

Marine Molluscs as Indicators of Environmental Change in Glaciated North America and Greenland During the Last 18 000 Years

Les mollusques marins et les changements du milieu dans la partie englacée de l'Amérique du Nord et du Groenland depuis 18 000 ans

Meeresweichtiere als Indikatoren für Umweltveränderungen im vereisten Nordamerika und in Gröniand während der letzten 18 000 Jahre

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[See table of contents](#)

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Article abstract

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MARINE MOLLUSCS AS INDICATORS OF ENVIRONMENTAL CHANGE IN GLACIATED NORTH AMERICA AND GREENLAND DURING THE LAST 18 000 YEARS*

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ABSTRACT Dated mollusc collections are classified in assemblages to map paleo-faunistic zones. *Hiatella arctica* and *Mya truncata* account for almost half the records and comprise a restricted arctic assemblage. Arctic assemblages comprise 70% and arctic-dominated assemblages 80% of the database. Fifteen species dominate but 170 taxa are recorded. At last glacial maximum, the arctic zone extended from the Arctic Ocean to the Grand Banks. The boreal zone in the western Atlantic was compressed. The subarctic zone, which today dominates eastern Canada, was small. The boreal zone was extensive in the eastern Pacific where subarctic and arctic zones were compressed. Zones shifted northward during deglaciation and the arctic zone diversified when Bering Strait submerged 10.5-10.3 ka BP. Western Arctic molluscs during Younger Dryas time indicate shallow waters warmer than present. Major North Atlantic currents were established 9.5-9.0 ka BP. The subarctic zone extended to the head of Baffin Bay and a boreal zone became established in West Greenland 9-8 ka BP, with intensive changes about 8.5 ka BP. We relate the latter to the reduction of Mackenzie River discharge and in sea ice export to the North Atlantic as Laurentide ice withdrew from Mackenzie headwaters. The extended subarctic zone in Baffin Bay persisted until 3 ka BP and then retreated about 1000 km on the Canadian side. Boreal-subarctic molluscs in the Gulf of St. Lawrence before 9.5 ka BP derived from the glacial refugium. High boreal-subarctic molluscs farther north probably migrated from Europe. We postulate that the Labrador Current acts as a one-way valve for mollusc migrations at glacial-interglacial scales.

RÉSUMÉ Les mollusques marins et les changements du milieu dans la partie englacée de l'Amérique du Nord et du Groenland depuis 18 000 ans. Les mollusques datés provenant de plus de 3000 collections ont été classés en paléo-zones fauniques. *Hiatella arctica* et *Mya truncata* comptent pour près de la moitié des relevés et comprennent un assemblage restreint à l'Arctique. Les assemblages arctiques ou à dominance arctique comptent respectivement pour 70% et 80% de l'ensemble des données. Sur les 170 taxons relevés, 15 espèces dominent. Au dernier pléniglaciaire, la zone arctique s'étendait de l'océan Arctique au Grand Banc. La zone boréale de l'Atlantique Ouest était comprimée. La zone subarctique, qui prédomine actuellement dans l'est du Canada, était peu étendue. La zone boréale occupait une grande superficie dans le Pacifique oriental alors que les zones arctique et subarctique étaient resserrées. Les zones se sont déplacées vers le nord au cours de la déglaciation et la zone arctique s'est diversifiée lorsque le détroit de Bering a été submergé de 10,5 à 10,3 ka BP. Les mollusques de l'Arctique occidental au cours du Dryas récent indiquent que les eaux peu profondes étaient plus chaudes que maintenant. Les principaux courants de l'Atlantique Nord se sont établis de 9,5 à 9,0 ka BP. La zone subarctique s'est étendue jusqu'à la tête (amont) de la mer de Baffin et une zone boréale s'est établie dans la partie ouest du Groenland vers 9-8 ka BP, avec des changements intenses vers 8,5 ka BP. La zone subarctique étendue s'est maintenue jusqu'à 3 ka BP, puis a reculé jusqu'à 1000 km du côté canadien. Les mollusques du Boréal-Subarctique présents dans le golfe du Saint-Laurent avant 9,5 ka BP provenaient du refuge glaciaire. Les mollusques du haut boréal-subarctique plus au nord provenaient probablement de l'Europe. Le courant du Labrador a sans doute agi comme pompe pour la migration des mollusques aux échelles glaciaire-interglaciaire.

ZUSAMMENFASSUNG Meeresweichtiere als Indikatoren für Umweltveränderungen im vereisten Nordamerika und in Grönland während der letzten 18 000 Jahre. Datierete Weichtier-Sammlungen wurden in Einheiten klassifiziert, um eine Karte der Paläo-Fauna-Zonen zu erstellen. *Hiatella arctica* und *Mya truncata* stellen fast die Hälfte der Aufstellungen und bestehen aus einer auf die Arktis beschränkten Einheit. Arktische Einheiten umfassen 70% und vorwiegend arktische Einheiten 80% der Datenbank. Fünfzehn Spezies überwiegen, aber 170 Taxa sind belegt. Beim letzten glazialen Maximum erstreckte sich die arktische Zone vom Arktischen Ozean bis zu den Grossen Bänken. Die Boreal-Zone im West-Atlantik war komprimiert. Die subarktische Zone, welche heute Ostkanada beherrscht, war klein. Die Boreal-Zone war im Ostpazifik sehr ausgedehnt, während die subarktische und die arktische Zone komprimiert waren. Die Zonen verlagerten sich nordwärts während der Enteisung, und die arktische Zone wurde abwechslungsreicher, als die Bering-Meerenge 10.5 - 10.3 ka v.u.Z. auftauchte. Die hauptsächlich Nordatlantikströmungen wurden 9.5 - 9.0 ka v.u.Z. festgelegt. Die subarktische Zone erstreckte sich bis zum Kopf der Baffin Bay, und eine Boreal-Zone etablierte sich 9 - 8 ka v.u.Z. in West-Grönland, mit intensiveren Veränderungen etwa um 8.5 ka v.u.Z. Die ausgedehnte subarktische Zone in der Baffin Bay erhielt sich bis 3 ka v.u.Z. und wich dann etwa 1000 km auf der kanadischen Seite zurück. Boreal-subarktische Weichtiere im Golf des Sankt-Lorenz vor 9.5 ka v.u.Z. stammten aus dem glazialen Refugium. Die Weichtiere aus dem subarktischen Hochboreal weiter im Norden kamen wahrscheinlich aus Europa. Wir behaupten, dass die Labrador-Strömung auf die Weichtier-Wanderungen im glazialen-interglazialen Massstab wie eine Klappe in einer Richtung wirkt.

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"Little is known of the fate of boreal species, and to a lesser extent arctic-boreal species in the northwest Atlantic during the last glacial maximum... Post-glacial species movements remain largely unknown..." (Franz and Merrill, 1980, p. 236-237).

INTRODUCTION

Mollusc shells, particularly pelecypod shells, are by far the most common macrofossils in Late Wisconsinan and Holocene raised marine deposits and more than 3000 collections from glaciated North America and Greenland have been radiocarbon dated at several laboratories. Although this is a large continental-scale paleoenvironmental data set, scant attention has been paid to changes in Late Quaternary mollusc assemblages through time. The taxonomic database has grown more through happenstance than through crafted research because collectors have most often submitted shells for dating in order to determine deglaciation and sea level histories rather than for paleoenvironmental research.

In this paper we examine changes in marine mollusc assemblages in glaciated North America (north of 40°N latitude) and Greenland from the last glacial maximum to today. We interpret nearshore marine conditions. Water mass temperatures and sea ice conditions modulate climate and broadly affect cyclogenesis and heat transfer to the atmosphere. Reconstructions of past conditions may be of use in validating paleoclimatic and paleoceanographic models and in evaluating feedbacks in the ocean-climate system. These are among the broad objectives of the Paleogeographic Atlas of Glaciated North America Project of the Geological Survey of Canada and the Climate Systems History and Dynamics Project. We use the radiocarbon time scale throughout. This departs increasingly from the calendar (sidereal) time scale back through time such that the last glacial maximum at 18 000 radiocarbon years ago corresponds to about 22 000 calendar years ago.

We summarize data below in three main sections: statistical summaries of species and assemblage percentages (see Fossil Mollusc Assemblages), "Regional Time Series of Mollusc Assemblages" for zoologically meaningful regions, and paleogeographic reconstructions of molluscan zones at 1000 year (1 ka) intervals (see Paleogeography). We then use the database to address the issue of species survival in the northwest Atlantic refugium alluded to in our opening quote (Franz and Merrill, 1980), followed by an examination of the record of *Mya pseudoarenaria*, which has experienced severe range retraction during the postglacial. Statistics and graphics are generated from computer databases that will be maintained and are available on request. Before these main sections we sketch the geological origins of mollusc groups of concern to this study and outline elements of oceanography and zoogeography that are necessary to interpret the fossil record. We also outline problems and biases inherent to the database that limit its utility but point to refinements. The term "mollusc" herein always refers to a marine mollusc.

