

Palaeoenvironmental Interpretation of Late Quaternary Marine Molluscan Assemblages, Canadian Arctic Archipelago

Interprétation paléoenvironnementale des faunes de mollusques marins de l'Archipel arctique canadien, au Quaternaire supérieur.

Interpretación paleoambiental de asociaciones marinas de moluscos del Cuaternario Tardío, Archipiélago Ártico Canadiense

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Article abstract

This study examines neontological and palaeontological data pertaining to arctic marine molluscs with the goal of reconstructing the palaeoecology of Late Quaternary ca. 12-1 ka BP glaciomarine environments in the Canadian Arctic Archipelago. A total of 26 taxa that represent 15 bivalves and 11 gastropods were recorded in shell collections recovered from Prince of Wales, Somerset, Devon, Axel Heiberg and Ellesmere islands. In spite of taphonomic bias, the observed fossil faunas bear strong similarities to modern benthic molluscan faunas inhabiting high latitude continental shelf environments, reflecting the high preservation potential of molluscan taxa in Quaternary marine sediments. The dominance of an arctic-boreal fauna represented by *Hiatella arctica*, *Mya truncata* and *Astarte borealis* is the product of natural ecological conditions in high arctic glaciomarine environments. Environmental factors controlling the distribution and species composition of the Late Quaternary molluscan assemblages from this region are discussed.

PALAEOENVIRONMENTAL INTERPRETATION OF LATE QUATERNARY MARINE MOLLUSCAN ASSEMBLAGES, CANADIAN ARCTIC ARCHIPELAGO

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ABSTRACT This study examines neontological and palaeontological data pertaining to arctic marine molluscs with the goal of reconstructing the palaeoecology of Late Quaternary ca. 12-1 ka BP glaciomarine environments in the Canadian Arctic Archipelago. A total of 26 taxa that represent 15 bivalves and 11 gastropods were recorded in shell collections recovered from Prince of Wales, Somerset, Devon, Axel Heiberg and Ellesmere islands. In spite of taphonomic bias, the observed fossil faunas bear strong similarities to modern benthic molluscan faunas inhabiting high latitude continental shelf environments, reflecting the high preservation potential of molluscan taxa in Quaternary marine sediments. The dominance of an arctic-boreal fauna represented by *Hiatella arctica*, *Mya truncata* and *Astarte borealis* is the product of natural ecological conditions in high arctic glaciomarine environments. Environmental factors controlling the distribution and species composition of the Late Quaternary molluscan assemblages from this region are discussed.

RÉSUMÉ *Interprétation paléoenvironnementale des faunes de mollusques marins de l'Archipel arctique canadien, au Quaternaire supérieur.* On étudie ici les données néontologiques et paléontologiques qui se rapportent aux mollusques marins de l'Arctique dans le but de reconstituer la paléocologie des milieux glaciomarins du Quaternaire supérieur entre 12 et 1 ka BP. Un total de 26 taxons composé de 15 bivalves et de 11 gastéropodes a été consigné dans les collections de coquillages assemblées dans les îles du Prince-de-Galles, Somerset, Devon, Axel Heiberg et Ellesmere. Malgré l'influence des processus taphonomiques, les faunes fossiles observées ressemblent beaucoup aux faunes de mollusques benthiques modernes habitant le plateau continental des hautes latitudes, ce qui reflète la grande capacité de préservation des taxons de mollusques dans les sédiments du Quaternaire. La dominance de la faune boréale-arctique représentée par *Astarte borealis*, *Hiatella arctica* et *Mya truncata* est le résultat des conditions écologiques naturelles qui prévalent dans les milieux glaciomarins du Haut Arctique. On étudie enfin les facteurs environnementaux qui déterminent la répartition et la composition des faunes de mollusques de la région, au Quaternaire supérieur.

RESUMEN *Interpretación paleoambiental de asociaciones marinas de moluscos del Cuaternario Tardío, Archipiélago Ártico Canadiense.* Este trabajo pretende la reconstrucción paleoecológica de ambientes glaciomarinos del Cuaternario Tardío ca. 12-1 ka BP del Archipiélago Artico Canadiense en base al análisis de datos neontológicos y paleontológicos relativos a moluscos marinos árticos. Se obtuvieron un total de 26 taxa que representan 15 bivalvos y 11 gasterópodos procedentes de las islas Prince of Wales, Somerset, Devon, Axel Heiberg y Ellesmere. A pesar de los sesgos tafonómicos, la fauna fósil observada guarda una gran similitud con las faunas actuales de moluscos bentónicos, lo que refleja alto potencial de preservación de los moluscos en sedimentos marinos del Cuaternario. La dominancia de una fauna boreal-ártica, representada por *Hiatella arctica*, *Mya truncata* y *Astarte borealis* obedece a las condiciones ecológicas imperantes en ambientes glaciomarinos de alta latitud. Finalmente, se discuten los factores ambientales que afectan la distribución de los moluscos del Cuaternario Tardío de esta región.

INTRODUCTION

Fossil marine molluscs from the Arctic region are of considerable interest to earth scientists studying the nature of environmental change at high latitudes during the Quaternary period. Firstly, they are common and well preserved forms in the Quaternary fossil record. Molluscs, especially bivalves, are by far the most common macrofossils recovered in Late Pleistocene and Holocene raised marine deposits from glaciated North America and Greenland (Feyling-Hanssen, 1955; Andrews *et al.*, 1981; Simonarson, 1981; Mode *et al.*, 1983; Aitken, 1990; Dyke *et al.*, 1996a). Despite the bias in preservation due to taphonomic processes, Quaternary fossil molluscan assemblages retain useful information pertaining to the life habit and habitats of the arctic marine benthos from which they are derived (Aitken, 1990). Comparing different marine environments in the eastern Canadian Arctic region, Aitken (1990) observed that molluscs inhabiting nearshore environments (depths < 50 m) exhibit the greatest preservation potential of all the arctic marine benthos.

Secondly, the Arctic is a critical region for the interpretation of faunal distributions in polar regions, as it lies between the Atlantic and the Pacific oceans. Molluscs recovered from Tertiary and Quaternary deposits have been used to follow periods of interchange and colonization between these two ocean basins. Information on this topic is provided through numerous publications, notably by Durham and Macneil (1967), Einarsson *et al.* (1967), Hopkins *et al.* (1972), Allison (1973), Troitskiy (1974), Bernard (1979), Gladenkov (1979), Lubinsky (1980), Evseev and Krasnov (1985), Golikov and Scarlato (1989), Fyles *et al.* (1991), Vermeij (1991) and Dyke *et al.* (1996a). In this regard, two geologic events appear to have had an important impact on the evolution of Canadian arctic molluscan faunas: (1) during the Tertiary, the opening of the Bering Strait at 3.5-3.0 Ma ago and (2) during the Late Quaternary, deglaciation of North America, Europe and Asia re-established the connection between the Pacific and the Atlantic oceans, after they were segregated by Quaternary glaciations and the emergence of the Bering Land Bridge. The information provided above demonstrates that the molluscs inhabiting nearshore environments in the Canadian Arctic Archipelago have particular significance as they provide a key to reconstructing palaeocommunities and to evaluating changes in faunal composition during the Quaternary period. This study attempts to reconstruct the palaeoecology of Late Quaternary marine macrofossil assemblages from the Canadian Arctic Archipelago based on a combination of neontological and palaeontological data.

