling benthic faunal biomass to increase to greater levels than in temperate or tropical regions with comparable food resources (Clarke, 1985, 1987).

The Antarctic is physically more constant and homogeneous than the Arctic and is characterized by greater environmental stability and diversity of benthic species (Table 2). In all major macrobenthic taxa, the number of Antarctic species greatly outnumber Arctic species (White 1984; Table 2). In addition, the Antarctic has extremely high benthic biomass on its deep continental shelves in spite of limited water column productivity, primarily due to the slow growth, delayed maturation and the longevity of benthic fauna (Clarke, 1985). However, periodic phytoplankton blooms and reduced pelagic consumption and recycling of descending organic carbon can transfer large amounts of organic carbon to the benthos that may be oxidized rapidly in some shelf areas (Dayton, 1990), suggesting that food supply is the dominant factor limiting benthic fauna biomass in these regions of the Antarctic. In comparison, low benthic biomass in the high Arctic and many of its marginal seas is probably directly due to low water column primary production rates (limited by low nutrient supplies and light regimes) and small carbon fluxes to the benthos, resulting in food limitation to the benthos and low benthic standing stock. For example, the biomass of benthic infauna on the shallow continental shelf of the northern Bering and Chukchi Seas is directly related to food supply, which is coincident with

TABLE 2

Comparison of the number of species recorded from certain groups of Antarctic and Arctic macrobenthos (modified from White, 1984).

Group	Antarctic	Arctic
Mollusks	875	224
Polychaetes	650	300
Amphipods	470	262
Bryozoans	310	200
Sponges	300	200
Isopods	299	49
Ascidians	129	47
Pycnogonids	100	29

high organic carbon utilization in the surface sediments due to benthic consumption (Grebmeier and McRoy, 1989; Lomstein et al., 1989).

Limited data exist describing macrobenthic standing stock for Antarctic benthos relative to Arctic studies. Instead, macrofaunal abundance is used as an indicator of benthic population levels, although faunal abundance only provides qualitative information on relative differences between various faunal groups, being limited by the screen size used (either 0.5 or 1 mm). In general, benthic macrofaunal abundance is an order of magnitude

greater in the Antarctic than Arctic (Knox and Lowry, 1977; Dayton 1990; Table 3). In the shallow subtidal habitats in McMurdo Sound up to 155,000 individuals (ind) can occur per m^2 , dropping an order of magnitude with depth (Dayton and Oliver, 1977). On the average, nearshore shelf values range from 10,000–30,000 $ind\ m^{-2}$. In comparison, average nearshore populations in the Arctic range from 1000–6000 $ind\ m^{-2}$. Benthic biomass also is generally higher in the Antarctic (20–4000 g wet weight m^{-2}) than in the Arctic (20–400 g wet weight m^{-2}), excluding the Bering/

TABLE 3

Comparison of abundance distribution of Antarctic and Arctic benthos (modified from Dunbar, 1977 and Dayton, 1990). Screen size is 1.0 mm unless indicated by *, which indicates screen size of 0.5 mm (ind = individuals)

Antarctic			Arctic			
Location	Depth (m)	Abundance ($ind\ m^{-2}$)	Location	Depth (m)	Abundance ($ind\ m^{-2}$)	
Off-Sabrina Coast	200	1363	Barents Sea	0–100	311	
	300	183–483		100–200	168	
	2000	28		200–300	93	
	3500	14		300–400	48	
Haswell Is., Davis Sea	14–28	1000–2000	Kara Sea	< 100	123	
	35–40	2000 +		100–200	13–25	
	45–50	up to 6000				
Indian Ocean Sector	100–500	450–500	Eastern Bering Sea	20–103	330–4414	
	3000 +	0.8–0.9	SW Bering Sea	23–30	1350	
McMurdo Sound * (east)	20	118,712–155,573		46–360	2120–2410	
	30	145,781		700	4330	
	(west)	30	2184–45,294		1700	1730
		40	10,036			
Ross Sea *	500	1960	Northern Bering Sea			
Arthur Harbor,	5–75	18,412	ACW † (east)	19–42	2413	
Anvers Is.	300–700	1530–2891	BSAW † (west)	20–51	4718	
King Edward Cove,	5	31,150	Chukchi Sea			
South Georgia	6	2490	ACW † (east)	22–51	1268	
	11	1618	BSAW † (west)	46–54	4461	
South Shetland Island	46–115	11,177	Northwest Baffin Bay	5	1133	
				26–52	5502	
				106–250	1983	
				751–1100	988	
			Central Baffin Bay	5	6193	
				26–52	1730	
	106–250	867				
	751–1100	231				

† ACW = Alaska Coastal Water

BSAW = Bering Shelf–Anadyr Water

Chukchi Seas and portions of the Barents and Greenland Seas (20–3500 g wet weight m^{-2} ; Stoker, 1981; Jazdzewski et al., 1986; Grebmeier et al., 1989). The higher standing stocks in the Antarctic are notable since water column primary production and carbon flux to the benthos is generally lower, indicating factors other than food supply are important for influencing benthic community composition in both the Antarctic (Dayton, 1990) and Arctic (Grebmeier et al., 1989). When consumption and recycling of organic carbon by zooplankton and bacteria, respectively, occur in the water column, less carbon is available for sinking to the benthos, particularly in the deep regions of these polar systems. This decoupling of food production in the surface waters from benthic secondary production appears to limit Arctic benthos to a greater extent than Antarctic benthos.

Benthic community structure: Organizing factors

Many environmental factors influence benthic faunal composition and biomass in polar regions, including sediment grain size, food supply, current regimes and hydrographic factors (salinity, temperature, freshwater input). In addition, biological factors, such as predation and competition, are important. Benthic biomass is influenced directly by the availability of food supplied to benthic populations. Primary production in the water column and benthic primary production both contribute to the energy budget of the benthos via sinking of organic material from the euphotic zone to the bottom, in situ production and by the horizontal advection of organic carbon from elsewhere. Primary production in the water column is variable in the Arctic and Antarctic and is influenced by ice cover, light regimes, nutrient availability and other factors. The amount of surface-produced organic carbon reaching the benthos is dependent on the level of heterotrophic grazing of material as it descends through the water column. Soft sediments can limit benthic macroalgal production due to the need for hold-fast sites. Ice gouging can also disrupt all types of macrobenthic life. Adaptations that allow benthic fauna to survive the dark and ice-covered winter

may include the consumption of resuspended phytodetritus, or the reduction of metabolic rate.

The influence of nutrient (e.g. nitrate, ammonium) resupply to the water column during both benthic carbon remineralization and utilization for secondary benthic production and the subsequent effect of this nutrient recycling on water column primary production levels has rarely been studied in polar systems, yet is potentially an important factor. Oxidation of organic carbon seems to occur rapidly in many regions of the Arctic and Antarctic shelf sediments, indicated by commonly observed low (1–2%) carbon contents, suggesting that these are carbon-limited sediments; yet benthic biomass values are often among the highest in the world. Only a limited number of studies have investigated bacterial production in polar ecosystems, yet it is likely an important factor in controlling the availability and quality of organic carbon reaching the benthos. In addition, the role of bacteria in the sediments has a direct impact on the amount of recycled nutrients and inorganic carbon returned to the overlying water column.

Unlike the Antarctic, the Arctic supports many fishes, crustaceans and marine mammals (e.g. halibut, king and tanner crab, gray whale, walrus and bearded seal) that forage directly on benthic fauna living either within or on the surface of sediments. In particular, the importance of these marine mammals in maintaining or reducing benthic populations is unclear, but some evidence indicates that marine mammal foraging maintains benthic macrofaunal communities in early successional states (Oliver et al., 1983, 1984). Moreover, these foraging activities suspend considerable volumes of sediment into the water column and may have significant effects on nutrient release from the sediments, particularly during the period of summer stratification (Nelson and Johnson, 1987). In the northern Bering Sea 50–70% of all benthic infauna are dominated by the amphipod *Ampelisca macrocephala* (Grebmeier et al., 1989). Recent studies by Highsmith and Coyle (1990) indicate that this species is the most productive benthic amphipod in the world, illustrating the paradigm of high productivity in a seasonally food-limited system.

