

# Ice scour disturbance to benthic communities in the Canadian High Arctic

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**ABSTRACT:** Seabed scouring by ice is a large-scale disturbance to polar coasts. Grounding ice modifies seabed topography, reworks the sediment, and ploughs and crushes the seabed biota. The effects of ice scour on soft-sediment benthos were examined in Barrow Strait in High Arctic Canada. Due to the variability of ice keel depths in this area, the Barrow Strait coast was found to exhibit a gradient of ice scour disturbance to 30 m depth. The inshore shallows were highly scoured by the abundant shallow draft ice. Deeper water scours caused by icebergs and portions of ice shelves were less frequent. The benthos paralleled this disturbance gradient, with the inshore consisting of a disturbance-associated fauna. Four recently formed ice scours were studied at 3 locations. Despite differences in exposure to currents and water depth, all scours were dominated by the same disturbance-associated fauna and were distinctive from the benthos outside. Scavenging amphipods and gastropods consumed bivalves that were dislodged and damaged, while predatory amphipods and opportunistic polychaetes burrowed in the gouged and displaced clays. Our expectation was that the topography of the ice scours would select for different colonizing species. However, there was no evidence of preferential occupation of the raised berms by suspension feeders or of the troughs by deposit feeders. The species that dominated the 4 scours also dominated the less recently disturbed areas of the inshore, despite the fact that these areas were situated 300 to 400 m inshore and at shallower depth. The prevalence of species that associate with ice scours indicates that ice disturbance is an important factor that molds coastal benthic zonation at this Arctic location.

**KEY WORDS:** Ice scour · Disturbance · Benthos · Arctic

## INTRODUCTION

Natural physical disturbance can have a major influence on both aquatic and terrestrial communities. Effects include opening of cleared patches, alteration of physico-chemical characteristics, opportunity for colonization by different species, altered community structure, and changed species interactions (Sousa 1984, Pickett & White 1985). Effects on the marine environment have been reviewed by Sousa (1985) for

intertidal communities, Connell & Keough (1985) for coral reefs, and Hall (1994) for soft sediment benthos. Common natural physical agents of seafloor disturbance are water motion, altered water temperature, unstable seabed, settling sediment, biotic foraging activity, and bioturbation (Sousa 1984, Connell & Keough 1985, Hall 1994). On polar coasts, the major chronic disturbance to both the shore and seafloor is scouring by grounding drift ice and pressure ridges. These erode hard and soft substrates alike, producing long scrapes and gouges, plough-shaped indentations, and basin-shaped depressions. Ice scour disturbance to soft sediments is a regular, predictable event on polar coasts. It differs from other such disturbances by ploughing and overturning the sediment and altering seabed topography, sometimes considerably. Icebergs have been known to scour a swath of seabed as wide as 1375 m and gouge an incision as deep as 11.5 m

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(Lewis & Blasco 1990). On deep seafloor, such disturbances may take millennia to disappear (Pereira et al. 1985, Josenhans & Woodworth-Lynas 1988).

The notion that ice scour can shape both the geology and biology of polar coasts was expressed by Darwin in 1837 (Levere 1993). Since then, considerable investigation of the physical effects of ice scour has been made, spurred by concerns for potential effects on man-made structures on the seabed (for reviews, see Barnes & Reimnitz 1974, Reimnitz & Barnes 1974, Reimnitz et al. 1977, Barnes et al. 1984, Weeks et al. 1984, Gilbert & Pedersen 1987, Clark 1990). The impact of ice scour may be similar to the effects of such anthropogenic physical disturbances as seabed dredging and trawling (Messieh et al. 1991, Thrush et al. 1995, Currie & Parry 1996).

Ice scouring is a large-scale coastal sediment reworking event on both the Arctic and Antarctic coasts. The coasts of Arctic and Atlantic Canada, Alaska, Russia, Svalbard, Norway, the Barents Sea, and Greenland, and the full coast of Antarctica are all vulnerable to ice disturbance. This amounts to some 149 000 km of coast (Munro 1988, Kurian 1989). In the Arctic, the Beaufort Sea is 100% scoured by pressure ridges and multiyear ice keels from shore to 40 m depth, and scouring reaches as deep as 72 m (Lewis & Blasco 1990). At 6 to 14 m water depth, the Beaufort seabed can be completely reworked within 50 yr (Reimnitz et al. 1977). On the Canadian Atlantic coast, icebergs from Greenland and the eastern Canadian Arctic scour as deep as 230 m (Lewis & Blasco 1990). The Antarctic ice shelves have produced 70 000 icebergs (more than 10 m wide) between 1981 and 1985 (Lien et al. 1989). These have scoured the seabed to water depths of up to 500 m (Barnes & Lien 1988, Lien et al. 1989). Relict Pleistocene scours are still visible on the Canadian Atlantic seabed to 700 m depth (Pereira et al. 1985, Josenhans & Woodworth-Lynas 1988), and iceberg scours are clearly visible on the former bed of glacial Lake Agassiz in central Canada (Woodworth-Lynas & Guigné 1990). During glacial periods, ice scouring would have reached considerably lower latitudes, to as low as 40° N in the North Atlantic (Bond et al. 1992).

Most information on the biological consequences of ice scour comes from intertidal habitats or rocky shores. In the subarctic and subantarctic intertidal zones, diversity is considerably reduced by ice scour and ephemeral algae quickly colonize denuded areas (Ellis & Wilce 1961, Kauffman 1977, O'Clair 1981, Bolton 1983, Gordon & Desplanque 1983, Keats et al. 1985, Wilson 1988, Hooper & Whittick 1990, McCook & Chapman 1993). Crevices on rocky shores provide refuges for recolonization (O'Clair 1981, Heine 1989). If scouring is sufficiently frequent, long-lived species with delayed reproduction are prevented from col-

onizing (Robertson & Mann 1984, Wethey 1985, Peck & Bullough 1993). Overall species diversity can be enhanced through removal of dominant competitors and clearing of patches for colonization by other species (DeLaca & Lipps 1976, Keats et al. 1985). Plant morphology can be altered by regular ice pruning (Mathieson et al. 1982). Ice detachment and rafting can introduce biota to new areas (Mathieson et al. 1982), while ice-damaged biota can provide nutrient supplies to other areas after rafting, deposition, and decomposition (Mathieson et al. 1982). In the Gulf of St. Lawrence, Canada, snow geese use ice-scoured depressions in marshes for foraging (Bélanger & Bédard 1994, 1995).

Recent work by Lenihan & Oliver (1995) on subtidal, soft sediment infauna in McMurdo Sound, Antarctica, showed that iceberg scouring removes late successional species and creates opportunity for colonization by early successional species. The purpose of our study was to further this analysis in a different soft-sediment environment (Barrow Strait, in the Canadian High Arctic). Pressure ridges and single- and multiyear drift ice are abundant along the eastern Canadian Arctic coast (Lewis & Blasco 1990). Less abundant deep draft icebergs and portions of ice shelves originate in Greenland and the northern Canadian Arctic archipelago (Lewis & Blasco 1990). Due to the variability of ice keel depths, we predicted that the Barrow Strait coast would exhibit a gradient of ice scour disturbance with depth, with the inshore shallows being highly scoured by the abundant shallow draft ice. Deeper water scours offshore would be less frequent. The benthos should parallel this disturbance regime, with the inshore consisting of a disturbance associated fauna similar to that found by Lenihan & Oliver (1995). However, since most Arctic benthic species have depth ranges that span the ice scour zone in Barrow Strait (0 to 30 m) (Macpherson 1971, Curtis 1972, Sekerek et al. 1976, Lubinsky 1980, Welch et al. 1992, Aitken & Fournier 1993), we predicted that deep water scours would have a species composition similar to that of the inshore benthos, in spite of separation and differences in depth. We also predicted that the topography of the ice scours would select for different colonizing species. Marine invertebrates preferentially colonize seabeds using a variety of physical, chemical, and biological cues including seabed topography (VanBlaricom 1982, Oliver & Slattery 1985, Oliver et al. 1985). Suspension feeders could predominate on the berms of sediment pushed up by the ice, which would elevate the substrate in the water column. The troughs could act as catchment basins for detritus, and favor deposit feeders.

