

Distribution patterns of Canadian Beaufort Shelf macrobenthos

Kathleen Conlan^{a,*}, Alec Aitken^b, Ed Hendrycks^a,
Christine McClelland^a, Humfrey Melling^c

^a Canadian Museum of Nature, P.O. Box 3443, Station D, Ottawa, Ontario, Canada K1P 6P4

^b Department of Geography, University of Saskatchewan, 9 Campus Drive, Saskatoon, Saskatchewan, Canada S7N 5A5

^c Institute of Ocean Sciences, Department of Fisheries and Oceans, P.O. Box 6000, Sidney, British Columbia, Canada V8L 4B2

Received 1 March 2007; received in revised form 27 September 2007; accepted 12 October 2007

Available online 24 October 2007

Abstract

Variation in macrofaunal composition in relation to sediment and water variables was analysed in nine regions of the western Canadian Arctic on the Beaufort Shelf and in Amundsen Gulf. We hypothesized that benthic community composition was distinctive (1) in a recurrent polynya in Amundsen Gulf and (2) in upwelling regions (Cape Bathurst and Mackenzie Canyon) and (3) changed in a linear gradient across the Beaufort Shelf. Analysis was based on 497 taxa >0.4 mm from 134 samples at 52 stations sampled over 2002–4 in 11–1000 m water depth. Abundance ranged from 490.7 m⁻² in eastern Amundsen Gulf to 17,950 m⁻² off Cape Bathurst. (1) Community composition in Amundsen Gulf was not significantly different from the Beaufort Shelf at similar depth, indicating a lack of benthic effect of the polynya in Amundsen Gulf. (2) The Mackenzie Canyon macrofauna, although abundant and diverse, were similarly indistinct from the shelf community at similar depth. However, there was a 10-fold increase in inshore abundance in the upwelling region of Cape Bathurst due to large numbers of the amphipod *Ampelisca macrocephala* and the polychaete *Barantolla americana*, species that were not abundant elsewhere. (3) In the inshore fast ice and flaw lead regions of the Beaufort Shelf, under the influence of ice scour, storm effects, coastal erosion and the Mackenzie River, the macrofauna were dominated by the bivalve *Portlandia arctica* and the polychaete *Micronephthys minuta*. Offshore, where these influences were less and upwelling of deep Atlantic water occurred, the polychaete *Maldane sarsi* dominated. Faunal distribution across the Beaufort Shelf correlated with depth, water and sediment changes but was not significantly linear.

Crown Copyright © 2007 Published by Elsevier B.V. All rights reserved.

Keywords: Benthos; Community structure; Polynya; Upwelling; Fast ice; Flaw lead; Canadian Arctic; Beaufort Shelf; Amundsen Gulf; Cape Bathurst

1. Introduction

Arctic benthic communities can be highly productive when closely coupled to the pelagic system (Highsmith and Coyle, 1990) and respond rapidly to external forces (Renaud et al., 2007a). They can be essential food resources for diving sea birds (Dickson and Gilchrist, 2002) and large mammals such as gray whales, walrus and bearded seals (Frost and Lowry, 1984). Soft

* Corresponding author. Tel.: +1 613 364 4063; fax: +1 613 364 4027.

E-mail addresses: kconlan@mus-nature.ca (K. Conlan),
aaitken@arts.usask.ca (A. Aitken), ehendrycks@mus-nature.ca
(E. Hendrycks), cmcclelland@mus-nature.ca (C. McClelland),
melling@dfo-mpo.gc.ca (H. Melling).

sediment benthic communities have numerous impacts on their surroundings (Pearson, 2001). They affect sediment microbiology (e.g. Papaspyrou et al., 2006), meiofaunal (e.g. Peachey and Bell, 1997) and macrofaunal (e.g. Callaway, 2006) composition, modify sediment chemistry (e.g. Norling et al., 2007), alter sediment stability and near-bed hydrodynamics (e.g. Norkko et al., 2001), release and draw down oxygen, nutrients and particulates from the water column (e.g. Kamp and Witte, 2005), supply and consume pelagic organisms (e.g. Snelgrove et al., 2001) and break down and recycle detritus and primary production (e.g. Duchêne and Rosenberg, 2001). They can rework the sediment to >20 cm depth (Dauwe et al., 1998). Although Arctic benthic communities can be abundant and diverse, they can also be sensitive to disturbance, such as from ice scour and be slow to recover (Conlan and Kvittek, 2005).

In the Canadian Beaufort region, benthic studies were spurred by hydrocarbon exploration during the 1970's and 1980's (Wacasey et al., 1977; Atkinson and Wacasey, 1989) but syntheses in the primary literature have been sparse until the recent review by Cusson et al. (2007). With the collapse of the Mackenzie gas pipeline development following the Berger Enquiry (Berger, 1977), benthic studies lapsed until settlement of Inuvialuit land claims and resumption of hydrocarbon exploration in this decade.

With improved logistic capabilities for widespread study of the Beaufort coastal region, such as the Canadian Arctic Shelf Exchange Study (CASES), Joint Western Arctic Climate Studies (JWACS) and the CCGS *Nahidik* programs and the development of improved multivariate analytical methods for benthic study (Clarke and Warwick, 2001), it is now possible to statistically test hypotheses of local community pattern in relation to environmental variation. Our purpose is to examine links in benthic macrofaunal community composition on the Beaufort Shelf to regional differences in geography, oceanography and ice processes.

The Canadian Beaufort Shelf is a broad platform extending over 64,000 km² to the 200 m isobath (O'Brien et al., 2006). The shelf is bordered by the Mackenzie Canyon to the west, the Amundsen Gulf to the east, the Mackenzie River delta to the south and the Beaufort Sea to the north (Fig. 1). The immense quantities of fresh water delivered by the Mackenzie River (~333 km³ yr⁻¹) make it the most estuarine of all the shelves. The Mackenzie River's sediment load (~127 million Mt yr⁻¹) exceeds the combined annual sediment load of all other rivers entering the Arctic Ocean (O'Brien et al., 2006). Most of this load is

delivered between late May and the end of August. Riverine discharge contributes both particulate (POC) and dissolved (DOC) organic carbon (Dunton et al., 2006) but the fate of this terrigenous carbon in the shelf ecosystem remains poorly understood. Beaufort Shelf sediments consist essentially of silts and clays discharged by the Mackenzie River or released by coastal erosion (Forest et al., 2008). Sand and gravel are largely confined to <10 m depth; coarse-grained sediments at greater depths are derived from drowned beaches or by ice-rafting (Héquette et al., 1995; Carmack and Macdonald, 2002). The upper waters to 220 m depth are mainly supplied by the relatively nutrient-rich Pacific. The water below 220 m is Atlantic in origin (Carmack et al., 2004).

Ice cover is markedly variable inter-annually (Carmack and Macdonald, 2002). Generally freeze-up begins in mid-October, break-up begins in late May and the shelf can be clear of ice by mid-July depending on winds. Winter landfast ice extends to about the 20 m isobath, bordered by a stamukhi zone of grounded ice and pressure ridges. Offshore of the stamukhi zone are intermittent open flaw leads and over the outer shelf, pack ice that tends to drift westward with the Beaufort Gyre. The flaw lead to the east widens into the Cape Bathurst polynya system centered at the mouth of Amundsen Gulf (Fig. 1). The flaw lead and polynya system are vital to marine mammals and migratory birds (Harwood and Stirling, 1992; Dickson and Gilchrist, 2002). The polynya, however, is markedly variable in the timing, extent and persistence of open water (Arrigo and van Dijken, 2004). Over 1998–2000, sustained open water in the polynya occurred over June–Oct (maximally Apr–Nov) with sea ice cover varying ±40% over an area maximally of 25,000 km² (Arrigo and van Dijken, 2004). This variation results in variable intensities, timing and duration of phytoplankton blooms, resulting in variable carbon supplies to the benthos, provided that supply is not circumvented by the microbial loop or zooplankton grazing (see Tremblay et al., 2006). Another potential effect of the polynya on the benthos is increased vertical mixing due to wind effects and brine release by newly forming sea ice. This would be manifested by greater flux of carbon to the seafloor than in summer-stratified waters where carbon production would be intercepted by zooplankton (Arrigo and van Dijken, 2004). Grebmeier and Cooper (1995) documented the enhanced flux of organic carbon to the benthos associated with brine release and convective mixing within a polynya in the central Bering Sea. That the benthos is responsive to surface processes was demonstrated by Renaud et al.

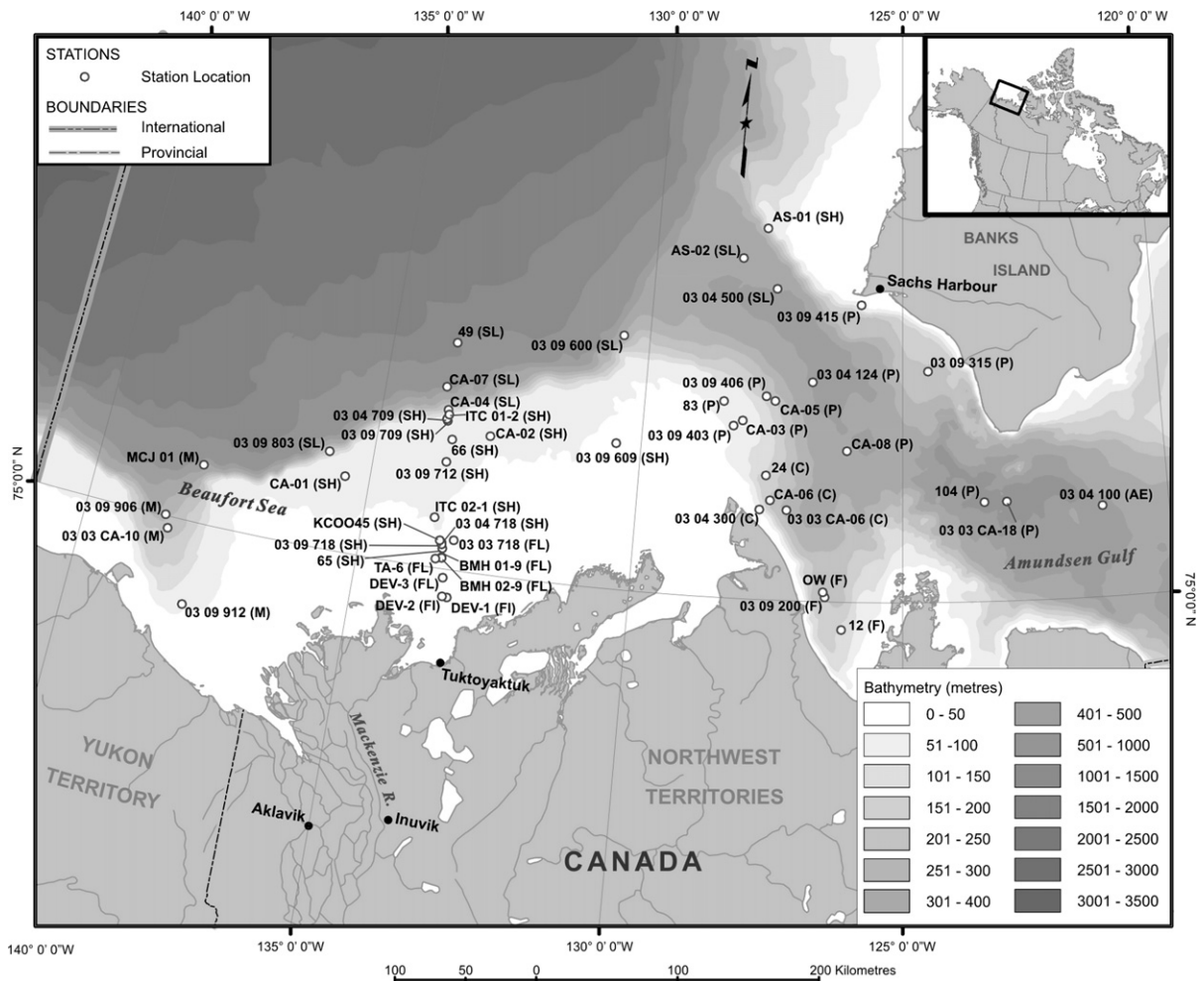


Fig. 1. Macrofaunal sample sites over the Beaufort study area with regions in brackets. M: Mackenzie Canyon; FI: fast ice; FL: flaw lead; SH: main shelf; SL: slope; C: Cape Bathurst; P: Cape Bathurst polynya; F: Franklin Bay; AE: Amundsen Gulf East. Base map produced by Elise Pietroniro (GIServices, University of Saskatchewan). Map data source: National Atlas of Canada 1:7.5 Million Scale, Natural Resources Canada, Government of Canada.

(2007), who measured a >10-fold increase in benthic sediment oxygen demand in the spring of 2004 at the time of the ice algal bloom. This study was adjacent to the polynya area, under the fast ice in the CASES overwintering site in Franklin Bay (Fig. 1). Beaufort Shelf benthos account for approximately 60% of annual new production (Renaud et al., 2007b), an amount indicative of their high importance to this area.

In polar regions, surface processes have been shown to influence the benthos directly below (Ambrose and Renaud, 1995; Grant et al., 2002; Schmid et al., 2006; Renaud et al., 2007) or through advection (Grebmeier and Cooper, 1995; Feder et al., 2007). Given the regional differences in ice cover, carbon supply, riverine influence, sedimentation and upwelling on the Beaufort

Shelf, we hypothesize that the benthos will reflect these processes in its species composition. Specifically, we hypothesize that:

1. Benthic community composition in the Cape Bathurst polynya (Amundsen Gulf) is distinctive from its immediate surroundings at similar depth.
2. Benthic community composition is distinctive also in upwelling regions (Cape Bathurst and Mackenzie Canyon).
3. The Beaufort Shelf shows an across-shelf gradient in benthic community composition relating to depth-related changes in ice cover, ice scour and water mass influences from the Mackenzie River and upwelling at the shelf edge.