Models of polar ecological systems-benthic perspective

Arctic

Climate and sea ice are severe in the Arctic Ocean, limiting both primary and secondary production, with the most variable ice cover occurring in the southeast half of the Barents Sea, the southern portion of the Chukchi Sea and the northern Bering Sea. We have developed three conceptual models to describe major ecosystems in the Arctic Ocean. The first focuses on the shallow continental shelves of the northern Bering and Chukchi Seas that are influenced directly by high nutrient water from the Pacific Ocean (Fig. 3). Next we discuss an ecological model of the high Arctic Ocean and its marginal seas (East Siberian, Laptev, Kara, Canadian Archipelago, Beaufort and northern Chukchi Seas), that are nutrient limited, have long seasonal or permanent ice cover and seasonal riverine input (Fig. 5). The third model describes the Arctic continental shelves influenced by warm Atlantic Ocean water, specifically the Barents Sea (Fig. 7).

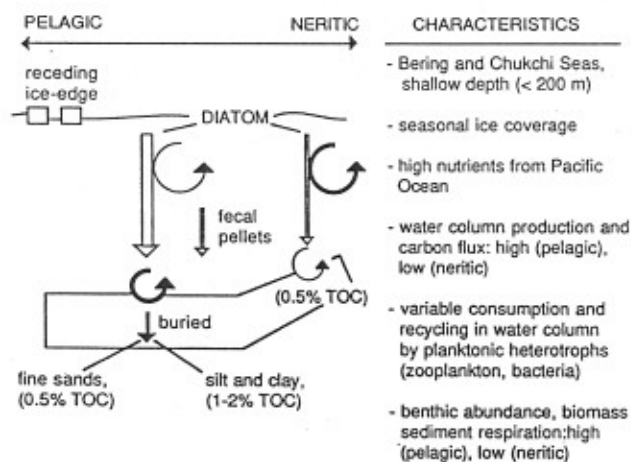


Fig. 3. Conceptual ecological model for the Pacific-influenced continental shelves of the Arctic Ocean. Vertical arrows indicate transport direction of organic carbon and circular symbol indicates recycling in the water column or at the sediment-water interface by heterotrophic organisms. Width of symbol indicates relative amount of organic carbon (e.g. thin arrow: low value, thick arrow: high value). TOC indicates total organic carbon in sediments.

Ecological model of the Arctic continental shelf—Pacific influenced (Fig. 3)

The shelves of the northern Bering and Chukchi Seas are shallow (30–70 m) and normally ice-covered from November to May (Fig. 1). Northward-flowing currents transport Pacific Ocean water through Bering Strait into the Chukchi Sea and Arctic Ocean. Water masses develop during the open-water season, each having different salinity, nutrient and phytoplankton dynamics (Walsh et al., 1989). The high nutrient load (20–40 $\mu\text{M NO}_3^-$) of the Anadyr Water provides a continuous source of nutrients for high primary production in the water column on the west side of the shelf from the Gulf of Anadyr to north of Bering Strait (250–300 $\text{gC m}^{-2} \text{yr}^{-1}$), but nutrient depletion limits production along the Alaska coastline in the east after the spring bloom (50–60 $\text{gC m}^{-2} \text{yr}^{-1}$; Walsh et al., 1989; Fig. 3). Andersen (1988) found that the microbial food web in the relatively oligotrophic Alaska Coastal Water utilizes 70–80% of the primary production, with the primary producers being dominated by pico- and nanoplanktonic forms. The microbial loop was least important in the water column at stations dominated by diatoms in the Anadyr and Bering Shelf waters, where only 5% of the primary production was processed through microbial activity. Recent studies by Fukuchi et al. (1990) indicate a water column organic carbon sedimentation rate ranging from 250–650 $\text{mg C m}^{-2} \text{d}^{-1}$ for the northern Bering Sea in Bering Shelf–Anadyr Water, with the C/N ratio (wt./wt.) of the sedimenting material averaging 6. Sinking rates were estimated at 30–60 m d^{-1} , indicating that fresh organic matter could reach the benthos in 1–2 days. The diatom *Thalassiosira* sp. was dominant during spring, with the diatom *Chaetocerus* sp. becoming abundant in the summer and sediment traps contained primarily fecal pellets in the late summer and fall (Taniguchi et al. 1990).

Rates of oxygen uptake by the sediments, used as an indicator of carbon use by the benthos, indicate the highest carbon supply to the benthos is in the highly productive Bering Shelf–Anadyr Water, with the lowest carbon supply to the sediments underlying the Alaska Coastal Water (Grebmeier and McRoy, 1989; Grebmeier, 1991).

The area of high organic carbon supply to the benthos supports a rich benthic biomass of amphipods and bivalves, which constitute the food base for benthic-feeding marine mammals in the region. Total benthic standing stock averages 20 gC m⁻² (300–400 g wet weight m⁻²), with values extending up to 50–60 gC m⁻² (2000 g wet weight m⁻²) in the southern Chukchi Sea (Grebmeier et al., 1988; Grebmeier, 1991; Fig. 4). Demersal fishes, common on the southeastern Bering Sea shelf, are apparently excluded from these northern shelves by low bottom water temperatures (Neiman, 1963). Sea stars, brittle stars and crabs are the major macroinvertebrate predators in the area (Jewett and Feder, 1980), but their populations are not a major limiting factor to benthic com-

munity structure and biomass in the highly productive regions of the Bering and Chukchi Seas (Jewett and Feder, 1980; Feder et al., 1989; Grebmeier et al., 1989).

A limited number of sediment respiration rates have been determined for the middle Bering Shelf region south of St. Lawrence Island as part of the U.S. National Science Foundation-funded PROBES project. Relatively higher respiration rates were observed in this slow-circulating, benthic-dominated regime than in either inner or outer shelf portions of the Bering Sea (Walsh and McRoy, 1986). The middle-shelf region also was the site of the highest biomass of benthic bivalves on the Bering Sea shelf, dominated by species of *Nucula* and *Macoma*. This enhanced benthic bio-