PHYSICAL CHARACTERIZATION

GLACIAL HISTORY

The study area covers a large part of the Canadian Arctic Archipelago that includes localities on western Axel Heiberg Island, western Ellesmere Island, Devon Island, Prince of Wales Island, Somerset Island and Boothia Peninsula (Fig. 1). Based on more than 130 radiocarbon dates, Dyke *et*

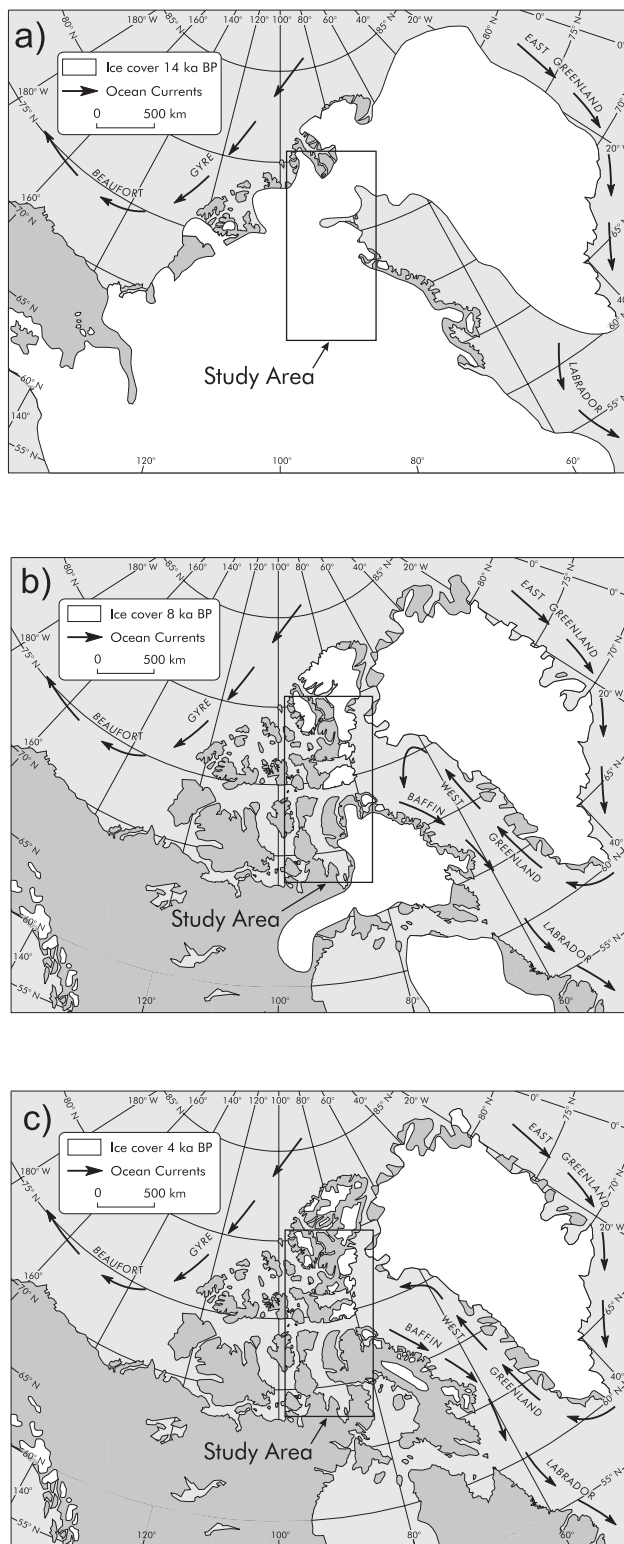


FIGURE 1. Maps of the Canadian Arctic Archipelago illustrating the study area, the distribution of glacial ice and the ocean currents at a) 14 ka BP; b) 8 ka BP; c) 4 ka BP (adapted from Dyke *et al.*, 1996a).

*Cartes de l'Archipel arctique canadien montrant le site à l'étude, le couvert glaciaire et les courants marins à a) 14 ka BP ; b) 8 ka BP ; c) 4 ka BP (à partir de Dyke *et al.*, 1996a).*

al. (1991) reconstruct the postglacial sea level history of Prince of Wales and Somerset islands. This region was affected by different ice masses during the Late Wisconsinan glacial maximum (ca. 18-14 ka BP; Dyke *et al.*, 1992). The Keewatin sector of the Laurentide Ice Sheet first flowed northwestward across Prince of Wales. Later ice flow switched to an eastward course, spreading from an ice divide located west of Prince of Wales. Somerset Island supported an independent ice cap that coalesced with Laurentide ice (Dyke *et al.*, 1991). There is no geologic evidence for an extensive regional ice sheet covering west-central Axel Heiberg Island (Lemmen *et al.*, 1994) or Fosheim Peninsula, Ellesmere Island (Bell, 1996). Trunk glaciers derived from inland ice caps occupied major through valleys while uplands supported small ice caps or cirque glaciers.

Deglaciation was regionally asymmetric. On Prince of Wales Island, the first area to become ice-free was in the northwest about 11 ka BP and final deglaciation occurred shortly after 9.2 ka BP (Dyke *et al.*, 1991). The ice cap on Somerset Island appears to have started to retreat about 9.3 ka BP, and probably melted entirely during a period of one or two centuries (Dyke, 1983). On western Axel Heiberg Island, initial retreat of trunk glaciers occurred at 8.4 ka BP followed by a rapid deglaciation (Lemmen *et al.*, 1994). On west Ellesmere Island, ice retreat is widely dated between 8.5 and 8.0 ka BP (Hodgson, 1985; England, 1990; Bell, 1996). Figure 1 illustrates the nature of deglaciation of the Canadian Arctic Archipelago over the period 12 ka BP to 4 ka BP.

Postglacial sediments on Prince of Wales and Somerset Islands consist predominantly of raised beach deposits, along with minor deltaic and alluvial deposits (Dyke, 1983; Dyke *et al.*, 1992). Among these features, ice-proximal glaciomarine deltas yielded most of the mollusc collections examined in this study. On Axel Heiberg and Ellesmere islands, early postglacial (ca. 10-8 ka BP) shell collections were recovered from laminated, fine-grained marine sediments interpreted as glaciomarine rhythmites deposited in near-shore environments proximal to glaciomarine deltas (Aitken and Bell, 1998). Mid-Holocene (ca. 8-5 ka BP) shell collections were recovered from massive marine muds interpreted to represent deposition of fine-grained sediments from suspension in nearshore environments distal to fiord-head deltas (Aitken and Bell, 1998).

WATER MASSES

The Canadian Arctic Archipelago is dominated by water masses from two major sources: Polar and Atlantic waters. From the surface to a depth of 200 m, the water column is occupied by Polar waters, characterized by temperatures between -1.5 and 0 °C and salinities ranging from 27 ‰ in the vicinity of the Mackenzie River to 34.5 ‰ in eastern Baffin Bay (Coachman and Aagaard, 1974). Beneath the Polar water, a mass of Atlantic water extends to approximately 500 m depth. It is composed of warmer (up to + 0. °C) and more saline water (around 34.9 ‰) (Lewis, 1982). In addition to the water masses, a Fiord water layer, 5-6 m thick and with positive temperatures, is formed by fresh water from rivers and by melting of sea ice. The Fiord water layer, which

exhibits salinities less than 20 ‰, only exists during the summer when the melting of large glaciers and sea ice is greatest (Ockelmann, 1958).

Movement of Polar waters southward and eastward through the archipelago maintains a predominantly arctic regime throughout the study area (Curtis, 1975). Polar waters flowing through the archipelago continue southward along the eastern coast of Canada as the Baffin and Labrador currents (Fig. 1c).

PALAEOECOLOGY

The fossil faunas that are the subject of this report were collected between 1975 and 1993 during various research projects supported by the Geological Survey of Canada. In the laboratory, specimens were sorted manually and identified to the level of species if possible. The autoecological characterization of the fossil taxa (mode of life, nature of locomotion and feeding, preferred substratum, ranges of water temperature, salinity and depth, and larval development) is derived from comparison with the ecology of extant taxa. A summary of the autoecology and biogeographic patterns of the fossil taxa is presented in Table I. Additional information on these topics may be found in the Appendix.

TAPHONOMIC CONSIDERATIONS

The preservational quality of a particular fossil specimen is largely determined by biostratigraphic and early diagenetic processes which occur in or near the original sedimentary environment and are characteristic of that environment (Brett and Baird 1986). Postmortem mechanical processes (*i.e.* disarticulation, fragmentation, corrosion and bioerosion) affecting macrofossil remains from the Prince of Wales Island region — included in the present work — are considered by Gordillo and Aitken (2001). General observations on taphonomic modification of the shell material in the collections indicate no signs of significant post-mortem transport (*e.g.* shell abrasion and/or fracturing, selective loss of size classes). Most of the shells have experienced post-mortem disarticulation, however, a great number of specimens of different taxa retain their periostracum. The populations of shells of the common taxa exhibit a wide range in size. Juvenile specimens are present in many of the samples examined in this study. The absence of encrusting organisms suggests rapid burial of the shell material on the seafloor as anticipated in nearshore glaciomarine environments characterized by high rates of sedimentation. These observations on the taphonomic modification of the shell material suggest that the macrofaunal assemblages as a whole most commonly represent parautochthonous assemblages, *i.e.* assemblages whose specimens have undergone minor taphonomic modification prior to burial on the seafloor.