BACKGROUND TO MOLLUSCAN DISTRIBUTIONS

All species of molluscs that occur in Late Pleistocene and Holocene deposits dealt with here are extant and many are of recent origin. Cold-water molluscs, common around northern North America today, originated during the Late Cenozoic (Franz and Merrill, 1980; Lubinsky, 1980). Before about 3.2 million years (Ma) ago the Arctic Ocean was separated from the Pacific by an emergent Bering Strait, and its Tertiary molluscan faunas were extensions of temperate Atlantic populations (Brouwers, 1994). A shallow Atlantic connection via Fram Strait was established 10-15 Ma ago (Lawver *et al.*, 1990).

Cold-water molluscs can exchange between the Pacific and Atlantic only via the Arctic. Such exchanges started in Late Tertiary time. Early exchanges of cold-water forms involved many more species migrating from Pacific to Atlantic than vice versa, probably because of current-controlled pelagic larvae dispersion (Durham and MacNeil, 1967); both Pacific and Atlantic surface waters flow into the Arctic but Arctic surface water today exits only to the Atlantic (Herman, 1989). The major transarctic migrations occurred when the Arctic Ocean was relatively warm, during 1 Ma or so between first submergence of Bering Strait and the onset of cyclic Northern Hemisphere glaciations about 2.4 Ma ago (Late Pliocene; Shackleton *et al.*, 1984). The first (or an early) opening of Bering Strait is recorded in Iceland by appearance of several Pacific boreal molluscs. Shortly thereafter Pacific-derived boreal species dominate the record (Einarsson *et al.*, 1967; Eiriksson, 1980). In arctic Canada, this event is known only from Meighen Island, where Beaufort Formation marine beds contain a mixture of Pacific-derived and Atlantic-derived molluscs believed to represent the time immediately after introduction of Pacific forms (Fyles *et al.*, 1991). The Arctic Ocean - Greenland Sea may have been relatively warm (nearshore sea bottom temperatures 4-9°C) during early (first?) glaciation(s) of northeast Greenland 2.4-2.6 Ma ago, as recorded in the Kap Kobenhavn and Lodin Elv formations (Penny, 1993), or they may have returned to warm conditions in the Late Pliocene (about 2 or 1.8 Ma ago; Funder, 1989; Bennike and Böcher, 1990; Repenning and Brouwers, 1992) depending on the age assigned to these formations. The Kap Kobenhavn Formation contains the boreal mollusc *Macoma balthica* (Funder, 1989). Mudie *et al.* (1990) place the onset of glaciation around the shores of the Arctic Ocean, possibly alpine glaciation of Ellesmere Island, at 4 Ma ago based on dropstone occurrences in cores from the submarine Alpha Ridge off the Canadian polar margin. Ice-rafted detritus first occurs in Late Miocene sediments in deep Baffin Bay (Cremer, 1989), but the pollen content of Baffin Bay sediment cores indicates persistence of boreal forests on Baffin Island and probably Greenland through the Pliocene and into the earliest Pleistocene (De Vernal and Mudie, 1989).

Mya arenaria, an important Pleistocene boreal mollusc, was the first Pacific form to reach the Atlantic via the Arctic. All but one species of *Mya* (*M. producta*) are of Pacific origin. *Mya truncata*, the second most common Late Quaternary molluscan fossil, occurred in the eastern North Atlantic by the

Early Pleistocene. Late Wisconsinan *M. truncata* were the oldest known to MacNeil (1965) from the western North Atlantic. However, we can now place it at the limit of radiocarbon dating, about 50 ka BP, and likely to the Sangamonian in eastern Canada; it comprises 22% of dated shells in the range 30-50 ka BP, all of which may be minimum ages. It occurs in the second lowest aminozone on eastern Baffin Island, which may be as young as 300 ka BP (Mode, 1985) or as old as Pliocene (Feyling-Hanssen, 1985). *Macoma calcarea*, one of the most common arctic-subarctic molluscs, migrated from Pacific to Atlantic as did *Clinocardium ciliatum*, *Serripes groenlandicus* and the boreal *Macoma balthica*, *Mytilus edulis*, and *Neptunea despecta*. *Hiatella arctica*, the most common Pleistocene mollusc in glaciated North America, and *Astarte alaskensis* (= *A. elliptica*) were the first Atlantic forms to reach the Pacific (Late Miocene-Early Pliocene; MacNeil, 1965; Durham and MacNeil, 1967). The important fossil *Chlamys islandica* also is suspected to have migrated from Atlantic to Pacific (Franz and Merrill, 1980). The most common Quaternary marine invertebrates discussed in this paper are illustrated on Plates I and II, drawn mostly from the type collections of the Geological Survey of Canada.

Important aspects of present mollusc distributions are thought to have resulted from stresses of Quaternary temperature fluctuations, from segregation of Pacific and Atlantic ranges during glaciations, and from extensions and retractions of ranges during and after deglaciation (Lubinsky, 1980). For example, many Pacific forms that made transarctic migrations during the Late Tertiary did not survive Pleistocene conditions in the North Atlantic; only 7 of 18 Pacific species in the Early Pleistocene of Iceland survive today (Franz and Merrill, 1980, quoting Einarsson, 1964). Only more adaptive species have survived the oceanographic changes associated with the earlier Quaternary glaciations, which explains the lack of extinctions during the last glaciation. In this context, the apparent ongoing extinction of *Mya pseudoarenaria*, discussed below, is puzzling.

The present distribution of mollusc species along eastern North America is discontinuous. There is no smooth gradient from cold-water species to warm-water species between Labrador and southern New England. Bousfield and Thomas (1975) hypothesized that the disjunctions resulted from postglacial environmental changes: following a range extension, especially favourable niches in newly occupied territory continued to be occupied after general range retraction.

For the time and water depths considered here, two kinds of range extensions occurred: arctic and boreal species extended southward as ice sheets expanded, and subarctic, boreal, and temperate species extended north of present limits during parts of postglacial time. Because temperate (Virginian) species ranged only marginally into the study area, this report primarily concerns arctic, subarctic, and boreal (cold-temperate) molluscs. We know from the stratigraphy of collection sites that most samples record shallow water conditions (<200 m; mostly <100 m).

OCEANOGRAPHY AND COASTAL ENVIRONMENTS

At a continental scale, shallow-water mollusc distributions are controlled by ocean surface water masses with contrasting temperatures, salinities, and sea-ice covers. Water mass distributions are dictated by the patterns and strengths of ocean surface currents (Fig. 1). Water masses at intermediate and greater depths have little or no effect on nearshore molluscs.

Arctic Surface Water (0 to -2°C ; 28-32.5 per mil salinity) carried by the Transpolar Drift continues southward through Fram Strait as the East Greenland Current. Other Arctic Surface Water, 30% of total (Arctic System Science, 1990), filters through the Canadian Arctic Archipelago and continues southward along the east coast of Canada as the Baffin and Labrador currents (-0.5 to 2.5°C ; 32-34 per mil for Inner Labrador Current). These sweep subarctic conditions into middle latitudes and deflect the Gulf Stream eastward off Cape Hatteras, about 40°N (Piper *et al.*, 1991).

Boreal (cool-temperate) Atlantic water is carried northward along the west coast of Greenland by the West Greenland Current ($4-6^{\circ}\text{C}$; 34-35 per mil) and subtropical (warm-temperate) Atlantic water is carried northward along the American and southeastern Canadian margins by the Gulf Stream and North Atlantic Drift. The Gulf Stream recurves southeastward off Nova Scotia but a branch continues northward as the North Atlantic Drift ($35-36$ per mil; $16-18^{\circ}\text{C}$, decreasing to 3°C in Barents Sea). Warm offshoots move westward and mix with arctic waters, forming the Irminger ($6-10^{\circ}\text{C}$)