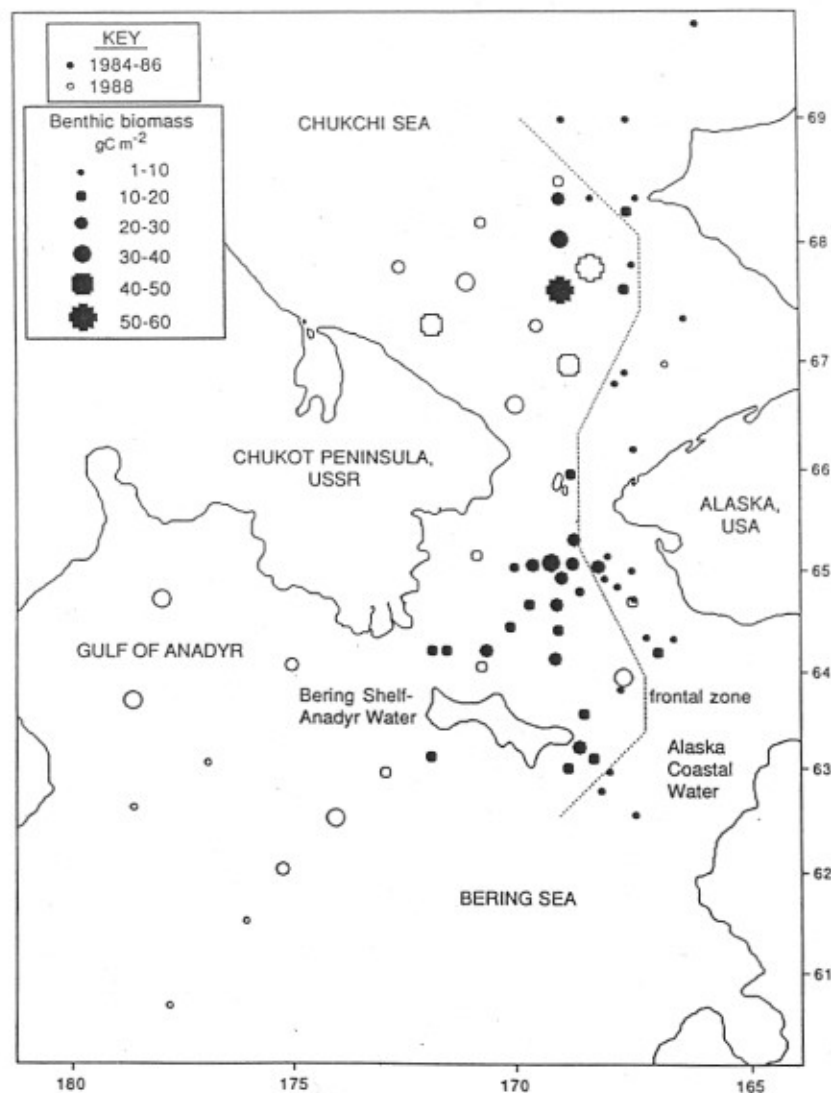


Fig. 4. Distribution of macrofaunal benthic biomass (gC m⁻²) for 1984–1986 (from Grebmeier et al., 1988) and 1988 (Grebmeier, 1991).

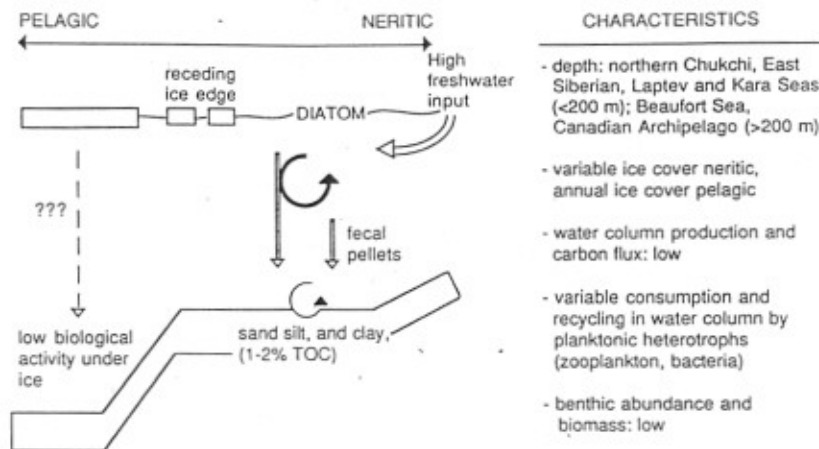


Fig. 5. Conceptual ecological model for the continental shelves and central basin of the Arctic Ocean. Vertical arrows indicate transport direction of organic carbon and circular symbol indicates recycling in the water column or at the sediment-water interface by heterotrophic organisms. Width of symbol indicates relative amount of organic carbon (e.g. thin arrow: low value, thick arrow: high value). TOC indicates total organic carbon in sediments.

mass was assumed to be due to a high flux of organic carbon to the benthos (Feder et al. 1980).

Both the quantity and quality of organic matter reaching the benthos influences benthic standing stock and sediment respiration (Grebmeier et al., 1988, Grebmeier and McRoy, 1989). Organic carbon in surface sediments was highest (1–2%) in the Gulf of Anadyr and the western region of the Chukchi Sea. The lowest values of organic carbon (0.1–0.5%) occurred in sediments under the Alaska Coastal Water (Grebmeier et al., 1988; Grebmeier, 1991). High quality organic carbon settles to the benthos in these shallow waters, as evidenced by the low C/N (5–7; wt./wt.) ratios in sediments under the highly productive Bering Shelf–Anadyr waters (Grebmeier et al., 1988). In contrast, highest C/N ratios (8–14, wt./wt.), indicative of low quality material, occurred in sediments underlying the Alaska Coastal Water. These results indicate the important influence of hydrodynamics on organic carbon loading and sediment composition, which in turn influences the structure and biomass of benthic populations in this region.

The supply of organic carbon from the water column is a major factor influencing the structure and biomass of benthic communities, along with carbon cycling, in the soft sediment habitats in the Bering and Chukchi Seas (Grebmeier et al., 1988, Grebmeier et al., 1989, Grebmeier and McRoy, 1989). Food supply to the benthos is greatest in the highly productive Bering Shelf–Anadyr Water,

resulting in high benthic biomass and low species diversity, whereas the food-limited system in the Alaska Coastal Water results in low benthic biomass and greater niche diversification (Grebmeier et al., 1989).

Ecological model of the Arctic Basin continental shelves and ocean basins (Fig. 5)

Information is extremely limited on primary productivity values in the central Arctic Basin and its marginal seas, such as the East Siberian, Laptev, Kara, northern Chukchi, Beaufort and the Canadian Archipelago (Fig. 1). Primary production is less than $1 \text{ gC m}^{-2} \text{ yr}^{-1}$ in the high Arctic, limited by multi-year ice cover and a deep freshwater lens on the surface (English, 1961). Calanoid copepods dominate the zooplankton in the high Arctic (e.g. *C. glacialis*) and its marginal seas (e.g. *Calanus hyperboreus*, *C. finmarchicus* and *Pseudocalanus* sp.; Zenkevitch, 1963; Loeng, 1989). Benthic populations in the deep (> 2000 m) Arctic basins are most likely food-limited (Zenkevitch, 1963). The biogenic carbon component of the sediments averages 1–2%, although values as high as 6% have been recorded sporadically in the abyssal plains of the central Arctic, where the greatest accumulation of fine sediments occurs (Darby et al., 1989). In addition, pebbles and cobbles are scattered throughout the Arctic basins due to ice rafting. It has been proposed that significant sediment remineralization occurs on

the wide continental shelves of the Arctic Ocean and that it has an important influence on nutrients recycled to the overlying water column, which eventually reach the arctic halocline (Anderson et al., 1986).

Marginal seas in the Arctic are limited by extreme yearly ice cover, seasonal riverine input with their load of suspended sediments and low nutrient supply (Fig. 5). No primary production values are available for the East Siberian, Laptev or Kara Seas (Walsh et al., 1989). The annual water column primary productivity in the northern Chukchi Sea ranges from 50–100 gC m^{-2} , dropping to 10–25 gC m^{-2} in the Beaufort Sea (Parish, 1988). With the low primary productivity observed in the Beaufort Sea, ice algae are likely an important source of organic carbon to the water column, potentially providing up to 5 $\text{gC m}^{-2} \text{yr}^{-1}$

(Alexander, 1974). Studies by Horner and Schrader (1982) found ice algae comprised 2/3 of the measured water column production. Only 1–10% of the water column production is estimated to reach the benthos in the Beaufort Sea, indicating that carbon limitation likely influences the low benthic biomass in this region (Carey and Ruff, 1977; Carey, 1987). Terrestrial peat is an additional carbon source to the nearshore Beaufort marine environment (Schell, 1983), although few benthic animals are able to digest peat-derived carbon and most of the peat is likely recycled through bacterial food webs (Griffiths et al., 1984).