In addition to biostratigraphic features, early diagenetic processes (*i.e.* skeletal dissolution, sediment fillings, and mineralization of fossils) may enhance or detract from the preservation of fossils. Early diagenetic processes are closely related to sediment geochemistry. Dyke *et al.* (1996a) state that for fossiliferous raised marine deposits in

TABLE I

Autoecology and biogeographic patterns of the mollusc species examined in this study (for details see the Appendix)

TAXA	AUTOECOLOGY (1)							FOSSIL RECORD (4)				
	LIFE HABIT	LOCOMOTION	SUBSTRATUM TYPE	DEPTH RANGE (m) (*)	FEEDING TYPE	NORMAL MINIMUM SALINITY (2)	TEMPERATURE (2)	GEOGRAPHIC DISTRIBUTION (3)	NORTH PACIFIC RECORD	ARCTIC-NORTH ATLANTIC RECORD	AREA OF ORIGIN	GEOLOGIC RANGE (**)
<i>Nuculana pernula</i> (MULLER)	IN	Bur	G,S,C	9 to 40	DF	25	-2 to 14(8)	Arc.-Bor.	Mio.	Plio.	Pac.	(Tri.) Mio.-R
<i>Portlandia arctica</i> (GRAY)	IN	Bur	C	4 to 81	DF	26	-2 to 4	H. Arc.	Pleist.	Pleist.	unc.	(Eoc.) Pleist.-R
<i>Batharca glacialis</i> (GRAY)	EP/SE	Bys	G+S	45 to 440	SF	32	-1.5 to 7	Arc.-Bor.	Pleist.	Pleist.	Atl.	(Eoc.) Pleist.-R
<i>Musculus niger</i> (GRAY)	EP/SE	Bys	Var.	7 to 50	SF	19	-1 to 14	Arc.-Bor.	Plio.	Plio.	Pac.	(Jur.) Pli.-R
<i>Delectopecten greenlandicus</i> (SOW.)	EP	Bys/Swi	Var.	6 to 150	SF	33	-2 to 9	H. Arc.	Mio.	Pleist.	Pac.	(Eoc.) Mio.-R
<i>Astarte borealis</i> (SCHUMACHER)	IN	Bur	S+C	Int. to 50	SF	15	-2 to 15.5	Arc.-Bor.	Plio.	Plio.	Atl.	(Jur.) Plio.-R
<i>Axinopsida orbiculata</i> (G.O.SARS)	IN	Bur	A,A+C	Int. to 59	DF	Euryha.	-2 to 9	Arc.-Bor.	Pleist.	Pleist.	Pac.	(Plio.) Pleist.-R
<i>Clinocardium ciliatum</i> (FABRICIUS)	IN	Bur	C,G+S	9 to 20	SF	Euryha.	-2 to 9	Arc.-Bor.	Mio.	Plio.	Pac.	(Eoc.) Mio.-R
<i>Serripes groenlandicus</i> (BRUGUIERE)	IN	Bur	S+C	Int. to 50	SF	Euryha.	-2 to 9	Arc.-Bor.	Mio.	Plio.	Pac.	(Mio.) Mio.-R
<i>Macoma calcarea</i> (GMELIN)	IN	Bur	S,C,S+C	Int. to 124	DF	13	-2 to 16(11)	Arc.-Bor.	Mio.	Plio.	Pac.	(Eoc.) Mio.-R
<i>Macoma moesta</i> (DESHAYES)	IN	Bur	S+C	7 to 47	DF	32	-1.5 to 7.5	Arc.-Bor.	Pleist.	R.	Pac.	(Eoc.) Pleist.-R
<i>Mya truncata</i> LINNAEUS	IN	Bur	Var.	Int. to 103	SF	17	-2 to 17	Arc.-Bor.	Mio.	Plio.	Pac.	(Eoc.) Mio.-R
<i>Hiatella arctica</i> (LINNAEUS)	EP/SE	Bys/Nes	Var.	Int. to 50	SF	20	Euryth.	Arc.-Bor.	Olig./Mio.	Olig.	unc.	(Jur.) Olig.-R
<i>Lyonsia arenosa</i> (MOLLER)	EP/SE	Bys/Nes	S+C,S	11 to 16	SF	32	-2 to 8.5	Arc.-Bor.	Pleist.	Pleist.	unc.	(Eoc.) Pleist.-R
<i>Thracia devexa</i> (G.O.SARS)	IN	Bur	S	4 to 90	SF	32	-1 to 8	H. Arc.	R	R	Atl.	(Jur.) -R
<i>Margarites</i> sp.	EP	Vag	M	shallow	BR	n/c	n/c	Arc.-Bor.	Plio.	Pleist.	Pac.	(Eoc.)-R
<i>Retusa obtusa</i> (MONTAGU)	IN	Vag	S+C,S	Int. to 88	CAR	15	n/d	Arc.-Bor.	Pleist.	Pleist.	Atl.	(Jur.) Pleist.-R
<i>Cylichna occulta</i> (MIGHELIS)	EP/IN	Vag	G,S,C	4 to 43	CAR	n/d	0 to 10	Arc.-Bor.	R	Pleist.	Atl.	(Cret.) Pleist.-R
<i>Trichotropis borealis</i> BROD. & SOW.	EP	Vag	G,S,C	4 to 32	SF	Stenoh.?	n/d	Arc.-Bor.	R	Plio.	Pac.	(Cret.) Plio.-R
<i>Colus</i> sp.	EP	Vag	C,S	shallow	CAR	n/c	n/c	Arc.-Bor.	Mio.	Plio.	unc.	(Eoc.)-R
<i>Buccinum glaciale</i> LINNAEUS	EP	Vag	Var.	5 to 119	CAR	Euryha.	-1 to 6	Arc.-Bor.	Pleist.	Plio.	Pac.	(Eoc.) Pli.-R
<i>Buccinum tenue</i> GRAY	EP	Vag	Var.	4 to 100	CAR	n/d	0 to 4	Arc.-Bor.	Pleist.	Pleist.	Pac.	(Eoc.) Pleist.-R
<i>Buccinum finmarkianum</i> VERKRUZEN	EP	Vag	Var.	5 to 40	CAR	n/d	n/d	Arc.-Bor.	n/d	Plio.	Pac.	(Eoc.) Pli.-R
<i>Oenopota decussata</i> (COUTHOUY)	IN	Vag	S+C,C	5 to 32	CAR	n/d	n/d	Arc.-Bor.	n/d	Plio.	Pac.	(Eoc.) Pli.-R
Naticidae	IN	Vag	C,S	shallow	CAR	n/c	n/c	n/c	n/c	n/c	n/c	(Cret.) -R

Explanations of the symbols:

EP: epifaunal; IN: infaunal; SE: semi-infaunal (partially buried).

Bur: burrower; Bys: bysally attached; Nes: nestler; Swi: swimmer; Vag: vagrant.

C: clay; G: gravel; S: sand; M: macroalgae; Var.: variable (clay, sand, gravel or rock).

int.: intermareal; shallow: < 200 m.

DP: deposit feeder; SF: suspension feeder; CAR: carnivorous.

Euryha.: euryhaline; Stenoh.: stenohaline; Euryth.: eurythermic.

Arc.-Bor.: Arctic-Boreal; H. Arc: High Arctic.

Atl.: Atlantic; Pac.: Pacific; unc.: uncertain.

Tri.: Triassic; Jur.: Jurassic; Cret.: Cretaceous; Eoc.: Eocene; Olig.: Oligocene; Mio.: Miocene; Pli.: Pliocene; Pleist.: Pleistocene; R: Recent.

(*) Range of depths based on living specimens recorded within the Canadian Arctic.

(**) genus range between brackets.

n/c: not considered; n/d: no data; ?: with doubt

Source of data:

(1) Thorson (1933, 1944); Vibe (1939); Lemche (1941); Ockelmann (1958); Ellis (1960); Bernard (1979); Dale (1985); Aitken and Gilbert (1986,1996); Dale *et al.* (1989) and Aitken and Fournier (1993).

(2) Aitken (1990) and Peacock (1993); salinity in parts per thousand and temperature range in °C; () minimum summer temperature.

(3) Feyling-Hanssen (1955); Ockelmann (1958); Macpherson (1971); Bernard (1979) and Fedyskov and Naumov (1989).