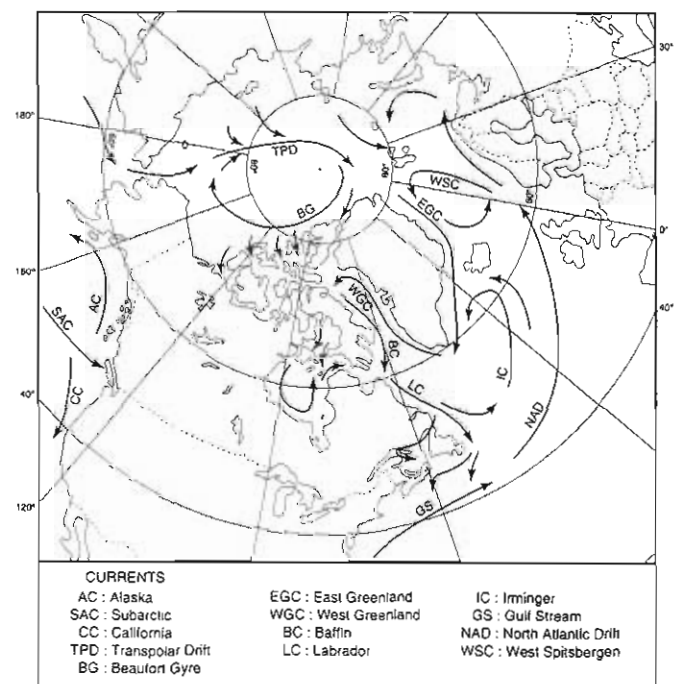
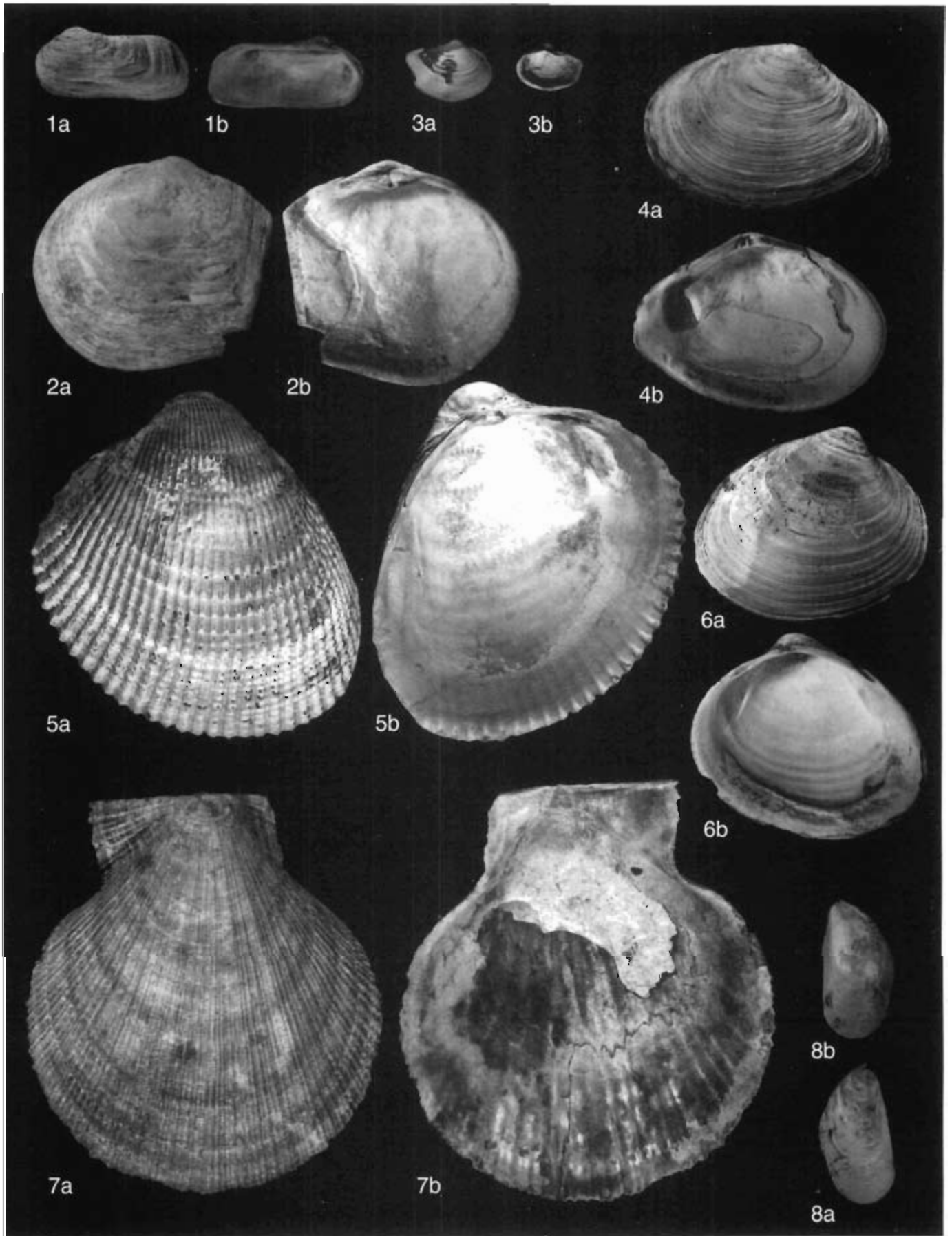


FIGURE 1. Ocean surface currents around northern North America and Eurasia.

Courants océaniques de surface autour du nord de l'Amérique du Nord et de l'Eurasie.



and West Spitsbergen currents. The former contributes the warm water to the West Greenland Current and the latter is responsible for the farthest northward extension today of boreal molluscs. A branch of the West Spitsbergen Current continues into the Arctic Ocean along the east side of Fram Strait. Its relatively warm (>3°C on entry) and saline (slightly above 35 per mil) waters then submerge to run below depths of 200-400 m (Coachman and Barnes, 1963). Most of this Atlantic Water re-exits the Arctic Ocean as an underlayer of the East Greenland Current after circulating counter-clockwise in the Arctic Ocean, below the opposing flow of the Beaufort Gyre. This two-way water flow through Fram Strait accomplishes 90% of the heat exchange between the Arctic Ocean and southern water masses (Kristoffersen, 1990). Shallow sills today prevent deep Atlantic water in the Arctic Ocean from traversing the Canadian Arctic Archipelago.

In the Pacific, the east-flowing, Subarctic Current strikes the coast at the latitude of Vancouver Island and splits to set up two opposing coastal currents: the Alaska Current carries warm water northward along the entire coast to the western Aleutian Islands while the California Current carries relatively cool (boreal) water southward nearly to the equator. This current pattern creates a much wider boreal zone in the eastern Pacific than its counterpart in the western Atlantic. Surface water from the North Pacific enters the Arctic Ocean via Bering Strait where it sweeps westward along the Siberian coast into the Beaufort Gyre and ultimately into the Transpolar Drift. Inflowing Pacific waters contribute much to the upper layers of the Arctic Ocean west of the submarine Lomonosov Ridge (10 times the annual inflow from all large Siberian rivers; Barry,

1989). Pacific water intruding the Beaufort Gyre forms a layer characterized by a shallow temperature maximum (50-100 m depth) above water of Atlantic origin and below Arctic Ocean Surface Water (Coachman and Barnes, 1961). A change in rate of Pacific inflow could affect the thickness of the Arctic Ocean surface layer.

MOLLUSCAN ZOOGEOGRAPHY

MOLLUSCAN ZONES

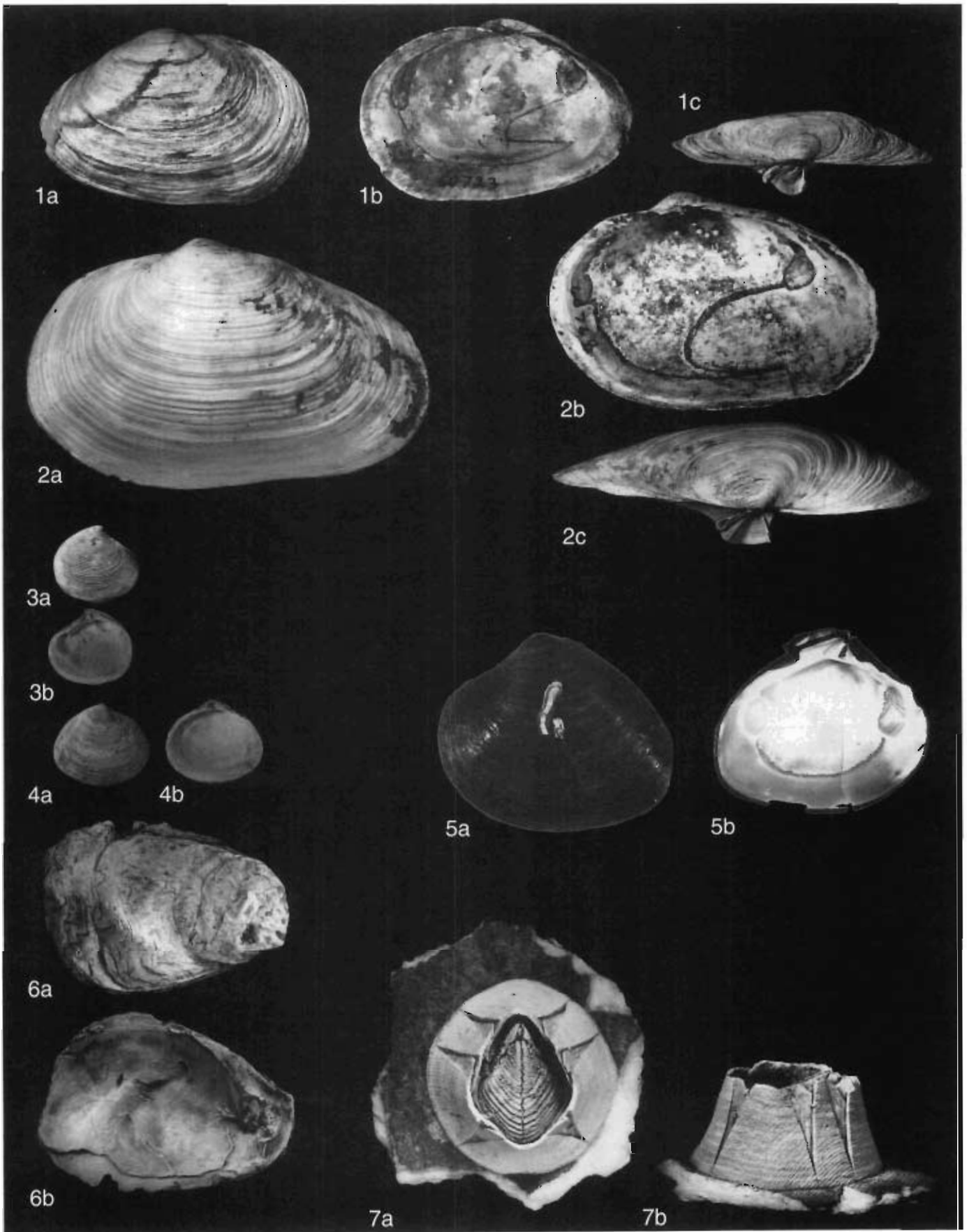
Marine molluscan zones are commonly, and herein, referenced to thermal conditions. Thus we refer to warm-temperate (Virginian; Californian), cold-temperate or boreal (Acadian, Oregonian), subarctic, and arctic zones, and to high and low arctic subzones. These zones have been defined for Greenland and North America (e.g. Madsen, 1936; Lubinsky, 1980; Bernard *et al.*, 1991). Franz and Merrill (1980) discussed the origins and determinants of the distribution of arctic-boreal, boreal, and temperate molluscs along the eastern seaboard of North America. They too found that an important influence on mollusc distribution was their thermal requirements. But they emphasized that species groups "...are not merely correlates of the existing marine environment, nor the products only of thermal/geographic barriers. Rather these groups have clearcut Tertiary origins and ...their present distribution patterns are the result of environmental conditions in the Pleistocene, and especially the Holocene". That is, evolutionary history is probably as important as the conditions of the present environment in determining faunal distributions.