The Alaskan Beaufort Sea has a narrow continental shelf and is characterized by low benthic biomass (40 g wet weight m^{-2} ; Thomson, 1982; Fig. 6). The Beaufort Sea is ice covered during most of the year, thus limiting primary produc-

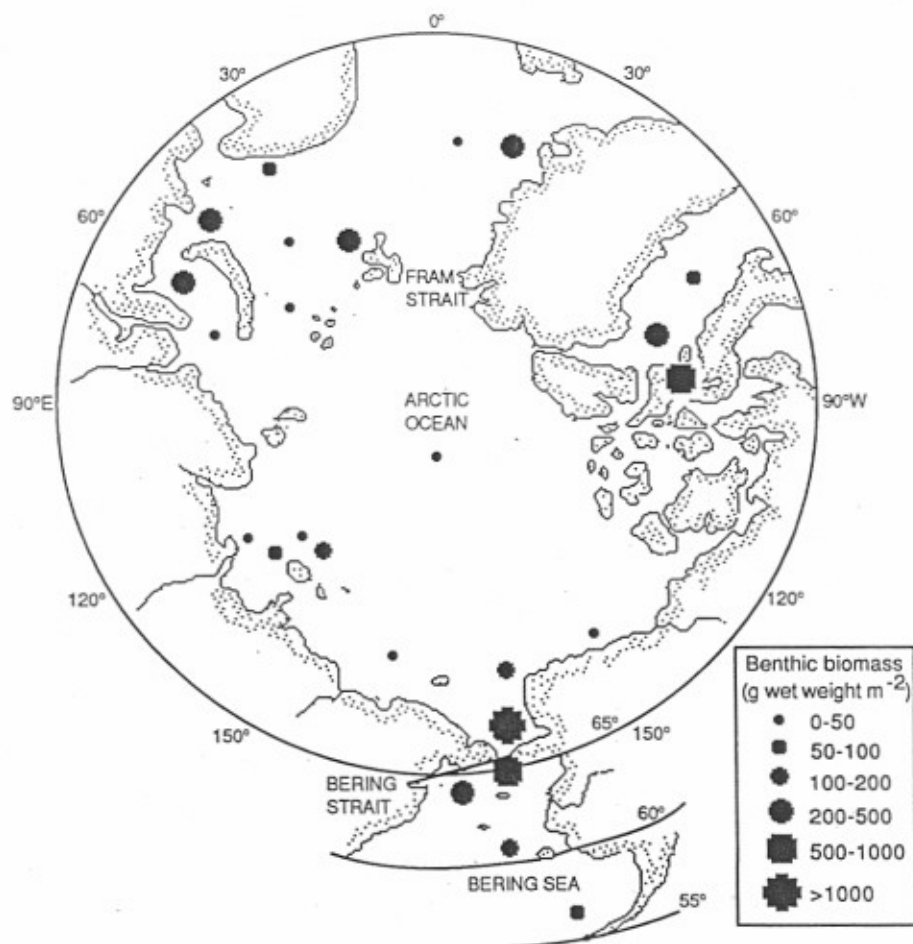


Fig. 6. Distribution of average benthic biomass ($\text{g wet weight m}^{-2}$) in various regions of the Arctic Ocean, based on data from the following authors: Bering and Chukchi Seas (Zenkevitch, 1963; Stoker, 1981; Grebmeier et al., 1989) Canadian Archipelago/Beaufort Sea (Thomson, 1982), Barents, Kara and East Siberian Seas (Zenkevitch, 1963), Laptev Sea (Golikov et al., 1990), East Greenland Sea (Zenkevitch, 1963) and the Arctic basin (Paul and Menzies, 1974; Golikov and Scalata, 1989).

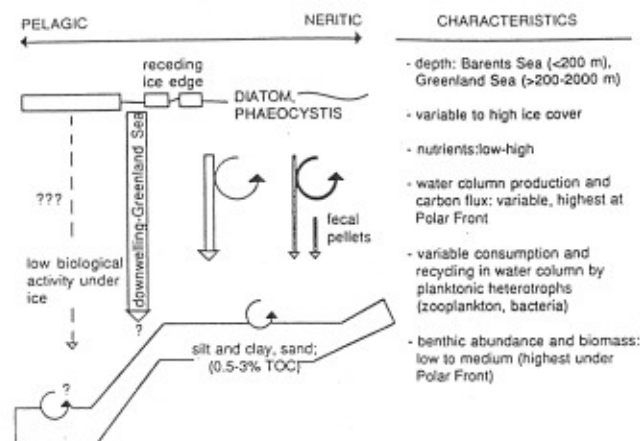


Fig. 7. Conceptual ecological model for the Atlantic-influenced continental shelves of the Arctic Ocean. Vertical arrows indicate transport direction of organic carbon and circular symbol indicates recycling in the water column or at the sediment-water interface by heterotrophic organisms. Width of symbol indicates relative amount of organic carbon (e.g. thin arrow: low value, thick arrow: high value). TOC indicates total organic carbon in sediments.

tion. Carey et al. (1977) related benthic community structure and diversity to water circulation, sediment distribution patterns and ice coverage. Benthic biomass in the northern Chukchi Sea ranges from 137–357 g wet weight m^{-2} (3.2–5.7 gC m^{-2} ; Feder et al., 1989). Feder et al. (1989) hypothesized that the high biomass in the northern Chukchi Sea under relatively low primary productivity Alaska Coastal Water resulted from advection of phytodetritus northward from the rich Bering Shelf–Anadyr water further south.

Although kelp communities are limited in the western Arctic due to fine-grained substrates and fast-ice disturbance, Dunton and Schell (1986) reported on a highly productive *Laminaria solidungula* community growing on boulders off the northern coast of the Beaufort Sea. The kelp community is able to utilize stored resources in the winter that were produced the previous open-water summer season, resulting in a net annual carbon production of 6–10 gC m^{-2} (Dunton and Schell, 1986). Using carbon isotope measurements ($\delta^{13}C$) Dunton and Schell (1987) traced kelp carbon utilization by many dominant benthic fauna in the region, indicating the importance of kelp as a food source in this extremely carbon-limited benthic system.

The highest benthic biomass in the Canadian

Archipelago occurs in northwestern Baffin Bay and Lancaster Sound (300–500 g wet weight m^{-2} , Fig. 6). Most of the rest of the Canadian Arctic (e.g. near Melville Island, central Baffin Bay) has much lower biomass (~ 40 –80 g wet weight m^{-2}) and the author suggested that these benthic communities were limited due to lower nutrients and primary production in the overlying water column (Thomson, 1982). The highest density and biomass of benthic fauna, dominated by suspension-feeding organisms, occurs in northwest Baffin Bay, where current speeds are greatest, while the lowest benthic fauna abundance and biomass, dominated by deposit feeders, occurs in low current regimes (Thomson, 1982).

Resuspension of surface sediments introduces phyto- and zoo-benthos, terrestrial and other detritus into the overlying water column, thus recycling organic matter for benthic deposit feeders as well as replenishing nutrients to the overlying water column for enhanced phytoplankton production. Few studies have estimated carbon flux to the benthos in the high Arctic. In Frobisher Bay, the flux of organic carbon to the sediments after the spring bloom is estimated to be 285 mg C $m^{-2} d^{-1}$ and this relatively high number may explain the high benthic biomass value observed in this region compared to the open water regions of Baffin Bay (Thomson, 1982; Fig. 6). In addition, fall-out of sea ice microalgae after the spring bloom can add detritus to benthic communities (Hsiao, 1987).

The Laptev and East Siberian Seas have the most severe climate, highest riverine input and lowest salinity of Arctic marginal seas, resulting in a highly stratified water column and low primary production, as well as greatly reduced benthic diversity and biomass (Zenkevitch, 1963; Fig. 6). Sediments in the Laptev Sea are primarily silt and clay, with total organic carbon content ranging from 0.6–1.6% (Holmes, 1967). Foraminifera abundance is low, similar to most regions of the Arctic, due to low temperatures and high ice cover (that limits primary production). Limited data from the East Siberian Sea indicates that total organic carbon in the sediments ranges from 0.4–1.5%, with organic carbon increasing with decreasing grain size in the offshore sediments (Naugler,

1967). Studies from the 1970's of the New Siberian shoals and adjacent waters of the Laptev Sea (up to 35 m depth) delineates 19 ecosystems, half of which are characterized by boreal-Arctic and brackish water species (Golikov et al., 1990). Benthic biomass values in the Laptev Sea ranged from 5–110 g wet weight m^{-2} . This study found the species abundance, diversity, biomass and production were higher in areas overlain by surface Arctic water compared to regions overlain by more brackish estuary-Arctic water, with maximum benthic values occurring in the centers of the water types (Golikov et al., 1990).