(4) Richards (1962); MacNeil (1965); Durham and McNeil (1967); Einarsson *et al.* (1967); Hopkins *et al.* (1972); Kaufman (1973); Gladenkov (1978, 1979); Bernard (1979); Franz and Merrill (1980); Simonarson (1981); Agapitov *et al.* (1985); Evseev and Krasnov (1985); Marincovich *et al.* (1985, 1990); Svitoch (1985); Golikov and Sirenko (1988); Marincovich (1990); Fyles *et al.* (1991); Vermeij (1991); Bandel (1993); Honda (1994); Suzuki and Akamatsu (1994); Crame (1996) and Mikkelsen (1996).

the Canadian arctic, the most important geological factors affecting shell preservation are probably the presence or absence of permafrost, sediment acidity, and sediment permeability. Fossils are much more commonly found in areas of permafrost, particularly in acidic terrain. In areas where permafrost is absent, fossils are better preserved in calcareous sediments than in acidic sediments; they are generally restricted to fine-grained sediments of low permeability (Dyke *et al.* 1996a). Burial in organic-rich sediments typically accelerates dissolution of shell material, due to the buildup of CO₂ and H₂SO₄ or both during anaerobic decay (Brett and Baird, 1986). Spjeldnaes (1978) refers to the presence of sulphides in Quaternary clays generated under anaerobic conditions in the sediments. When these sediments are uplifted, they become oxidized and the resulting acidity may destroy all or part of the carbonate fossils. Under these conditions, refractory organic matter (*i.e.* periostracum) may be selectively preserved, while shell carbonates are entirely dissolved (Brett and Baird, 1986). Lemmen *et al.* (1994) describe an example of this type of fossil preservation in glaciomarine sediments on Axel Heiberg Island.

FAUNAL CHARACTERIZATION

Shell collections were organized into four geographic groups: western Ellesmere Island, Axel Heiberg Island, Devon Island and Prince of Wales Island and adjacent areas. For each group, the relative abundance of species and trophic groups is given by the [(number of individuals for a taxon (or trophic group) / total number of individuals) x 100 %]. A total of 6678 specimens (103 samples) were examined from sites within the study area (Fig. 1). A summary of the faunal composition and relative abundances of taxa and trophic groups represented in the collections is presented in Table II. Twenty-six taxa (15 bivalves, 11 gastropods) are represented in the samples. Each taxa is presently extant within the Canadian Arctic Archipelago. The most common species represented in the fossil collections were *Hiatella arctica* (28.5-35.7 %), *Mya truncata* (21.3-48.7 %) and *Astarte borealis* (13.9-32.0 %) which together represent near the 88.3 % of the total fauna. Russell (1991) compared Pleistocene fossil assemblages and modern death assemblages from California and concluded that habitat or substratum type could be inferred from relative abundance measures of the species present within fossil assemblages. Following this line of reasoning, our observations on the species composition of the Canadian Arctic fossil assemblages record the dominance of infaunal suspension-feeding taxa (*i.e.* *Astarte*, *Clinocardium*, *Hiatella*, *Macoma*, *Mya*, *Serripes* and *Thracia*) that occur most abundantly on soft substrates deposited in nearshore environments.

The samples are composed mainly of bivalves. Various authors have observed that bivalves contribute significantly to the biomass of continental shelf benthic communities in the study area, but gastropods only appear as a minor fraction of the total biomass (Ellis, 1960; Curtis, 1975; Thomson *et al.*, 1986). Thus, the dominance of bivalves (99.2 %; n = 6623) with respect to gastropods (0.8 %; n = 55) appears to be the result of natural ecological conditions encountered in

high latitude nearshore environments. Other taxa represented in our samples include barnacles (*Balanus* sp.) that appeared in low proportions, and foraminifers that were collected only in a single sample from Axel Heiberg Island.

Suspension-feeding taxa represent 93 % of the fossil molluscan fauna collected from the study area. Deposit-feeders, carnivores and browsers represent 6.3 %, 0.7 % and 0.05 %, respectively, of the macrofossil assemblage. The relative abundance of trophic groups represented in the fossil faunas differs markedly from the trophic composition of the modern fiord benthos observed in Baffin Island and Greenland fiords. Aitken and Fournier (1993) noted that the relative abundance of trophic groups in Baffin Island benthic communities is as follows: deposit-feeders > suspension-feeders > carnivores > browsers. Thorson (1933, 1944), Bertelsen (1937) and Schmid and Piepenburg (1993) noted similar trends in benthic communities inhabiting Greenland fiords. Deposit-feeding taxa tend to dominate the benthos on soupground substrates in fiord-head environments characterized by cold temperatures, variable salinities and rapid rates of clastic sedimentation. Suspension-feeding taxa occur more abundantly on softground substrates (*i.e.* infaunal forms) and firmground substrates (*i.e.* epifaunal forms) in distal estuarine environments that experience a reduction in the rate of clastic sedimentation and an increase in salinity and primary production.

With regards to the preservation potential of the taxa, Aitken (1990) and Palmqvist (1990) associate differences in shell preservation between trophic groups with (1) different initial abundances (*i.e.* primary consumers like bivalves are usually more abundant than higher trophic groups like carnivorous gastropods) and (2) differences in preservation related to mobility and the nature of mineralized body parts (*i.e.* carnivorous gastropods like *Buccinum* or *Colus* are vagrant and exhibit relatively less robust shells in comparison to more sedentary infaunal taxa like *Astarte* or *Mya*). The combination of these factors should produce palaeo-communities whose trophic composition is as follows: suspension-feeders > deposit-feeders > carnivores > browsers (Aitken, 1990). This is precisely the situation recorded in the macrofossil assemblages from the study region. The overrepresentation of infaunal suspension-feeding mollusc taxa in Late Quaternary macrofossil assemblages from the Canadian Arctic reflects the greater preservation potential of these taxa relative to other benthic organisms.

COMPARISON WITH LIVING ARCTIC COMMUNITIES

A comparison of the species composition of different benthic mollusc communities inhabiting high latitude fiords and shallow marine environments is presented in Table III. These data will be employed in reconstructing the structure of the macrofossil assemblages represented in the shell collections.

Studies examining the structure of modern benthic communities are based commonly on the abundance of taxa recovered by various methods of collection (trawl or grab). In this regard it is important to note that both benthic trawls and

TABLE II
Faunal composition and relative abundances of mollusc species and trophic groups

TAXA	Axel Heiberg Is. (14)		Ellesmere Island (38)		Devon Island (22)		Prince of Wales (29)	
	# of specim.	Relative abund.	# of specim.	Relative abund.	# of specim.	Relative abund.	# of specim.	Relative abund.
<i>Astarte borealis</i>	306 (12)	27,18	263 (8)	13,91	453 (12)	32,04	671 (15)	29,86
<i>Axinopsida orbiculata</i>	2 (1)	0,18		-		-		-
<i>Batharca glacialis</i>		-	1 (1)	0,05		-		-
<i>Buccinum finmarkianum</i>		-		-		-	1 (1)	0,04
<i>Buccinum glaciale</i>		-		-		-	1 (1)	0,04
<i>Buccinum spp.</i>	4 (1)	0,36		-		-	5 (3)	0,22
<i>Buccinum tenue</i>		-		-		-	2 (1)	0,09
<i>Clinocardium ciliatum</i>		-		-	7 (2)	0,50	23 (7)	1,02
<i>Colus sp.</i>	3 (1)	0,27		-		-		-
<i>Cylichna occulta</i>	2 (1)	0,18		-		-		-
<i>Delectopecten greenlandicus</i>		-	13 (1)	0,69		-		-
<i>Hiatella arctica</i>	402 (14)	35,70	565 (29)	29,88	403 (20)	28,50	784 (21)	34,89
<i>Lyonsia arenosa</i>	3 (2)	0,27		-	3 (2)	0,21		-
<i>Macoma calcarea</i>	2 (1)	0,18	1 (1)	0,05	19 (8)	1,34	90 (4)	4,01
<i>Macoma moesta</i>	4 (3)	0,36		-	116 (14)	8,20	48 (6)	2,14
<i>Margarites sp.</i>	3 (1)	0,27		-		-		-
<i>Musculus niger</i>	7 (4)	0,62		-		-		-
<i>Mya truncata</i>	240 (12)	21,31	920 (32)	48,65	357 (21)	25,25	580 (22)	25,81
Naticidae		-		-		-	1 (1)	0,04
<i>Nuculana pernula</i>	5 (1)	0,44		-		-		-
<i>Oenopota sp.</i>	24 (1)	2,13	1 (1)	0,05		-		-
<i>Portlandia arctica</i>		-	111 (6)	5,87	4 (4)	0,28	21 (6)	0,93
<i>Retusa obtusa</i>		-	1 (1)	0,05		-		-
<i>Serripes groenlandicus</i>	109 (6)	9,68	15 (5)	0,79	51 (12)	3,61	18 (6)	0,80
<i>Thracia devexa</i>	4 (3)	0,36		-	1 (1)	0,07	1 (1)	0,04
<i>Trichotropis borealis</i>	6 (1)	0,53		-		-	1 (1)	0,04
Bivalvia = 6623 (99.18 %)	1084	96,27	1889	99,89	1414	100	2236	99,51
Gastropoda = 55 (0.82 %)	42	3,73	2	0,11		-	11	0,49
Suspension feeders = 6207 (92.95 %)	1077	95,65	1777	93,97	1275	90,17	2078	92,48
Deposit feeders = 423 (6.33 %)	13	1,15	112	5,92	139	9,83	159	7,08
Carnivora = 45 (0.77 %)	33	2,93	2	0,11		-	10	0,44
Browsers=3 (0.05%)	3	0,27		-		-		-
Total Number of Taxa = 26		17		10		10		15
Total Number of specimens = 6678		1126		1891		1414		2247