We assessed scour disturbance along the Barrow Strait coast near the Hamlet of Resolute Bay, Northwest Territories, Canada. We determined scour distribution and compared the biota along a gradient of

depths in 3 locations, using 4 scours. This is part of a larger study determining the impact of ice scour and sequence and rate of recolonization and scour degradation. Other publications from this study are Fournier & Conlan (1994) and Kvittek et al. (1998). Our results will improve our understanding of the effects of a common and widespread natural disturbance to the benthos of polar oceans.

## MATERIALS AND METHODS

Fig. 1 shows the Barrow Strait study area along the southern coast of Cornwallis Island. This area was chosen for its accessibility and good visibility for scuba divers. The glacial clay sediment retained a clear record of scour events, such that the raised berms and incised troughs of ice scours were clearly discernable from level, unscoured areas. Criteria for recency of scour were the degree of weathering of the scour berms and troughs (sharp berms, no subsidence of sediment, presence of ice impressions and grooves in the trough) and the presence of dislodged and damaged fauna lying on the surface. Physical parameters of the scours, such as berm height, incision depth, trough length, and water depth, were measured by scuba divers. Currents in Resolute Bay and Barrow Strait were measured by 3-replicate S-4 current meters placed on the seabed for 24 h. Distance from shore was determined from aerial observation and differential GPS (Global Positioning System). The scours were mapped by sidescan sonar using an EG&G 260TH Dual Frequency (100/500 kHz) sidescan sonar. Bathymetry was determined using a 208 kHz Innerspace 448 digital fathometer. Amount of seabed disturbance was calculated from sidescan sonar images taken in August 1996 along the Barrow Strait coast from Cape Martyr to the mouth of Resolute Bay. Area of sidescan coverage was from 5 to 50 m depth. Three 100 m wide depth transects were selected on records that covered uniformly sloping seabed from in-shore to 50 m depth. Disturbance was calculated as the number of grid points out of a total of 38 that touched a scour trough or berm on the sidescan images at each 25 m interval. This method had a 5% error rate, based on repeat measurements of the same transect. Old scour marks, which are still physically recognizable but are biologically

indistinguishable from reference seabed (Conlan unpubl. data), were designated as biologically undisturbed. Ongoing assessment of scour degradation rate indicates that these scours are over 50 yr old (Conlan unpubl. data).

Fauna were sampled inside and in the proximity of 2 scours in Resolute Bay and 1 each in Assistance Bay and Barrow Strait (Fig. 1). These scours were located 300 to 400 m offshore. All sampling occurred in August 1991, during which time weather and ice conditions allowed access to the seabed. Nevertheless, pack ice inundations made the study sites inaccessible for more than 60% of the field season. The opportunity to replicate scours was limited by the large amount of underwater search time needed to locate scours that were relatively large, distinct, and obviously recent in origin.

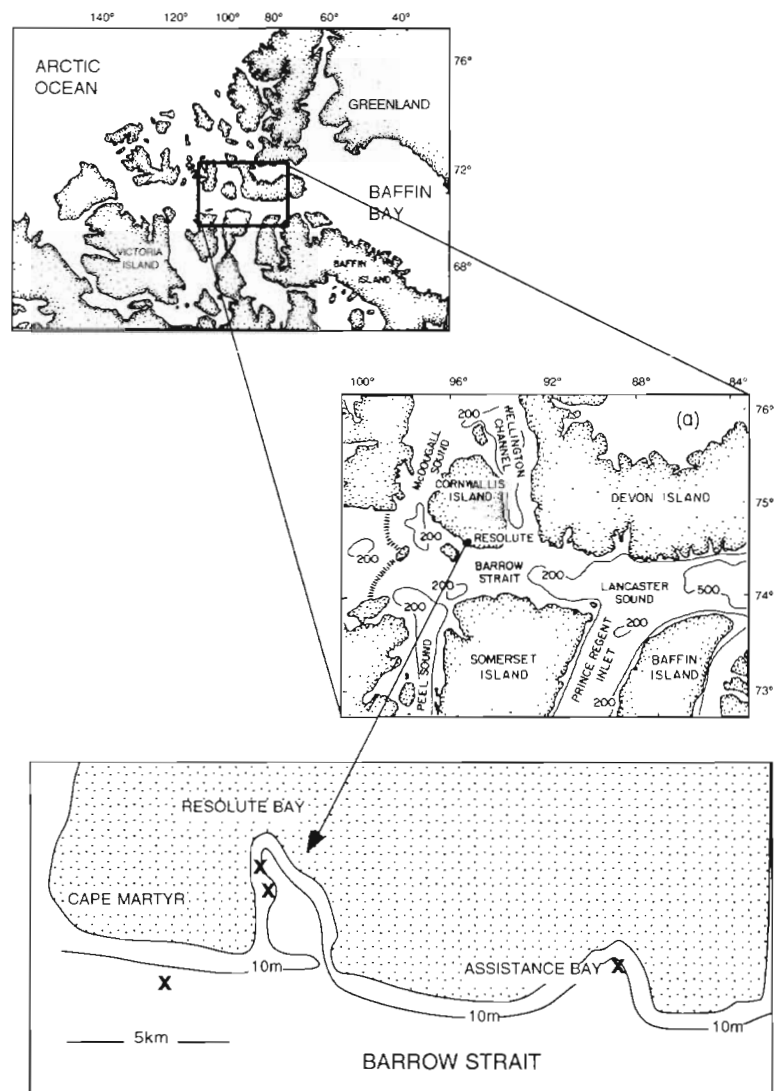


Fig. 1 The 3 study areas on the coast of Cornwallis Island in High Arctic Canada: Assistance Bay, Resolute Bay, and Barrow Strait between Cape Martyr and the mouth of Resolute Bay. X: scour locations

Each of the 4 scours was sampled for benthic fauna on the trough, berm, and at 2 locations outside. The one outside site was next to the scour, while the other was 50 m away. All samplers were placed haphazardly. Large epifauna were counted by divers in 4 replicate 1 m × 10 m transects. The transects were placed along depth contours in order to maintain a constant sampling depth. The siphons of large individuals of the bivalves *Mya truncata* and *Serripes groenlandicus* were counted in 4 replicate 1 m<sup>2</sup> quadrats. Size frequency was measured from bivalves that were suction sampled in 1 m<sup>2</sup> of seabed to 20 cm sediment depth. Small macrofauna were collected with 6 replicate 0.0075 m<sup>2</sup> cores to 10 cm sediment depth. To compare community composition of the offshore scours to that of the inshore shallows, the 2 sampling sites outside each scour were extended inshore and offshore as depth transects. Six replicate core samples were taken along each transect at 3 m depth intervals from 3 to 15 m at sites that had not obviously been recently disturbed. Criteria for undisturbed conditions were presence of large kelps, even terrain, lack of ice scour marks, and cobbles with dense cover of coralline algae. These are termed 'outside' sites herein. Sediment samples were taken at each site and analyzed for grain size distribution by standard sieve methods.

The bivalve suction samples and the core samples for small fauna were sieved on a 0.5 mm mesh. The suctioned bivalves were sorted into species, enumerated, and weighed after drying on absorptive tissue for 1 min (damp-dry) while alive. The core-sampled fauna were fixed in 5% formalin-seawater, preserved in 70% glycerated ethanol, returned to the lab, microscopically sorted and identified to the lowest possible taxonomic level, enumerated, and weighed damp-dry. Feeding and burrowing characteristics of the fauna were determined from Reid & Reid (1969), Stanley (1970), Bernard (1979), Fauchald & Jumars (1979), Barnes (1980), E. L. Bousfield (Royal Ontario Museum pers. comm.), and J. Fournier and A. Martel (Canadian Museum of Nature pers. comm.).

Two-way ANOVA was applied to test for significant differences in abundance of large scuba-surveyed fauna, using the 4 scours and the substrate types (outside, berm, and trough) as crossed, fixed factors. Normality was tested using the Kolmogorov-Smirnov test, and heterogeneity of variances was tested with a Levene Median test.  $\log_{10}(x+1)$  or  $\sqrt{x+0.5}$  transformations were applied to achieve normality and equal variance. Post hoc multiple comparisons within main effects were made using the Tukey test. The significance level for all tests was  $p < 0.05$ .