Major changes in species composition occur around Cape Hatteras and Cape Cod. Warm Transhatteran species decline sharply north of Cape Cod, as do cold arctic-boreal species south of there. The boreal group displays maximum success where the other two decline. The boreal species are largely endemic to the western North Atlantic (65%), having evolved there after formation of the Labrador Current System in the Tertiary (Franz and Merrill, 1980). This current separated European from American warm-water shelf areas, whereas earlier the Gulf Stream and its offshoots had warmed the Labrador Sea. Berggren and Hollister (1977) correlated the onset of the Labrador Current with the onset of Northern Hemisphere glaciation in the Late Tertiary at 2.4 Ma ago. However, the Labrador Current operates under interglacial conditions today. In as much as it derives its cold water from the Arctic Ocean via the arctic archipelago and Fram Strait, its onset may correlate with formation of the arctic inter-island channels during the Middle to Late Tertiary rather than with glaciation (Kerr, 1980; Mudie *et al.*, 1990; Dyke *et al.*, 1992). Bohrman *et al.* (1990) suggested the onset of cold surface currents at 4 Ma ago in the Labrador Sea (East Greenland Current) based on the beginning of biogenic opal accumulation. Gradstein and Srivastava (1980) placed the establishment of a Labrador Current in the Late Miocene to Middle Pliocene (5-3 Ma ago), as Arctic Ocean outflows formed, but also suggested that the Labrador Shelf was not "fully swept" by cold southward currents until the Pleistocene.

The Transhatteran species are derived largely from American Miocene species that predate the transarctic migrations

PLATE I. All shells are shown at actual size. 1) *Hiattella arctica* Linné. 1a, exterior; 1b, interior; GSC hypotype 20164; GSC negatives 113092K, L. 2) *Mya truncata uddevallensis* Forbes. 2a, exterior; 2b, interior; GSC hypotype 20162; GSC negatives 113096D, E. 3) *Portlandia arctica* Gray. 3a, exterior; 3b, interior; GSC hypotypes 20148, 20147; GSC negatives 113092M, N. 4) *Macoma calcarea* Gmelin. 4a, exterior; 4b, interior; GSC hypotype 20158; GSC negatives 113092M, N. 5) *Clinocardium ciliatum* Fabricius. 5a, exterior; 5b, interior; sample 69-1 (GSC-1337), L.A. Dredge; GSC negatives 1966-066B, C. 6) *Serripes groenlandicus* Bruguière. 6a, exterior; 6b, interior; GSC hypotype 20156; GSC negatives 103094F, H. 7) *Chlamys islandica* Müller. 7a, exterior; 7b, interior; sample 69-1 (GSC-1337), L.A. Dredge; GSC negatives 1966-066E, D. 8) *Mytilus edulis* Linné. 8a, exterior; 8b, interior; GSC hypotype 20149; GSC negatives 113096F, G.

PLANCHE I. Tous les coquillages sont illustrés grandeur nature. 1) *Hiattella arctica* Linné. 1a, extérieur; 1b, intérieur; hypotype de la CGC 20164; négatifs de la CGC 113092K, L. 2) *Mya truncata uddevallensis* Forbes. 2a, extérieur; 2b, intérieur; hypotype de la CGC 20162; négatifs de la CGC 113096D, E. 3) *Portlandia arctica* Gray. 3a, extérieur; 3b, intérieur; hypotypes de la CGC 20148, 20147; négatifs de la CGC 113092M, N. 4) *Macoma calcarea* Gmelin. 4a, extérieur; 4b, intérieur; hypotype de la CGC 20158; négatifs de la CGC 113092M, N. 5) *Clinocardium ciliatum* Fabricius. 5a, extérieur; 5b, intérieur; échantillon 69-1 (GSC-1337), L.A. Dredge; négatifs de la CGC 1966-066B, C. 6) *Serripes groenlandicus* Bruguière. 6a, extérieur; 6b, intérieur; hypotype de la CGC 20156; négatifs de la CGC 103094F, H. 7) *Chlamys islandica* Müller. 7a, extérieur; 7b, intérieur; échantillon 69-1 (GSC-1337), L.A. Dredge; négatifs de la CGC 1966-066E, D. 8) *Mytilus edulis* Linné. 8a, extérieur; 8b, intérieur; hypotype de la CGC 20149; négatifs de la CGC 113096F, G.



of cold-water forms. In contrast, 82% of the arctic-boreal faunas have an amphiatlantic/Pacific distribution and only 8% are endemic to the western North Atlantic. This group originated largely from transarctic migrations from the Pacific in the Late Tertiary.

While not negating the evolutionary overprint, thermal regime appears to play an important role in species diversity (Bernard *et al.*, 1991). Species diversity declines with temperature in both Pacific and Atlantic oceans. However, cold-water species have wider distributions because they inhabit lower latitudes by submerging to cooler waters at depth. Thus, there is a vertical zonation in non-arctic regions. Conversely, the small temperature difference between deep and shallow water in arctic seas results in relatively unrestricted depth ranges for some arctic molluscs there.

Minimum winter temperatures are not critical to molluscan distributions. Instead, Hall (1964) suggested that the number of consecutive days in summer when shallow water temperatures are warm enough for spawning and larval activity is critical. Bernard *et al.* (1991) found a strong positive correlation between mean annual surface temperatures and the number of intertidal bivalve species in the northeast Pacific. A weaker correlation was found for subtidal molluscs.

Our study area extends marginally into the warm-temperate zone in the Atlantic. In the Pacific, the boreal contacts the arctic zone along the Aleutian Islands and its southern boundary is at 34°N. All Pacific fossil sites considered here lie in the present boreal zone; there are no dated molluscs from the arctic Bering Sea due to the lack of raised marine sediments.

PLATE II. All shells are shown at actual size. 1) *Mya arenaria* Linné. 1a, exterior; 1b, interior; 1c, dorsal view; GSC hypotype 20160; GSC negatives 113095J, H, I. 2) *Mya pseudoarenaria* Schlesch. 2a, exterior; 2b, interior; 2c, dorsal view; GSC hypotypes 20163, 20163a; GSC negatives 113094D, 113097F, 113094E. 3) *Astarte striata* Leach. 3a, exterior; 3b, interior; GSC hypotype 20151; GSC negatives 113092E, F. 4) *Macoma balthica* Linné. 4a, exterior; 4b, interior; GSC hypotype 20159; GSC negatives 113095C, D. 5) *Astarte borealis* Schumacher. 5a, exterior; 5b, interior; ¹⁴C sample GSC-4853; GSC negatives 1966-066A, B. 6) *Crassostrea virginica* Gmelin. 6a, exterior; 6b, interior; GSC hypotype 20150; GSC negatives 113097C, D. 7) *Balanus hameri* Ascanius. 7a, top view of adult individual attached to a scallop shell; 7b, side view; GSC hypotype 20193; GSC negatives 113234I, B.