Table 1

Mean (s.e.) sampling time, abundance, diversity, bottom water and sediment characteristics site⁻¹ in the 5 regions on the Canadian Beaufort Shelf (fast ice (<20 m depth), flaw lead (20–40 m), shelf (40–200 m), slope (>200 m) and Mackenzie Canyon) and the 4 regions in Amundsen Gulf (Cape Bathurst, Cape Bathurst polynya, Franklin Bay and Amundsen Gulf east (outside of the polynya))

	Beaufort shelf				
	Fast ice	Flaw lead	Shelf	Slope	Mackenzie Canyon
No. sites	2	5	15	7	4
No. biotic samples	6	15	37	18	11
Month	7.0 (1.7)	9.1 (0.1)	8.6 (0.4)	8.4 (0.5)	8.3 (0.8)
Year (2=2002 etc.)	3.3 (0.7)	2.2 (0.2)	2.7 (0.2)	2.7 (0.4)	3.3 (0.5)
Abundance m ⁻²	1726.2 (437.2)	3636.2 (1355.1)	2041.2 (228.1)	828.1 (212.1)	2658.2 (680.2)
Taxonomic diversity m ⁻²	65.8 (3.2)	47.2 (5.8)	71.0 (3.3)	78.3 (1.9)	74.1 (5.9)
Water depth, m	11.0 (0)	32.8 (2.14)	69.7 (7.92)	440.5 (102.1)	271.3 (94.5)
Bottom water fluorescence, mg l ⁻¹	0.50 (0.10)	0.49 (0.10)	0.37 (0.10)	0.06 (0.02)	0.08 (0.02)
Bottom water temp, °C	0.19 (0.01)	-0.80 (0.08)	-1.31 (0.05)	0.00 (0.20)	-0.29 (0.43)
Bottom water salinity, ‰	22.65 (0.15)	27.07 (2.77)	32.21 (0.12)	34.61 (0.15)	34.13 (0.52)
Bottom water oxygen, ml l ⁻¹	7.60 (0)	7.97 (0.07)	7.14 (0.20)	6.13 (0.18)	6.11 (0.21)
Sediment % nitrogen	0.06 (0.01)	0.13 (0.02)	0.15 (0.02)	0.15 (0.01)	0.24 (0.05)
Sediment % organic carbon	0.58 (0.04)	0.66 (0.04)	1.17 (0.20)	1.43 (0.44)	2.31 (0.84)
Sediment C/N	10.06 (2.34)	5.32 (0.71)	7.50 (1.27)	6.91 (1.68)	8.91 (1.93)
Sediment δ ¹³ C, ‰	-26.25 (0.05)	-26.18 (0.05)	-25.03 (0.35)	-24.40 (0.70)	-25.20
Sediment % clay	13.63 (2.46)	26.05 (5.27)	33.74 (4.36)	38.93 (2.82)	48.77 (4.68)
Sediment % silt	82.30 (2.57)	71.59 (4.72)	46.30 (4.17)	57.82 (2.92)	50.19 (4.14)
Sediment % vf sand	1.56 (0.58)	0.56 (0.20)	1.96 (0.57)	1.06 (0.38)	0.43 (0.43)
Sediment % f sand	0.48 (0.04)	0.29 (0.04)	8.43 (3.67)	0.57 (0.27)	0.14 (0.14)
Sediment % m sand	0.17 (0.01)	0.53 (0.14)	4.50 (2.57)	0.69 (0.23)	0.18 (0.18)
Sediment % c sand	1.02 (0.31)	0.58 (0.33)	1.31 (0.71)	0.39 (0.19)	0
Sediment % vc sand	0.84 (0.41)	0.40 (0.23)	0.91 (0.63)	0.18 (0.12)	0
Sediment F&W phi mean	7.06 (0.21)	8.20 (0.43)	6.91 (0.79)	8.33 (0.23)	8.34 (0.31)
Sediment F&W phi sorting	1.95 (0.06)	2.33 (0.14)	2.45 (0.15)	2.33 (0.20)	2.31 (0.26)
Sediment F&W phi skewness	0.25 (0.01)	0.36 (0.02)	0.24 (0.07)	0.15 (0.10)	0.21 (0.04)
Sediment F&W phi kurtosis	1.50 (0.07)	1.18 (0.18)	1.09 (0.16)	0.99 (0.13)	1.50 (0.41)
	Amundsen Gulf				
	Cape Bathurst	Cape Bathurst polynya	Franklin Bay	Amundsen Gulf East	
No. sites	4	11	3	1	
No. biotic samples	10	28	6	3	
Month	9.8 (0.5)	8.6 (0.4)	7.0 (1.7)	10	
Year (2=2002 etc.)	2.5 (0.3)	2.9 (0.3)	3.3 (0.7)	3	
Abundance m ⁻²	6884.7 (3459.4)	2577.9 (730.0)	5052.9 (278.5)	490.7	
Taxonomic diversity m ⁻²	73.4 (4.6)	74.5 (1.8)	79.0 (2.2)	77	
Water depth, m	162.7 (47.0)	259.1 (63.5)	204.5 (29.8)	484.0	
Bottom water fluorescence, mg l ⁻¹	0.09 (0.03)	1.05 (0.93)	0.05 (0.02)	0.02	
Bottom water temp, °C	-0.83 (0.38)	-0.52 (0.23)	-0.65 (0.44)	0.24	
Bottom water salinity, ‰	33.46 (0.61)	33.62 (0.37)	33.83 (0.56)	34.72	
Bottom water oxygen, ml l ⁻¹	6.10 (0.59)	6.34 (0.36)	6.07 (0.51)	5.18	
Sediment % nitrogen	0.13	0.17 (0.04)			
Sediment % organic carbon	0.70	1.74 (0.30)	2.13	2.77	
Sediment C/N	5.60	7.73 (1.12)			
Sediment δ ¹³ C, ‰	-25.70	-24.30 (0.29)			
Sediment % clay	24.49 (11.62)	31.79 (3.94)	32.19 (9.09)	37.63	
Sediment % silt	56.74 (8.46)	56.64 (3.97)	50.08 (8.45)	45.91	
Sediment % vf sand	7.10 (5.06)	1.33 (0.52)	0.45 (0.45)	1.79	
Sediment % f sand	8.24 (7.77)	5.16 (3.16)	0.08 (0.08)	1.48	
Sediment % m sand	2.30 (2.16)	4.48 (2.96)	0.35 (0.35)	0.90	
Sediment % c sand	0.49 (0.33)	0.47 (0.28)	6.40 (6.40)	4.66	
Sediment % vc sand	0.57 (0.31)	0.13 (0.08)	10.37 (10.37)	7.63	
Sediment F&W phi mean	6.61 (1.00)	7.30 (0.55)	6.66 (0.98)	8.80	
Sediment F&W phi sorting	2.21 (0.17)	2.20 (0.18)	1.71 (0.31)	2.68	
Sediment F&W phi skewness	0.22 (0.05)	0.24 (0.07)	0.12 (0.15)	0.41	
Sediment F&W phi kurtosis	1.25 (0.22)	0.85 (0.06)	0.88 (0.08)	0.71	

2. Materials and methods

2.1. Sample collection and identification

Nine regions within the Beaufort Shelf and Amundsen Gulf study area (Fig. 1 and Table 1) were identified based on geography and ice regime according to O'Brien et al. (2006) and Carmack and Macdonald (2002): Mackenzie Canyon offshore of the Mackenzie delta, the Beaufort Shelf encompassing the inshore fast ice area (<20 m), flaw lead (20–35 m), main part of the shelf (>35 m to 200 m) and the slope (>200 m) and four regions in Amundsen Gulf: Cape Bathurst, the Cape Bathurst polynya, Franklin Bay and the part of the gulf sampled east of the polynya. Sampling occurred over 6 ship cruises in 2002–2004. CCGS *Sir Wilfrid Laurier* samples were collected in Sept 2002, CCGS *Radisson* samples in Oct 2002 and CCGS *Amundsen* legs 1, 2, 6 and 8 samples in Sept–Oct 2003, Oct–Nov 2003, April 2004 and July 2004, respectively. A 0.25 m² box corer was used for sampling on the *Radisson* and *Amundsen* cruises and a 0.1 m² van Veen grab on the *Laurier* cruise. The constraints of shared ship use minimized replication to 3 reps. station⁻¹ with 1 rep. station⁻¹ on the *Radisson* cruise. Shared sediment requirements limited collection of biota to 0.063–0.13 m² of the box corer. Depth sampled was mostly 15 cm. Despite these constraints, a total of 134 samples at 52 stations were collected, which comprised 30,802 individuals >0.4 mm at an abundance of 230.1 ± 18.7 ind. sample⁻¹.

Macrofauna were elutriated from the sediment, fixed in buffered 5% formalin and seawater and preserved in 70% ethanol. Organisms traditionally considered meiofauna (nematodes and harpacticoid copepods) were excluded from the data. The smaller mesh size used in this study (0.4 mm) than the usual 0.5 mm did not capture any additional species but augmented the abundance of smaller bodied species, particularly tanaids (Table 2). Re-sieving of 27 randomly selected samples (comprising 52% of the stations) on 0.5 mm mesh yielded only a 2.8 ± 0.7% difference in abundance between the two mesh sizes. Every effort was made to find taxonomic experts to identify the macrofauna to species level. This resulted in the identification of 497 taxa (227 crustaceans (identified by E. Hendrycks and C. McClelland), 111 mollusks (A. Aitken), 122 polychaetes (P. Pocklington and K. Conlan), 26 echinoderms (P. Lambert, C. McClelland and K. McKendry) and 11 others (P. Lambert, K. Conlan and C. McClelland)). Of the 497 taxa, 3.8% were identified to phylum or order, 6.2% to family, 12.5% to genus and 77.5% to species. All samples are housed at the Canadian Museum of Nature, Ottawa.

Bottom water characteristics were measured at the time of faunal and sediment collection. Seasonal variations in current speed, temperature and salinity were recorded by instruments on oceanographic moorings. Moorings were established by the Institute of Ocean Sciences (DFO) in the vicinity of Kugmallit Valley (134° W) north of Tuktoyaktuk on the inner shelf (site 9, corresponding to BMH01-9 and BMH02-9 in Fig. 1), at mid-shelf (site 1, corresponding to ITC02-1) and at shelf edge (site ITC03-2 corresponding to 03 09 709; site 2, corresponding to ITC01-2). A comparative mooring operated on the outer shelf north-west of Sachs Harbour on Banks Island (site 8, corresponding to AS-01). All moorings were equipped with an acoustic Doppler current profiler (RD Instruments narrow-band ADCP) and most with a temperature-conductivity recorder (Sea Bird Instruments SBE37). The former instrument measured current speed at half-hourly intervals at discrete levels between the surface and about 6 m above the seabed. The latter delivered data on temperature and salinity at the same interval 2 m above the seabed. For the purposes of this discussion, the means and variances (s.d.) of data have been computed for three-month intervals of measurement. There are data from October through September for two years at site 9 (2001–03), at site 2 (2001–03) and site 8 (1999–2001). Only one year of data has been used from site 1 (2001–02) and site 2a (2003–04). Data from seabed temperature recorders adjacent to moorings have demonstrated the equivalence of temperature and salinity at the seabed and 2 m above it. The 6 m level for current recordings provides a good measure of relative magnitude of the flow which would transport

Table 2
Proportion of macrofauna >0.4 mm and <0.5 mm relative to >0.4 mm averaged over 27 samples

Major taxon	No. indiv. >0.4 mm		% indiv. >0.4 mm and <0.5 mm	
	Mean	s.e.	Mean	s.e.
Amphipods	26.89	21.41	0.00	0.00
Mollusks	26.41	5.54	0.00	0.00
Holothurians	0.07	0.07	0.00	0.00
Cumaceans	6.74	1.64	1.42	1.03
Isopods	1.37	0.49	1.76	1.76
Ophiuroids	4.19	1.34	0.00	0.00
Ostracods	46.15	15.75	1.52	0.70
Others	1.52	0.28	0.90	0.90
Polychaetes	99.00	13.61	2.23	0.62
Sipunculids+Priapulids	2.11	0.63	0.00	0.00
Tanaids	11.19	4.01	8.59	3.49
All taxa	233.59	44.26	2.78	0.66

detritus from one place to another and of the force of current at the seabed.

Sediment samples taken from a separate section of the macrofaunal sample were frozen and analyzed for grain size, % N, % organic C and $\delta^{13}\text{C}$ at the University of Calgary or the Geological Survey of Canada. Analytical procedures are as follows.

2.1.1. Particle size (sediment grain size) analysis

Sediment samples were air-dried for at least 24 h and ground by mortar and pestle until homogeneous. The coarser 2 mm fraction was removed by sieving. A 15 to 25 ml (<2 mm) portion was then separated through a riffler (Humboldt Manufacturing Company micro splitter with sixteen 1/8 in. chutes) to reduce sample size to the recommended weight of 0.15 to 0.20 g. Sandier samples were reduced to a recommended weight of 0.80 to 0.90 g. Samples were treated with a 30% solution of H_2O_2 to remove the organic matter and then analyzed by a Malvern Instruments Mastersizer 2000 with Hydro G sample dispersion unit.

2.1.2. Organic matter and carbonates

An estimate of total carbon was determined by the loss on ignition method given in McKeague (1976). A 10–20 g sample was dried overnight at 105 °C. The samples were brought to room temperature in a desiccator and weighed. The samples were then heated to 420 °C in a muffle furnace and allowed to soak at 420 °C for 1.5 h to burn off the organic matter. The samples were removed to a desiccator, brought to room temperature and weighed. Subsequently they were heated to 850 °C. Then the samples were allowed to soak for 0.5 h. The samples were removed to a desiccator, allowed to come to room temperature and weighed. Percent organic carbon and percent carbonates were calculated using the following equations:

$$\begin{aligned} \% \text{ OM (LOI\% at 420 }^\circ\text{C)} \\ = \frac{\text{wt after 105 }^\circ\text{C} - \text{wt after ignition 420 }^\circ\text{C}}{\text{wt after oven dry 105 }^\circ\text{C}} \times 100 \end{aligned}$$

$$\begin{aligned} \% \text{ total C (LOI 850 }^\circ\text{C)} \\ = \frac{\text{wt after 105 }^\circ\text{C} - \text{wt after ignition 850 }^\circ\text{C}}{\text{wt after oven dry 105 }^\circ\text{C}} \times 100 \end{aligned}$$

$$\% \text{ carbonate} = \% \text{ total C} - \% \text{ OM}$$

A conversion factor of 0.58 was used to convert the amount of organic matter into an estimate of the % organic carbon: % OC = % OM \times 0.58.

2.1.3. Nitrogen (nitrogen digest)

Analysis for total nitrogen was done using a Kjeldahl digestion procedure given in Schuman et al. (1973). A 15 ml sample was air dried at 105 °C for 8 h and removed to a desiccator. A 0.5 g sample was placed into digestion tubes along with one piece of pumice, about 3.4 g of a prepared catalyst (96% K_2SO_4 and 3% CuSO_4) and 10 ml of concentrated H_2SO_4 . The samples were placed in a Technicon block digester, model BD-40, heated to 375 °C and heated for 2.5 h. The samples were cooled and distilled water was added to bring the volume to 75 ml. Samples were filtered under vacuum and analysed using a Technicon autoanalyzer with an ammonia module and the Technicon Industrial Method 98-70W/A. Determination of % N is considered accurate to ± 0.014 (Schuman et al., 1973).

2.1.4. Carbon isotopes

Analysis of $\delta^{13}\text{C}$ was performed using Continuous Flow-Elemental Analysis-Isotope Ratio Mass Spectrometry technology. Samples were air dried, mixed with 60 ml of 1 M HCl and left overnight. The solution was then filtered under vacuum, washed and re-dried at 60–80 °C. Samples were then analysed with a Finnigan Mat Delta+XL mass spectrometer interfaced with a Carlo Erba NA 1500 elemental analyzer at the Isotope Science Laboratory, University of Calgary. Isotopic abundances are reported in parts per thousand (per mil, ‰), with a precision typically of $\pm 0.2\text{‰}$.