Multivariate analyses were applied to the core collections of small fauna (which constituted the bulk of benthic abundance). The data were analysed using the

PRIMER software package described in Clarke (1993). Dominance-diversity was computed with the DOMPLOT program as cumulative dominance on the total faunal matrices for each location ( $k$ -dominance curves; Lamshead et al. 1983). The degree of multivariate dispersion of the replicates in each site was determined by the MVDISP procedure (Warwick & Clarke 1993). Non-metric multidimensional scaling (MDS) (Kruskal 1964) and UPGMA (unweighted pair-group method using arithmetic averages; Sokal & Mitcheener 1958) cluster analysis using the Bray-Curtis (1957) similarity coefficient were applied to  $\log_{10}(x+1)$ -transformed abundances following removal of taxa that occurred in less than 5% of the samples. Environmental variables were linked to the multivariate community patterns using the BIO-ENV program described in Clarke & Ainsworth (1993). Differences among the scours were computed by ANOSIM, a multivariate form of ANOVA described in Clarke (1993). Species responsible for the major groups generated by cluster analysis were determined with the SIMPER program.

## RESULTS

### Physical characteristics

The coastal seabed in the Barrow Strait study region is a mixed glacial till covered by a cobble veneer. Scouring removes the cobble cover and exposes the underlying clay. At 20 m water depth, the glacial till is about 5 m in thickness above the underlying bedrock. This cover is reduced to near zero at 0 to 5 m water depth. The seabeds of Assistance and Resolute Bays are also a mixed glacial till, but lack the cobble veneer. The 3 areas differ somewhat in that Resolute Bay has little current (not detectable over 1 tidal cycle in August 1994) and is protected from scouring beyond 11 m depth by a sill at the mouth (Fig. 1). Assistance Bay resembles Resolute Bay in aspect, but is not protected from deep draft ice by a sill. Barrow Strait has tidal currents at the sediment surface that reach 31 cm s<sup>-1</sup> (measured over 1 tidal cycle in August 1994) and receives the full range of scour from small annual ice to large icebergs and multiyear ice keels.

Fig. 2 shows the process by which a moving ice keel scours the seabed. The incision left by the ice is the scour trough, and the mounds of sediment pushed up to either side are the scour berms. Uneven keels may produce parallel grooves in the trough, and movement pressures may create fractures in the trough. Ice keels may also wallow in a stationary position on the seabed, in which case a more circular pit may be formed.

Fig. 3 shows the intensity of scouring observed along the 3 depth transects in Barrow Strait. As predicted,

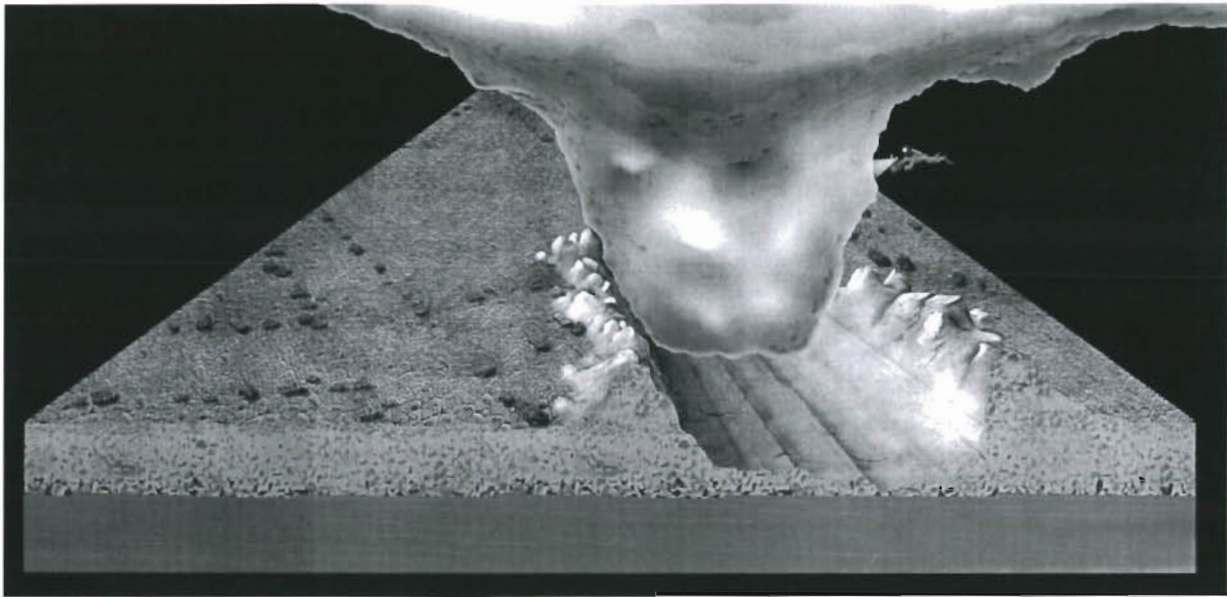


Fig. 2. Process of seabed scouring in Barrow Strait, showing the scour trough incised by the ice keel and the berms of sediment pushed up to either side. Parallel grooves produced by the uneven keel form in the scour trough, along with periodic fractures. The seabed is mixed glacial clay overlying bedrock. Remains of old scours appear as parallel rows of boulders left of the now eroded berms

scours were most abundant inshore and declined in frequency offshore. Seabed at water depths of 0 to 5 m was nearly 100% scoured, and 26 to 100% scoured at 6 to 10 m. Diver observation and sidescan images indicated that the incisions were usually less than 0.5 m deep, and the scours tended to be narrow (<5 m wide).

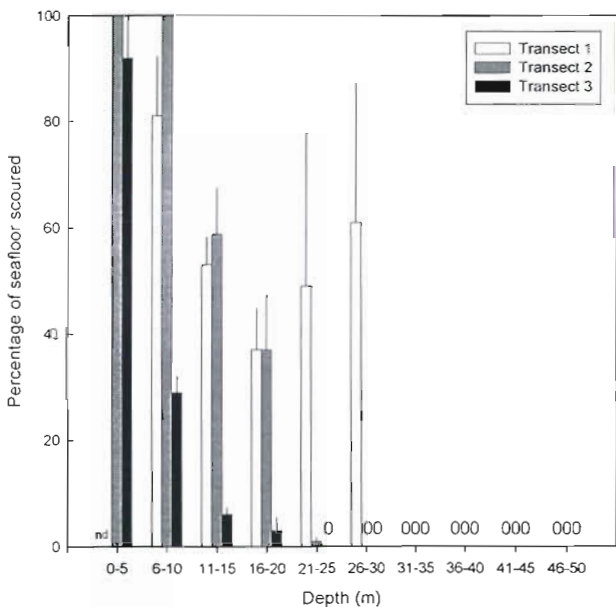


Fig. 3. Percentage of seafloor scoured ( $\pm$ SE) in three 100 m wide belt transects in Barrow Strait. nd = no data

The occurrence of pitting was common inshore, resulting from tidal lifting and grounding of ice. Despite the apparent 100% scour frequency inshore as shown by sidescan sonar, finer resolution by divers indicated areas of dense kelp cover between the scours. Diver observation of the ice-scouring process showed that the ice crushed the kelp, tore the blades from the stipes, or removed the algae entirely. Thus, areas that were densely covered with long-bladed kelp were considered to have not been recently scoured and were used as reference sites for biological sampling. At 11 to 30 m, the amount of seabed scoured was highly variable. This was due to the presence of infrequent, but large, scours. Transect 1 crossed such a scour, which paralleled the shore and was 100 m wide. This scour accounts for the increase in scouring seen at 21 to 30 m in Fig. 3. Scours at this depth typically incised 0.5 to 1.0 m of sediment, with the greatest penetration being 2.5 m. From 30 to 50 m depth, scours were rare and often subdued in contour, suggesting that they were old. Sidescanning in Resolute Bay revealed that the seabed was more often characterized by the pitting and scraping of stationary, wallowing ice keels than by long gouges. Scouring was restricted to depths less than 11 m by the sill at the mouth of the bay. Assistance Bay was not surveyed by sidescan sonar. Diver observation indicated a mix of pitting and longer scrapes.