number of samples between brackets; main taxa in bold letters

grab samplers underestimate the presence of deeply buried (> 5 cm depth) infaunal organisms. For example, Thomson *et al.* (1986) and Schiøtte (1989) note that the abundance and biomass of the large deeply buried bivalve *Mya truncata* are underestimated in grab samples acquired from near-shore environments.

A comparison of the species composition of the macrofossil assemblages (Table II) with that of modern benthic mollusc communities (Table III) indicates that 30-60 % of the modern mollusc fauna is represented in the fossil faunas. The large relative abundance of *Mya truncata* in the macrofossil assemblages stands in sharp contrast to its apparent absence in the modern faunas. This latter situation is probably due to the sampling bias discussed above.

Amongst the taxa not represented in the macrofossil assemblages are molluscs that may have been excluded from the study region as a result of environmental factors. *Kelliella miliaris*, recorded by Rozycki (1984) in Spitsbergen fiords, is absent in Canadian arctic waters. It is a Norwegian species (Ockelmann, 1958) and its presence in Spitsbergen fiords is considered as incidental by Rozycki (1984). The other three species that characterize the fauna of Van Keulen Fiord are *Astarte elliptica*, *Astarte montagui* and *Crenella decussata*, all of which occur off the eastern shores of the Canadian Archipelago. *Boreacola vadosa* and *Lio-cyma fluctosa* are endemic species restricted to western North America (Bernard, 1979; Lubinsky, 1980).

The relatively low abundance and/or absence of other taxa, notably *Nucula*, *Portlandia*, *Thyasira* and *Yoldiella*, in the

TABLE III

Faunal compositions of different living communities from the Arctic region indicating the taxa in common with fossil assemblages in Table II

Locality: (region): Source of data:	Van Keulen Fjord (Spitsbergen) Rozycki (1984, 1987)	Jorgen Bronlund Fjord (North Greenland) Schiotte (1989)	Expedition Fjord (Canadian Arctic) Aitken and Gilbert (1996)	SE Beaufort Sea (Canadian Arctic) Wagner (1977)	SW Beaufort Sea (North Alaska) Carey et al. (1984)	
Sampling method: Abundance: Depth:	dredge % of occurrence (1) 15-18 m	trawl and grab abund. m2 5-48 m	dredge abund. x sample 4-80 m	trawl and grab % of occurrence (1) 6-35 m 35-60 m	grab abund. m2 (2) 5-25 m	
TAXA	TAXA IN COMMON WITH FOSSIL ASSEMBLAGES IDENTIFIED IN TABLE II					
<i>Astarte borealis</i>	33,3	3,39	12,88	1.1	2.8	-
<i>Axinopsida orbiculata</i>	-	0,07	-	0.7	1.1	19,12
<i>Bathyrca glacialis</i>	-	0,18	-	-	1.1	-
<i>Clinocardium ciliatum</i>	5,5	-	0,95	1.9	2.8	-
<i>Cylichna occulta</i>	1	0,14	4,85	21,0	8,9	-
<i>Delectopecten greenlandicus</i>	-	-	1,89	-	-	1,78
<i>Hiatella arctica</i>	1,6	53,46	3,66	-	2,2	0,18
<i>Lyonsia arenosa</i>	-	-	-	0,7	-	0,36
<i>Macoma calcarea</i>	-	2,65	0,71	5,5	6,2	6,26
<i>Macoma moesta</i>	-	-	-	0,7	0,6	1,16
<i>Margarites sp.</i>	-	-	-	0,4 (3)	0,6 (4)	-
<i>Musculus niger</i>	-	1,06	-	1,9	2,8	-
<i>Mya truncata</i>	2,3	0,35	0,47	0,4	-	-
Naticidae	-	-	0,83	-	-	-
<i>Nuculana pernula</i>	-	-	0,36	0,4	1,7	0,12
<i>Oenopota sp.</i>	-	0,07	0,59	-	0,6 (5)	-
<i>Portlandia arctica</i>	-	24,03	10,4	1,9	5	15,48
<i>Retusa obtusa</i>	-	1,55	-	-	-	-
<i>Serripes groenlandicus</i>	7,1	-	-	1,1	-	1,14
<i>Thracia devexa</i>	-	0,18	0,59	1,1	1,1	0,14
<i>Trichotropis borealis</i>	-	0,11	3,19	-	-	-
NOT SHARED TAXA WITH FOSSIL ASSEMBLAGES IDENTIFIED IN TABLE II	<i>Astarte elliptica</i> (13.5) <i>Crenella decussata</i> (12.7) <i>Astarte montagui</i> (8.7) <i>Kellyella militaris</i> (6.3) minor taxa (8)	<i>Nucula belloti</i> (3.2) <i>Astarte warhami</i> (2.08) <i>Cylichna alba</i> (1.41) minor taxa (6.07)	<i>Astarte warhami</i> (40.9) <i>Thyasira gouldi</i> (7.21) <i>Yoldiella lenticula</i> (4.61) minor taxa (5.91)	<i>Portlandia a. siliqua</i> (26.9) <i>Portlandia arctica</i> <i>aestuvariorum</i> (5.2) <i>Liocyma fluctuosa</i> (5.9) minor taxa	<i>Yoldiella lenticula</i> (8.9) <i>Nucula tenuis</i> (6.2) minor taxa	<i>Boreacola vadosa</i> (32.8) <i>Liocyma fluctuosa</i> (13.18) minor taxa (8.28)
Total Number of Taxa	15	26	21	45	49	31
Number of Taxa in common	6 (40 %)	13 (50 %)	13 (62 %)	13 (28.9 %)	14 (28.6 %)	10 (32.3 %)
Abundance of taxa in common	50.8 %	87.24 %	41.37 %	N/C	N/C	04.6%
Total Number of specimens	N/C	2830	846	N/C	N/C	5000

(1) % of occurrence used by Wagner (1977) and Rozycki (1984) refers to the number of samples containing one species / the samples in the series under examination X 100;

(2) The data by Carey et al. (1984) is based on bivalves;

(3) *M. costalis*;(4) *M. olivaceus*;(5) *O. decussata*.