The Kara Sea is shallow (< 200 m), receives 1/3 of the total freshwater input to the polar basins and is an important area for production and export of ice to the central Arctic (Hanzlick and Aagaard, 1980). Both the extreme ice conditions and high freshwater content severely limit benthic productivity on this wide shelf, which is dominated by echinoderms (Zenkevitch, 1963). Benthic diversity and biomass are highest in the shallow regions, where sediments are silt and sand and are influenced by the inflow of Atlantic water via the Barents Sea (Fig. 6). The finer grained brown muds of the deep, offshore regions contain extremely low amounts of benthic life compared to similar depths in the Barents Sea, although it is unclear why this is the case. Besides the fact that a limited amount of organic matter reaches the benthos, it is possible that manganese toxicity, resulting from the high levels of manganese and iron oxides in the sediments, limit benthic production (Zenkevitch, 1963). Benthic biomass averages 50 g wet weight m^{-2} in the western regions, but only 5 g wet weight m^{-2} in the central brown muds and rises to 300 g wet weight m^{-2} in the shallow areas where fish also occur (Zenkevitch, 1963). Sediment organic carbon ranges from 0.3–2%, characteristic of other Arctic shelves.

In their review of the Arctic benthos, Golikov and Scarlato (1989) characterized the high Arctic benthic biomass as being dominated by macrobenthic organisms, with the percentage of meiobenthic biomass to total biomass averaging ≤ 6 –15%. They observed that meiobenthic biomass increases near estuaries and at depth beneath the permanent pack ice where macrofaunal biomass is

limited and conclude that meiobenthic organisms feed on the finest grained and dissolved particulate matter not available for the macrobenthos to feed upon. In general, the highest mean benthic biomass (300 g wet weight m^{-2}) occurs at salinities $> 24\text{‰}$ in ice-free regions, with values < 150 g wet weight m^{-2} beneath the pack ice or in areas where salinities are 6–7‰.

Ecological model of Arctic continental shelves—Atlantic influenced (Fig. 7)

The Barents Sea has the most diverse bottom fauna in the Arctic Ocean (1400 species), with numbers dropping to 200 species in the Laptev Sea (Zenkevitch, 1963). Only in the southern Chukchi Sea are species numbers somewhat elevated due to the influence of immigration northward of Pacific Ocean species through Bering Strait. The Polar Front in the Barents Sea exists as a transitional zone between Arctic and Atlantic water masses. The Barents Sea, unlike other Arctic seas, has low river input and low suspended sediment load. A distinguishing feature of the southern Barents Sea is the large biomass of benthic macroalgae, including *Fucus* sp., *Laminaria* sp. and red algae, that is consumed within narrow nearshore foodwebs or advected offshore (Belyaeva et al., 1989).

Primary productivity ranges from 40–80 gC $m^{-2} yr^{-1}$, most of which occurs during the spring bloom (Loeng, 1989). In addition to diatoms, the prymensiophyte *Phaeocystis pouchetii* is an important phytoplankton component in summer and fall in the Barents Sea (Wassman et al., 1990), though whether it is used as a food source in the water column and/or benthos is uncertain. Until recently, this gelatinous community was considered unused by zooplankton, but recent studies have found they can be grazed upon by a variety of copepods (*Calanus finmarchicus*, *C. hyperboreus* and *C. glacialis*), with predation level dependent upon the physiological state of the *Phaeocystis* colony (Estep et al., 1990). In addition, *Phaeocystis* blooms can form a large percentage of the organic carbon settling out of the euphotic zone, although most of it degrades in the water column (Wassman et al., 1990), thus diminishing the possible significance of this carbon input to the un-

derlying benthos. However, *Phaeocystis* has been observed intact on the shallow bottom of McMurdo Sound, Antarctica, although its role in benthic productivity is unknown (Dayton, 1990). True Arctic zooplankton, such as *Calanus glacialis*, along with the boreal Atlantic species *C. finmarchicus* and *C. hyperboreus*, are the major zooplankton consumers of primary production in the Barents Sea (Hansen et al., 1990).

The Barents Sea is well oxygenated and the sediments have 0.5–3% organic carbon content, with organic C/N ratios ranging from 6 to 8 (wt./wt.), indicating the availability of high quality material (Fig. 7; Zenkevitch, 1963). The northern Barents Sea contains fine-grained brown sediments, with low content of organic carbon. The benthic fauna of the northern and eastern portions of the Barents sea are impoverished primarily due to ice conditions, in a manner similar to the Laptev Sea (Fig. 8; Zenkevitch 1963). Many areas of the Barents Sea have sandy sediments and rich benthic life, but have a low content of organic carbon in the surface sediments. These sandy sediments result from the removal of fine-grained particles by high horizontal and vertical water motion. The highest benthic biomass in the Barents Sea occurs at the Polar Front separating Atlantic water and

Arctic Ocean water in the southeastern Barents Sea (Fig. 8; Zenkevitch, 1963). The dominant macrobenthic fauna include bivalves, gastropods, polychaetes, echinoderms, crustaceans, sponges, hydroids, bryozoans, ascidians and foraminifera.

Meiobenthic studies on the northeastern Svalbard shelf in the Barents Sea and in the Nansen Basin found a significant correlation between the abundance and biomass of meiofauna and sedimenting organic detritus, indicating the importance of food quantity to benthic stocks (Pfannkuche and Thiel, 1987). The northeast Svalbard shelf is normally ice covered, except when the ice-edge retreats northward in the summer. The Nansen Basin is covered with multi-year ice and receives water transported from the Norwegian Sea through Fram Strait. Sediment oxygen consumption rates are 3–10 times lower in the northern Barents Sea than in the eastern Atlantic, although data indicate a comparable input of organic matter (Pfannkuche and Thiel, 1987). These data suggest that Arctic fauna in this region have low turnover rates due to slow growth rates and long individual life spans, resulting in high benthic biomass. Macrofauna dominated the benthos at shelf stations, where biomass was highest and the faunal composition was dominated by suspension feeders (indicative of the high current regime), whereas meiofauna became more important at the deeper stations, where biomass was lowest and the fauna were primarily deposit feeders (Pfannkuche and Thiel, 1987).

At 80°N north of Svalbard, annual primary production is only about 10 g C m^{-2} , although ice-edge production is likely to be important during parts of the year (Strömberg, 1989), which suggests that lateral transport of phytodetritus on the northeast Svalbard shelf may be an important food source to benthic communities. High levels of sediment-bound chlorophyll were measured northeast of Svalbard and on the continental shelf, indicating a substantial transport of phytodetritus to the seabed and a downslope transport of phytodetritus to the Nansen Basin (Pfannkuche and Thiel, 1987), possibly due to formation of dense water by brine rejection on the Barents shelf. Studies by both Pfannkuche and Thiel (1987) and Belyaeva et al. (1989) suggest that the high benthic

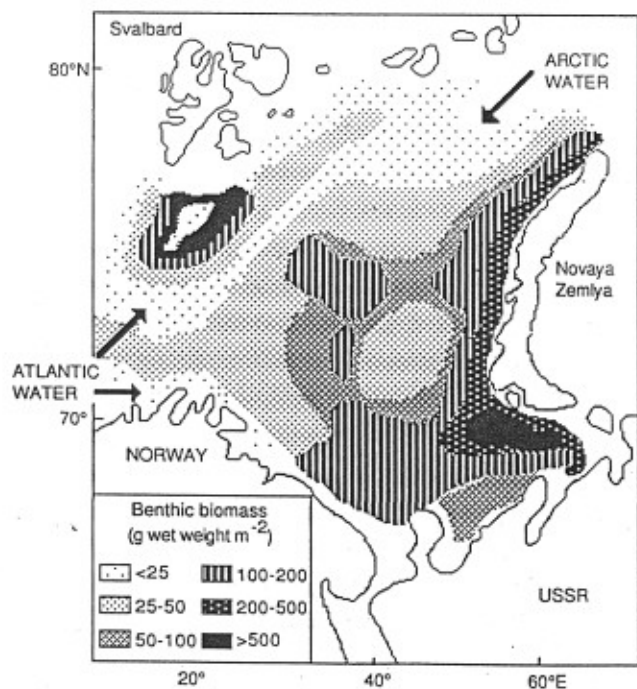


Fig. 8. Distribution of benthic biomass ($\text{g wet weight m}^{-2}$) in the Barents Sea (from Zenkevitch, 1963).

productivity of regions in the Barents Sea is due to the relatively high primary productivity of the water column, short food chains, low temperature of organic matter decomposition and long life span of the fauna.