Physical characteristics of the 4 scours used for biological study are summarized in Table 1. The scours were located 300 to 400 m offshore. Water depths

Table 1. Physical characteristics of the 4 ice scours

Location	Water depth (m)	Distance from shore (m)	Scour length (m)	Scour width (m)	Average berm height (m)	Average incision depth (m)	Sediment grain size (mean phi)	
							Berm	Trough
Resolute Bay	6	300	40	3	1.0	0.25	2.33	2.34
Resolute Bay	9	300	13	13	1.5	1.0	0.58	2.91
Assistance Bay	6	400	50	6	1.0	0.5	-0.82	1.24
Barrow Strait	15	400	40	3–4	1.5	1.5–2.0	1.34	0.79

varied from 6 to 15 m. Of the 4, the Barrow Strait scour was at greatest water depth and incised the seabed most deeply. Each scour consisted of clay with buried cobble, gravel, and shell. All scours appeared to have been formed since ice breakup 2 wk before sampling. The Resolute and Assistance Bay scours contained uprooted and damaged clams that had not yet lost their tissue to scavengers. The Barrow Strait scour lacked dislodged infauna and therefore was possibly older. However, like the other scours, it had sharp berms and a smooth clay trough, which contrasted with the cobble-veneered clay outside. None of the scours contained anoxic, discolored water as described by Kvittek et al. (1998).

### Biotic characteristics

#### Comparison of the scours with the outside

Most large fauna that could be quantified by scuba diving showed low abundance within the ice scours. The large bivalves *Mya truncata* and *Serripes groenlandicus*, which were inaccessible by core collection, were quantified by a siphon count. Mean density of their siphons differed significantly among the 4 scours across the 3 substrates (outside, berm, and trough) (Table 2). Mean density was significantly greater outside the Barrow Strait scour ( $41.8 \pm 3.7 \text{ m}^{-2}$ ) than outside the 2 Resolute Bay scours ( $23.0 \pm 4.7 \text{ m}^{-2}$  and  $26.0 \pm 2.8 \text{ m}^{-2}$ ) (Tukey tests,  $p < 0.05$  for both comparisons) (Table 3). At both locations, mean density was

significantly lower inside the scours than outside (post hoc Tukey tests; Table 3). Shell size-frequency analysis of suction samples at 12 m depth revealed that *M. truncata* was significantly smaller in Barrow Strait than in Resolute Bay ( $t = 3528.5$ ,  $p < 0.001$ ). Mean shell length in Barrow Strait averaged  $3.6 \pm 0.08 \text{ cm}$  ( $n = 156$ ), while in Resolute Bay it was  $5.0 \pm 0.17 \text{ cm}$  ( $n = 26$ ).

The relative abundance of other large, widely dispersed fauna was also determined by scuba survey. Buccinid gastropod distribution exhibited a significant difference among scours and substrates (Table 2). However, there was not a significantly lower abundance inside the scours than outside as there was for the bivalves (Table 3). Indeed, at the Barrow Strait scour, abundance on the berm was significantly greater than abundance outside. Buccinids were found scavenging damaged individuals of *Mya truncata* and *Serripes groenlandicus* that were uprooted and lying exposed on the scours. Other scavengers present in the scours but not quantified were various lysianassid amphipods (*Onisimus* spp., *Boeckosimus affinis*, and *Anonyx nugax*). These amphipods were abundant inshore as well, burrowing into the sediment and descending en masse if offered damaged fauna.

Several other large invertebrates were found in relatively high abundance outside the Barrow Strait scour, but were absent or in low abundance inside the scour. These were the sea urchin *Strongylocentrotus* spp. (*S. droebachiensis* and *S. pallidus*), the soft coral *Gersemia rubriformis*, the sea cucumber *Cucumaria* sp., infaunal anemones, and solitary tunicates. Mean abundance ranged from  $155.0 \pm 19.4 \text{ 10m}^{-2}$  for the urchins to  $2.5 \pm 0.6 \text{ 10m}^{-2}$  for the tunicates ( $n = 4$ ). All but the urchins were entirely absent within the scour. Urchin density varied significantly with substrate (1-way ANOVA,  $F = 26.585$ ,  $p < 0.001$ ), with mean density being significantly lower both on the berm and inside the trough than outside, but not significantly different between berm and trough (Tukey test,  $p < 0.05$ ). These species were too rare to be quantified in Resolute and Assistance Bays.

Table 2. Results of 2-way ANOVA of large bivalves and buccinid gastropods. Data were log-transformed for the bivalves and untransformed for *Buccinum* spp. abundance

	Bivalves (siphons $\text{m}^{-2}$ )				<i>Buccinum</i> spp. (ind. $10 \text{ m}^{-2}$ )			
	df	MS	F-ratio	p-value	df	MS	F-ratio	p-value
Scour (a)	2	0.269	27.982	<0.001	2	11.194	5.422	0.010
Substrate (b)	2	6.113	635.075	<0.001	2	15.361	7.439	0.003
a × b	4	0.494	51.330	<0.001	4	8.694	4.211	0.009
Residual	27	0.010			27	2.065		

Table 3. Mean ± SE abundance (n = 4) of the species in Table 2 and post hoc Tukey test q-values for comparisons between outside and inside the scour. Differences are significant at p < 0.05 (\* significant; ns: not significant)

Species	Location	Outside	Scour berm	q (berm vs outside)	Scour trough	q (trough vs outside)
Bivalves (siphons m <sup>-2</sup> )	Resolute Bay, 6 m	23.0 ± 4.7	8.8 ± 0.85 <sup>a</sup>	7.504*	0.5 ± 0.3 <sup>a</sup>	24.498*
	Resolute Bay, 9 m	26.0 ± 2.8	6.2 ± 0.55 <sup>a</sup>	11.562*	0	29.040*
	Assistance Bay, 6 m	No data	No data	No data	No data	No data
	Barrow Strait, 15 m	41.8 ± 3.7	0	33.156*	0	33.156*
<i>Buccinum</i> spp. (ind. 10m <sup>-2</sup> )	Resolute Bay, 6 m	2.0 ± 0.9	0.5 ± 0.5	2.088ns	1.0 ± 0.4	1.392ns
	Resolute Bay, 9 m	2.8 ± 0.5	3.5 ± 0.6	1.044ns	0.8 ± 0.5	2.784ns
	Assistance Bay, 6 m	No data	No data	No data	No data	No data
	Barrow Strait, 15 m	2.2 ± 0.8	5.8 ± 1.3	4.871*	1.3 ± 0.5	1.392ns

<sup>a</sup>Dislodged and damaged

Fig. 4 shows the relative abundance and biomass (wet weight) of the small, core-collected fauna at the 3 sites. In the undisturbed sediments outside the scours, mean abundance ranged from 70.3 to 399.7 ind. core<sup>-1</sup>. Mean wet weight ranged from 0.3 to 25.6 g core<sup>-1</sup>. In Barrow Strait abundance and biomass increased with depth. In the 2 bays no consistent trend was apparent. Within the ice scours, abundance was significantly lower than outside in the 2 scoured troughs at Resolute Bay and on the scour berm at Barrow Strait (Tukey test, p < 0.05). Differences in abundance between the scour and the outside sediment were not significant in Assistance Bay. Biomass was significantly lower than outside at all 3 sites, however.