N/C not considered in the original source; bold characters = main taxa

macrofossil assemblages may be attributed to a variety of factors: "patchy" distribution on the seafloor, operator sampling bias and the lower preservation potential of these taxa. For example, *Portlandia arctica* exhibits a relative abundance of 25 % of the molluscan fauna from Jørgen Brønlund Fiord as opposed to 0-6 % in the macrofossil assemblages. Firstly, *Portlandia arctica*-*Thyasira* spp. represent a facies fauna strongly associated ice-proximal and/or fiord-head environments characterized by rapid rates of sedimentation (Dale et al., 1989; Schiøtte, 1989; Syvitski et al. 1989; Aitken and Gilbert, 1996) and this sedimentary environment may be under-represented in our samples. Secondly, in these fiord-head environments *Portlandia* exhibits a "patchy" distribution on the seafloor as noted by Dale et al. (1989) and Syvitski and Hein (1991) in Baffin Island fiords. Given this situation it is unlikely

that all outcrops of ice-proximal sediments in the raised marine record will yield a *Portlandia*-*Thyasira* fauna, thus contributing to the relatively low abundance of *Portlandia* in the shell collections. Thirdly, underrepresentation of small-sized taxa may also result from collector bias. Field collectors may overlook these small-sized taxa in favour of collecting the shells of large taxa such as *Astarte*, *Clinocardium*, *Hiatella*, *Mya* and *Serripes*. Finally, acidic sediments may contribute to the destruction of carbonate fossils via solution (Spjeldnaes, 1978; Dyke et al., 1996a). The small, thin shells of *Portlandia*, *Thyasira*, etc. makes them more susceptible to postmortem solution relative to larger and/or thick-shelled taxa such as *Mya*, *Hiatella* and *Astarte*. Selective solution of small shells is not likely to occur in the carbonate-buffered surficial sediments on Prince of Wales, Somerset and Devon islands, but Lemmen

et al. (1994) have observed significant postmortem solution of mollusc shells recovered from acidic sediments on western Axel Heiberg Island.

Environmental energy also plays an important role in determining fossil preservation under background sedimentation conditions; even with rapid deposition, fragile fossils may be fragmented if burial involves high-energy conditions (Brett and Baird, 1986).

The arctic-boreal taxa *Colus* spp. and *Buccinum* spp. are widely distributed in the Canadian Arctic and Greenland (Thorson, 1944; Macpherson, 1971; Thomson *et al.*, 1986), however, they are never common. For example, *Buccinum* spp. represents > 1 % of the total abundance of invertebrates recorded in nearshore habitats in northern Baffin Island fiords (Syvitski *et al.*, 1989) and neither taxa has been collected from shallow water habitats in Expedition Fiord, Axel Heiberg Island (Aitken and Gilbert, 1996), nor Disko Fjord and Jørgen Brønlund Fiord, Greenland (Schjøtte, 1989; Schmid and Piepenburg, 1993). These authors do not provide reasons for the absence of these taxa in their collections, however, their low abundance and the sampling bias (*i.e.* small sample area) associated with benthic trawls and grab samplers may be contributing factors.

In relation to *Astarte warhami*, the species is a member of the modern fiord benthos from Axel Heiberg Island (Aitken and Gilbert, 1996). The oldest postglacial records of *Astarte* correspond to the start of a period of climatic amelioration at ca. 8500 BP (Dyke *et al.*, 1996a), but *Astarte warhami* was not found in our samples as a fossil. The absence of this species cannot be explained by changes in water mass properties, since during deglaciation of the central Canadian Arctic Archipelago the surface waters must surely have been Polar in character (Fig. 1); similar to waters where the modern species is adapted to living (Lubinsky 1980). *A. warhami* is notably not recorded as a fossil in the database used by Dyke *et al.* (1996a) for the reconstruction of postglacial faunal succession in North America and Greenland. We postulate that its absence as a fossil can be related to taxonomic difficulties related with this group (Lubinsky 1980), or natural ecological conditions of its distribution. *Astarte warhami* is probably an artificially united species belonging to a group of small *Astarte* referred to collectively under the name of "*Astarte montagu*" (Lubinsky, 1980).

Finally, time averaging, which refers to the mixing of portions of non-contemporaneous benthic communities during the creation of fossil assemblages (Staff *et al.*, 1986) is another factor that produces differences in species composition when comparing modern communities with fossil assemblages. Modern benthic communities are sampled at discrete time intervals, but the fossil assemblages include organisms that occupied the seafloor for variable periods of time, hence the fossil assemblages may be time-averaged. The temporal dimension determines how similar a palaeo-community will be to an ecological one. In another work (Gordillo and Aitken, 2001), we considered the biostratigraphy and taphonomy of the shell collections examined in this study. It was determined that the bulk of the fossil assem-

blages represent parautochthonous assemblages as defined by Kidwell *et al.* (1986); assemblages consisting of specimens that have suffered only minor postmortem disturbance and/or destruction.

Several distinct fossil assemblages were identified in the Canadian Arctic shell collections that resemble, based on similarities in species composition and habitat, modern benthic mollusc assemblages. The fossil assemblages are 1) *Portlandia* only; 2) *Portlandia-Hiatella-Mya*; 3) *Mya-Hiatella-Astarte-Macoma*; 4) a diversified *Astarte* assemblage including *Clinocardium*, *Serripes*, *Colus*, *Buccinum*, and other taxa. Assemblages 1) and 2) occur in late Pleistocene-early Holocene ice-contact/ice-proximal environments and in comparable environments today, whereas assemblages 3) and 4) occur in middle to late Holocene ice-distal, shallow water (< 50 m) environments and in comparable environments today. Thus, the species composition and habitats occupied by the fossil assemblages varied through space and time. The factors influencing the temporal and spatial variation of Late Quaternary mollusc assemblages observed in the Canadian Arctic Archipelago are examined in more detail by Dyke *et al.* (1996a).

In summary, differences in the species composition of modern and fossil mollusc assemblages may be attributed to several factors: (1) biases in the methods of collecting modern and fossil organisms; (2) bias in the preservation potential of some taxa (*e.g.* *Portlandia arctica*); (3) the presence of local taxa in the various benthic communities (*e.g.* *Kelliella miliaris*); (4) ecological factors related to the patchy distribution of certain species on the seafloor (*e.g.* *Portlandia arctica*) or species represented by small numbers of individuals (*e.g.* *Colus* and *Buccinum* spp.); (5) taxonomic difficulties (*e.g.* *Astarte warhami*); (6) time-averaging of fossil assemblages.

TROPHIC RELATIONSHIPS

We recognize that taphonomic bias in fossil preservation places limitations on reconstructions of the trophic dynamics of the Quaternary marine benthos. Soft-bodied taxa, which are numerically abundant in benthic faunas (Schopf, 1980; Aitken, 1990; Palmqvist 1990) cannot be incorporated into our model due to their absence in the fossil record, either as body fossils or trace fossils (however, see Thomsen and Vorren [1986] for examples of unique soft-body preservation in glaciomarine sediments). Consequently, attributes of living communities and palaeocommunities related to trophic structure are not equivalent. Acknowledging the information loss inherent in the fossil record, we have combined observations of modern trophic interactions with observations of trophic relationships documented in the fossil record, *e.g.* naticid gastropod predation (Petersen, 1982; Aitken and Risk, 1988), to partially reconstruct the trophic dynamics of Late Quaternary benthic communities represented in fossil assemblages from the Canadian Arctic Archipelago.

Previous research has shown that molluscs constitute an important component of the arctic food web and are fed upon by a variety of marine organisms. Among vertebrates,

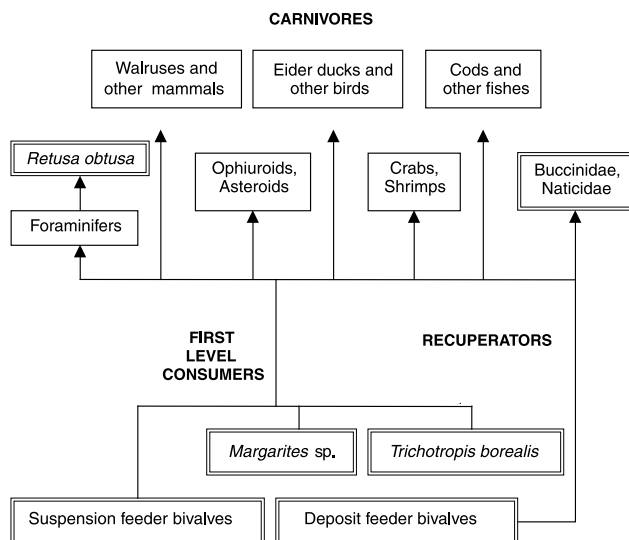


FIGURE 2. Probable trophic relationships for Quaternary marine molluscs in the Canadian Arctic Archipelago. Sources of data are listed in the text. References: DF: deposit feeder. SF: suspension feeder. Mollusca are in double boxes.