2.2. Multivariate analyses

The common practice of conversion of smaller samples to 1 m² can over-estimate abundance if the sample area is small (De Grave et al., 2001). However, sample area always exceeded the recommended 0.0137 m² area recommended as necessary for accurate estimation for muddy habitats. Therefore, only for the purpose of illustrating the distribution of abundance were values converted to no. m⁻². Otherwise, abundance was standardized by totals to adjust for variable sample size and square root transformed to prevent over-domination of abundant species. Abundances varied from 0 to 508 ind. sample⁻² and so required only a light transformation.

Because of the variable sample sizes, only the taxonomic diversity index of Warwick and Clarke (1995) was used for comparisons of diversity because this is not influenced by sample size while commonly reported indices such as the Shannon–Wiener index and species richness are (Clarke and Warwick, 1998). Taxonomic diversity is also a more sensitive univariate

measure of community structure because it considers taxonomic relationships. Taxonomic diversity is a measure of the average path length between all pairs of species in a sample. It includes an evenness component (a form of Simpson's index) (Clarke and Warwick, 1998).

Resemblances were calculated by the Bray–Curtis measure of similarity based on species and abundances in common among the sites. Resemblances were mapped by multidimensional scaling and differences among regions (replicates averaged) were tested for significance using the one-way ANOSIM procedure in Primer 6.1.5 (Clarke and Green, 1988; Clarke, 1993; Clarke and Gorley, 2006). The ANOSIM procedure compares the difference in rank similarities between regions with rank similarities within the regions (R statistic) in relation to the number of samples, then rearranges the sample labels in the two regions and recalculates R . If the resemblance remains high under repeated rearrangements, it can be concluded there is no significant difference between the two regions. However, if resemblance declines considerably upon label rearrangement, resulting in few iterations where resemblance is high, then it can be concluded that differences between the groups are significant. The significance level is calculated by dividing the number of times the rearranged R is \geq the non-rearranged R . The maximum number of iterations per comparison is constrained to 999. Two regions had too few samples to allow many label rearrangements (Amundsen Gulf east with 1 sample and the fast ice region with 2), resulting in conservative comparisons.

Taxa typifying or distinguishing the regions were identified by the SIMPER procedure in Primer. This routine determines species contributions to within-group similarity, comparing these to their contributions to distinguishing groups. Small scale variation in species composition was examined by analysis of multivariate dispersion of the station replicates (MVDSP procedure) based on within-group Bray–Curtis dissimilarity.

The samples differed in sampling method, date, location, bottom water and sediment characteristics. The BEST procedure was applied to examine which single or multiple variables most highly correlated with biotic abundance patterns. Percent sand fractions were summed. The abiotic data were individually transformed ($\log_{10}x+1$) or square root transformed (for percentage data) if skewed, then all variables were normalized ($(x - \text{mean}) / \text{sd}$) and then site similarities were calculated by Euclidean distance. The biotic data were standardized by total and square root transformed. The Spearman rank

correlation was calculated between the species resemblance matrix and the normalized abiotic resemblance matrix using different combinations of up to five environmental variables.

3. Results

3.1. Regional variation

Table 1 summarizes the collection, environmental and biological characteristics of the nine sampling regions. Spearman rank correlation of the site similarities based on macrofaunal abundance vs. the abiotic factors (BEST procedure) found that water depth gave the highest correlation (0.631). Spearman rank correlation with the four water parameters alone was highest for fluorescence, temperature and oxygen combined (0.463). Species distributions correlated very low with sediment measures. The highest Spearman rank correlation was 0.047 for measures of grain size distribution (sorting, skewness and kurtosis) and correlations were lower for proportions of clay, silt and sand. Further analysis of a subset of the deeper samples (>100 m), which would be less prone to the seasonally variable influence of the Mackenzie River and other surface and coastal influences indicated that for these samples, water depth was still the single most important variable, but with a lower correlation (0.445). Of significance is that in both analyses, variability in time of sampling and type of gear did not correlate highly with faunal distribution patterns.

Regional macrofaunal abundance varied from 490.7 m^{-2} in Amundsen Gulf East to $6884.7 \pm 3459.4 \text{ m}^{-2}$ off Cape Bathurst (Table 1). Highest abundance of $17,950 \text{ m}^{-2}$ was recorded at station 03 04 300–3 (Fig. 1), the station closest inshore at Cape Bathurst. Taxonomic diversity (which incorporates an evenness component) ranged from $47.2 \pm 5.8 \text{ m}^{-2}$ in the flaw lead region of the Beaufort Shelf to $78.3 \pm 1.9 \text{ m}^{-2}$ on the slope. Bottom water (mostly summer and fall (Table 1)) showed highest fluorescence in the Cape Bathurst polynya region ($1.05 \pm 0.93 \mu\text{g l}^{-1}$). Bottom water temperature was lowest on the Beaufort Shelf (-1.31 ± 0.05 °C averaged over 15 stations) and salinity was lowest close to the Mackenzie River delta (22.65 ± 0.15 ‰ averaged over 2 stations in the fast ice region). Bottom water oxygen levels were high throughout the area ($5.18\text{--}7.97 \pm 0.07 \text{ ml l}^{-1}$).

Sediment C/N ranged from 5.32 ± 0.71 (flaw lead) to 10.06 ± 2.34 (fast ice). Sediment $\delta^{13}\text{C}$ was more negative inshore on the Beaufort Shelf (-26.25 ± 0.05 ‰ in the fast ice zone and less negative offshore (-24.40 ± 0.70 ‰ on

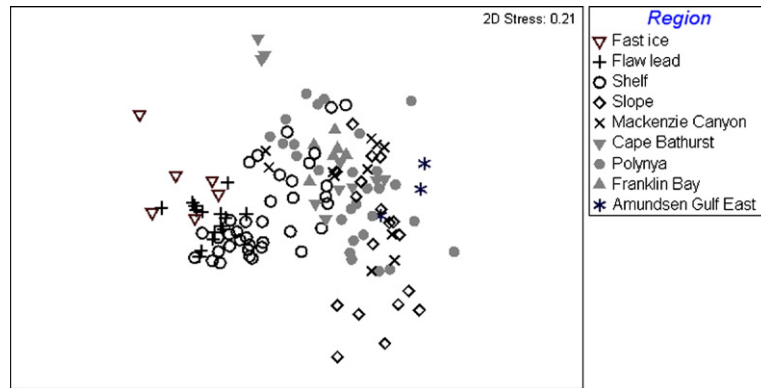


Fig. 2. Non-metric multidimensional scaling plot of sample similarities in each region of the Beaufort study area.

the slope). The sediments in all regions were well sorted silt-clays (Folk and Ward phi mean 6.61 ± 1.00 to 8.34 ± 0.31) but higher sand fractions were found at some stations on the shelf (stn. AS01 (up to 41.9%) and stn. 03 09 709 (up to 78.9%)), off Cape Bathurst (stn. 83 (up to 83.1%) and stn. 03 04 300 (up to 62.8%)) and Franklin Bay (stn. 03 09 200 (up to 100%)).

Fig. 2 shows a Multidimensional Scaling (MDS) plot of all of the biotic samples based on the Bray–Curtis index of similarity. The flaw lead and Franklin Bay samples show high intra-regional similarity while the others are more variable. The three replicates taken at the shallowest station at Cape Bathurst (stn. 03 04 300) cluster tightly and are dissimilar to other samples taken in this region. Other regional samples are broadly cohesive, however and grade across the MDS plot from the fast ice samples on the left to the Beaufort slope samples on the right. Mackenzie Canyon samples mix with all but the fast ice and flaw lead samples. In Amundsen Gulf, the polynya samples intermingle with samples from neighbouring Cape Bathurst, Franklin Bay and Amundsen Gulf east.

Appendix A lists the macrofauna that typify (account for cumulatively 75% of the within-group similarity in) each region. Polychaetes dominate the communities, with *Maldane sarsi*, *Tharyx kirkegaard/marioni* (comprising mostly *T. kirkegaard*), *Lumbrineris impatiens* and *Prionospio cirrifera/steenstrupi* (comprising mostly *P. cirrifera*) being common to most regions. The deep-burrowing bamboo worm *M. sarsi* is one of the most abundant dominants at depth. The small, shallow-burrowing polychaete *Micronephthys minuta* occurs there as well but is much more abundant in the inshore fast ice and flaw lead regions. The tanaid *Paraleptognathia gracilis*, the cumacean *Etkonodiatylis nimia* and the ostracod *Philomedes brenda* are the most

widespread crustacean dominants. The isopod *Saduria sabini* is common in the flaw lead and on the shelf but with its large size it is more often captured as wandering megafauna than macrofauna. The deposit feeders *Thyasira flexuosa* and various *Portlandia* spp. are the dominant bivalves in the regions. *Portlandia arctica* is especially abundant in the fast ice zone.

3.2. Small scale variation

Multivariate dispersion of the replicates at each station was computed (MVDS) based on within-group Bray–Curtis dissimilarity. Multivariate dispersion was positively correlated with water depth (Spearman rank correlation, $R=0.404$, $p=0.006$, $n=45$) and also with taxonomic diversity m^{-2} ($R=0.345$, $p=0.020$, $n=45$). Multivariate dispersion was not correlated with region ($R=0.173$, $p=0.257$, $n=45$).

3.3. H1. Benthic community structure in the Cape Bathurst polynya is distinctive from its immediate surroundings at similar depth

Table 3 shows pairwise ANOSIM comparisons of the nine regions, with replicates averaged. The polynya community does not significantly differ from communities in nearby Amundsen Gulf East, Franklin Bay and Cape Bathurst. It is significantly different from the geographically more distant Beaufort shelf and inshore regions, but it does not significantly differ from communities on the Beaufort slope and in the Mackenzie Canyon. A re-analysis, comparing only sites central to the polynya (stations 124, 500, 406, CA-05 and CA-08) with sites at similar depths elsewhere confirmed a lack of significant distinctness of the polynya community.

Table 3
Pairwise ANOSIM comparisons of the 9 regions based on macrofaunal abundance (replicates averaged)

Groups	R Statistic	Significance Level	Possible Permutations	Actual Permutations	No. \geq Observed
Franklin Bay, Cape Bathurst	0.185	0.257	35	35	9
Franklin Bay, Slope	0.302	0.067	120	120	8
Franklin Bay, Shelf	0.447	0.003 **	680	680	2
Franklin Bay, Polynya	-0.073	0.621	364	364	226
Franklin Bay, Flaw lead	1	0.018 *	56	56	1
Franklin Bay, Mackenzie Canyon	-0.019	0.543	35	35	19
Franklin Bay, Amundsen Gulf East	1	0.025 *	4	4	1
Franklin Bay, Fast ice	1	0.010 **	10	10	1
Cape Bathurst, Slope	0.225	0.094	330	330	31
Cape Bathurst, Shelf	0.487	0.002 **	3060	999	1
Cape Bathurst, Polynya	-0.003	0.431	1365	999	430
Cape Bathurst, Flaw lead	0.725	0.008 **	126	126	1
Cape Bathurst, Mackenzie Canyon	-0.104	0.914	35	35	32
Cape Bathurst, Amundsen Gulf East	0.25	0.40	5	5	2
Cape Bathurst, Fast ice	0.321	0.333	15	15	5
Slope, Shelf	0.667	0.001 **	116280	999	0
Slope, Polynya	0.125	0.106	31824	999	105
Slope, Flaw lead	0.947	0.001 **	792	792	1
Slope, Mackenzie Canyon	0.093	0.245	330	330	81
Slope, Amundsen Gulf East	-0.02	0.625	8	8	5
Slope, Fast ice	0.948	0.028 *	36	36	1
Shelf, Polynya	0.52	0.001 **	4457400	999	0
Shelf, Flaw lead	0.01	0.367	11628	999	366
Shelf, Mackenzie Canyon	0.509	0.004 **	3060	999	3
Shelf, Amundsen Gulf East	0.622	0.067	15	15	1
Shelf, Fast ice	0.363	0.067	120	120	8
Polynya, Flaw lead	0.751	0.001 **	4368	999	0
Polynya, Mackenzie Canyon	-0.024	0.518	1365	999	517
Polynya, Amundsen Gulf East	-0.24	0.833	12	12	10
Polynya, Fast ice	0.836	0.013 *	78	78	1
Flaw lead, Mackenzie Canyon	0.856	0.008 **	126	126	1
Flaw lead, Amundsen Gulf East	1	0.167	6	6	1
Flaw lead, Fast ice	0.491	0.048 **	21	21	1
Mackenzie Canyon, Amundsen Gulf East	-0.417	0.80	5	5	4
Mackenzie Canyon, Fast ice	0.643	0.067	15	15	1
Amundsen Gulf East, Fast ice	1	0.333	3	3	1

* Significant at $p < 0.05$.

** Significant at $p < 0.01$.

SIMPER analysis (Table 4) demonstrated that the significant difference of the polynya community from the Beaufort shelf and inshore is due to relative differences in the abundance of a large number of fauna. The polychaetes *M. sarsi*, *Pholoe minuta*, *Barantolla americana*, *Ophelina cylindricaudata* and *Terbellides stroemi*, the bivalves *T. flexuosa* and *Portlandia sp.*, the ostracods *Cypridina megalops* and *P. brenda* and the cumacean *E. nimia* and the isopod *Gnathia sp.* are more abundant in the polynya than on the Beaufort shelf. The contrast between the two areas is even greater inshore, where the polynya species are rare or absent. The polychaetes *Levinsinea gracilis*, *Micro-nephtys minuta*, *Heteromastus sp.*/*Mediomastus sp.*,

Aricidea spp. and *Pectinaria hyperborea*, the bivalve *P. arctica*, the cumacean *Leucon nasicus*, the tanaid *P. gracilis*, the amphipod *Ponotoporeia femorata* and the brittle star *Ophiocten sericeum* are more abundant on the shelf than in the polynya. The contrast between the two areas is even greater inshore, where many of the polynya species are rare or absent.