While nemerteans, priapulids, sipunculids, and echinoderms (holothurians) were present outside the scours in many of the cores, over 90% of the species were polychaetes, molluscs, and crustaceans. In total, 131 taxa were identified: 33 were polychaetes, 26 were molluscs, and 52 were crustaceans. The bulk of the polychaetes were in the families Capitellidae, Cirratulidae, Hesionidae, Maldanidae, Paraonidae, Orbiniidae, Pholoidae, Phyllodocidae, Sabellidae, and Spionidae. Molluscan dominants were the gastropods *Cingula castanea*, *Philine lima* and *Retusa obtusa*, and the bivalves *Astarte* spp. (*A. borealis*, *A. cf. montagui*, and *A. cf. warhami*), *Axinopsida orbiculata*, *Macoma* spp. (*M. calcarea*, *M. loveni*, and *M. moesta*), *Musculus dis-*

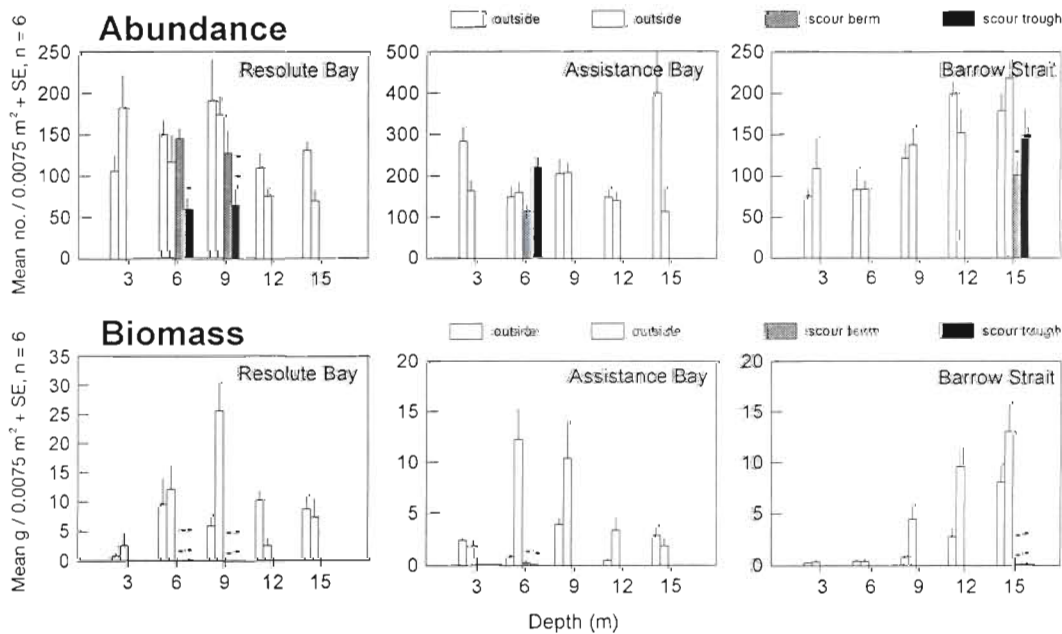


Fig. 4. Total abundance and wet weight biomass of core-collected fauna outside and inside the scoured berms and troughs at the 3 locations. Mean abundance or biomass in the scours are significantly less than outside the scours when marked by a minus sign (-) (Tukey test, p < 0.05). A double negative indicates that abundance or biomass in the scour is significantly less than both sites outside the scour at that same depth

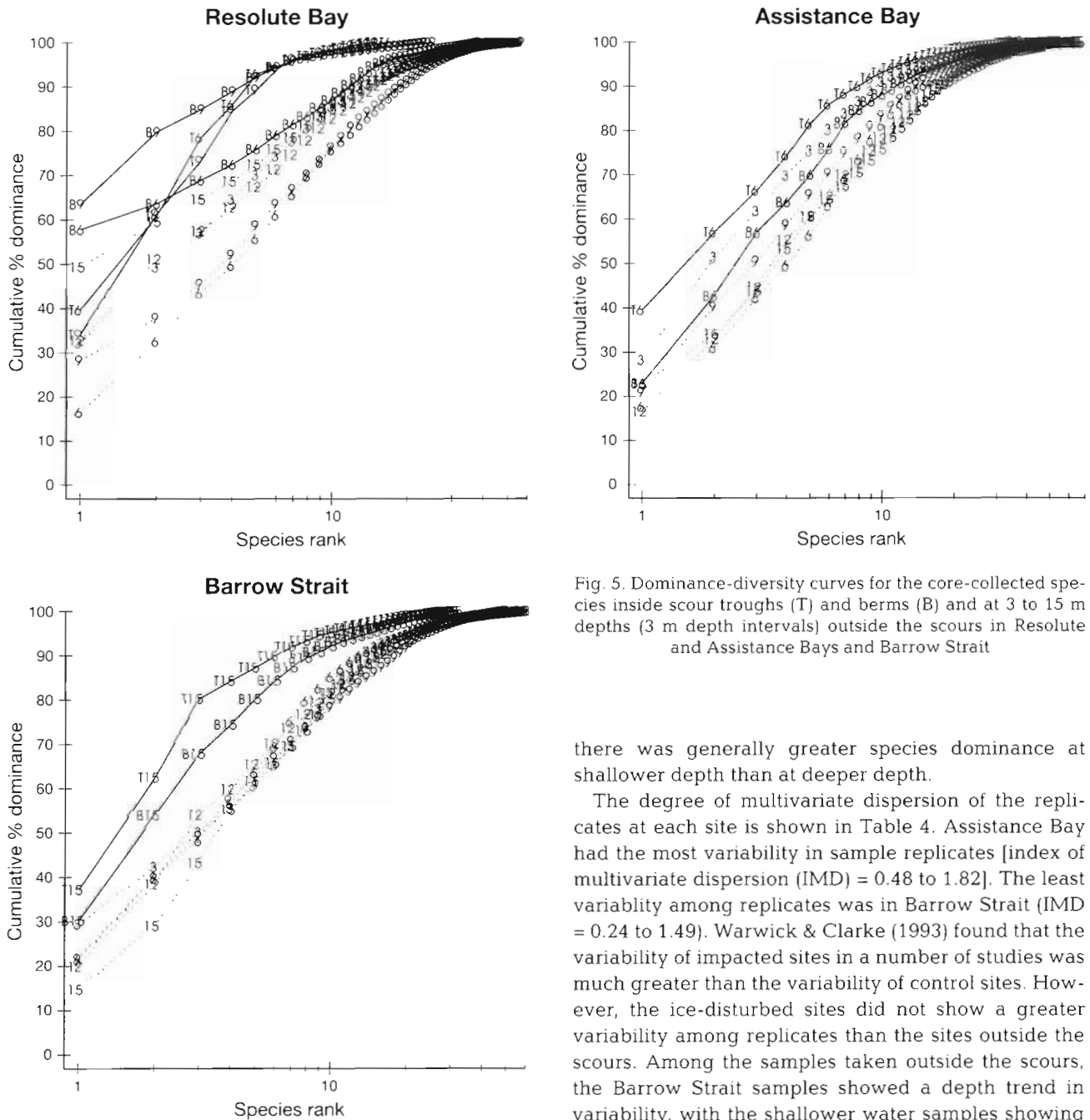


Fig. 5. Dominance-diversity curves for the core-collected species inside scour troughs (T) and berms (B) and at 3 to 15 m depths (3 m depth intervals) outside the scours in Resolute and Assistance Bays and Barrow Strait

there was generally greater species dominance at shallower depth than at deeper depth.

The degree of multivariate dispersion of the replicates at each site is shown in Table 4. Assistance Bay had the most variability in sample replicates [index of multivariate dispersion (IMD) = 0.48 to 1.82]. The least variability among replicates was in Barrow Strait (IMD = 0.24 to 1.49). Warwick & Clarke (1993) found that the variability of impacted sites in a number of studies was much greater than the variability of control sites. However, the ice-disturbed sites did not show a greater variability among replicates than the sites outside the scours. Among the samples taken outside the scours, the Barrow Strait samples showed a depth trend in variability, with the shallower water samples showing more variation among the replicates. There was no consistent depth trend in the Resolute and Assistance Bay samples.