PLANCHE II. Tous les coquillages sont illustrés grandeur nature. 1) *Mya arenaria* Linné. 1a, extérieur; 1b, intérieur; 1c, vue dorsale; hypotype de la CGC 20160; négatifs de la CGC 113095J, H, I. 2) *Mya pseudoarenaria* Schlesch. 2a, extérieur; 2b, intérieur; 2c, vue dorsale; hypotypes de la CGC 20163, 20163a; négatifs de la CGC 113094D, 113097F, 113094E. 3) *Astarte striata* Leach. 3a, extérieur; 3b, intérieur; hypotype de la CGC 20151; négatifs de la CGC 113092E, F. 4) *Macoma balthica* Linné. 4a, extérieur; 4b, intérieur; hypotype de la CGC 20159; négatifs de la CGC 113095C, D. 5) *Astarte borealis* Schumacher. 5a, extérieur; 5b, intérieur; échantillon GSC-4853; négatifs de la CGC 1966-066A, B. 6) *Crassostrea virginica* Gmelin. 6a, extérieur; 6b, intérieur; hypotype de la CGC 20150; négatifs de la CGC 113097C, D. 7) *Balanus hameri* Ascanius. 7a, vue verticale d'un individu adulte attaché à un coquillage; 7b, vue de côté; hypotype de la CGC 20193; négatifs de la CGC 113234I, B.

ARCTIC MOLLUSCS

After Late Cenozoic cooling created a thermal barrier to transarctic migrations, waters from the Atlantic Ocean played the prominent role in the distribution of arctic species. Most arctic taxa have affinities with Atlantic boreal species (Fedyakov and Naumov, 1989; Golikov, 1989). Influence of Pacific waters has been less significant. Only Pacific species that can move through the cold waters of Bering Strait can spread into the Canadian Arctic and Greenland. *Macoma inconspicua* is one of few Pacific endemics found in the south-western Canadian Arctic Archipelago. Of 101 species of molluscs identified by Wagner from the Canadian Beaufort Sea, 33% are known from both Atlantic and Pacific oceans; 51% are recorded from the Atlantic but not the Pacific, and only 6% are reported from the Pacific but not the Atlantic (Vilks *et al.*, 1979). Although the 6% shared with the Pacific distinguishes the Beaufort region from the rest of the Canadian Arctic, Atlantic affinity dominates the present fauna even there. However, data presented below show that the last opening of Bering Strait had an important impact on postglacial evolution of Canadian arctic faunas.

Interest has increased recently in the marine biology, sedimentology, and oceanography of cold regions of Canada, but many important concepts were established by Danish researchers in Greenland. Madsen (1936, 1940) first divided Greenland waters into arctic and subarctic (or boreo-arctic) zoogeographical zones. The boundary is marked by the northern limits of certain littoral animals, such as *Littorina saxatilis*, *Mytilus edulis*, and *Balanus balanoides*. This boundary was placed 1100 km farther north on the west coast of Greenland (73° 05'N) than on the east (66° 67'N). Madsen (1936) correctly speculated that the farther penetration of warm fauna on the west coast was due to admixing of warm water from the Irminger Current with polar water in the West Greenland Current.

Dunbar (1946) recognized the significance of Madsen's zones to the distribution of littoral and other northern faunas and to hydrographic conditions in the Canadian Arctic. The northern limit of boreal molluscs occurs along Cumberland Peninsula near Cape Dyer (67°N) on the Canadian side of Baffin Bay, about 1000 km south of the limit on the Greenland side (Andrews *et al.*, 1980). This dramatically illustrates the influence of the cold Baffin Current off eastern Canada. Madsen's observations have been confirmed by further research on Greenland shores (Bertelsen, 1937; Vibe, 1939). The Canadian limits were confirmed by Ellis (1955, 1960).

Investigation of arctic mollusc communities and environmental tolerances began with Thorson's (1933, 1934) work in northeast Greenland. He defined several communities, the most extensive being the *Macoma calcarea* community in water depths of 3-45 m. He also studied larval development and determined that temperatures <4°C exclude most boreal species; only fauna capable of reproduction at lower temperatures can inhabit arctic waters. About 70% of species studied spawned successfully at temperatures <2.5°C. About 95% of benthic invertebrates from northeast Greenland complete their larval development without a pelagic stage. Non-pelagic development is particular to all species found solely in the

Arctic and to some deep-sea species, but to few cosmopolitan shallow-water forms. Those species with pelagic larval development present in the Arctic extend into lower latitudes. Pelagic stages are short (<1 month), suggesting high metabolism. Thorson noted that some species that exhibit non-pelagic development in the North switch to pelagic modes in the South. For many benthic organisms, the planktonic larval stage is the main means of dispersal. However, Martel and Chia (1991) found that juveniles and small adults of *Mytilus edulis*, *M. californianus*, and *Hiatella arctica* can drift to new sites. This was an advantage to these species in extending their ranges during deglaciation.

Cold-water molluscs have a further advantage in postglacial dispersion because they tolerate wide ranges of marine conditions. They exploit short ice-free periods and tolerate long winters with negative water temperatures and seasonally varying salinities; some robust species such as *Hiatella arctica* and *Mya truncata* can survive the abrasive action of sea ice in the intertidal zone. Some have evolved reproductive strategies where large-yoked eggs or nurse eggs increase probability of success.

Thorson (1936) suggested that low temperatures were responsible for slow growth rates, great longevity, and late maturity (third summer or later) of arctic bivalves. Slow growth rates have been confirmed for Canadian arctic species, notably *Mya truncata* (Hewitt and Dale, 1984). Consequently one would expect to find a high proportion of juveniles in arctic environments. Ockelmann (1958) studied the bivalves of eastern Greenland. He identified characteristic bivalves that occur in East Greenland Current and fiord waters and noted Holocene range extensions. East Greenland Current waters with temperatures of 0° to -1.7°C hosted, among others, *Portlandia arctica*, *P. (= Yoldiella) lenticula*, *P. (= Yoldiella) frigida*, *P. (= Yoldiella) fraterna*, *Lima hyperborea*, and *Pandora glacialis*.

Recent studies of mollusc-sediment relationships may be useful in interpreting fossil records. Gulliksen *et al.* (1985) showed that a high suspended sediment content of water reduces phytoplankton production and thus faunal abundance. Görlich *et al.* (1987) noted reduced biomass of macrobenthos in Hornshund Fjord, Svalbard due to settling of suspended sediment from tidewater glaciers.

Canadian research is less comprehensive than work accomplished in Greenland. The most extensive early faunal collections were made during the second Norwegian Arctic Expedition (1898-1902) in Jones Sound (Grieg, 1909). The Canadian Arctic Expedition (1913-18; Verrill, 1922) and Fisheries Research Board *Calanus* cruises (1948-61; Dunbar and Grainger, 1952) provided the first lists and descriptions of marine invertebrates from large areas. Ellis (1957) and Curtis (1975) list other early studies of Canadian arctic benthic fauna. These and other studies outlined the distributions of common molluscs (Bousfield, 1960; Macpherson, 1971; Bernard, 1979; 1983; Lubinsky, 1980; Smith, 1981; Wagner, 1984). More recent surveys include those of Clarke (1974) and Syvitski *et al.* (1989) in Baffin Bay, Wagner (1975) in Strait of Canso, and Vilks *et al.* (1979) on the Beaufort Shelf.

Quantitative studies of cold-water molluscs are few because of limited accessibility. This constrains understanding of modern molluscan ecology and zoogeography and limits our ability to draw generalizations from the fossil record. Few quantitative studies have concentrated on intertidal and upper subtidal zones, and the works of Ellis (1955, 1960) and Ellis and Wilce (1961) still provide benchmarks for the Canadian Arctic, particularly for southern Baffin Island. They described a seaward-increasing density of fauna below the generally barren zone above mean tide level. Intertidal molluscs of southern Baffin Island have been further studied by McCann *et al.* (1981), Aitken and Gilbert (1986, 1989), and Dale (1992). McCann *et al.* noted that gastropods are most common on inner intertidal flats and bivalves on the outer. In areas of emergence, the outer tidal flat environment, with its thicker sediments, has better preservation potential which would tend to bias the record in favour of bivalves. *Mya truncata* survives well on the outer flat where firm, cohesive sediment prevents burrows from collapsing.

The typical arctic, shallow-water community is the *Macoma* community on sandy sites. This is dominated by *Macoma calcarea* with *Mya truncata*, *Serripes groenlandicus*, and *Hiatella arctica*. The large intertidal flats of Baffin Island contain pockets of *Cyrtodaria kurriana*, *Thracia myopsis*, and *Astarte borealis*. *Portlandia arctica* dominates deeper mud bottoms. In contrast, high arctic intertidal sites on eastern Ellesmere Island exhibit lower densities and diversities of organisms: *Axinopsida orbiculata*, *Hiatella arctica*, and *Mya truncata* occur in low densities along with gastropods such as *Cylichna alba* and *Oenopota bicarinata* (Dale, 1985).

Subtidal molluscs in Canadian arctic fiords have been studied recently. Syvitski *et al.* (1989) compared a number of Baffin Island fiords but local environmental effects are difficult to separate from possible latitudinal controls on differences in communities. Aitken and Fournier (1993) and Dale *et al.* (1989) examined the macrobenthos, including molluscs, in several east-central Baffin Island fiords. A *Portlandia* association there occupies prodelta environments, characterized by abundant *P. arctica* and other motile deposit feeders such as *Axinopsida orbiculata* and *Nucula bellotti*. Aitken and Gilbert (in press) described molluscs along shallow to deep-water transects in Expedition Fiord (79°N), Axel Heiberg Island, the most northerly such study site in Canada. They found 36 species of molluscs (including 8 gastropods and 17 bivalves) forming two associations. A *Portlandia* - *Thyasira* association, with two molluscs only, occupies the deep prodelta environment with summer temperatures <0°C and salinities <25 per mil. Away from the delta this association diversifies to include *Yoldiella* spp. and *Delectopecten greenlandicus*. A *Macoma* - *Astarte* association, with 7 common high arctic species, occupies shallower water (3-32 m) away from the brackish river mouth and its areas of high suspended sediment. The upper 3 m are barren due to destruction of molluscs by sea ice.