Relations trophiques probables s'appliquant aux mollusques marins quaternaires dans l'Archipel arctique canadien. Les sources des données sont signalées dans le texte. Le nom des mollusques apparaît dans les encadrés doubles.

the list includes walrus (Thorson, 1944; Vibe, 1950; Feder *et al.*, 1994; Fisher and Stewart, 1996), bearded and ringed seals (Vibe, 1950), foxes (Vibe, 1950), common eider ducks (Vibe, 1950) and fishes (Thorson, 1944; Macpherson, 1971; Feder *et al.*, 1994). Benthic invertebrate predators include: sea stars (Feder *et al.*, 1994), brittle stars (Ockelmann, 1958; Feder *et al.*, 1994), shrimps and crabs, (Feder *et al.*, 1994) and naticid, buccinid and muricid snails (Petersen, 1982; Aitken and Risk, 1988; Siferd and Welch, 1992; Feder *et al.*, 1994). Based on this information and the feeding habits of molluscs described previously, a general reconstruction of probable predator-prey interactions in Late Quaternary marine benthic faunas is illustrated in Figure 2.

Fisher and Stewart (1996) found that *Mya truncata* and *Hiatella arctica* contribute 81.4 % and 7.5 %, respectively of the total gross energy in the diet of the Atlantic walrus (*Odobenus rosmarus rosmarus*) inhabiting the Arctic Canadian Archipelago. Walrus and whales have an excellent fossil record in the Late Quaternary (Dyke *et al.*, 1996b, 1999) but they are not represented in our samples. Naticid gastropod predation is well documented in Quaternary bivalves from Baffin Island (Aitken and Risk, 1988), but this kind of predation was recorded infrequently from the shells examined in this study. It is also noted that many of the carnivorous taxa identified in Figure 2 are unknown or poorly represented in the Late Quaternary fossil record of the Canadian Arctic Archipelago. (*i.e.* ducks and echinoderms are known from very few localities (*e.g.* Bell, 1996) and crustaceans and fishes have not been recorded from Quaternary sediments in this region of the Canadian Arctic.

CONCLUSIONS

Late Pleistocene and Holocene fossil assemblages recorded in the Canadian Arctic Archipelago differ significantly with respect to species composition from modern nearshore benthic communities. Non-preservation of soft-bodied organisms in combination with the selective destruction of hard body parts may result in the loss of a great proportion of the taxa composing arctic nearshore benthic communities. The basic requirement for meaningful palaeo-community reconstruction is a clear recognition of the differences between the fossil assemblage and the original community. This requires an understanding of the processes that form the fossil assemblage.

Some ecological factors make it unlikely that any sample will contain a complete species-for-species correspondence between its live and dead components, even if no post-mortem transportation or early diagenetic processes had taken place. According to Warne (1969), these factors are: (1) living species populations that are distributed in patches or clumps (irregular spacing of individuals); and (2) natural habitats are commonly occupied by communities in which a few species are represented by a large number of individuals, and many more species by smaller number of individuals (rarity of some species within communities).

The present work illustrates that the Late Quaternary fossil record can yield a great deal of ecological information relating to the habitats occupied by fossil molluscan assemblages and the trophic relationships among their component species if the nature of preservational biases is understood. In spite of a probable bias in the preservation of some taxa (*e.g.* *Portlandia arctica*), the molluscan fauna, as a whole, apparently exhibits a high preservation potential. Thus, the dominance of a boreal-arctic fauna represented by *Hiatella arctica*, *Mya truncata* and *Astarte borealis* would be the result of natural ecological conditions in glaciomarine environments.

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APPENDIX

AUTOECOLOGY AND BIOGEOGRAPHIC PATTERNS

The binomial nomenclature is based on Bernard (1979) and Lubinski (1980) for bivalves, on Macpherson (1971) for gastropods, and on Thorson (1944) and Schiøtte (1989) for some specific taxa.

LIFE HABIT (Table I, column 1)

The majority of the mollusc species represented in the collections belong to the benthic infauna. Another group, formed by taxa such as *Bathyarca glacialis*, *Hiatella arctica*, *Lyonsia arenosa* and *Musculus niger*, is able to live epifaunally or partially buried. This "plasticity" allows them to inhabit both rocky and unconsolidated bottoms. In the eastern Canadian Arctic, *Hiatella arctica* is associated with an epifaunal mode of life on coarse substrates, but it also lives infaunally, partially buried in unconsolidated sediments (Aitken *et al.*, 1988). The adults of *Mya truncata* belong to the infauna, whereas the young ones are often found attached to algae (Ockelmann, 1958). The typical infaunal form of *Mya truncata* burrows deeply into soft sediment (as deep as 60 cm), but this species is also able to live buried shallowly within small patches of shell, silt and clay amongst cobbles as noted by Siferd and Welch (1992) in Barrow Strait.

LOCOMOTION (Table I, column 2)

Most of the species represented in the collections are mobile forms that burrow into the substrata. Only five species live byssally attached to coarse substrates or rocks (*Bathyarca glacialis*, *Delectopecten greenlandicus*, *Hiatella arctica*, *Lyonsia arenosa* and *Musculus niger*). *Delectopecten greenlandicus* lives byssally-attached as juveniles and are free-swimming as adults (Thomsen and Vorren, 1986). In the fiords of eastern Canada, Dale *et al.* (1989) note that the motile form of *Delectopecten* is a common member of the benthos inhabiting fine-grained substrates. In comparison, the attached form of *Delectopecten* appears to be associated with isolated ice-rafted cobbles and boulders on unconsolidated (softground) substrates, which provide these organisms with suitable substrates for attachment, creating the "faunal islands" described by Dale *et al.* (1989). Besides the byssally-attached mode of life, both *Hiatella arctica* and *Lyonsia arenosa* are capable of nestling without a byssus. The predominance of mobile forms is related with the prevalence of unconsolidated bottoms in nearshore glaciomarine environments. It can also be related with the ability of the arctic benthos to adapt to unstable substrates subjected to mass wasting, disturbance by currents and ice-scour, and relatively high rates of sediment deposition in nearshore glaciomarine environments. Under these conditions the ability to burrow rapidly and move freely may be important attributes of both the infaunal and epifaunal benthos. The conditions described above should strongly limit the distribution of attached and/or nestling epifauna. In Canadian arctic fiords, these organisms are largely restricted

to outer fiord environments that are characterized by low rates of sedimentation or erosion, and firmground substrates (Dale *et al.*, 1989; Syvitski, 1989).

SUBSTRATA (Table I, column 3)

The ability of most of the observed taxa to live on a wide variety of substrates from hard to unconsolidated sediments has been well documented by Ockelmann (1958), Ellis (1960) and Siferd and Welch (1992). Dale *et al.* (1989) divide the floors of fiords into soupgrounds, softgrounds, firmground and hardgrounds based on the definitions of Ekdale *et al.* (1984). Amongst the fossil taxa recorded in this study, *Nuculana pernula* and *Portlandia arctica* are well represented on soupground substrates (*i.e.* fine-grained sediments exhibiting high water contents) at the head of the fiords. As noted previously, *Delectopecten greenlandicus* is common over softground substrates towards the fiord mouth. *Delectopecten greenlandicus*, *Hiatella arctica*, and *Macoma calcarea* are the most common taxa on firmground substrates (*i.e.* coarse-grained substrates composed of shell debris and gravel) in the sill area at the mid-fiord and at the fiord mouth. Finally, hardground substrates (*i.e.* rocky sidewalls, exposed bedrock at sills, and faunal islands) are suitable environments for byssally-attached forms (*e.g.*, *Delectopecten greenlandicus* and *Hiatella arctica*). *Astarte borealis* inhabits bottoms with coarse sediments composed of gravel and mud, but is best represented on muddy bottoms where the species occur in abundance (Ellis, 1960; Rozycki, 1987). In the Arctic region, benthic macroalgae (mainly laminariales) also live wherever rock substrates form a suitable site for attachment (Thomson *et al.*, 1986). These algae constitute another common substrate for byssally-attached taxa such as *Hiatella arctica*, *Margarites* sp. and *Musculus niger* as observed Ockelmann (1958) and Rozycki (1984).