Ordination of the core collections by non-metric multidimensional scaling (MDS) (Fig. 6) demonstrated a change with depth in the fauna outside the ice scours. The samples taken inside the scours grouped apart from their same-depth counterparts outside and were closest in similarity to the shallow water collections. There was some separation of trough from berm samples in Resolute Bay and Barrow Strait. Analysis of all sites combined indicated that there was consider-

cors, *Mya truncata*, and *Thyasira gouldi*. Crustacean dominants were cumaceans, tanaids, myodocopid and podocopid ostracods, and the burrowing amphipods *Monoculodes latimanus*, *Monoculodes vibei*, *Orchomene minutus*, and *Pontoporeia femorata*. Dominance-diversity plots of the samples are shown in Fig. 5. In each location, the communities of the scour troughs and berms showed lower diversity and greater species dominance than did the communities outside the scours. Among the depth transects outside the scours,



Table 4. Sample sites at Resolute Bay, Assistance Bay, and Barrow Strait ordered from lowest to highest multivariate dispersion (IMD) among the replicates (n = 6). Ice scour samples are given in bold

Resolute Bay		Assistance Bay		Barrow Strait	
Site	IMD	Site	IMD	Site	IMD
<b>Trough 6 m</b>	0.38	Outside 3 m	0.48	Outside 15 m	0.24
Outside 12 m	0.57	<b>Trough 6 m</b>	0.56	Outside 12 m	0.42
Outside 15 m	0.62	Outside 9 m	0.72	Outside 12 m	0.69
Outside 9 m	0.65	Outside 9 m	0.86	Outside 15 m	0.87
<b>Berm 9 m</b>	0.78	Outside 6 m	0.88	Outside 9 m	0.88
Outside 6 m	0.93	Outside 12 m	0.90	<b>Trough 15 m</b>	1.09
Outside 3 m	1.05	Outside 15 m	1.00	Outside 9 m	1.16
Outside 12 m	1.17	Outside 3 m	1.06	<b>Berm 15 m</b>	1.21
Outside 6 m	1.18	Outside 6 m	1.13	Outside 3 m	1.24
<b>Trough 9 m</b>	1.23	Outside 12 m	1.18	Outside 6 m	1.28
Outside 9 m	1.29	<b>Berm 6 m</b>	1.37	Outside 6 m	1.44
<b>Berm 6 m</b>	1.30	Outside 15 m	1.82	Outside 3 m	1.49
Outside 3 m	1.37				
Outside 15 m	1.47				

able overlap in species composition at the 3 locations. The single environmental factor that best explained sample groupings was state of disturbance [weighted Spearman or harmonic rank correlation,  $r = 0.441$  (BIOENV procedure)]. Sediment structure (mean phi) was least influential on sample groupings ( $r = 0.096$ ). Disturbance and depth were the best double combination of environmental factors, but reduced the rank correlation to  $r = 0.396$ . Addition of substrate improved the rank correlation to  $r = 0.424$ , but this was still less than the single effect of state of disturbance.

Two-way crossed ANOSIM of the 4 scours showed that each scour differed significantly in community structure

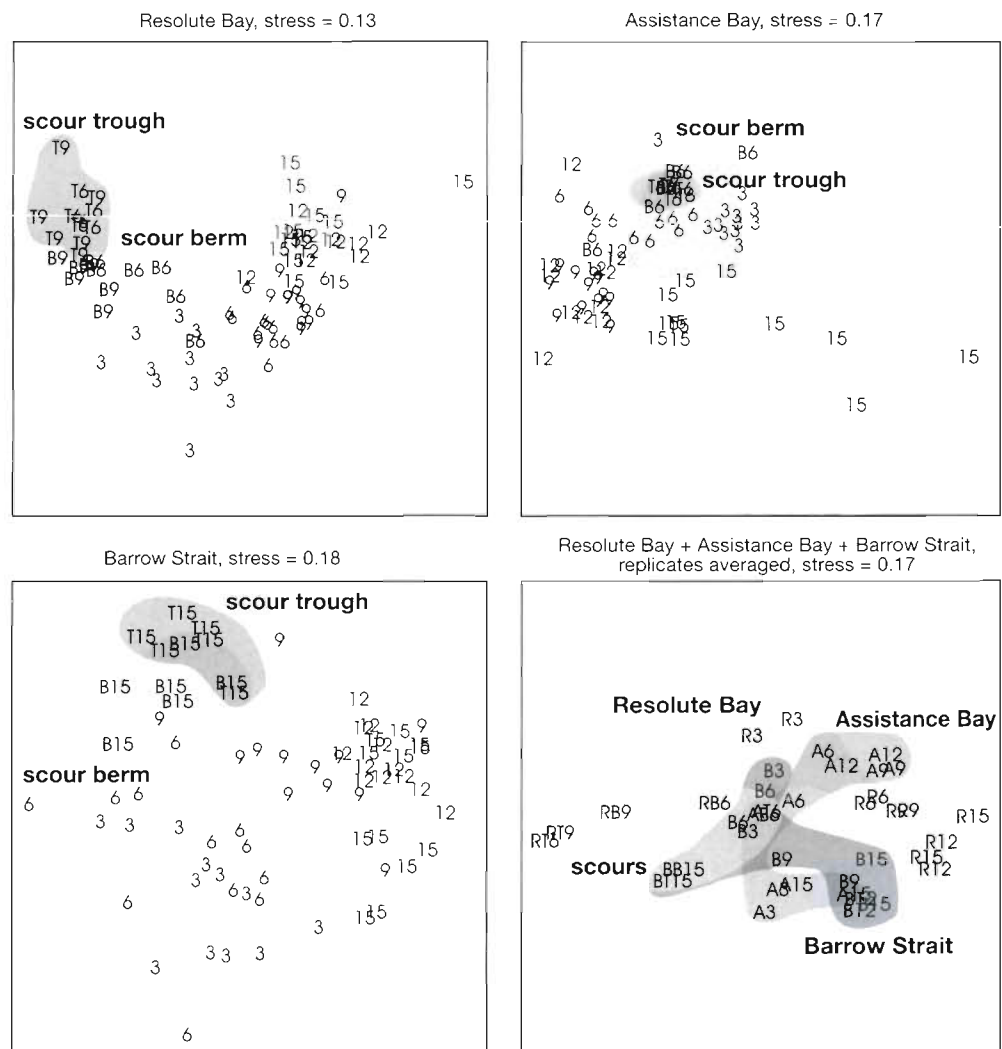


Fig. 6. MDS plots of sample similarity according to species composition inside scour troughs (T) and berms (B) and at 3 to 15 m depths (3 m depth intervals) outside the scours in Resolute (R) and Assistance (A) Bays and Barrow Strait (B)

Table 5. One-way ANOSIM comparison of species composition in the 4 scours

Pair comparison	R statistic	Possible permutations	Permutations used	Significant statistics	Significance level (%)
Resolute 6 m and Resolute 9 m	0.059	$1.352 \times 10^6$	5000	599	12.0
Resolute 6 m and Assistance 6 m	0.730	$1.352 \times 10^6$	5000	0	0
Resolute 6 m and Barrow 15 m	0.662	$1.352 \times 10^6$	5000	0	0
Resolute 9 m and Assistance 6 m	0.815	$1.352 \times 10^6$	5000	0	0
Resolute 9 m and Barrow 15 m	0.691	$1.352 \times 10^6$	5000	0	0
Assistance 6 m and Barrow 15 m	0.738	$1.352 \times 10^6$	5000	0	0

from the community immediately outside (0% of permuted statistics  $\geq R = 0.848$ , no. permutations = 5000). Comparison of species composition within the scours by 1-way ANOSIM showed that the fauna within the Resolute Bay, Assistance Bay, and Barrow Strait scours differed significantly in composition from each other. However, there was no significant difference between the 2 Resolute Bay scours (Table 5).

Cluster analysis grouped the collections taken outside the scours into shallow and deep water clusters. The scour samples clustered with the shallow water samples. Species that dominated these groups are shown in Table 6. Within the scours and the shallow water collections outside the scours, spionid and capitellid polychaetes were the species most responsible for group formation. Several other polychaetes were important as well: ampharetids, phyllodocids, sabellids, the hesionid *Nereimyra punctata*, and the dorvilleid *Ophryotrocha spatula*. Some crustaceans were also important. Two genera of amphipods, *Orchomene* and *Monoculodes*, were important in Resolute Bay. *Monoculodes* was important in Barrow Strait, as were cumaceans. Fauna responsible for formation of the deep water clusters were more numerous and varied. Bivalves figured more prominently than in the scours and shallows, with *Axinopsida orbiculata*, *Macoma* spp., and *Musculus discors* exhibiting some importance in group formation. Some polychaete families overlapped with the scour cluster, indicating that greater taxonomic distinction would be necessary for refinement of relationships. Table 6 also shows the feeding and burrowing characteristics of these fauna. The scour and shallow water clusters were dominated by deposit feeders and predators, while the deep water clusters contained a larger proportion of suspension feeders. Most of these species were subsurface burrowers. However, in the deeper water some surface living and deep-burrowing species were dominant as well.