3.4. H2. Benthic community composition is distinctive also in upwelling regions (Cape Bathurst and Mackenzie Canyon)

Cape Bathurst is steeply contoured (Fig. 1) and inshore it is marked by extremely high faunal abundance (Table 1),

Table 4

Mean abundances (s.e.) m^{-2} of the dominant macrofauna in the Cape Bathurst polynya compared with the Beaufort shelf, flaw lead and fast ice regions

	Polynya	Shelf	Flaw lead	Fast ice
<i>Philomedes brenda</i>	520.9 (329.4)	14.3 (10.6)	153.3 (153.3)	1.9 (1.9)
<i>Maldane sarsi</i>	212.4 (55.0)	128.3 (48.3)	1.5 (0.9)	0
<i>Tharyx kirkegaarde</i> + <i>T. marioni</i>	133.7 (41.3)	160.1 (23.2)	264.9 (108.8)	38.9 (38.9)
<i>Cypridina megalops</i>	112.9 (69.7)	14.8 (10.1)	0	0
<i>Pholoe minuta</i>	93.0 (61.2)	11.8 (7.8)	0.7 (0.7)	0
<i>Thyasira flexuosa</i>	73.3 (22.9)	0.6 (0.4)	0	0
<i>Prionospio cirrifera</i> + <i>P. steenstrupi</i>	69.1 (18.8)	49.8 (27.5)	39.7 (16.8)	31.5 (27.8)
<i>Levinsinea gracilis</i>	49.0 (29.4)	83.5 (20.3)	104.1 (35.0)	5.6 (5.6)
<i>Micronephthys minuta</i>	43.7 (19.9)	536.5 (133.8)	2341.0 (1158.4)	735.2 (227.8)
<i>Barantolla americana</i>	31.4 (17.6)	16.8 (4.5)	7.3 (3.1)	7.4 (3.7)
<i>Lumbrineris impatiens</i>	30.0 (14.9)	46.5 (15.6)	12.5 (5.3)	1.9 (1.9)
<i>Normanicythere leioderma</i>	29.9 (26.3)	0.8 (0.5)	0	31.5 (5.6)
<i>Ektonodiatylis nimia</i>	29.1 (11.7)	9.0 (6.2)	0	0
<i>Paraleptognathia gracilis</i>	28.3 (10.5)	75.8 (29.2)	47.5 (42.2)	13.0 (1.9)
<i>Ophelina cylindricaudata</i>	27.0 (9.3)	10.2 (5.3)	0	0
<i>Portlandia</i> sp.	24.7 (15.6)	5.6 (3.8)	2.6 (1.4)	0
<i>Terebellides stroemi</i>	22.2 (5.4)	5.5 (3.3)	5.7 (3.9)	1.9 (1.9)
<i>Haploops</i> sp.	18.4 (14.5)	0.3 (0.3)	8.9 (8.9)	33.3 (33.3)
Sipuncula	17.8 (6.1)	16.0 (9.3)	0.7 (0.7)	0
<i>Xestoleberis depressa</i>	15.9 (12.9)	14.0 (7.5)	14.1 (10.1)	101.9 (61.1)
<i>Eudorella</i> sp.	11.1 (5.5)	1.2 (0.7)	3.0 (1.8)	0
<i>Cossura longocirrata</i>	10.6 (6.7)	13.0 (7.3)	18.5 (6.7)	18.5 (3.7)
<i>Ampharete balthica</i> + <i>A. vega</i>	9.9 (4.0)	2.4 (1.6)	0	3.7 (0)
Nemertea	9.8 (2.7)	5.6 (1.3)	8.2 (3.0)	1.9 (1.9)
<i>Heteromastus</i> sp.+ <i>Mediomastus</i> sp.	9.6 (4.5)	16.2 (8.0)	6.7 (3.0)	42.6 (31.5)
Sabellidae	9.5 (4.0)	2.6 (1.3)	0	0
<i>Aricidea albatrossae</i>	8.8 (3.0)	11.0 (5.2)	3.0 (3.0)	3.7 (3.7)
<i>Leitoscoloplos</i> sp.+ <i>Scoloplos</i> sp.	8.3 (3.2)	15.9 (5.4)	10.4 (5.0)	11.1 (0)
<i>Lumbrineris tenuis</i>	8.3 (3.8)	2.6 (1.5)	2.1 (2.1)	27.8 (1.9)
<i>Ophiocten sericeum</i>	7.2 (3.1)	69.0 (29.1)	1.1 (0.7)	0
<i>Gnathia</i> sp.	6.1 (2.7)	0.5 (0.5)	0	0
<i>Aricidea catherinae</i> + <i>A. nolani</i> + <i>A. suecica</i>	4.7 (2.9)	20.4 (6.1)	70.1 (28.5)	7.4 (3.7)
<i>Pontoporeia femorata</i>	1.6 (1.1)	22.9 (13.8)	28.2 (14.5)	9.3 (9.3)
<i>Saduria sabini</i>	1.5 (1.5)	5.3 (1.8)	8.1 (2.9)	0
<i>Haploops laevis</i>	1.3 (1.3)	10.9 (4.8)	5.0 (3.6)	50.0 (24.1)
<i>Leucon nasicus</i>	1.0 (1.0)	20.1 (6.9)	14.1 (7.3)	0
<i>Trochochaeta multisetosa</i>	1.0 (1.0)	2.2 (1.5)	0.7 (0.7)	48.1 (11.1)
<i>Portlandia arctica</i>	0.9 (0.6)	0.6 (0.6)	23.7 (21.9)	133.3 (18.5)
<i>Pectinaria hyperborea</i>	0	37.0 (18.6)	109.0 (109.0)	0
Podocypid 3b	0	1.3 (1.3)	0	113.0 (24.1)

reaching $17,127.7 \pm 647.6$ ind. m^{-2} at 38 m depth (station 03 04 300). This is due to high numbers of the tube-dwelling amphipods *Ampelisca macrocephala* (8250.0 ± 113.4 ind. m^{-2}) and *Photis* spp. (927.8 ± 253.2 ind. m^{-2}), the ostracod *P. brenda* (1016.7 ± 76.4 ind. m^{-2}), the cumacean *Brachydiastylis nimia* (644.4 ± 55.6 ind. m^{-2}) and the capitellid polychaete *B. americana* (2005.6 ± 349.9 ind. m^{-2}). Faunal composition is distinctive relative to shallow sites sampled on the Beaufort shelf (Table 3). Offshore of Cape Bathurst, abundance declines and the faunal composition resembles that in nearby Franklin Bay and the polynya (Fig. 2).

Although abundance does not reach anything like that at Cape Bathurst (Table 1), the Mackenzie Canyon fauna are similar to the offshore communities at Cape Bathurst, in the polynya and on the Beaufort slope (Table 3). The dominant species (Appendix A) comprise a range of small amphipod, ostracod and cumacean crustaceans and surface feeding polychaetes. The same dominants characteristic of the deeper regions of the Beaufort shelf and Amundsen Gulf (the polychaetes *M. sarsi*, *T. kirkegaarde/marioni*, *L. impatiens*, *T. stroemi* and *P. cirrifera/steenstrupi*, the bivalve *T. flexuosa*, the tanaid *P. gracilis*, cumacean *E. nimia* and ostracod *P. brenda*) typify the

Mackenzie Canyon (Appendix A) and distinguish it from the flaw lead and fast ice regions of the Beaufort Shelf.

3.5. H3. The Beaufort Shelf shows a latitudinal gradient in benthic community composition relating to depth-related changes in ice cover, ice scour and water mass influences from the Mackenzie River and offshore upwelling

Fig. 3 shows the gradient in faunal abundance and diversity with environmental variables measured in Sept.–Oct. 2002 across the Beaufort Shelf and slope in the area of Kugmallit Valley (133°18' N–133°53' W). This time period was selected for analysis in order to minimize temporal and sampling gear variation and because the majority of transect samples were taken at that time. Macrofaunal abundance in the fast ice, flaw lead and on the shelf ranges from 1289 ± 227.8 to 3200 ind. m^{-2} and declines to 178 ind. m^{-2} at the deepest station on the shelf edge (station 49 at 1000 m depth). Taxonomic diversity is lowest in the flaw lead

(32.7 ± 1.1) and highest at the shelf edge (82.8 ± 3.0). However, in some parts of the inshore (e.g., 47 km offshore) it is nearly as high (68.9 ± 1.9) as farther offshore. Changes in faunal composition across the Beaufort Shelf do not progress linearly, however. When the 2002 transect was compared to a perfectly seriated similarity matrix, the Spearman rank correlation with the faunal similarity matrix was significantly different (0.566 , $p < 0.001$). Water depth, bottom temperature, bottom oxygen, sediment % sand and phi mean combined most highly correlated ($R = 0.828$) with changes in faunal composition across the shelf (BEST procedure). Bottom water temperature shows a decline from 0.18 °C inshore to -1.45 °C on the shelf, then increasing to 0.40 °C on the slope. Bottom water salinity increases from 16.0 ‰ inshore to 30.0 ‰ 75 km from shore and thereafter increases gradually to 34.9 ‰ at the end-point of sampling at 1000 m depth. Fluorescence declines with distance from shore from a maximum of 0.75 $\mu g\ l^{-1}$ in the flaw lead region to a minimum of 0.03 $\mu g\ l^{-1}$ on the slope. Bottom water oxygen is high

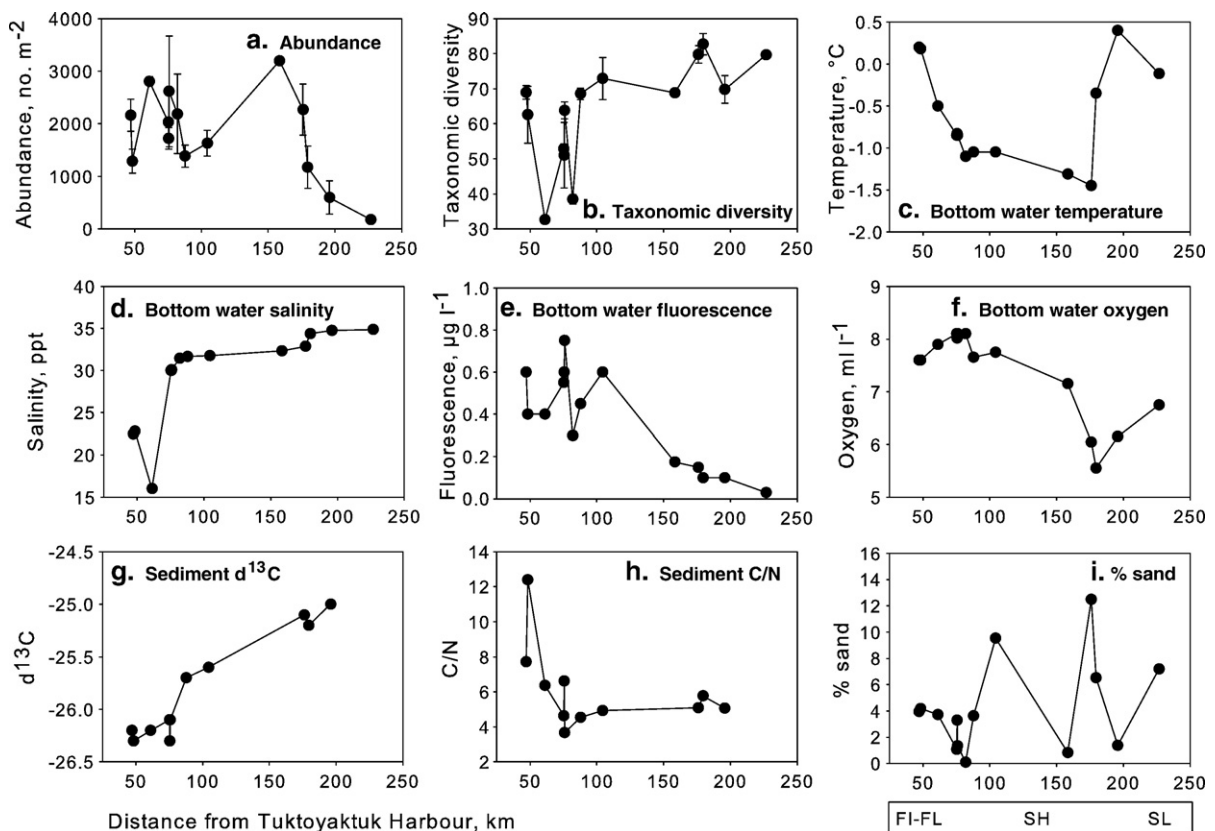


Fig. 3. Changes in benthic macrofaunal abundance (a) and taxonomic diversity (b) with bottom water temperature (c), salinity (d), fluorescence (e) and oxygen (f) and sediment $\delta^{13}C$ (g), C/N (h) and % sand (i) across the Beaufort Shelf in Sept.–Oct. 2002 in Kugmallit Valley. Replicate samples were averaged (mean and s.e.). FI: fast ice; FL: flaw lead; SH: shelf; SL: slope.

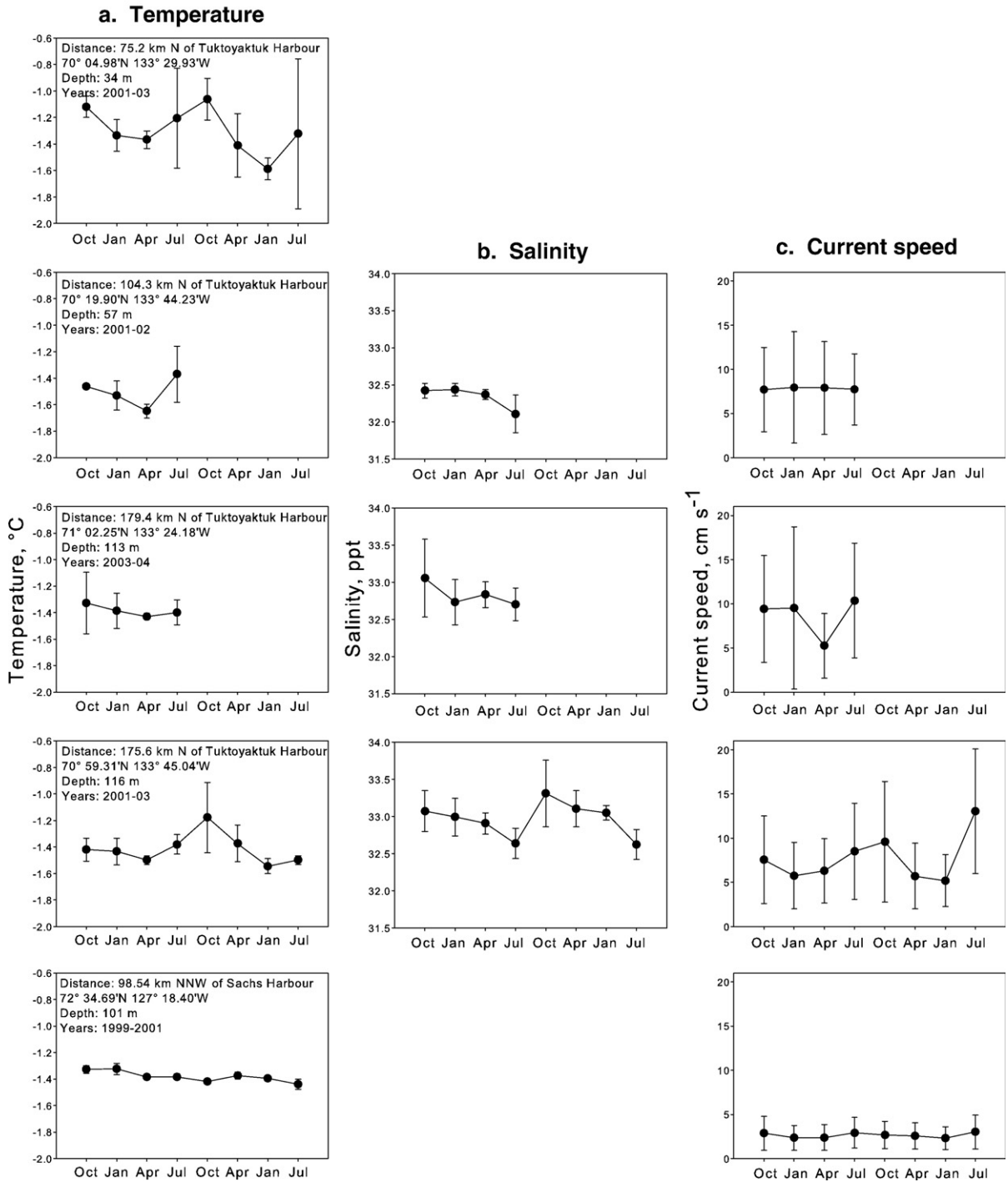


Fig. 4. Seasonal variation (mean and s.d.) in water temperature (column a) and salinity 2–3 m above the seabed (column b) and current speed 6 m above the seabed (column c) for years just prior to or during benthic sampling. There are data from four sites within Kugmallit Valley off Tuktoyaktuk Harbour (69°25'59" N, 132°58'09" W) that spans the Beaufort Shelf near 134° W and from a comparative site near the edge of the Banks Island Shelf northwest of Sachs Harbour (72°22'67" N, 127°49'04" W). Each row represents a site. The coordinates, water depth and period of measurement are indicated on each row. $n=126-21,840$. Note that the x axis is not comparable between sites due to different years of sampling.