LATE WISCONSINAN AND HOLOCENE MOLLUSCS -PREVIOUS WORK

Paleontological interest in postglacial molluscs seems to have been greatest before radiocarbon dating. Careful early

inventories of fossils were made by Dawson (1893), Laursen (1950), and Richards (1962; reporting work mainly before 1950). Systematic inventories for several arctic regions by Wagner (1969 and in Craig, 1960, 1961, 1963, and unpublished) and her survey of Champlain Sea fossils (Wagner, 1970) had limited radiocarbon support. Similarly, the treatment of marine Pleistocene faunas of southwestern British Columbia by Wagner (1959) is not supported by radiocarbon dates, even though some were in hand (Armstrong, 1956; Fyles, 1963). Bousfield and Thomas (1975) interpreted the disjunct nature of shallow-water molluscan and crustacean faunas between Labrador and southern New England in terms of possible postglacial migrations. They inferred a water temperature history that involved a Hypsithermal 2.5°C warmer than present, but the paleoenvironmental sequence that they presented was entirely hypothetical in that they did not utilize fossil mollusc data. Many more recent studies include lists of postglacial marine invertebrates and these have been incorporated in our database. Below we outline those that document dated ecostratigraphic zonation or range extensions.

Matthews (1967a) discussed postglacial changes in molluscan faunas in Frobisher Bay. He identified three species with age estimates of 6-6.5 ka BP that do not occur in Canadian arctic waters at present: *Volshellia demissa*, *Nucula delphinodonta*, and *Lyonsia hyalina*. The first and last of these represent extreme range extensions in that they do not now occur north of the southwestern Gulf of St. Lawrence, and hence have a Virginian distribution. *N. delphinodonta* ranges north to Hudson Strait. Because they are not directly dated and their fragmented nature suggests the possibility of misidentification, they are not included in the present database. The surprising presence of Virginian taxa in this area has not been confirmed despite much additional work. Deposits estimated by Matthews to be older than 6.5 ka BP contain only *Hiatella arctica* and *Mya truncata*.

Matthews (1967b) reported a rich cirriped and mollusc (31 pelecypods, 20 gastropods) assemblage from postglacial raised marine deposits of the Ungava shore of Hudson Strait. The dated faunas are included in the present database. He identified 8 species that represent range extensions, mostly of boreal-subarctic species now occurring along the Labrador coast but also including the temperate *L. hyalina*, during the period 5.2-3.9 ka BP. He pointed out that the apparent marine temperature optimum here was displaced in time from that in Frobisher Bay. Wagner (1969) documented 26 pelecypod and 27 gastropod species in Tyrrell Sea fossil collections. Those that have been dated are included here. She concluded that samples collected at altitudes >122 m indicated more brackish conditions than present but similar water temperatures (<0°C). These samples contained only *Hiatella arctica*, *Mya truncata*, *Clinocardium ciliatum*, and *Macoma balthica*. The last of these is a boreal-subarctic species but the first two are much more common. Specimens collected at altitudes <61 m indicated modern low arctic marine conditions, with salinities ≤33 per mil. Wagner interpreted this zonation as reflecting deglaciation - decreasing meltwater influx and land uplift.

Andrews (1972) documented growth rates and range extensions of Holocene molluscs on Baffin Island. The southern species *Mytilus edulis*, *Chlamys islandica*, and *Macoma balthica* extended their ranges in the middle Holocene (8.2-2.8 ka BP) and retreated during the Neoglacial. The database for this region has since been expanded and care has been taken to document range extensions. Hjort and Funder (1974) dated subfossil occurrences of *Mytilus edulis* in central East Greenland to 8-5.5 ka BP. They suggested that it migrated from Svalbard via the West Spitsbergen Current, rather than advancing from southern Greenland where it occurs today.

Funder and Weidick (1991) documented range extensions of boreal molluscs in West Greenland between 8.4 and 4.9 ka BP. These include 6 species now regionally extinct: the gastropod *Emarginula fissura* and the bivalves *Heteranomia squamula*, *Modiolus modiolus*, *Arctica islandica*, *Panopea norvegica*, and *Zirphaea crispata*. The first two are not directly dated and hence not included in our database. They estimated that water temperatures rose 1-3°C above present. Temperatures there are controlled by the mix of polar versus Atlantic waters in the West Greenland Current.

Champlain Sea molluscs are the best studied in Canada, with a history of investigation that dates back to 1837 (Bayfield, 1837; Lyell, 1841; Wagner, 1970; Elson, 1969a, b; Hillaire-Marcel, 1980; Rodrigues, 1987; Rodrigues and Richard, 1983, 1985, 1986). Wagner (1970) analyzed extensive collections and concluded that the Champlain Sea did not attain normal salinities even in its central basin. Relatively high salinities of >20 per mil were associated with deep water areas where *Portlandia arctica* lived. She considered that the mollusc assemblages represented boreal conditions. But she also reported five species that appear to represent early range extensions of temperate faunas into the eastern Champlain Sea. These species now range north only to southwestern Gulf of St. Lawrence and their first appearance in the region may well be represented by the still undated collections of Wagner. *Neptunea despecta tornata* is recorded at five localities, *Crassostrea virginica* and *Yoldia limatula* at two, *Mysella planulata* and *Lyonsia hyalina* each at one. Ardley (1912) had earlier reported a collection of oyster fossils from a depth of 3 m below the surface at Montreal. Oysters require water temperatures of at least 20°C for viability.

Rodrigues and Richard (1986) reviewed earlier work on the Champlain Sea. Elson's (1969a, b) suggestion of a two-fold biostratigraphy - a cold, deep-water, *Hiatella arctica* phase succeeded by a warmer, shallow-water, *Mya arenaria* phase - has proven too simple. Rodrigues and Richard recognized 5 ecostratigraphic pelecypod and cirriped associations and showed that the *Hiatella* association persisted to near the end of the sea. Salinity and substrate exerted the major controls over these associations, with the barnacle *Balanus hameri* indicating deep, high salinity (30-34 per mil) water. Hillaire-Marcel (1980) detailed changes of species during deglaciation in the Tyrrell, Goldthwait, and Champlain seas. He recognized 6 pelecypod communities of the Champlain Sea that shifted with changing water depths and other conditions following deglaciation.

PROBLEMS AND BIASES

PRESERVATION

The faunal assemblage at a fossil site is only the record of species that were preserved and the complete faunal community can not be reconstructed. Soft-bodied species have been lost. In addition, many smaller shells may not have survived burial or may be overlooked during collection.

Burial rates, transport history, sediment chemistry (acidity), and ground temperature (permafrost) all partly determine preservation potential of shelled taxa. These control rates of abrasion, fragmentation, dissolution, and staining of shells (Powell and Davis, 1990). For example, Valentine (1989) compared molluscs inhabiting the California shelf with species collected in onshore Pleistocene deposits. He found that 77% of living species were preserved in the fossil record. Post-burial destruction appeared responsible for most loss of species, not initial lack of shells. He also found that differences in preservation between gastropods (76%) and bivalves (80%) were due to a predominance of epifaunal species in the former and infaunal species in the latter. Aitken (1990) calculated that 66% of modern shelled macrobenthos of Baffin Island (mainly bivalves and gastropods) are represented in the local Quaternary fossil record but that 68-86% of all genera (mainly soft bodied) have no preservation potential; infaunal suspension feeders and epifaunal browsers are preferentially preserved.

Palmqvist (1991) suggested that differences in preservation between trophic groups are due to initial abundances; primary consumers like pelecypods are usually more abundant than higher trophic groups like carnivorous gastropods. Other differences in preservation may relate to variations in mobility, size, and skeletal nature. For example, many primary consumers are sessile and large and grow thick shells to protect against predators; secondary consumers tend to be mobile and smaller and grow thinner shells.

For the raised marine deposits that hold the fossils of concern to this paper, the most important geological factors affecting preservation probably are presence or absence of permafrost, sediment acidity, and sediment permeability. Fossils are much more commonly found in areas of permafrost than farther south, particularly in acidic terrain. South of permafrost, fossils are better preserved in calcareous than in acidic sediments. In acidic terrain, they are generally restricted to fine-grained sediments of low permeability. It appears that carbonate shells are leached from coarser sediments over the course of a few thousand years.