Antarctic

Antarctic benthic communities, like those in Arctic regions, are controlled by the vertical flux of material from the euphotic zone. In the Antarctic, however, the greater depth of the continental shelf, highly variable ice cover and its effects on hydrodynamic processes that control primary production, the minimal terrestrial runoff, among other factors, result in benthic biological dynamics divergent from Arctic systems. Hempel (1985) discusses three zones that characterize biological systems in Antarctic seas. We have generated 3 ecological models for the dynamics of Antarctic benthos that correspond to Hempel's zones. These models encompass the biological dynamics of the water column, the flux of organic material to the benthos and sediment characteristics.

Ecological model of Antarctic continental shelves-offshore (Fig. 9)

The first Antarctic model (Fig. 9) typifies the ice free zones of the West Wind Drift, such as the

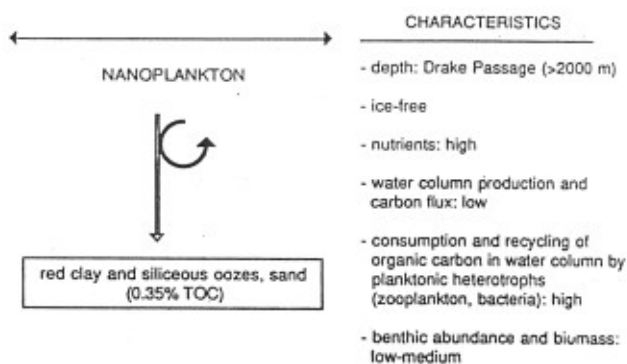


Fig. 9. Conceptual ecological model for the offshore continental shelves of Antarctica. Vertical arrows indicate transport direction of organic carbon and circular symbol indicates recycling in the water column or at the sediment-water interface by heterotrophic organisms. Width of symbol indicates relative amount of organic carbon (e.g. thin arrow: low value, thick arrow: high value). TOC indicates total organic carbon in sediments.

Drake Passage. Like most Antarctic seas these pelagic systems have high levels of inorganic nutrients, but phytoplankton productivity often is limited by light due to deep vertical mixing of the surface waters. Rates of primary production are fairly low (ca. 0.1 to 0.4 gC m⁻² d⁻¹; Fogg, 1977) and nanoplankton contribute 50% or more of the total phytoplankton biomass (Bröckel, 1981, Hewes et al., 1983, 1985) and up to 90% of the primary production (Clarke, 1985). This high proportion of nanoplankton suggests that consumption and recycling of organic material within the water column by zooplankton grazing and in situ microbial degradation, respectively, are major factors that may restrict the vertical transport of organic material to the benthos. Copepods, euphausiids (other than krill) and salps dominate the zooplankton, with krill in low abundance compared to more productive Antarctic seas (Hempel, 1985). Low rates of primary production, coupled with a high proportion of nanoplankton with slow sinking rates, and great depths (ca. 2000-5000 m) result in a limited vertical flux of carbon to the benthos.

Fluxes of organic carbon to sediment traps suspended in the water column in Drake Passage are quite variable and have been determined to be from 6 gC m⁻² y⁻¹ in the upper 50 m to 1-5 gC m⁻² y⁻¹ in depths from 1000 to 2500 m (Wefer et al., 1982; Clarke, 1984; Noriki and Tsunogai, 1986; Fig. 9). Benthic sediments are composed of red clays and siliceous oozes with an organic carbon content near 0.35%. Benthic abundance is low in deep water (60 ind m⁻²) and higher along the Shetland Islands (ca. 8000 ind m⁻²; 200 g wet weight m⁻²), but still not high compared to temperate latitudes and similar to many Arctic basin sites (Mills and Hessler, 1974). This low abundance and standing stock of benthic organisms and the low levels of organic carbon in the sediments suggest that benthic communities are food limited due to the restricted flux of organic material from the euphotic zone, particularly to deep benthic habitats. Because rates of disturbance in Antarctic benthos are lower than in the Arctic where macroinvertebrate and vertebrate predators are abundant (e.g. Bering Sea), biomass can accumulate over longer periods and produce

higher standing stocks under potentially lower rates of secondary production.

Ecological model of Antarctic continental shelves—nearshore, variable ice cover (Fig. 10)

A second conceptual model for Antarctic benthic–pelagic coupling characterizes regions with large seasonal fluctuations in ice cover, such as the Ross Sea, Bransfield Strait, parts of the Bellinghousen Sea and Scotia Arc region (Fig. 10). Nutrients generally are high and meltwater produced by the deterioration of the annual ice enhances water column stability and “seeds” regional plankton blooms with sea ice algae (Hempel, 1985). Though these systems differ considerably in some aspects, all are typified by somewhat higher primary production than the Drake Passage, with seasonally intense blooms of phytoplankton (ca. 0.2 to 2.0 gC m⁻² d⁻¹). Recent studies have found nanoplankton contribute a major portion of the biomass and production of phytoplankton over most of the southern ocean (Hewes et al., 1985, Weber and El-Sayed, 1987). However, larger diatom species (predominately *Nitzschia* and *Thalassiosira*) and prymeniophyte flagellates (*Phaeocystis*) can be much more abundant in marginal ice zone phytoplankton blooms (Holm-Hansen et al., 1989; Legendre, 1990). Zooplankton in this system

are dominated by krill (*Euphausia* spp.), particularly in the Scotia Arc area. Krill preferentially consume microplankton over nanoplankton (Meyer and El-Sayed, 1981; Quetin and Ross, 1985) and can effectively graze algae from bloom areas.

Nanoplankton and microplankton fractions appear to contribute differentially to recycling within the water column and sedimentation, respectively, due to the differences in their rates of settlement through the water column. Nanoplankton and the mucilaginous flagellate *Phaeocystis* sp. have slower sinking rates and probably contribute greatly to microbial loop dynamics. In contrast, microplankton sink towards the bottom as intact particles or within fecal pellets of krill. The larger diatom fraction clearly is important with up to 90% of the sedimenting material in some areas being composed of euphausiid fecal pellets (Dunbar, 1984). Nevertheless, much of the primary production in the surface waters appears to be recycled in situ and supports the high production of pelagic food webs of such regions, including krill, squid and vertebrate predators. Benthic sediments are dominated by siliceous biogenic material and sandy glacial materials, with an organic carbon content ranging from 0.5 to 2.0%. The benthos of this model system (Fig. 10) are richer than regions from the previous model (Fig. 9), with higher standing stock and, presumably, higher productivity. Nevertheless, these benthic systems still are food limited compared to some highly productive regions of the Arctic seas, such as the northern Bering Sea shelf.