#### Comparison of scour berms and troughs

Two-way crossed ANOSIM showed that the scour troughs and berms differed significantly in species

composition (0% of permuted statistics  $\geq R = 0.390$ , no. permutations = 5000). However, many of the dominants were common to both troughs and berms (Table 7). Spionid and capitellid polychaetes dominated all 4 scours. The dorvilleid polychaete *Ophryotrocha spatula* dominated the Resolute and Assistance Bay scours. The amphipods *Monoculodes* spp. and *Orchomene* spp. dominated the Resolute Bay and Barrow Strait scours. Most of the dominants were subsurface dwelling deposit feeders. Contrary to our expectation, the berms were not populated by suspension feeders.

#### DISCUSSION

The results showed that ice scour had a significant impact on the benthos in Barrow Strait. Species composition inside the scours was markedly different from outside, and was dominated by small polychaetes and crustaceans. Ice scouring eliminated or damaged large organisms such as kelp, sea urchins, and bivalves. Considering that ice scour affects the full Arctic coastline, this loss may be of ecological significance. Laminarian kelp are large primary producers and provide cover for associated organisms. Sea urchins control the distribution of kelps and coralline algae (Vadas 1977, Larson et al. 1980, Keats et al. 1984). The large bivalves *Mya truncata* and *Serripes groenlandicus* are a significant energy resource for walrus (Welch et al. 1992). These and smaller bivalves deposit undigested phytoplankton, which then enters the deposit-feeding food web (Welch et al. 1992).

Some species were found in elevated numbers inside the scours. Buccinid gastropods and lysianassid amphipods were found scavenging the remains of damaged and dislodged bivalves. Deposit feeding polychaetes and scavenging crustaceans were abundant both within the scours and in the shallows outside the scours. Suspension feeders and predators were more abundant in deeper water where scouring was less evident. Thus, ice scouring appears to favor deposit feeders and scavengers. This differential effect of disturbance on certain feeding guilds has also been

Table 6. Species accounting for 75% of the average similarity within the major groups identified by cluster analysis. Species are ordered from the greatest contribution to the least. Taxonomic category, feeding guild, and benthic distribution of these species follow in the same order

Scours + shallow water samples outside the scours			Deep water samples outside the scours		
Resolute Bay (scours)	Assistance Bay (scour + 3–6 m)	Barrow Strait (scour + 3–9 m)	Resolute Bay (3–15 m)	Assistance Bay (6–15 m)	Barrow Strait (9–15 m)
<b>Taxa</b>					
Spionidae	Spionidae	Capitellidae	Cirratulidae	Syllidae	Cirratulidae
<i>Orchomene</i> spp.	Capitellidae	Spionidae	Spionidae	<i>Nereimyra punctata</i>	Spionidae
<i>Monoculodes</i> spp.	Ampharetidae	Phyllodocidae	<i>Axinopsida orbiculata</i>	Myodocopid Ostracoda	Capitellidae
	Phyllodocidae	Cumacea	Capitellidae	<i>Pholoe minuta</i>	Nemertea
	<i>Nereimyra punctata</i>	<i>Monoculodes</i> spp.	Syllidae	Spionidae	<i>Axinopsida orbiculata</i>
	<i>Ophryotrocha spatula</i>	Nemertea	<i>Nereimyra punctata</i>	Capitellidae	<i>Macoma</i> spp.
	Sabellidae	<i>Nereimyra punctata</i>	Sabellidae	Phyllodocidae	<i>Pholoe minuta</i>
			Phyllodocidae	Cirratulidae	Tanaidacea
			<i>Pholoe minuta</i>	Ampharetidae	Cumacea
			<i>Retusa obtusa</i>	<i>Musculus discors</i>	Myodocopid Ostracoda
			<i>Macoma</i> spp.	Sabellidae	
<b>Taxonomic group</b>					
Polychaete	Polychaete	Polychaete	Polychaete	Polychaete	Polychaete
Crustacean	Polychaete	Polychaete	Polychaete	Polychaete	Polychaete
Crustacean	Polychaete	Polychaete	Bivalve	Crustacean	Polychaete
	Polychaete	Crustacean	Polychaete	Polychaete	Nemertean
	Polychaete	Crustacean	Polychaete	Polychaete	Bivalve
	Polychaete	Nemertean	Polychaete	Polychaete	Bivalve
	Polychaete	Polychaete	Polychaete	Polychaete	Polychaete
			Polychaete	Polychaete	Crustacean
			Polychaete	Polychaete	Crustacean
			Gastropod	Bivalve	Crustacean
			Bivalve	Polychaete	
<b>Feeding guild</b>					
Deposit feeder	Deposit feeder	Deposit feeder	Deposit feeder	Predator	Deposit feeder
Scavenger	Deposit feeder	Deposit feeder	Deposit feeder	Predator	Deposit feeder
Predator	Deposit feeder	Predator	Suspension feeder	Suspension feeder	Deposit feeder
	Predator	Suspension feeder	Deposit feeder	Predator	Predator
	Predator	Predator	Predator	Deposit feeder	Suspension feeder
	Deposit feeder	Predator	Predator	Deposit feeder	Deposit feeder
	Suspension feeder	Predator	Suspension feeder	Predator	Predator
			Predator	Deposit feeder	Suspension feeder
			Predator	Deposit feeder	Suspension feeder
			Unknown	Suspension feeder	Suspension feeder
			Deposit feeder	Suspension feeder	
<b>Benthic distribution</b>					
Subsurface	Subsurface	Subsurface	Subsurface	Surface	Subsurface
Subsurface	Subsurface	Subsurface	Subsurface	Subsurface	Subsurface
Subsurface	Subsurface	Subsurface	Subsurface	Surface	Subsurface
	Subsurface	Subsurface	Subsurface	Subsurface	Surface
	Subsurface	Subsurface	Surface	Subsurface	Subsurface
	Subsurface	Subsurface	Subsurface	Subsurface	Deep
	Surface	Surface	Subsurface	Subsurface	Subsurface
	Deep	Subsurface	Deep	Subsurface	Subsurface
			Subsurface	Subsurface	Subsurface
			Subsurface	Subsurface	Subsurface
			Surface	Surface	Surface
			Deep	Deep	

observed in dredge and trawl tracks (Brylinsky et al. 1994, Currie & Parry 1996) and in areas of organic enrichment (Pearson & Rosenberg 1978, Rhoads & Boyer 1982, Weston 1990).

The scour communities closely resembled the inshore, shallow water benthos outside the scours. This similarity was in spite of the 300 to 400 m separation of the scours from the inshore area, differences in water

depth (the scours were 3 to 12 m deeper), and differences in kelp cover (the scours lacked kelp cover, while the inshore samples had nearly 100% kelp cover). Cumaceans, the amphipods *Monoculodes* spp. and *Orchomene* spp., and spionid, capitellid, dorvilleid, phyllodocid, ampharetid, hesionid, and sabellid polychaetes were common to both the scours and the inshore area. Of the 3 environmental factors measured



The presence of numerous polychaetes in the scours suggests either that there was rapid migration of adults and/or larval recruitment, or that these species survived the scouring event, possibly by being plowed up onto the berm and subsequently tumbling back into the trough. Spionid and capitellid polychaetes tolerate disturbance and are characteristic early colonizers of defaunated habitat (Grassle & Grassle 1974, McCall 1977, Pearson & Rosenberg 1978, Lenihan & Oliver 1995, Olsgard & Gray 1995, Warwick & Clarke 1995). Species discrimination of the capitellid polychaetes indicated that *Capitella cf. capitata* predominated in the scour and inshore samples. *Capitella cf. capitata* has a small range of dispersal (Levin 1984) and can colonize local disturbances within days (Grassle & Grassle 1974). It also requires enriched sediment for normal growth (Tsutsumi 1990). Spionids have prolonged spawning periods and relatively brief pelagic larval development. As adults they leave their tubes when disturbed, settling nearby to rapidly rebuild new tubes from the surrounding sediment (McCauley et al. 1976). The scours are patches of newly revealed clay, as well as sites of decomposition of buried fauna and depressions with different water properties (Kvitek et al. 1998). Movement of these polychaetes into patch depressions has been implicated as food related in other studies (Thistle 1981), and this is probably also the case for these ice scours. Various species of *Monoculodes* and *Orchomene* (primarily *Monoculodes vibei* and *O. minutus*) also dominated some scours. These are more mobile than the polychaetes, and could have been using the disturbed sediments to consume