COLLECTING, REPORTING, AND IDENTIFICATION

Radiocarbon dating has been done mostly on monospecific groups of robust shells, with preference for well-preserved shells collected from growth positions. Although this reduces the risk of incorporating age mixtures in dated subsamples, it can introduce a bias in any taxonomic database based on radiocarbon dates. This bias is alleviated when the submitter reports other taxa in the collection or at the site. But this is not always done. An extreme sampling bias occurs when only one or a few large, easily recognized species, those most

commonly used in radiocarbon dating, are collected or recorded. The extent of this bias can be assessed only by re-examination of hundreds of samples scattered in dozens of collections at various institutions. However, 17% of the radiocarbon dates have been published without identification of even the dated shells, which suggests that the bias may be substantial. On the other hand, many radiocarbon dates are published with comprehensive species lists. It would be exceedingly helpful to future research if collectors of radiocarbon samples ensured that all species are included in their samples and if full documentation of dated samples were deposited in the Canadian Radiocarbon database. Ideally, all samples should eventually reside in a national collections.

Identification of species is problematic for some entries in the database. Generally, samples identified only to genera are those that were too fragmented for specific assignment. Some problems arise from evolving nomenclature but can be impossible to correct without access to original samples. For example, the few *Mya arenaria* recorded from the Canadian Arctic are likely *M. pseudoarenaria* in that the former has never been identified in modern arctic collections (Lubinsky, 1980). Further inconsistencies of identification may have resulted from the many researchers, usually sample submitters, involved. We assume original identifications to be correct but have updated archaic nomenclature (Appendix). Few obvious cases of misidentification (e.g. a Pacific species reported from the Atlantic) are retained in the database but not used.

Mixing of Arctic and Atlantic waters results in mixing of arctic and boreal species. Arctic species tend to occupy deeper water with decreasing latitude and live below boreal communities. This creates a potential for conflicting interpretation of paleoenvironments. However, most shells in the database were collected above present sea level and at a known altitude below the postglacial marine limit. Many were dated because of their sedimentological affinity to former shorelines. Most represent communities that lived in water depths of a few metres to a few tens of metres. A small subset of samples from continental shelf sediment cores are generally of shells in growth position, and hence from known paleo-water depths.

METHODS

Radiocarbon dates on marine shells dating <20 ka BP were compiled from the literature, yielding a database of 3083 entries. Radiocarbon ages are corrected for the marine reservoir effect by subtracting 400 years whenever pertinent protocol information was available; otherwise dates are used as originally published. No taxa identifications were found (other than "marine shells") for 503 dated samples (16.6% of database) and a further 115 samples (3.7%) recorded only widespread taxa, many identified only to genera. Thus analysis herein relies on 2465 identified assemblages of known age and location (Table I). Every effort, including correspondence with submitters and reference to unpublished and limited-circulation data files (e.g. Robertson, 1987; Bigras and Dubois, 1987), was made to compile a full list of taxa in dated samples, rather than just the dated taxon. The database, which is in spreadsheet format and is current as of 1993, is filed

TABLE I

Abundances of dated mollusc and cirriped assemblages as percent of classified samples

Assemblage	No. of samples	%
1. <i>Hiatella arctica</i> only	540	21.9
2. <i>Mya truncata</i> only	360	14.6
3. <i>H. arctica</i> and <i>M. truncata</i>	268	10.9
Restricted arctic (1+2+3; RA)	1168	47.4
4. <i>Portlandia arctica</i>	91	3.7
Restricted arctic (1+2+3+4; RA)	1259	51.1
5. <i>Mya pseudoarenaria</i> ± 1,2,3,6	33	1.3
6. Other arctic species ± 1,2,3	437	17.7
Diverse arctic (5+6; DA)	470	19.1
Arctic only (subtotal)	1729	70.1
7. <i>H. arctica</i> + 1 boreal species	42	1.7
8. <i>M. truncata</i> + 1 boreal species	11	0.4
9. Both (7 & 8) + 1 boreal species	30	1.2
10. <i>P. arctica</i> + 1 boreal species	2	0.0
11. <i>M. pseudoarenaria</i> + 1 boreal species	6	0.2
12. Other arctic species + 1 boreal species	112	4.5
Arctic assemblages + 1 boreal species	203	8.2
13. <i>M. truncata</i> + 2 boreal species	2	0.0
14. <i>H. arct.</i> & <i>M. tr.</i> + 2 boreal species	4	0.2
15. <i>M. pseudoarenaria</i> + 2 boreal species	5	0.2
16. Other arctic species + 2 boreal species	39	1.6
Arctic assemblages + 2 boreal species	50	2.0
17. <i>M. pseudoarenaria</i> + 3 boreal species	3	0.1
18. Other arctic species + 3 boreal species	10	0.4
Arctic assemblages + 3 boreal species	3	0.5
Arctic assemblages with boreal species (AB)	266	10.8
Arctic dominated (subtotal)	1995	81.9
19. 2 boreal species + <i>H. arctica</i>	8	0.3
20. 2 boreal species + <i>M. truncata</i>	2	0.0
21. 2 boreal species + <i>H.a.</i> & <i>M.t.</i>	2	0.0
22. 2 boreal species + <i>P. arctica</i>	1	0.0
Restricted boreal assemblage with arctic species	13	0.5
23. 3 boreal species + <i>H. arctica</i>	4	0.2
24. 3 boreal species + <i>M. truncata</i>	4	0.2
25. 3 boreal species + <i>H.a.</i> & <i>M.t.</i>	2	0.0
26. 3 boreal species + <i>M. pseudoarenaria</i>	2	0.0
Boreal assemblages with arctic species	12	0.5
27. 4 boreal species + <i>H. arctica</i>	2	0.0
28. 4 boreal species + <i>M. truncata</i>	2	0.0
29. 4 boreal species + <i>H.a.</i> & <i>M.t.</i>	2	0.0
30. 4 boreal species + <i>M. pseudoarenaria</i>	1	0.0
31. 4 boreal species + other arctic species	6	0.2
32. 6 boreal species + <i>H. arctica</i>	2	0.0
33. 6 boreal species + <i>M. truncata</i>	1	0.0
Diverse boreal assemblages with arctic species	16	0.6
Boreal assemblages with arctic species (BA)	41	1.7
34. Boreal species only (B)	396	16.1
35. Boreal assemblage with a Virginian species (BV)	3	0.1
36. Virginian assemblage with a boreal and an arctic species (mixed population?)	1	0.0
37. Virginian assemblage (V)	29	1.2
Total classified in assemblages	2465	
38. Widespread	115	
39. Not identified	503	
Total	3083	

Note: the ± symbol above stands for 'with or without'.

with the Radiocarbon Dating Laboratory, Geological Survey of Canada.

All taxa identified and dated are listed in the Appendix along with information on current geographic ranges and synonymy. Addition of reported but undated taxa would increase the list by a few percent. In total 170 shelled taxa have a dated fossil record, with most identified to species. These include 160 molluscs - 47 gastropods and 113 pelecypods - 7 cirripeds, 1 brachiopod, and 3 echinoderms. Although gastropods comprise 27% of the list, they are mainly from south-eastern sample sites. Gastropods appear to be a less prominent part of marine invertebrate faunas in the Arctic. Thorson (1933) found they make up <1% of biomass weight in Frans Joseph Fjord, East Greenland. Similarly, Dale (1992) found that gastropods accounted for <10% of taxa collected in Pangnirtung Fjord, Baffin Island.

FOSSIL MOLLUSC ASSEMBLAGES

Marine mollusc and mollusc-cirriped assemblages are classified in this paper as widespread, arctic, boreal, temperate (Virginian), or intergrades of these according to geographic ranges (Appendix) and within-sample diversity. Classification was conducted at two levels. A detailed (39-part) classification (Table I) is retained in the database. This was collapsed to a more general classification (see below) for mapping and interpreting environments at a continental scale.

The assemblages defined here are based on the most common groupings that can be discerned from within-sample lists of fossils. They do not necessarily have formally recognized modern counterparts, but our approach does not differ fundamentally from that used in defining modern associations, which are based on relative abundance and diversity at a site. Ideally one should use abundance of species within each sample of fossils to classify that sample, but the database is not sufficiently detailed for this approach. Instead, we use diversity within a sample and relative abundance within groups of samples to characterize assemblages. Hence, assemblages are discussed below according to a gradient of diversity and, we believe, generally of water-mass temperature.

RESTRICTED ARCTIC ASSEMBLAGE (RA)

Despite the large number (170) of taxa identified, samples are dominantly of arctic assemblages with few species (Table I); Plates I and II illustrate the 15 most common species). By far the most abundantly dated molluscs are *Hiatella arctica* and *Mya truncata*, which account for 47.4% of records. Of the 1168 samples reporting only these species, *H. arctica* occurs in 69.2% and *M. truncata* in 53.8%. Dominance of the overall record by an apparently low-diversity arctic fauna partly reflects under-reporting of other species by submitters of radiocarbon samples, who may have no particular paleontological interests.

Both species range throughout the Arctic and subarctic, submerging to cooler water southward. They inhabit a wide range of depths from intertidal to hundreds of metres but prefer shallow sites, 2-45 m depth, in arctic waters. *H. arctica* exhibits a wide range of habitat adaptations. This suspension feeder is capable of infaunal habits by boring into soft rock

and sediment or of epifaunal habits by byssate attachment to clasts. It thus occurs as a fossil in various sediments which partly explains its abundance. *M. truncata*, the most widespread species of its genus, exhibits a narrower range of habitats. This burrowing, infaunal, suspension feeder prefers finer substrates of the upper sublittoral. As a fossil in the Arctic, it is most commonly collected from deltaic and sandy fore-shore facies.