Ecological model of Antarctic continental shelves—persistent ice cover (Fig. 11)

A third model includes habitats, such as continental shelf areas covered by floating glaciers (Ross Ice Shelf, Ronne Ice Shelf) and continental margins (McMurdo Sound, Southern Weddell Sea) with persistent to permanent ice cover (Fig. 11). The reduction in down-welled light by ice cover severely restricts in situ primary production (ca. 0.01 to 0.25 gC m⁻² d⁻¹; Bunt, 1964; Barry and Dayton, unpubl.) and benthic communities must rely upon the horizontal advection of organic materials produced further north in ice-free areas,

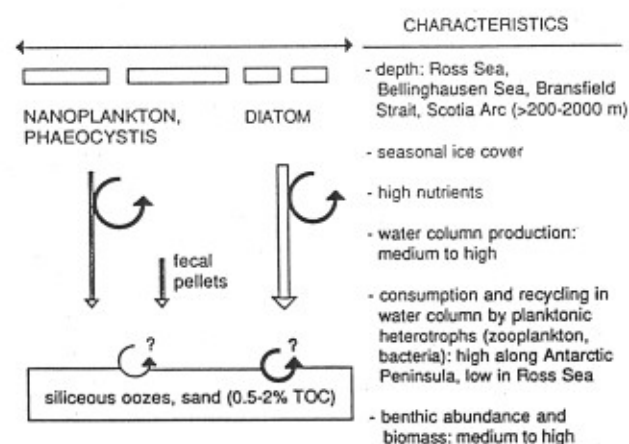


Fig. 10. Conceptual ecological model for continental shelves off Antarctica with seasonally variable ice cover. Vertical arrows indicate transport direction of organic carbon and circular symbol indicates recycling in the water column or at the sediment–water interface by heterotrophic organisms. Width of symbol indicates relative amount of organic carbon (e.g. thin arrow: low value, thick arrow: high value). TOC indicates total organic carbon in sediments.

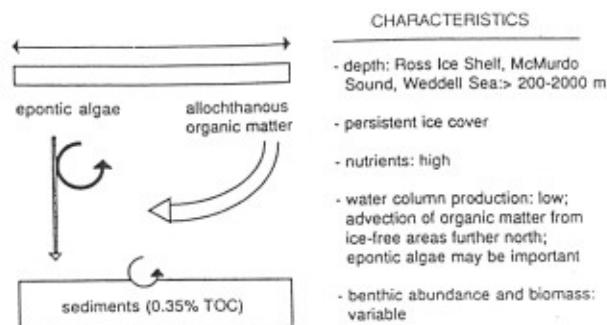


Fig. 11. Conceptual ecological model for continental shelves off Antarctica with persistent ice cover. Vertical arrows indicate transport direction of organic carbon and circular symbol indicates recycling in the water column or at the sediment-water interface by heterotrophic organisms. Width of symbol indicates relative amount of organic carbon (e.g. thin arrow: low value, thick arrow: high value). TOC indicates total organic carbon in sediments.

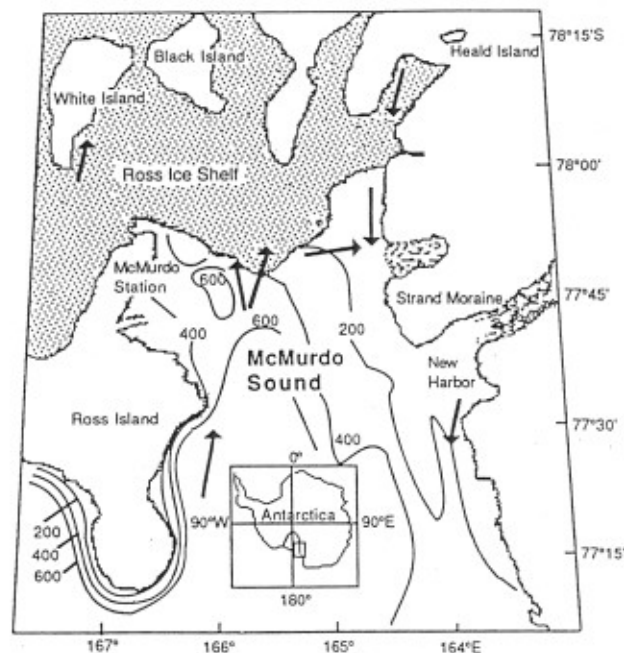


Fig. 12. McMurdo Sound, Antarctica. Arrows indicate general circulation flow and depth contours are in meters (modified from Barry and Dayton, 1988).

rather than on the sinking of phytoplankton from above. Even where sea ice melts seasonally for short periods, in situ primary production is limited. In these regions the relative contribution of epontic algae is increased (Palmisano and Sullivan, 1985). Although photosynthetic production under ice shelves clearly must be negligible, Horrigan (1981) speculates, based on her measurements of production for ¹⁴C incubations under the Ross Ice Shelf, that chemosynthesis may provide a small amount (1.5 gC m⁻² y⁻¹) of energy for benthic populations. In McMurdo Sound, the importance of advective transport of carbon from source areas is shown by the close correspondence of benthic community patterns and current patterns within the Sound. Sites in the eastern Sound are bathed by plankton-rich waters flowing southward from the Ross Sea and have correspondingly higher benthic biomass and turnover rates than do sites in the western Sound where the source waters are relatively plankton-poor (Fig. 12, Table 4; Dayton and Oliver, 1977; Barry, 1988; Barry and Dayton, 1988). Sedimentation rates in the eastern and western Sound corroborate the importance of horizontal advection to patterns of benthic production in McMurdo Sound with 10 times the rates of sedimentation in the western Sound (Dunbar et al., 1989; Barry and Dayton, unpubl.). The standing stock of benthic microalgae reflects these sedimentation rates with an average of 300–900 and 18–60 mg m⁻² chl *a* for eastern and

western Sound sediments, respectively (Table 4; Dayton et al., 1986).

Benthic habitats under permanent ice shelves are entirely dependent upon the horizontal advection of organic material for food sources. The

TABLE 4

Summary of standing stock and productivity from sea ice, water column and benthic communities in McMurdo Sound, Antarctica (modified from Barry and Dayton, 1988).

Parameter	East Sound	West Sound
Sea ice		
chl <i>a</i> (mg m ⁻²)	93.1	188.0
Water column		
chl <i>a</i> (mg m ⁻³)	0.69	0.13
diatom flux (no. m ⁻² d ⁻¹)	390	90.0
microalgal production		
---mgC m ⁻² d ⁻¹	1.1	0.0
---gC m ⁻² d ⁻¹	2.0	0.4–1.0
bacterial abundance		
(no. L ⁻¹ × 10 ³)	6.5	0.65
microbial ATP assimilation	85.0	4.5
Benthos		
chl <i>a</i> (mg m ⁻²)	300–900	18–60
Macrofauna		
Arthropoda (no. m ⁻²)	102,273	216
Polychaetes (no. m ⁻²)	3893	10,882
Total	140,021	15,855

ventilation of the sub-ice shelf cavity of the Ross Ice Shelf appears to provide adequate food to support limited benthic communities (Bruchhausen et al., 1979; Lipps et al., 1979; Azam et al., 1981). The organic carbon content of benthic sediments at a station several hundred kilometers from the shelf edge under the ice was 0.35%, similar to the Drake Passage. Currently, little information concerning the standing stocks of the benthos under permanent ice shelves is available, though several taxa are known to occur.

Ecological model of Arctic and Antarctic ice-edge systems and polynyas (Fig. 13)

Polynyas are open water areas within ice covered seas, which form due to physical and meteorological processes. These persistent features are thought to be important in sustaining primary and secondary productivity in polar regions (Massom, 1988; Smith et al. 1990). Studies at marginal ice zones indicate that the water-ice boundary is the site of the earliest spring water column phytoplankton blooms in polar regions (Alexander and Niebauer, 1981; Johannessen et al., 1982; Niebauer and Alexander, 1985; Fig. 13). Wind-driven upwelling along the ice edge, along with density stratification from ice melt, result in high chlorophyll concentrations and nutrient depletion (Alexander and Niebauer, 1981; Johannessen et al., 1982; Niebauer and Alexander, 1985). Although some data are available that describe

physical dynamics of these systems, little is known about biological interactions within polynyas, especially at the lower trophic levels. The regular occurrence of polynyas in polar systems and the association of large populations of marine seabirds and mammals within these open-water areas, indicate that polynyas are important biological habitats (Stirling, 1980; Dunbar, 1981; Massom 1988). The presence of large benthic-feeding marine mammals in the Arctic that are associated with Arctic leads and polynyas suggest an additional association with rich benthic communities.