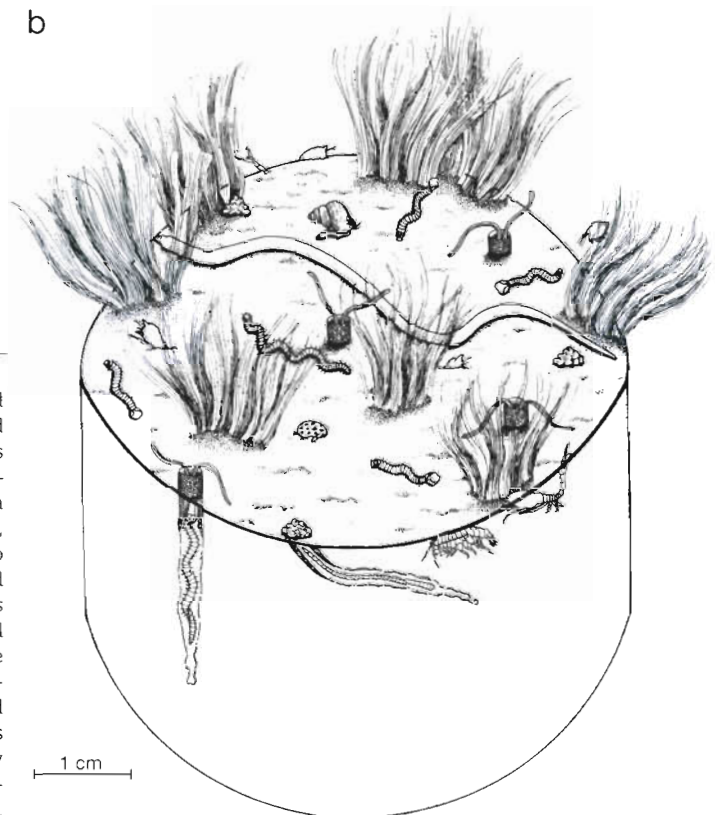
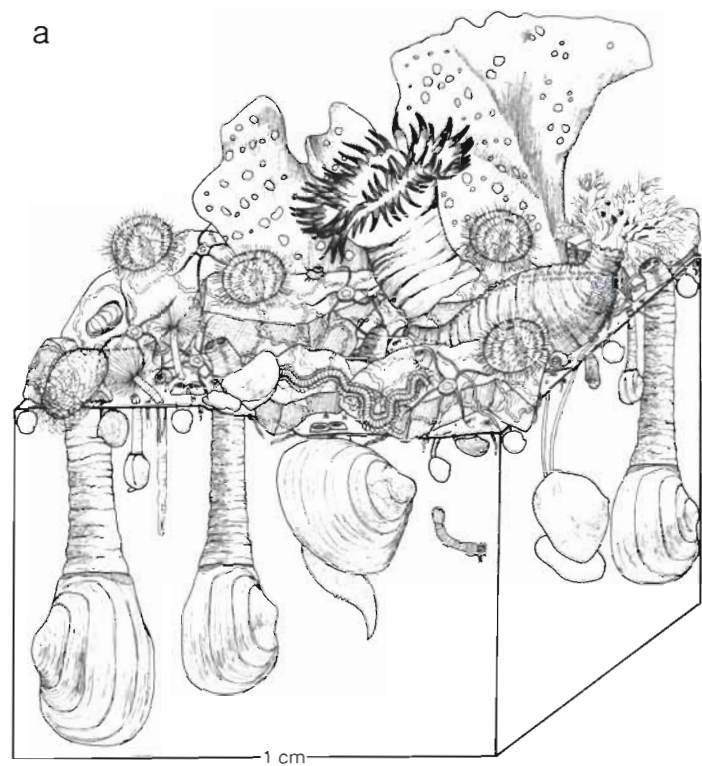


Fig. 7. Dominant fauna (a) outside and (b) inside a 1 yr old scour in Barrow Strait at 20 m depth. The undisturbed seabed (a) is dominated in biomass by the large bivalves *Mya truncata*, *Serripes groenlandicus*, and *Macoma calcaria*, the sea urchin *Strongylocentrotus pallidus*, the sea cucumber *Cucumaria frondosa*, the anemone *Telia* sp., the polychaete *Phyllodoce groenlandicus*, and the kelp *Agarum cribrosum*. Dominant occupants of a 1 yr old scour berm (b) are tubicolous polychaetes [the spionids *Prionospio steenstrupi* and *Pygospio elegans* (vertical tubes) and *Capitella cf. capitata* (horizontal tube)], the wandering polychaetes *Ophryotrocha spatula* (with spatulate posterior) and *Nereimyra punctata*, the amphipod *Monoculodes vibei*, and various cumaceans. Nemertean and ostracods may also frequent new scours. Diatoms may colonize in abundance. The tufts shown here are composed of the tube-forming pennate diatom *Parlibellus* sp.

detritus, scavenge remains, and capture newly invading prey. The highly scoured inshore could serve as source areas for early recolonization of these offshore scours.

These results can be compared with several other studies of soft-bottom ice scouring. Similarities are evident. In McMurdo Sound, Antarctica, Lenihan & Oliver (1995) found elevated numbers of *Capitella* sp. and *Ophryotrocha claperedii* in iceberg scours relative to unscoured sediment. *Capitella* cf. *capitata* and *O. spatula* were found to dominate scours in this study as well. In scours of soft mud on the Antarctic Peninsula, Kauffman (1977) found an initial increase of the large nemertean scavenger *Parborlasia corrugatus*, and mobile fauna recolonized quickly. Similarly, Gutt et al. (1996) found that the first immigrants of deep sea Arctic and Antarctic scours were mobile organisms such as fish, echinoderms, and bivalves. In this study, the first large epifauna to appear in new scours were buccinid gastropods and lysianassid amphipods, which scavenged the remains of damaged and uprooted fauna. Scours in crustacean-dominated sediment in the Bering Sea exhibited similar declines of fauna as seen in this study, but no infilling by opportunistic polychaetes and crustaceans (Klaus et al. 1990). However, Oliver & Slattery (1985) found that the scavenging amphipods *Anonyx* spp. and *Orchomene minutus* invaded and attacked fauna dislodged by gray whale feeding, a finding similar to this study. These and many other lysianassid amphipods are cold water scavengers and are quick to be attracted to bait traps (Bousfield 1973, Slattery & Oliver 1986, Conlan 1994).

The fact that the large bivalve *Mya truncata* did not achieve as great a size in the exposed Barrow Strait as in the protected Resolute Bay may be attributable to the frequency of ice disturbance, although other factors, such as current speed and sediment type, also differ. The 12 m sampling depth was outside the range of influence of ice in Resolute Bay but within range of deep draft ice in Barrow Strait. Peck & Bullough (1993) found that ice scour limited the upper age attainable by a dense population of *Yoldia eightsi* at subantarctic Signy Island. Energetically, *M. truncata* is important to the Arctic benthos, filtering out phytoplankton and releasing it as undigested pseudofeces on the bottom, where it becomes available to deposit feeders (Welch et al. 1992). Individual *M. truncata* can attain a high biomass but growth is slow. The oldest specimen aged for this region is 55 yr (Welch et al. 1992).

Ice scouring is a large-scale event that affects Arctic and Antarctic coasts alike. This study has shown that, although ice scouring is initially destructive, it provides opportunities as well. It alters seabed topography by gouging troughs and pushing up berms of sediment. It reveals fresh, cleared sediment, which is

rapidly colonized by small polychaetes and amphipods. It also provides feeding opportunities for scavenging gastropods and amphipods. Depth-related faunal transitions along ice-scoured coastline may well predict the course of succession in offshore ice scours. Recently formed scours will resemble the inshore benthos, as illustrated in Fig. 7b, and gradually shift to resemble their same-depth counterparts outside, as shown in Fig. 7a. Many of the species that first colonize these scours are widespread in the Canadian Arctic. Congeners of these Arctic species also inhabit ice scours in Antarctica. Thus, the benthos may respond consistently wherever ice scour is a force.

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