inshore, increasing slightly from 7.6 ml l^{-1} close to shore to a maximum of 8.10 ml l^{-1} in the flaw lead region, then declining to 5.55 ml l^{-1} on the slope. Thereafter it increases to 6.75 ml l^{-1} at the sampling endpoint. Sediment $\delta^{13}\text{C}$ increases with distance from shore from a low of -26.3 in the fast ice region to a high of -24.9 at the deepest offshore station on the slope. Sediment C/N is higher inshore, peaking at 12.4 at 48.2 km from shore, then plateauing after 75 km from shore to about 4.5–5.0. Mean sediment phi (and also % sand) was determined by the BEST procedure to contribute to the environmental variables that correlated most highly with changes in species composition. Mean sediment phi varied little throughout Kugmallit Valley. The lowest value was 6.86, describing the sediment as fine silt by the Wentworth scale, up to 9.11, describing the sediment as clay. Percent sand was relatively low throughout Kugmallit Valley as well, varying from 1.1 to 12.6%.

Fig. 4 shows the seasonality in bottom water temperature, salinity and current speed on the Beaufort shelf in the area of Kugmallit Valley (off Tuktoyaktuk Harbour) compared to that of the Banks Island shelf (off Sachs Harbour). Bottom temperature is more variable on the Beaufort shelf than off Banks Island at similar depth, where the variation in seasonal average is less than one tenth of a degree over the year. On the Beaufort shelf the range in seasonal average is about half a degree, from a spring low of $-1.6 \pm 0.1 \text{ }^\circ\text{C}$ to a fall high of $-1.1 \pm 0.2 \text{ }^\circ\text{C}$. Near the shelf edge temperature can also be relatively high in the summer months (June–August average). The seasonal range of variation is greater inshore (lesser depth) than offshore (greater depth). Data from the two mooring sites that are 175 and 179 km offshore (13 km along shelf separation) span three years (2001–2004) and reveal year-to-year differences in the seasonal cycle. The range of seasonal variation in temperature and current at the seabed off Banks Island

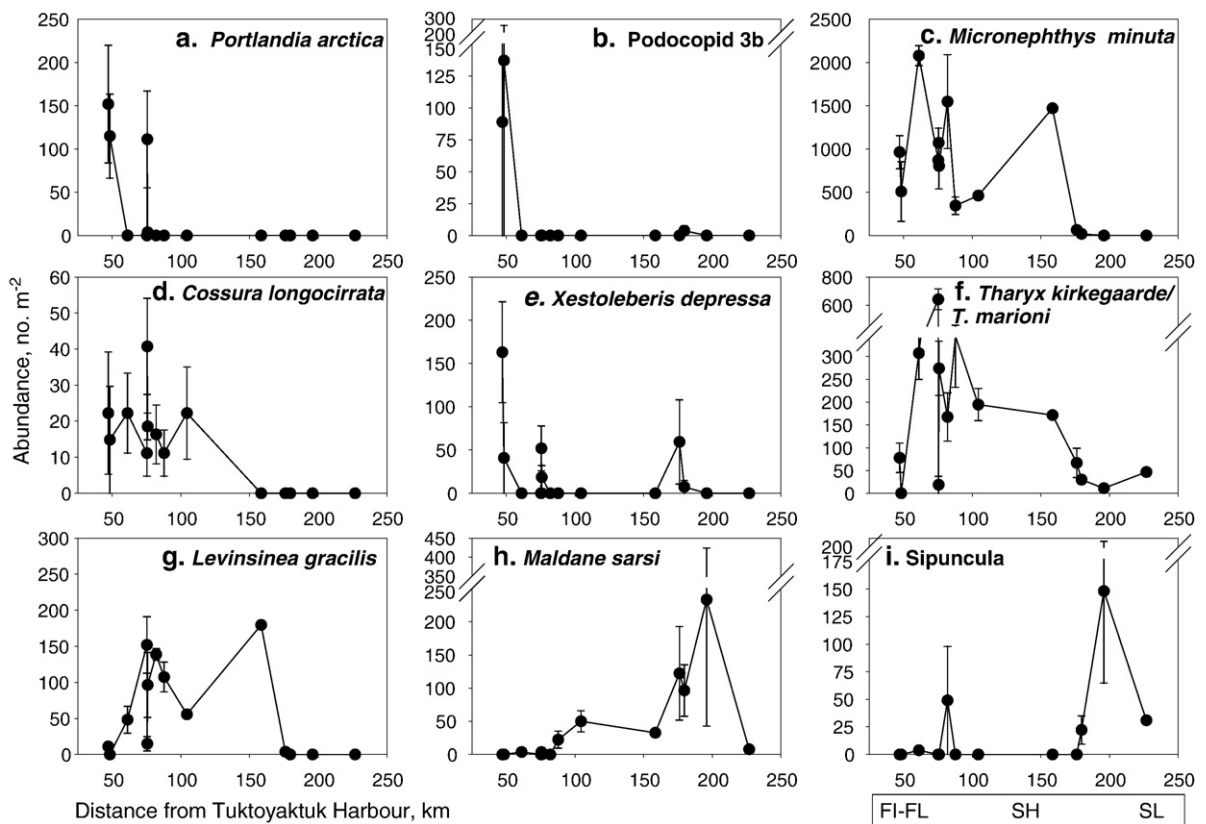


Fig. 5. Changes in abundance of dominant species across the Beaufort Shelf in Sept.–Oct. 2002 in the region of Kugmallit Valley. The bivalve *Portlandia arctica* (a), Podocopid ostracod 3b (b), the polychaetes *Micronephthys minuta* (c) and *Cossura longocirrata* (d), the ostracod *Xestoleberis depressa* (e), the polychaetes *Tharyx kirkegaarde/T. marioni* (f), *Levinsinea gracilis* (g) and *Maldane sarsi* (h) and *Sipuncula* (i). Two other dominants are not shown: the brittle star *Ophiocten sericeum*, which resembles *Levinsinea gracilis* in abundance and the polychaete *Lumbrineris impatiens* which resembles *M. sarsi* in abundance. Replicate samples were averaged (mean and s.e.). FI: fast ice; FL: flaw lead; SH: shelf; SL: slope.

appears to be very small, but temperature did gradually decrease during 1999–2001 from -1.3 ± 0.0 °C to -1.4 ± 0.0 °C. Greater variation in the Beaufort Shelf records make it difficult to determine whether a decline is evident here as well, although the data from 75 km offshore of Tuktoyaktuk Harbour is suggestive of a decline. Bottom current speed is higher and more variable seasonally on the Beaufort shelf than off Banks Island. Seasonal averages vary from 7.7 ± 4.8 cm s⁻¹ to 13.0 ± 7.0 cm s⁻¹ in the former area, whereas off Banks Island the range is only 2.3 ± 1.4 cm s⁻¹ to 3.0 ± 1.9 cm s⁻¹. As was noted for temperature, the annual variation of current speed differs between sites on the shelf edge at 175 and 179 km offshore, but this is probably attributable to inter-annual variability. In general there is a decline in winter to an average 5 cm s⁻¹ with increase in the summer and fall to an average 9 cm s⁻¹. Current speeds as high as 41.5 and 67.5 cm s⁻¹ were recorded for short periods at the two sites, respectively.

Fig. 5 shows changes in abundance of the top four dominant species in the Kugmallit Valley portion of the fast ice, flaw lead, shelf and slope regions. The polychaete *M. minuta* is the most abundant of these species, reaching 2077 ± 116.0 ind. m⁻² in the flaw lead region. Other species that show peak abundances inshore are the bivalve *P. arctica*, the ostracods Podocopid 3b and *Xestoleberis depressa* and the polychaetes *Cossura longocirrata* and *T. kirkegaardel/T. marioni*. The polychaete *L. gracilis* and the brittle star *O. sericeum* are more abundant on the shelf than inshore or on the slope while sipunculids and the polychaetes *M. sarsi* and *L. impatiens* peak in abundance on the slope. None of these species are abundant at the most offshore station, however.

4. Discussion

4.1. Macrofaunal patterns on the Beaufort Shelf

The abundance of the Beaufort Shelf and Amundsen Gulf macrofauna >0.4 mm (this study, Table 1) was within range of the abundance of macrofauna >1.0 mm in the Bering and Chukchi Seas (Grebmeier and Cooper, 1995; Feder et al., 2007), macrofauna >0.5 mm in the eastern Canadian Arctic (Cusson et al., 2007) on the northeast Greenland Shelf (Ambrose and Renaud, 1995) and Barents Sea (Denisenko et al., 2007) and an order of magnitude more abundant than macrofauna >1.0 mm in the Barents and Kara Seas (Grebmeier and Barry, 1991). In comparing studies it is important to consider differences in sieve mesh size. Our study used 0.4 mm, which increased macrofaunal abundance by

about 3% over a 0.5 mm mesh sieve (Table 2). As was found in the Laptev Sea (Steffens et al., 2006), the broad regional variation of the macrofauna correlated most highly with water depth. However, the correlation was low (0.631) between the environmental and biotic similarity matrices. Two reasons can be suggested for this: (1) The Mackenzie River has a broad and temporally variable influence and so single measures will not capture the full range of variation experienced by the benthos. (2) Many of the benthic species are sufficiently long lived and adaptable to integrate environmental variability.

Essentially, the fauna on the Beaufort Shelf and in Amundsen Gulf consisted of a mud-associated community dominated by the deep burrowing polychaete *M. sarsi* that differed inshore near the Mackenzie River and at Cape Bathurst (Fig. 6). These inshore communities were dominated by *P. arctica* and *M. minuta* around the Mackenzie River and by *A. macrocephala* and *B. americana* at Cape Bathurst. These species occurred in small numbers elsewhere, but appeared to be favoured by estuarine conditions and upwelling respectively.

The Cape Bathurst polynya in Amundsen Gulf did not appear to influence community structure as the community here was not significantly different from the Beaufort shelf and slope fauna to the west at similar depth. This suggests that processes within the polynya that influence carbon production and export to the benthos are not sufficient to produce a footprint on the benthos. Although the benthos relies on surface organic carbon, this supply can be advected. Indeed, re-suspended shelf sediment and sediment from the Mackenzie River reach the Amundsen Gulf during onshore wind storms, which create an easterly coastal current (O'Brien et al., 2006). In addition, the series of sills and basins in the polynya region, which would isolate bottom water masses, would restrict bottom circulation. This bathymetry would not be conducive to supporting elevated benthic abundance in the polynya.

Barry et al. (2003) found that the spatial distribution of megabenthos under the Antarctic Ross Sea polynya associated more closely with benthic environmental variables than with the timing of ice cover or primary productivity. However, tight coupling of benthic metabolism to the St. Lawrence Island, Northeast Water and North Water polynyas in the Arctic were observed by Grebmeier and Cooper (1995), Ambrose and Renaud (1995) and Grant et al. (2002) respectively. The St. Lawrence Island polynya was dominated by deposit-feeding nuculid, nuculanid and tellinid bivalves and capitellid polychaetes (Grebmeier and Cooper, 1995). Piepenburg and Schmid (1996) reported

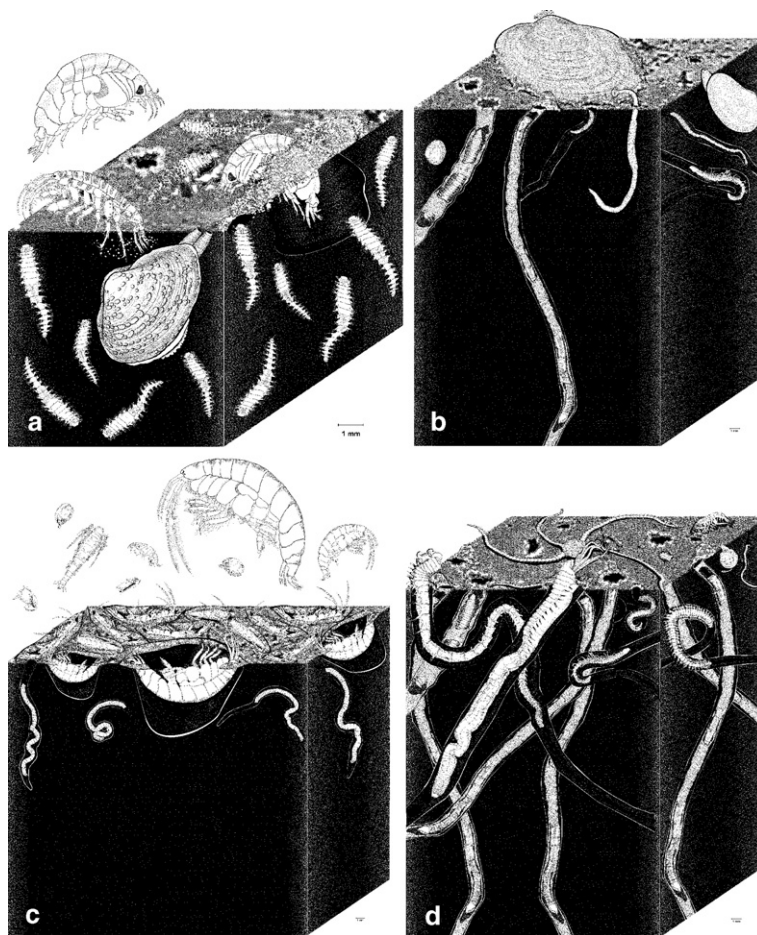


Fig. 6. Contrasting communities on the Beaufort Shelf and in Amundsen Gulf. Clockwise from top left: the community typical of the inshore fast ice and flaw lead regions of the Beaufort Shelf dominated by the polychaete *Micronephthys minuta* and the bivalve *Portlandia arctica* and the amphipods *Protomedea* sp. and *Anonyx* sp. (near stn. DEV-3 in Fig. 1, 20 m) (a); low density community on the Beaufort slope at 1000 m (stn. 49) dominated by the polychaetes *Maldane sarsi*, *Lumbrineris impatiens*, *Tharyx kirkegaarde/marioni*, a sipunculid and the bivalves *Bathyarca* sp. and *Yoldiella* sp. (b); the high density community at 38 m depth off Cape Bathurst (stn. 03 04 300) dominated by the amphipods *Ampelisca macrocephala* and *Photis* sp., the ostracods *Cypridina megalops* and *Philomedes brenda* and the polychaete *Barantolla americana* (c); the Cape Bathurst polynya community also characteristic of the Beaufort shelf at similar depth (stn. CA-08, 390 m) dominated by the abundant deep burrowing polychaete *M. sarsi* and the polychaetes *Terebellides stroemi*, *Melinna cristata*, *T. kirkegaarde/marioni* and the brittle star *Ophiocten sericeum* (d). Abundances are relative to 0.125 m²; scale 1 mm. Illustrations by Susan Laurie-Bourque in consultation with Pat Pocklington (Arenicola Marine) and the authors.