Three polynyas in the Arctic are currently the focus of interest to the scientific community: the St. Lawrence Island polynya in the northern Bering Sea, the North Water polynya in Baffin Bay, Canadian Archipelago and the Northeast Water polynya off the northeastern Greenland coast (Arctic Ocean Sciences Board, 1989; Smith et al., 1990). These polynyas result from a variety of physical oceanographic interactions, yet all are hypothesized to influence increased water column production due to ice-edge dynamics at the marginal ice zone. Although few studies have investigated pelagic-benthic coupling processes in polynyas, Piepenburg (1988) found that the benthos in the area of the Northeast Water polynya had enhanced benthic epifaunal abundance compared to the benthos underlying the pack ice.

Polynyas and receding ice edges are also likely to be very important for benthic communities in Antarctica, such as the Terra Nova polynya in the Antarctic Ross Sea. Little work has been completed at this time on the role of these features and the characteristics of associated benthic communities. Nevertheless, there is evidence that polynyas are important to Antarctic benthos. The high production and standing stock of eastern McMurdo Sound is due to the southward advection of phytoplankton from northeast of Ross Island, an area with frequent winter polynya formation (Fig. 12; Zwally et al., 1985). Polynyas can be formed by high winds that break up thin ice layers and transport ice away from shorelines or ice shelf edges. Relaxation of the wind, even for short periods can result in renewed ice cover. Variation in the wind field can result in repeated ice formation and removal events. The process reduces ice

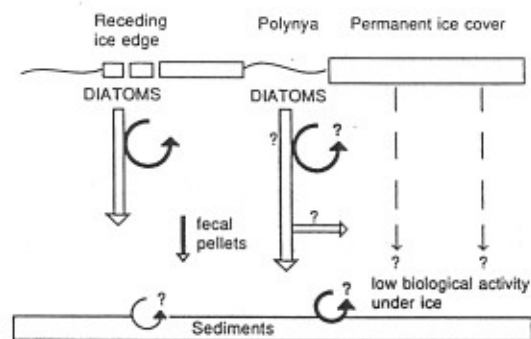


Fig. 13. Conceptual ecological model for Arctic and Antarctic ice-edge systems and polynyas. Vertical arrows indicate transport direction of organic carbon and circular symbol indicates recycling in the water column or at the sediment-water interface by heterotrophic organisms. Width of symbol indicates relative amount of organic carbon (e.g. thin arrow: low value, thick arrow: high value).

cover, but also increases the mean rate of ice formation in the area. Because thin ice grows much faster than thick ice, the rates of ice formation can be very high in polynya areas (Zwally et al., 1985). This results in an increase in the salinity of the surface waters and an unstable water column, thus increasing vertical mixing and presumably inhibiting primary production, even though light levels, while low during winter, still are higher than ice-covered areas. Nevertheless, any negative effects of the salinization process on primary production may be offset during spring and summer by elevated light levels and water column stability, thus enhancing secondary production in benthic communities located downcurrent.

Discussion and direction for future research

A major objective of this review paper has been to demonstrate the influence of oceanographic processes on pelagic-benthic coupling in polar regions from a "bottom-up" perspective, using benthic studies from various regions in both the Arctic and Antarctic. An important question for our studies is whether benthic communities are food-limited in polar regions. Various studies from the Arctic and Antarctic indicate that a large percentage of organic carbon produced in surface water is either consumed by zooplankton or recycled in the water column by microorganisms, reducing the amount of organic material settling out to feed benthic fauna. Exceptions in the Arctic occur in the shallow shelf regions (< 200 m), such as the Bering/Chukchi shelf system and certain regions of the Barents Sea, where a tight coupling between pelagic and benthic productivity occurs with higher food supply to the benthos influencing high benthic standing stock. A major difference between the Antarctic and Arctic is that the nearshore deep Antarctic has high abundance and biomass within the macrobenthos despite low water column production, suggesting that the cold bottom temperatures, stability and low disturbance levels of these deep water regions enable species to grow larger and live longer than in Arctic systems. As the ice retreats shoreward during summer in the Antarctic, ice edge and water column production provides a limited food supply;

in some regions, intense phytoplankton blooms can contribute large quantities of food to the benthos.

Anderson and Dyrssen (1989) suggest that reduced pelagic bacterial activity in low temperature waters on the shallow shelf of the Arctic Ocean increases the probability that a large proportion of biogenic organic matter ends up in shelf sediments. These authors conclude that the sediment-seawater interface plays an important role in cycling chemical constituents in the Arctic Ocean. Jones and Anderson (1986) proposed that recycling at the sediment-water interface on the shallow shelves in the Arctic directly influences the nutrient maximum of the Arctic halocline. In addition, wind mixing on the shallow shelves could resupply the overlying water column with nutrients and enhance water column production. In contrast, the extreme depth of the nearshore Antarctic benthos and the high stability and deep pycnocline of the overlying water likely inhibit any feedback to the euphotic zone of organic carbon recycled at the sediment-water interface.

The magnitude of benthic biomass can vary both as a result of the amount of organic carbon available for consumption as well as in response to disturbance levels. Disturbance levels on sediments are high in the marginal seas of the Arctic, both physically (ice gouging, freshwater and sediment input, variable ice cover) and biologically (marine mammal feeding effects and macrobenthic predation). These factors can limit benthic productivity. Permanent ice in the high Arctic limits primary productivity except in open leads, polynyas and in thinning ice regions where ice algae production can occur. Freshwater input, low nutrient resupply after algal utilization, ice cover and suspended sediment act to limit primary production in many Arctic marginal seas, as well as the high Arctic, resulting in food limitation for the benthos. Only on the relatively shallow shelves of the Bering, Chukchi and Barents Sea under highly productive waters do benthic communities reach abundance and biomass levels comparable to many Antarctic systems, in spite of high disturbance levels. By comparison, on the deep Antarctic shelf, low water column primary production and high water column consumption and recycling of this

organic carbon work in concert to limit benthic productivity. Apparently the low disturbance levels in the Antarctic enable benthic populations to grow to high levels of biomass in spite of low water column production. In addition, some Antarctic systems are like the shallow Arctic shelves and are not seasonally food-limited, thus maintaining rich benthic populations (e.g. portions of the Antarctic Peninsula).

Further studies are required to fully understand the paradox of low water column production and high benthic populations in many areas of the Antarctic and the role of disturbance in the Arctic. In a general sense, we need to quantify the relative importance of ice algal, water column and benthic algal production and their contribution to benthic communities. What is the fate of nano-, micro- and total plankton on both shallow and deep shelves and deep ocean floors? Do all groups of plankton sink, or do some groups get recycled in the water column preferentially, thus limiting the underlying benthos for food supply? What is the importance of bacteria and meiofauna in benthic communities?

Specific questions for future benthic work include:

- (1) What is the relative role of the different benthic fauna size classes (macro- and meiofauna) and microorganisms, along with their standing stocks, in polar ecosystems?
- (2) What are the overwintering strategies of benthic fauna in polar regions?
- (3) What are the rates of secondary production in Arctic and Antarctic benthic communities? (Standing stock alone is inadequate for comparisons between polar systems, particularly where rates of physical and biological disturbance vary).
- (4) What is the potential influence of global climate change on factors having a direct impact on benthic populations; e.g. will reduced ice cover open up more marginal polar seas to light in spring/summer, thus increasing overlying primary productivity and deposition of organic matter to the benthos? Will increased freshwater input and suspended load from continental rivers to the Arctic Ocean and its marginal seas change food web population structure?

- (5) What is the comparative importance of the flux of organic carbon to the benthos relative to internal adaptations of benthic fauna (e.g. lower metabolism, longer life span) on overall benthic productivity?

The increasing awareness that polar systems are a vital component of regional and global biogeochemical cycles and are important in global climatic changes emphasizes the need for a comprehensive and coordinated study of polar regions. In addition, these global changes may act as a major disturbing force, particularly in the shallow Arctic. Investigations into processes influencing pelagic-benthic coupling and recycling between the water column and sediments in a variety of polar environments will provide insight into ecological processes directly influencing the global carbon cycle.

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