DEPTH (Table I, column 4)

We know from the stratigraphy of the collection sites that Late Quaternary molluscs from the Canadian High Arctic record shallow water conditions (mostly < 100 m depth; Dyke *et al.*, 1996a). The molluscan fauna recorded in the collections typically inhabits shallow Arctic waters, but can extend their ranges to hundred of meters depth. Only *Bathyarca glacialis* and *Delectopecten greenlandicus* are more closely associated with deep-water environments. *Bathyarca* spp. inhabits depths from 255-750 m in fiords and across the continental shelf of eastern Baffin Island (*cf.* Aitken and Fournier, 1993, Table 4) and depths of 40-550 m in eastern Greenland fiords (*cf.* Aitken and Fournier, 1993, Table 4). Similarly, *Delectopecten greenlandicus* inhabits depths of 30-150 m in eastern Baffin Island fiords (Dale *et al.*, 1989), 45-200 m in eastern Greenland fiords (*cf.* Aitken and Fournier, 1993, Table 4) and 10-180 m in high Arctic fiords (*cf.* Aitken and Gilbert, 1996, Table 3).

An important environmental feature of arctic shores is the presence of sea-ice. A barren zone devoid of benthic macrofauna can extend to depths of 10-20 m. Mortality due to the direct freezing of benthic organisms during the development of landfast ice, abrasion by sea ice during breakup in early summer, and physiological stress associated with lowered salinities created by melting snow and sea ice in summer are believed to contribute to the absence of shallow-water macrofauna. In general, below 10 m depth these effects are less pronounced, permitting establishment of benthic macrofaunal communities (Alexander, 1980). Several taxa, including *Axinopsida orbiculata*, *Hiatella arctica*, *Macoma calcarea*, *Margarites* sp., *Mya truncata*, *Retusa obtusa* and *Serripes groenlandicus*, recorded by Dale (1985) and Aitken and Gilbert (1986) from intertidal habitats on Ellesmere and Baffin islands indicate that these species can survive the ecological challenges associated with the presence of sea ice in shallow-water environments.

FEEDING (Table I, column 5)

Most of the bivalve taxa represented in the shell collections are filter feeders. Only *Axinopsida orbiculata*, *Macoma calcarea*, *Macoma moesta*, *Nuculana pernula* and *Portlandia arctica* are surface deposit feeders. With respect to the gastropods, *Buccinum* sp., *Colus* sp., *Cylichna occulta*, Naticidae, *Oenopota* sp. and *Retusa obtusa* are carnivorous, but *Trichotropis borealis* is a filter feeder and *Margarites* sp. is a browser. With regards to the carnivorous taxa, *Retusa obtusa* preys mainly on foraminifers and hydrobiid mud snails (Berry *et al.*, 1992; Stamm, 1995). Naticids are predators of bivalves such as *Astarte borealis* and *Hiatella arctica* (Petersen, 1982; Aitken and Risk, 1988). The carnivorous *Buccinum* sp. and *Colus* sp. *sensu lato* also act as scavengers (Aitken and Risk, 1988).

In modern Canadian glaciomarine environments, various authors (Dale *et al.*, 1989; Syvitski *et al.*, 1989; Aitken and Gilbert, 1996) have noted that deposit feeding taxa, notably *Portlandia arctica*, dominate environments characterized by high rates of sedimentation proximal to retreating tidewater glaciers. In comparison, suspension feeding taxa (*e.g.*, *Hiatella arctica* and *Mya truncata*) inhabit more distal environments, where a reduction in the rate of clastic sedimentation, coupled with greater marine primary production, allows for this feeding habit. In Greenland fiords, Schiøtte (1989) noted the predominance of the deposit feeder *Portlandia arctica* in the inner fiord and the predominance of the suspension feeder *Hiatella arctica* in the outer fiord, which agrees well with observations from Canadian fiords.

Carey *et al.* (1984) and Feder *et al.* (1994) have analyzed the trophic structure of mollusc communities inhabiting shallow-water environments in the southwestern Beaufort Sea and northeastern Chukchi Sea, respectively. These authors observed distributional patterns related to water depth and sediment type. Nearshore sand and gravel substrates are dominated by suspension feeding bivalves (*e.g.*, *Astarte* spp., *Boreacola vadosa*), whereas silt and clay substrates offshore are dominated by deposit-feeding bivalves (*e.g.*, *Macoma calcarea*, *Nucula* spp., *Portlandia arctica*).

SALINITY AND TEMPERATURE (Table I, columns 6 and 7)

Estimates of the range of temperatures and salinities tolerated by taxa represented in the shell collections were taken from Aitken (1990) and Peacock (1993). These data were derived from a comparison of modern mollusc distributions with hydrographic data. The data suggest that the macrofauna represented in the collections was able to inhabit polar waters with temperatures ranging from -2 to 0 °C and the reduced salinities (< 30 ‰) found near tidewater ice margins and river deltas.

GEOGRAPHIC DISTRIBUTION (Table I, column 8)

Based on the water masses that prevail in the arctic region, Dunbar (1951) defines "arctic regions" as composed of Polar water only and "subarctic regions" as composed of a mixture of Polar and Atlantic waters. The term "panarctic" refers to species inhabiting both arctic and subarctic regions. The majority of the species represented in the collections (87.5 %) exhibit panarctic circumpolar distributions. Only three species (*Delectopecten greenlandicus*, *Portlandia arctica* and *Thracia devexa*) are restricted to Polar waters of the high arctic region. Ockelmann (1958) considers *Macoma moesta* as a high arctic species. Notwithstanding this observation, the species has been recorded from northern Baffin Island but not southwestern Greenland (Ellis, 1960). Thus, it is considered here as an Arctic-boreal species that exhibits a more restricted pattern in its southern distribution.

Lubinsky (1980) states that the present distribution of Arctic mollusc species reflects the segregation of the polar region from Pacific and Atlantic oceans during Northern Hemisphere Quaternary glaciations, and the extension and retraction of species ranges during and after deglaciation. Dyke *et al.* (1996a) examined postglacial macrofaunal successions and gross shifts in mollusc distribution ranges in response to deglaciation and associated oceanographic changes on a regional scale throughout the Canadian Arctic. According to these authors only *Hiatella arctica* and *Portlandia arctica*, survived in unglaciated regions of the polar continental shelf. The majority of the species with an arctic-boreal distribution, therefore, may have sought refugia by moving into subarctic regions and/or deeper water during periods of extensive continental glaciation as suggested by Crame (1996). These taxa subsequently reoccupied continental shelf habitats as they became available to colonize as a result of deglaciation and sea level rise.

FOSSIL RECORD AND AREA OF ORIGIN (Table I, columns 9-12)

Information on temporal geographic ranges were obtained primarily from Durham and Macneil (1967), Evseev and Krasnov (1985; bivalves) and Vermeij (1991). Additional information was provided by Richards (1962), Macneil (1965), Einarsson *et al.* (1967), Hopkins *et al.* (1972), Allison (1973), Troitskiy (1974), Gladenkov (1978, 1979), Bernard (1979), Franz and Merrill (1980), Simonarson (1981), Agapitov *et al.* (1985), Marincovich *et al.* (1985), Golikov and

Scarlato (1989), Marincovich (1990), Fyles *et al.* (1991) and Suzuki and Akamatsu (1994). Information on the geologic ranges of various genera was obtained from Kauffman (1973), Hallam (1979), Golikov and Sirenko (1988), Honda (1994), Titova (1994), Crame (1996) and Mikkelsen (1996).

The Late Quaternary fauna of Arctic Canada is composed of elements from the Atlantic or from the Pacific (Durham and McNeil, 1967; Bernard, 1979; Evseev and Krasnov, 1985; Vermeij, 1991; among others). Two different groups are recognized. Firstly, Tertiary elements that participated in the Pliocene interchange between the Pacific and Atlantic

Ocean basins. The list includes *Astarte borealis*, *Buccinum finmarkianum*, *Buccinum glaciale*, *Clinocardium ciliatum*, *Colus* spp., *Hiatella arctica*, *Macoma calcarea*, *Musculus niger*, *Mya truncata*, *Nuculana pernula*, *Oenopota decussata*, *Serripes groenlandicus* and *Trichotropis borealis*. Secondly, Quaternary elements derived mainly from the Atlantic Ocean formed taxa of Arctic origin. These taxa are *Axinopoda orbiculata*, *Bathyarca glacialis*, *Buccinum tenue*, *Cylindrina occulta*, *Delectopecten greenlandicus*, *Lyonsia arenosa*, *Macoma moesta*, *Margarites* sp., *Portlandia arctica*, *Retusa obtusa* and *Thracia devexa*.