increased benthic epifaunal abundance (dominated by brittle stars) under the Northeast Water polynya compared to the benthos underlying the pack ice. Common to these polynyas is that benthic metabolism is not fuelled directly by the vertical sinking of ungrazed organic matter in the water column above the seafloor. Instead, organic material produced at the margins of the polynya begins to sink and is subsequently advected to the regions where high benthic respiration and increases in infaunal abundance occur. Ice edge blooms can also show considerable delays of supply to the benthos while they are being processed by bacteria (4–11 mo. —

Lovvorn et al., 2005). For the Cape Bathurst polynya, there may be tighter coupling in benthic activity than in species composition and abundance. Renaud et al. (2007) measured a rapid increase in respiration of the macrofauna in Franklin Bay at the time of the spring ice algal bloom, suggesting that the nearby polynya could have a similar effect, so long as organic production within the polynya is not intercepted pelagically. Seuthe et al. (2007) measured a corresponding initiation of feeding by the major pelagic grazers *Calanus glacialis* and *C. hyperboreus* with consequent increase in fecal pellet production. Phytoplankton standing stocks were

high in the polynya in June. The lower $\delta^{13}\text{C}$ of the sediment organic carbon on the eastern edge of the Beaufort Shelf ($-23.62 \pm 0.28\%$, $n=4$) than on the north and western edge ($-25.12 \pm 0.05\%$, $n=4$) suggests that the polynya fauna are influenced by a more ocean-based carbon supply than fauna to the west in the Mackenzie Canyon and northern edge of the Beaufort Shelf. These results correspond with those reported by Dunton et al. (2006).

Cape Bathurst is a region of high macrofaunal abundance and diversity which extends northward along the shelf edge. High bottom water oxygen levels here and at the western edge of Banks Island are likely due to upwelling. Low sediment C/N ($4\text{--}7$ wt. wt. $^{-1}$), indicative of high quality organic carbon occurs here. Abundances $>15,000$ m $^{-2}$ were recorded at 38 m depth. This abundance exceeds most abundances recorded elsewhere in the Arctic (Grebmeier and Barry, 1991) with the exception of that found in some parts of the Bering and Chukchi Seas (Grebmeier and Cooper, 1995; Feder et al., 2007). It is within range of some of the high levels found at similar depth in the Antarctic (with the exception of below the fast ice in east McMurdo Sound). The very high abundance at Cape Bathurst is mainly due to the capitellid polychaete *B. americana* and the tubicolous amphipod *A. macrocephala* (Fig. 6). Capitellids are non-selective deposit feeders (Fauchald and Jumars, 1979) while ampeliscid amphipods can be suspension or surface deposit feeders (Mills, 1967; Highsmith and Coyle, 1990). *A. macrocephala* is a prime food resource for California gray whales (*Eschrichtius robustus*) in the Bering and Chukchi Seas (Oliver et al., 1983) and is highly productive (Highsmith and Coyle, 1990). Averaging 8250 ± 113.5 ind. m $^{-2}$ at Cape Bathurst, this ampeliscid abundance is twice the mean ampeliscid abundance in the Chirikov Basin (Bering Sea) that feeds the California gray whale (Highsmith and Coyle, 1990). Gray whales were sighted on the Beaufort Shelf in the summer of 2007 (Hamlet of Sachs Harbour, pers. comm., 2008) and bowhead whales (*Balaena mysticetus*) forage as far east as Cape Bathurst and Amundsen Gulf in the summer (Frost and Lowry, 1984). Indeed, this part of Cape Bathurst is locally known as Whale Bluff. Generally considered to be pelagic zooplankton feeders (Harwood and Smith, 2002; Lee et al., 2005), bowhead whales also feed benthically (Frost and Lowry, 1984). Thus, it is possible that the rich *A. macrocephala*–*B. americana* community at Cape Bathurst is consumed by summer foraging gray and bowhead whales. The community is also a significant potential resource for such local diving seabirds as the surf scoter (*Melanitta perspicillata*),

white wing scoter (*Melanitta fusca*), common eider (*Somateria mollissima* v *nigra*), king eider (*Somateria spectabilis*) and long-tailed duck (*Clangula hyemalis*) (Dickson and Gilchrist, 2002) if it extends into the shallows.

The sampling transect across the Beaufort Shelf demonstrated a certain gradient of environmental and faunistic change with depth, although the latter was not significantly linear. Benthos in the inshore fast ice and flaw lead zones are subject to frequent disturbance by ice scour (Gilbert and Pedersen, 1987; Lewis and Blasco, 1990; Myers et al., 1996). Inside the 24 m isobath, 97% is disturbed in <100 years (S. Blasco, pers. comm., 2006). The variation in abundance and diversity inshore (Fig. 3) likely reflects this major benthic disturbance. Disturbance by storm effects and coastal erosion, variable salinity, temperature and turbidity influences of the Mackenzie River also would shape community structure. Fauna here are taxonomically diverse, however and some species, such as the small polychaete *M. minuta* can be highly abundant (Fig. 6). It was most abundant (6882.8 ± 3128.6 ind. m $^{-2}$) where there was an offshore rise (station 03 03 718). Coincidentally, *A. macrocephala* was also abundant here (244.8 ± 71.5 ind. m $^{-2}$) relative to other sites on the transect, although an order of magnitude less so than at Cape Bathurst. Nephtyid polychaetes are considered to be active subsurface predators. However, the small size of *M. minuta* suggests that it may concentrate on meiofauna. Nematodes are very abundant on the Beaufort Shelf (P. Buat, pers. comm., 2007). Other dominants on the inshore shelf are several ostracod species and the small deposit feeding bivalve *P. arctica*. The large scavenging and predaceous isopod *S. sabinii* can aggregate in large numbers around food falls and is a conspicuous component of the megabenthos in this region. The inshore fauna bear a strong resemblance to the shallow water (<30 m depth) fauna that inhabit muddy substrates on the Laptev Sea shelf, which is dominated by the bivalve *P. arctica*, the mysid shrimp *Mysis oculata* and the isopod *Saduria entomon* (Schmid et al., 2006; Steffens et al., 2006). The flaw-lead zones on the Beaufort Shelf and off Banks Island are important spring staging areas for eiders and long-tailed ducks (Dickson and Gilchrist, 2002).

Further offshore, a larger mix of species characterizes the shelf, many of which are common also in Amundsen Gulf and Mackenzie Canyon. This would account for the observed increase in multivariate dispersion among station replicates correlated with increased depth and taxonomic diversity. Some of the offshore dominants are the deposit feeding polychaetes *T. kirkegaarde/marioni*,

L. gracilis, *Prionospio cirrifera* and *M. sarsi*, the tanaid *P. gracilis* and the brittle star *O. sericeum*. *M. sarsi* is a deep burrowing, head-down, non-selective deposit feeder which defecates at the surface and therefore likely is important in sediment mixing, pore water oxygenation and surface nutrient replenishment (Holte, 1998). Its gardening action likely benefits the surface microbial and meiofaunal community, which in turn would benefit larger surface micropredators and deposit feeders such as *O. sericeum*, *P. gracilis* and *Prionospio cirrifera* (Fauchald and Jumars, 1979; Jangoux and Lawrence, 1982; Błażewicz-Paszkowycz and Ligowski, 2002). The maldanid polychaete *Praxillella* sp. benefits burrowers >10 cm below the surface through subduction of surface carbon (Levin et al., 1997) but it is unknown whether *M. sarsi* has similar deep-sediment effects. *M. sarsi*, *Lumbrineris fragilis*, *P. arctica*, *L. gracilis*, *Prionospio cirrifera*, *P. gracilis* and others in this Beaufort study were found dominating glacial fjords or estuarine areas in the eastern Canadian Arctic (Curtis, 1972; Aitken and Gilbert, 1996), Svalbard (Holte and Gulliksen, 1998), Spitsbergen (Błażewicz-Paszkowycz and Sekulska-Nalewajko, 2004; Włodarska-Kowalczyk and Pearson, 2004) and Siberia (Golikov and Averintzev, 1977), indicating that these species are tolerant of high rates of clastic sedimentation.

At the shelf edge, warmer bottom water temperatures than on the shelf (Fig. 3) reflect the presence of different water masses (Atlantic deeper and Pacific shallower). The general pattern of bottom water salinity decrease in summer followed by a rapid increase in the fall likely reflects the strengthening of upwelling-favourable easterly winds in the latter season. The greater range in salinity over the steeper slope of the outer shelf (>100 m) than over the flatter middle shelf is also consistent with upwelling. Variations exceeding ‰ can occur on time scales shorter than seasonal. At stations CA-04 and CA-07, the sediment has a high terrigenous carbon content (25–60%) despite its distance from shore (177.6 and 195.9 km from Tuktoyaktuk Harbour, respectively) (Héquette et al., 1995; Forest et al., 2007). Winter supply of POC to the benthos comes from resuspension and advection of shelf bottom particles via the benthic nepheloid layer (Forest et al., 2007). Ice algae supply a short duration boost of POC in spring, followed by summer sedimentation of remaining ice algae, phytoplankton and zooplankton fecal pellets. Currents can be stronger on the shelf edge than inshore (O'Brien et al., 2006), although in our study average values were not greatly different (Fig. 4). However, currents were consistently higher on the Beaufort shelf than further east off Banks Island. Macrofaunal

abundance on the Beaufort shelf edge and slope is variable and declines at the deepest site (1000 m) but here, taxonomic diversity is still high. Species typical of the shelf are still present but in smaller numbers (Fig. 6).

Several factors favour the Mackenzie Canyon as habitat for benthos. The Mackenzie Canyon receives seven times greater annual deposition than in the region of stations CA-04 and CA-07 on the shelf edge (O'Brien et al., 2006). Moreover, the shape and location of the canyon focuses upwelling so that water from more than 180 m deep frequently reaches shallow depth. During the short ice-free season, upwelling and downwelling of sub-surface waters on the Beaufort shelf and slope are forced directly by wind storms. For most of the year, however, they are driven by ice motion. The upwelling response to westward ice movement (easterly winds) is actually stronger than that to wind alone. However, the compensating downwelling during westerly winds is weak because the strength of pack ice inhibits rapid and prolonged eastward ice drift (Williams et al., 2006). The effect is a net upwelling that is stronger than would result from the wind-stress without the intervention of pack ice. Moreover, the net upwelling in Mackenzie Canyon brings a flux of nitrate, phosphate and silicate to the head of the trough and adjacent areas of the shelf because there is a peak in nutrient concentrations between 100 and 200 m depth in the southern Beaufort Sea. The abundant and diverse fauna in the Mackenzie Canyon (Tables 1 and 3) are indicative of an abundant water-borne food supply and active sediment bioturbation.

4.2. Climate change projections for the Beaufort Shelf benthos

Carmack and McLaughlin (2001) and Piepenburg (2005) have predicted a number of changes resulting from shrinking pack ice in the Arctic that will affect continental shelf benthos. These are, longer ice-free periods, particularly in the seasonal ice zone; increased wind-mixing, upwelling and wintertime brine rejections, which will increase the availability of nutrients to phytoplankton; increased availability of underwater light to phytoplankton (and benthic primary producers), especially in the seasonal ice zone; increased river flow and export of organic terrestrial material (POC, DOC) to the coast (therefore increasing turbidity); a decrease in extent of ice algae (thereby decreasing flux to the benthos); increased coastal erosion (resulting in increased turbidity); and shifting water mass fronts and currents (e.g., buoyancy boundary flow) (resulting in different migration pathways and potential for

introduction of foreign species that may have large impacts on benthic communities). The consequence to the benthos would be less carbon supply if it is intercepted by zooplankton and the microbial loop and changes in the quality, timing and source of carbon (Lovvorn et al., 2005). This would favour changes in species composition based on feeding and reproductive characteristics and likely reduced or redistributed benthic biomass due to lower pelagic carbon supply. Lower benthic biomass would affect bottom predators, including mammals and sea birds and favour smaller predators such as fish. Warmer water also has physiological consequences for stenothermal, cold-adapted animals, most importantly limitations for oxygen uptake (Peck, 2002; Pörtner and Knust, 2007).

On the Canadian Beaufort Shelf, the Mackenzie River influence already selects for inshore fauna that are adaptable to changeable conditions. Climate warming in this area would likely first affect these fauna (through greater river inflow, more wave effects, thinner ice and shorter duration of ice cover) and more storms (leading to greater mixing and supply of nutrients, enhanced sediment transport and coastal erosion). The expected outcome would be expansion of these stress-tolerant fauna over the shelf and immigration of other species with corresponding adaptations. Also anticipated would be a greater import of Pacific origin species via increased buoyancy boundary flow from the Pacific (Carmack and McLaughlin, 2001).

Upwelling zones will also be subject to climate change (Carmack and McLaughlin, 2001), expanding if ice edges and steep topography are spatially coincident. However, if the ice edge retreats too far, the effect of ice edge amplification will be lost. Either change would have an impact on the dense shallow water populations at Cape Bathurst. This benthic community is less subject to the extremes of salinity, turbidity and temperature that is felt by the Beaufort Shelf community closer to the Mackenzie River's influence and so therefore may be less adaptable to climate-induced changes. Community expansion would be favoured by upwelling increase, provided that pelagic interception does not counterbalance the benthic advantage. However, loss of sea ice cover will dampen upwelling, resulting in diminished populations, with ramifications for their large predators.

5. Conclusion

The Beaufort Shelf and Amundsen Gulf macrofauna are abundant, ranging from 320 to 16,840 m⁻² on the shelf, 1104–4844 m⁻² in Mackenzie Canyon and 533–

7967 m⁻² in the Cape Bathurst polynya. Highest abundance found was 17,950 m⁻² off Cape Bathurst. Taxonomic diversity is generally high throughout the shelf and slope, though more variable inshore, in the Amundsen Gulf basins and close to the Mackenzie River. Regional variation in community composition is correlated most highly with water depth, although the correlation is not high ($R=0.631$ for all samples and $R=0.828$ in combination with other variables in Kugmallit Valley). The macrofaunal community in the Cape Bathurst polynya (centred in Amundsen Gulf) is not significantly different from elsewhere on the shelf or in the gulf, indicating that community composition is not altered by the polynya. High faunal abundance off Cape Bathurst (>15,000 m⁻²), caused by large numbers of the suspension feeding amphipod *A. macrocephala* and the deposit feeding polychaete *B. americana* may provide a food supply for local diving seabird colonies and summer foraging whales. The benthic community on the Beaufort Shelf grades from dominance by the surface deposit feeding bivalve *P. arctica* and the predaceous polychaete *M. minuta* to a mixed polychaete–crustacean community where the non-selective deposit feeding polychaete *M. sarsi* gardens the sediment deeply. Climate change predictions suggest that the inshore *Portlandia*–*Micronephthys* community would be favoured to expand over the shelf. However, the rich Cape Bathurst community may contract due to reduced upwelling caused by loss of sea ice, potentially affecting benthic feeding birds and mammals.

Acknowledgements

We are grateful to the following for their assistance in many different capacities: for assistance with sampling, Philippe Archambault and Mélanie Simard (Université du Québec à Rimouski), Karen McKendry (Canadian Museum of Nature) and Megan Foss (University of Victoria); for assistance with lab processing and identification of samples and analysis of moorings data, Karen McKendry (Canadian Museum of Nature), Kathryn Wallace (Dalhousie University), Megan Foss (University of Victoria), Phil Lambert (Royal British Columbia Museum) and Pat Pocklington (Arenicola Marine); for illustration of the communities, Susan Laurie-Bourque; for GIS mapping, Elise Petroniro (University of Saskatchewan); for water chemistry data, Yves Gratton (INRS-Eau, Terre et Environnement); for sediment analysis, Andrea Freeman (University of Calgary) and the Geological Survey of Canada, Ottawa; for logistical support, Aurora Research Institute, crews of CCGS *Laurier*, *Radisson*, *Amundsen* and *Nahidik* and staff of

the University of Saskatchewan and the Canadian Museum of Nature. Moorings for long-term ocean and ice measurements were supported by the federal Program on Energy Research and Development (PERD) under the Northern Hydrocarbons Objective. Funding was also

provided by the Canadian Museum of Nature and by the Natural Sciences and Engineering Research Council for the CASES Program, lead by Louis Fortier (Université Laval). We would also like to thank two anonymous reviewers for their constructive criticisms.

Appendix A

Dominant taxa (cumulatively accounting for 75% of the within-group similarity) in each region. Amundsen Gulf East is not listed because it comprises only one site

Taxa	% Contribution to within-group similarity
Fast ice. Average within-group similarity: 58.93	
<i>Micronephthys minuta</i> (Theel, 1879) (Polychaete)	23.04
<i>Portlandia arctica</i> (J. E. Gray, 1824) (Bivalve)	9.73
Podocopid 3b (Ostracod)	7.44
<i>Xestoleberis depressa</i> G.O. Sars, 1866 (Ostracod)	6.53
<i>Trochochaeta multisetosa</i> (Oersted, 1844) (Polychaete)	6.08
<i>Normanicythere leioderma</i> (Norman, 1869) (Ostracod)	4.80
<i>Haploops laevis</i> Hoek, 1882 (Amphipod)	4.02
<i>Lumbrineris tenuis</i> (Verrill, 1873) (Polychaete)	4.02
<i>Cossura longocirrata</i> Webster and Benedict, 1887 (Polychaete)	3.72
<i>Heteromastus</i> sp. + <i>Mediomastus</i> sp. (Polychaete)	3.41
<i>Paraleptognathia gracilis</i> (Kroyer, 1842) (Tanaid)	3.04
Flaw lead. Average within-group similarity: 43.56	
<i>Micronephthys minuta</i> (Polychaete)	40.70
<i>Tharyx kirkegaarde</i> Blake, 1991 + <i>T. marioni</i> St. Joseph, 1894 (Polychaete)	10.22
<i>Levinsinea gracilis</i> (Tauber, 1879) (Polychaete)	7.64
<i>Prionospio cirrifera</i> Wiren, 1883 + <i>P. steenstrupi</i> Malmgren, 1867 (Polychaete)	4.57
<i>Aricidea catherinae</i> Laubier, 1967 + <i>A. nolani</i> Webster and Benedict, 1887 + <i>A. suecica</i> Eliason, 1920 (Polychaete)	3.57
<i>Cossura longocirrata</i> (Polychaete)	2.91
<i>Lumbrineris impatiens</i> (Claparède, 1868) (Polychaete)	2.53
<i>Pontoporeia femorata</i> Kroyer, 1842 (Amphipod)	2.31
<i>Saduria sabini</i> (Kroyer, 1849) (Isopod)	2.05
Shelf. Average within-group similarity: 32.95	
<i>Micronephthys minuta</i> (Polychaete)	19.97
<i>Tharyx kirkegaarde</i> + <i>T. marioni</i> (Polychaete)	13.29
<i>Maldane sarsi</i> Malmgren, 1865 (Polychaete)	7.64
<i>Levinsinea gracilis</i> (Polychaete)	6.40
<i>Paraleptognathia gracilis</i> (Tanaid)	3.94
<i>Ophiocten sericeum</i> (Forbes, 1852) (Ophiuroid)	3.58
<i>Prionospio cirrifera</i> + <i>P. steenstrupi</i> (Polychaete)	2.90
<i>Lumbrineris impatiens</i> (Polychaete)	2.84
<i>Leucon nasicus</i> (Kroyer, 1841) (Cumacean)	2.15
<i>Barantolla americana</i> Hartman, 1963 (Polychaete)	2.04
<i>Aricidea catherinae</i> + <i>A. nolani</i> + <i>A. suecica</i> (Polychaete)	1.91
<i>Pectinaria hyperborean</i> (Malmgren, 1866) (Polychaete)	1.85
Nemertea	1.38
<i>Heteromastus</i> sp. + <i>Mediomastus</i> sp. (Polychaete)	1.33
<i>Pontoporeia femorata</i> (Amphipod)	1.30
<i>Leitoscoloplos</i> sp. + <i>Scoloplos</i> sp. (Polychaete)	1.29

Appendix A (continued)

Taxa	% Contribution to within-group similarity
Shelf. Average within-group similarity: 32.95	
<i>Saduria sabini</i> (Isopod)	1.12
<i>Cossura longocirrata</i> (Polychaete)	1.11
Slope. Average within-group similarity: 29.75	
<i>Maldane sarsi</i> (Polychaete)	15.62
<i>Tharyx kirkegaarde</i> + <i>T. marioni</i> (Polychaete)	11.38
Sipuncula	8.90
<i>Thyasira flexuosa</i> (Montagu, 1803) (Bivalve)	8.29
<i>Portlandia</i> sp. (Bivalve)	6.26
<i>Lumbrineris tenuis</i> (Polychaete)	4.93
<i>Lumbrineris impatiens</i> (Polychaete)	3.47
<i>Aricidea albatrossae</i> Pettibone, 1957 (Polychaete)	2.29
<i>Gnathia</i> sp. (Isopod)	1.79
<i>Paraleptognathia gracilis</i> (Tanaid)	1.76
Indeterminate bivalves	1.59
<i>Prionospio cirrifera</i> + <i>P. steenstrupi</i> (Polychaete)	1.51
<i>Thyasira</i> sp. (Bivalve)	1.38
Nemertea	1.36
<i>Haploops</i> sp. (nr. <i>tubicola</i>) (Amphipod)	1.35
<i>Ehlersia cornuta</i> (Rathke, 1843) (Polychaete)	1.31
<i>Ektonodiastylis nimia</i> (Hansen, 1920) (Cumacean)	1.30
<i>Philomedes brenda</i> (Baird, 1850) (Ostracod)	1.30
Mackenzie Canyon. Average within-group similarity: 28.99	
<i>Thyasira flexuosa</i> (Bivalve)	10.43
<i>Tharyx kirkegaarde</i> + <i>T. marioni</i> (Polychaete)	9.32
<i>Lumbrineris impatiens</i> (Polychaete)	6.72
<i>Prionospio cirrifera</i> + <i>P. steenstrupi</i> (Polychaete)	5.35
<i>Terebellides stroemi</i> Sars, 1835 (Polychaete)	5.33
<i>Paraleptognathia gracilis</i> (Tanaid)	5.28
Nemertea	5.21
Sipuncula	4.88
<i>Aricidea albatrossae</i> (Polychaete)	4.59
<i>Ektonodiastylis nimia</i> (Cumacean)	3.04
<i>Maldane sarsi</i> (Polychaete)	2.98
<i>Pholoe minuta</i> (Fabricius, 1780) (Polychaete)	2.68
<i>Micronephthys minuta</i> (Polychaete)	1.97
<i>Ehlersia cornuta</i> (Polychaete)	1.87
<i>Philomedes brenda</i> (Ostracod)	1.87
<i>Trochochaeta multisetosa</i> (Polychaete)	1.64
<i>Rabilimis mirabilis</i> (Brady, 1868) (Ostracod)	1.62
<i>Cypridina megalops</i> G.O. Sars, 1872 (Ostracod)	1.44
Cape Bathurst. Average within-group similarity: 27.81	
<i>Paraleptognathia gracilis</i> (Tanaid)	7.12
<i>Ektonodiastylis nimia</i> (Cumacean)	6.74
<i>Maldane sarsi</i> (Polychaete)	6.39
<i>Thyasira flexuosa</i> (Bivalve)	6.09
<i>Prionospio cirrifera</i> + <i>P. steenstrupi</i> (Polychaete)	6.01
<i>Philomedes brenda</i> (Ostracod)	5.68
<i>Cypridina megalops</i> G.O. Sars, 1872 (Ostracod)	4.49
<i>Tharyx kirkegaarde</i> + <i>T. marioni</i> (Polychaete)	4.44
<i>Micronephthys minuta</i> (Polychaete)	3.98
<i>Lumbrineris impatiens</i> (Polychaete)	3.68
<i>Terebellides stroemi</i> (Polychaete)	3.30
<i>Paraleptognathia</i> sp. manca (Tanaid)	3.08
<i>Aricidea albatrossae</i> (Polychaete)	3.01
<i>Heteromastus</i> sp.+ <i>Mediomastus</i> sp. (Polychaete)	2.25

(continued on next page)

Appendix A (continued)

Taxa	% Contribution to within-group similarity
Cape Bathurst. Average within-group similarity: 27.81	
<i>Harpinia</i> sp. (Amphipod)	2.19
<i>Portlandia frigida</i> (Torell, 1859) (Bivalve)	2.05
Nemertea	2.05
<i>Ophelina cylindricauda</i> (Hansen, 1878) (Polychaete)	1.74
<i>Cossura longocirrata</i> (Polychaete)	1.68
Polynya. Average within-group similarity: 29.33	
<i>Maldane sarsi</i> (Polychaete)	12.82
<i>Tharyx kirkegaarde</i> + <i>T. marioni</i> (Polychaete)	9.68
<i>Prionospio cirrifera</i> + <i>P. steenstrupi</i> (Polychaete)	7.39
<i>Thyasira flexuosa</i> (Bivalve)	5.54
<i>Philomedes brenda</i> (Ostracod)	4.66
<i>Terebellides stroemi</i> (Polychaete)	3.69
<i>Pholoe minuta</i> (Polychaete)	3.17
<i>Ophelina cylindricauda</i> (Polychaete)	2.81
<i>Paraleptognathia gracilis</i> (Tanaid)	2.72
Sipuncula	2.60
<i>Ehtonodiastylis nimia</i> (Cumacean)	2.37
<i>Lumbrineris impatiens</i> (Polychaete)	2.32
<i>Micronephthys minuta</i> (Polychaete)	2.24
<i>Portlandia</i> sp. (Bivalve)	1.64
<i>Aricidea albatrossae</i> (Polychaete)	1.62
Nemertea	1.54
<i>Cypridina megalops</i> (Ostracod)	1.23
<i>Eudorella</i> sp. (Cumacean)	1.21
<i>Haploops</i> sp. (Amphipod)	1.15
Sabellidae (Polychaete)	1.15
<i>Ampharete balthica</i> Linnaeus, 1758+ <i>A. vega</i> (Wirén, 1883)	1.08
<i>Lumbrineris tenuis</i> (Polychaete)	1.02
<i>Heteromastus</i> sp.+ <i>Mediomastus</i> sp. (Polychaete)	1.01
<i>Gnathia</i> sp. (Isopod)	1.00
Franklin Bay. Average within-group similarity: 46.23	
<i>Tharyx kirkegaarde</i> + <i>T. marioni</i> (Polychaete)	7.71
Podocopid 1a (Ostracod)	6.94
<i>Lumbrineris impatiens</i> (Polychaete)	6.69
<i>Prionospio cirrifera</i> + <i>P. steenstrupi</i> (Polychaete)	6.14
<i>Philomedes brenda</i> (Ostracod)	4.82
<i>Maldane sarsi</i> (Polychaete)	4.54
<i>Rabilimis mirabilis</i> (Ostracod)	4.47
<i>Thyasira flexuosa</i> (Bivalve)	4.14
<i>Barantolla americana</i> (Polychaete)	3.91
<i>Pholoe minuta</i> (Polychaete)	3.84
<i>Aricidea albatrossae</i> (Polychaete)	3.65
<i>Portlandia intermedia</i> (M. Sars, 1865) (Bivalve)	3.63
<i>Cypridina megalops</i> (Ostracod)	3.38
<i>Micronephthys minuta</i> (Polychaete)	3.31
<i>Ehtonodiastylis nimia</i> (Cumacean)	2.80
<i>Cossura longocirrata</i> (Polychaete)	2.32
<i>Normanicythere leioderma</i> (Ostracod)	2.27
<i>Pseudotanaia macrocheles</i> G. O. Sars, 1882 (Tanaid)	2.02

References

- Aitken, A.E., Gilbert, R., 1996. Marine Mollusca from Expedition Fiord, Western Axel Heiberg Island, Northwest Territories, Canada. *Arctic* 29, 29–43.
- Ambrose, W.G., Renaud, P.E., 1995. Benthic response to water column productivity patterns: evidence for benthic–pelagic coupling in the Northeast Water Polynya. *J. Geophys. Res.* 100, 4411–4421.
- Arrigo, K.R., van Dijken, G.L., 2004. Annual cycles of sea ice and phytoplankton in Cape Bathurst polynya, southeastern Beaufort Sea, Canadian Arctic. *Geophys. Res. Lett.* 31 (L08304), 1–4.

- Atkinson, E.G., Wacasey, J.W., 1989. Benthic invertebrates collected from the western Canadian Arctic, 1951 to 1985. Can. Data Rep. Fish. Aquat. Sci. 745.
- Barry, J.P., Grebmeier, J.M., Smith, J., Dunbar, R.B., 2003. Oceanographic versus seafloor-habitat control of benthic megafaunal communities in the S. W. Ross Sea, Antarctica. In: DiTullio, G.R., Dunbar, R.B. (Eds.), Biogeochemistry of the Ross Sea. Antarctic Research Series, vol. 78. American Geophysical Union, Washington, D. C., pp. 327–354.
- Berger, T.R., 1977. Northern Frontier, Northern Homeland. The report of the Mackenzie Valley Pipeline Inquiry: Volume One. Ministry of Supply and Services Canada.
- Blażewicz-Paszkwycz, M., Ligowski, R., 2002. Diatoms as food source indicator for some Antarctic Cumacea and Tanaidacea (Crustacea). *Antarct. Sci.* 14, 11–15.
- Blażewicz-Paszkwycz, M., Sekulska-Nalewajko, J., 2004. Tanaidacea (Crustacea, Malacostraca) of two polar fjords: Kongsfjorden (Arctic) and Admiralty Bay (Antarctic). *Polar Biol.* 27, 222–230.
- Callaway, R., 2006. Tube worms promote community change. *Mar. Ecol., Prog. Ser.* 308, 49–60.
- Carmack, E.C., Macdonald, R.W., 2002. Oceanography of the Canadian Shelf of the Beaufort Sea: A setting for marine life. *Arctic* 55 (Supplement 1), 29–45.
- Carmack, E.C., McLaughlin, F., 2001. Arctic Ocean change and consequences to biodiversity: A perspective on linkage and scale. *Mem. Natl. Inst. Polar Res., Spec. Issue* 54, 365–375.
- Carmack, E.C., Macdonald, R.W., Jasper, S., 2004. Phytoplankton productivity on the Canadian Shelf of the Beaufort Sea. *Mar. Ecol., Prog. Ser.* 277, 37–50.
- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Clarke, K.R., Gorley, R.N., 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.
- Clarke, K.R., Green, R.H., 1988. Statistical design and analysis for a 'biological effects' study. *Mar. Ecol., Prog. Ser.* 46, 213–226.
- Clarke, K.R., Warwick, R.M., 1998. A taxonomic distinctness index and its statistical properties. *J. Appl. Ecol.* 35, 523–531.
- Clarke, K.R., Warwick, R.M., 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition. PRIMER-E Ltd., Plymouth.
- Conlan, K.E., Kvitek, R.G., 2005. Recolonization of ice scours on an exposed Arctic coast. *Mar. Ecol., Prog. Ser.* 286, 21–42.
- Curtis, M.A., 1972. Depth distributions of benthic polychaetes in two fiords on Ellesmere Island, N.W.T. *J. Fish. Res. Board Can.* 29, 1319–1327.
- Cusson, M., Archambault, P., Aitken, A., 2007. Biodiversity of benthic assemblages on the Arctic continental shelf: historical data from Canada. *Mar. Ecol., Prog. Ser.* 331, 291–304.
- Dauwe, B., Herman, P.M.J., Heip, C.H.R., 1998. Community structure and bioturbation potential of macrofauna at four North Sea stations with contrasting food supply. *Mar. Ecol., Prog. Ser.* 173, 67–83.
- De Grave, S., Casey, D., Witaker, A., 2001. The accuracy of density standardization of infaunal benthos. *J. Mar. Biol. Assoc. U.K.* 81, 541–542.
- Denisenko, N.V., Denisenko, S.G., Lehtonen, K.K., Andersin, A.-B., Sandler, H.R., 2007. Zoobenthos of the Cheshskaya Bay (southeastern Barents Sea): spatial distribution and community structure in relation to environmental factors. *Polar Biol.* 30, 735–746.
- Dickson, D.L., Gilchrist, H.G., 2002. Status of marine birds of the southeastern Beaufort Sea. *Arctic* 55, 46–58.
- Duchêne, J.-C., Rosenberg, R., 2001. Marine benthic faunal activity patterns on a sediment surface assessed by video numerical tracking. *Mar. Ecol., Prog. Ser.* 223, 113–119.
- Dunton, K.H., Weingartner, T., Carmack, E.C., 2006. The nearshore western Beaufort Sea ecosystem: circulation and the importance of terrestrial carbon in arctic coastal food webs. *Prog. Oceanogr.* 71, 362–378.
- Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds. *Oceanogr. Mar. Biol.* 17, 193–284.
- Feder, H.M., Jewett, S.C., Blanchard, A.L., 2007. Southeastern Chukchi Sea (Alaska) macrobenthos. *Polar Biol.* 30, 261–275.
- Forest, A., Sampei, M., Hattori, H., Makabe, R., Sasaki, H., Fukuchi, M., Wassmann, P., Fortier, L., 2007. Particulate organic carbon fluxes on the slope of the Mackenzie Shelf (Beaufort Sea): Physical and biological forcing of shelf-basin exchanges. *J. Mar. Syst.* 68 (1–2), 39–54.
- Frost, K.J., Lowry, L.F., 1984. Trophic relationships of vertebrate consumers in the Alaskan Beaufort Sea. In: Barnes, P.W., Schell, D.M., Reimnitz, E. (Eds.), *The Alaskan Beaufort Sea: Ecosystems and Environments*. Academic Press, Orlando, pp. 381–401.
- Gilbert, G., Pedersen, K., 1987. Ice scour data base for the Beaufort Sea. Environmental Studies Revolving Funds Report No. 055.
- Golikov, A.N., Averintzev, V.G., 1977. Distribution patterns of benthic and ice biocenoses in the high latitudes of the polar basin and their part in the biological structure of the world ocean. In: Dunbar, M.J. (Ed.), *Polar oceans*. McGill University, Montreal, pp. 331–364.
- Grant, J., Hargrave, B., Macpherson, P., 2002. Sediment properties and benthic–pelagic coupling in the North Water. *Deep-Sea Res.* 49, 5259–5275.
- Grebmeier, J.M., Barry, J.P., 1991. The influence of oceanographic processes on pelagic–benthic coupling in polar regions: a benthic perspective. *J. Mar. Syst.* 2, 495–518.
- Grebmeier, J.M., Cooper, L.W., 1995. Influence of the St. Lawrence Island polynya upon the Bering Sea benthos. *J. Geophys. Res.* 100, 4439–4460.
- Harwood, L.A., Smith, T.G., 2002. Whales of the Inuvialuit settlement region in Canada's Western Arctic: an overview and outlook. *Arctic* 55 (Suppl.1), 77–93.
- Harwood, L.A., Stirling, I., 1992. Distribution of ringed seals in the southeastern Beaufort Sea during late summer. *Can. J. Zool.* 70, 891–900.
- Héquette, A., Desrosiers, M., Barnes, P.W., 1995. Sea ice scouring on the inner shelf of the southeastern Canadian Beaufort Sea. *Mar. Geol.* 128, 201–219.
- Highsmith, R.C., Coyle, K.O., 1990. High productivity of northern Bering Sea benthic amphipods. *Nature* 344, 862–863.
- Holte, B., 1998. The macrofauna and main functional interactions in the sill basin sediments of the pristine Holandsfjord, North Norway, with autecological reviews for some key-species. *Sarsia* 83, 55–68.
- Holte, B., Gulliksen, B., 1998. Common macrofaunal dominant species in the sediments of some north Norwegian and Svalbard glacial fjords. *Polar Biol.* 19, 375–382.
- Jangoux, M., Lawrence, J.M., 1982. Echinoderm nutrition. A.A. Balkema, Rotterdam.
- Kamp, A., Witte, U., 2005. Processing of ¹³C-labelled phytoplankton in a fine-grained sandy-shelf sediment (North Sea): relative importance of different macrofauna species. *Mar. Ecol., Prog. Ser.* 297, 61–70.
- Lee, S.H., Schell, D.M., McDonald, T.L., Richardson, W.J., 2005. Regional and seasonal feeding by bowhead whales *Balaena mysticetus* as indicated by stable isotope ratios. *Mar. Ecol., Prog. Ser.* 285, 271–287.
- Levin, L., Blair, N., DeMaster, D., Plaia, G., Fornes, W., Martin, C., Thomas, C., 1997. Rapid subduction of organic matter by malदानaid polychaetes on the North Carolina slope. *J. Mar. Res.* 55, 595–611.

- Lewis, C.F.M., Blasco, S.M., 1990. Character and distribution of sea-ice and iceberg scours: keynote address. In: Clark, J.I. (Ed.). Workshop on ice scouring and design of offshore pipelines, Calgary, Alberta, April 18–19, 1990. Canada Oil and Gas Lands Administration, Energy, Mines and Resources Canada and Indian and Northern Affairs Canada.
- Lovvorn, J.R., Cooper, L.W., Brooks, M.L., De Ruyck, C.C., Bump, J.K., Grebmeier, J.M., 2005. Organic matter pathways to zooplankton and benthos under pack ice in late winter and open water in late summer in the north-central Bering Sea. *Mar. Ecol., Prog. Ser.* 291, 135–150.
- McKeague, J.A., Editor, 1976. Manual of soil sampling and methods of analysis. Soil Research Institute, pp. 81–155.
- Mills, E.L., 1967. The biology of an ampeliscid amphipod crustacean sibling species pair. *J. Fish. Res. Board Can.* 24, 305–355.
- Myers, R., Blasco, S., Gilbert, G., Shearer, J., 1996. 1990 Beaufort Sea ice scour repetitive mapping program. Volume 1. Environmental Studies Research Funds Report No. 129.
- Norkko, A., Hewitt, J.E., Thrush, S.F., Funnell, G.A., 2001. Benthic–pelagic coupling and suspension-feeding bivalves: linking site-specific sediment flux and biodeposition to benthic community structure. *Limnol. Oceanogr.* 46, 2067–2072.
- Norling, K., Rosenberg, R., Hulth, S., Grémare, A., Bonsdorff, E., 2007. Importance of functional biodiversity and species-specific traits of benthic fauna for ecosystem functions in marine sediment. *Mar. Ecol., Progr. Ser.* 332, 11–23.
- O'Brien, M.C., Macdonald, R.W., Melling, H., Iseki, K., 2006. Particle fluxes and geochemistry on the Canadian Beaufort Shelf: implications for sediment transport and deposition. *Cont. Shelf Res.* 26, 41–81.
- Oliver, J.S., Slattery, M.A., Silberstein, M.A., O'Connor, E.F., 1983. A comparison of gray whale, *Eschrichtius robustus*, feeding in the Bering Sea and Baja California. *U. S. Nat. Mar. Fish. Serv. Fish. Bull.* 81, 513–522.
- Papaspyrou, S., Gregersen, T., Kristensen, E., Christensen, B., Cox, R.P., 2006. Microbial reaction rates and bacterial communities in sediment surrounding burrows of two nereidid polychaetes (*Nereis diversicolor* and *N. virens*). *Mar. Biol.* 148, 541–550.
- Peachey, R.L., Bell, S.S., 1997. The effects of mucous tubes on the distribution, behaviour and recruitment of seagrass meiofauna. *J. Exp. Mar. Biol. Ecol.* 209, 279–291.
- Pearson, T.H., 2001. Functional group ecology in soft-sediment marine benthos: the role of bioturbation. *Oceanogr. Mar. Biol.* 39, 233–267 (an Annual review).
- Peck, L.S., 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. *Polar Biol.* 25, 31–40.
- Piepenburg, D., 2005. Recent research on Arctic benthos: common notions need to be revised. *Polar Biol.* 28, 733–755.
- Piepenburg, D., Schmid, M.K., 1996. Distribution, abundance, biomass, and mineralization potential of the epibenthic megafauna of the Northeast Greenland shelf. *Mar. Biol.* 125, 321–332.
- Pörtner, H.O., Knust, R., 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315, 95–97.
- Renaud, P.E., Riedel, A., Michel, C., Morata, N., Gosselin, M., Juul-Pedersen, T., Chiuchiolo, A., 2007a. Seasonal variation in benthic community oxygen demand: a response to an ice algal bloom in the Beaufort Sea, Canadian Arctic? *J. Mar. Syst.* 67, 1–12.
- Renaud, P.E., Morata, N., Ambrose Jr., W.G., Bowie, J.J., Chiuchiolo, A., 2007b. Carbon cycling by seafloor communities on the eastern Beaufort Sea shelf. *J. Exp. Mar. Biol. Ecol.* 349, 248–260.
- Schmid, M.K., Piepenburg, D., Golikov, A.A., von Juterzenka, K., Petryashov, V.V., Spindler, M., 2006. Trophic pathways and carbon flux patterns in the Laptev Sea. *Prog. Oceanogr.* 71, 314–330.
- Schuman, G.E., Stanley, M.A., Knudsen, D., 1973. Automated total nitrogen analysis of soil and plant samples. *Soil Sci. Soc. Am. Pro.* 37, 480–481.
- Seuthe, L., Darnis, G., Riser, C.W., Wassmann, P., Fortier, L., 2007. Winter–spring feeding and metabolism of Arctic copepods: insights from faecal pellet production and respiration measurements in the southeastern Beaufort Sea. *Polar Biol.* 30, 427–436.
- Snelgrove, P.V.R., Grassle, J.F., Grassle, J.P., Petrecca, R.F., Stocks, K.I., 2001. The role of colonization in establishing patterns of community composition and diversity in shallow-water sedimentary communities. *J. Mar. Res.* 59, 813–831.
- Steffens, M., Piepenburg, D., Schmid, M.K., 2006. Distribution and structure of macrobenthic fauna in the eastern Laptev Sea in relation to environmental factors. *Polar Biol.* 29, 837–848.
- Tremblay, J.-E., Hattori, H., Michel, C., Ringuette, M., Mei, Z.-P., Lovejoy, C., Fortier, L., Hobson, K.A., Amiel, D., Cochran, K., 2006. Trophic structure and pathways of biogenic carbon flow in the eastern North Water Polynya. *Prog. Oceanogr.* 71, 402–425.
- Wacasey, J.W., Atkinson, E.G., Derick, L., Weinstein, A., 1977. Zoobenthos data from the southern Beaufort Sea, 1971–1975. *Fish. Mar. Serv. Data Rep.* 41, 187 pp.
- Warwick, R.M., Clarke, K.R., 1995. New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar. Ecol., Progr. Ser.* 129, 301–305.
- Williams, W.J., Carmack, E.C., Shimada, K., Melling, H., Aagaard, K., Macdonald, R.W., Ingram, R.G., 2006. Joint effects of wind and ice motion in forcing upwelling in Mackenzie Trough, Beaufort Sea. *Cont. Shelf Res.* 26, 2352–2366.
- Wlodarska-Kowalczyk, M., Pearson, T., 2004. Soft-bottom macrobenthic faunal associations and factors affecting species distributions in an Arctic glacial fjord (Kongsfjord, Spitsbergen). *Polar Biol.* 27, 155–167.