No known zoogeographic region today is characterized exclusively by these two molluscs (Lubinsky, 1980). However, many fossil sites, certainly those in deglacial marine sediments in the Canadian High Arctic (Dyke, unpublished observations), Spitsbergen (Feyling-Hanssen, 1955; Feyling-Hanssen and Olssen, 1960), Greenland (*e.g.* Bennike, 1987), and apparently many in deglacial sediments south to the Gulf of St. Lawrence, contain only these two molluscs. Therefore, we suggest that this restricted assemblage is a legitimate paleontological group whose distribution is albeit exaggerated by incomplete site inventories of fossils. Hillaire-Marcel (1980) suggested that the *H. arctica* - *M. truncata* association of the Champlain Sea indicates cold waters (<0°C) and salinities >30 per mil in depths greater than 30 m. This depth constraint would not apply to arctic sites.

The greater reported abundance of *H. arctica* than of *M. truncata* in this group agrees with the authors' field experience for arctic sites and accords with the broader range of habitats of *H. arctica*. This relative abundance cannot be explained by different preservation potentials or by a sampling bias for radiocarbon dating because the less-reported *M. truncata* has a larger shell and would tend to be favoured for both reasons.

Another commonly occurring species is included in this group. *Portlandia arctica* is an obligate arctic species, especially in shallow water. This burrowing deposit feeder is a common fossil of fine-grained, ice-proximal glaciomarine sediment that accumulated in turbid, brackish water; a so-called facies fauna. It occurs in 3.7% of identified samples and 7.2% of samples in the restricted arctic group, commonly alone. In a detailed (regional) analysis it should be considered another restricted arctic assemblage and this distinction is retained in the database. But because its distribution reflects local (substrate) rather than regional environments, we included it in a broader grouping. Its most common associates are *Yoldiella fraterna* and *Y. frigida*. *P. arctica siliqua* can indicate more boreal conditions but is rarely distinguished in fossil collections.

DIVERSE ARCTIC ASSEMBLAGE (DA)

A more diverse community appeared in arctic areas shortly after deglaciation (Lemmen *et al.*, 1994a; Bennike, 1987; Dyke, unpublished). In the High Arctic, diversification is marked at most sites first by appearance of *Astarte borealis*. According to data at hand (Table II), a typical diverse arctic assemblage consists of *Macoma calcarea* (in 40.6% of samples), *Clinocardium ciliatum* (18.7%), *Serripes groenlandicus* (13.6%), *Astarte borealis* (13.0%), and *Mya pseudoarenaria* (7.4%), along with the barnacle *Balanus balanus* (6.2%). However, *M. truncata* and *H. arctica* dominate this assemblage,

TABLE II
Taxa in the diverse arctic assemblage (470 samples)

Species	No. of Samples	%
Gastropods:		
<i>Buccinum</i> sp.	1	0.2
<i>Buccinum (hancocki) glaciale</i>	1	0.2
<i>Buccinum physematum</i>	1	0.2
<i>Buccinum (tenuis) scaliforme</i>	2	0.4
<i>Lepeta caeca</i>	1	0.2
<i>Natica clausa</i>	3	0.6
<i>Oenopota</i> sp.	1	0.2
<i>Trichotropis borealis</i>	3	0.6
unidentified gastropods	5	1.1
Pelecypods:		
<i>Astarte</i> sp.	37	7.9
<i>Astarte borealis</i>	61	13.0
<i>Astarte crenata</i>	2	0.4
<i>Astarte montagui</i>	13	2.8
<i>Bathyarca glacialis</i>	9	1.9
<i>Bathyarca raridentata</i>	1	0.2
<i>Clinocardium ciliatum</i>	88	18.7
<i>Clinocardium echinatum?</i>	1	0.2
<i>Cyrtodaria kurriana</i>	4	0.9
<i>Delectopecten greenlandicus</i>	1	0.2
<i>Hiatella arctica</i>	240	51.1
<i>Macoma</i> sp.	34	7.2
<i>Macoma calcarea</i>	191	40.6
<i>Macoma moesta</i>	1	0.2
<i>Musculus</i> sp.	1	0.2
<i>Musculus discors</i>	1	0.2
<i>Musculus niger</i>	1	0.2
<i>Mya</i> sp.	18	3.8
<i>Mya pseudoarenaria</i>	35	7.4
<i>Mya truncata</i>	250	53.2
<i>Mya truncata uddevalensis</i>	4	0.9
<i>Nucula belloti</i>	3	0.6
<i>Nucula sulcata?</i>	1	0.2
<i>Nuculana</i> sp.	1	0.2
<i>Nuculana pernula</i>	3	0.6
<i>Nuculana tenuisulcata</i>	1	0.2
<i>Palliolium greenlandicum</i>	1	0.2
<i>Portlandia</i> sp.	3	0.6
<i>Portlandia arctica</i>	34	7.2
<i>Portlandia intermedia</i>	1	0.2
<i>Serripes groenlandicus</i>	64	13.6
<i>Thyasira</i> sp.	3	0.6
<i>Yoldia hyperborea</i>	2	0.4
<i>Yoldiella fraterna</i>	5	1.1
<i>Yoldiella frigida</i>	3	0.6
Cirripeds:		
<i>Balanus</i> sp.	42	8.9
<i>Balanus balanus</i>	29	6.2
<i>Balanus crenatus</i>	18	3.8
Brachiopods:		
<i>Hemithyris psittaceae</i>	3	0.6

occurring in 53.2% and 51.1% of samples, respectively. This diverse assemblage is most commonly recovered from deltaic and prodeltaic sediments, which accounts for the nearly equal abundance of *M. truncata* and *H. arctica*.

Mya pseudoarenaria, considered in more detail below, is presently a low arctic mollusc that was formerly more widespread. Today it inhabits shallow water, 2-30 m deep, in eastern Hudson Bay. As a fossil, it usually occurs in diverse arctic associations or in boreal-arctic mixtures. The other prominent taxa of this assemblage are panarctic. The diverse arctic assemblage accounts for 19.1% of classified records. Future research will likely define important regional variants within this assemblage.

In contrast to the dominant taxa listed above, 62.5% of the elements in Table II occur in <1% of samples. Restricted and diverse arctic assemblages together account for 70.1% of the database (Table I).

ARCTIC ASSEMBLAGE WITH BOREAL SPECIES (AB)

Nearly 82% of the database consists of **arctic-dominated** assemblages. Nearly 11% is an arctic assemblage with boreal species. However, only one boreal species occurs in 80% of these samples. The samples form two main groups: a northern and a southeastern group.

The northern samples (Table IIIA) are from sites near the present arctic-subarctic marine boundary and within its zone of postglacial oscillation. Samples are mostly diverse arctic assemblages, as described above, to which are added most commonly *Mytilus edulis* (48.6% of samples), *Chlamys islandica* (31.8%), *Macoma balthica* (13.3%), *Astarte (montagui) striata* (8.1%), and *Mya arenaria* (8.1%). These are the only boreal species that occur in >5% of samples. Near their northern limits they are restricted to shallow water. As mentioned above, it would be worth re-examining the *M. arenaria* specimens in this group of samples to see if some are *M. pseudoarenaria*.

The southeastern samples (Table IIIB), from sites within present boreal and low subarctic waters, similarly are diverse arctic assemblages, to which are added most commonly, *Macoma balthica* (43.2%), *Mytilus edulis* (27.3%), *Mya arenaria* (18.2%), *Chlamys islandica* (9.1%), and *Balanus hameri* (6.8%). Again these are the only boreal species that occur in >5% of samples.

Both regional, arctic-dominated associations are similar in the major species included. But they differ in order of abundance of these species. As might be expected, the southeastern group also has a more diversified overall assemblage (Table IIIB). Hence, early postglacial, arctic-dominated assemblages in the southeast are not strictly analogous to modern or Holocene assemblages near the subarctic-arctic boundary in that they included more temperate elements. Boreal species that occur in the poorly represented (5 samples) early postglacial, arctic-dominated assemblages of the Pacific include *Colus halli*, *Chlamys rubida*, *Cyclocardia ventricosa*, *Macoma obliqua*, and, *Nuculana fossa*.

BOREAL ASSEMBLAGE WITH ARCTIC SPECIES (BA)

A dominantly boreal assemblage with arctic species comprises only 1.7% of the database, 41 samples (Table I). *Hiatella arctica* and *Mya truncata* are the only arctic species reported in 75% of these samples. In that these species range throughout the subarctic today, their presence does not necessarily represent strong polar water influence. The five most

TABLE III
Boreal species in arctic-dominated assemblages

Species	No. of Samples	%
A. Northern and northeastern region - Amundsen Gulf to northern Labrador and Hudson Bay (173 samples)		
Gastropods:		
<i>Buccinum undatum</i>	2	1.2
<i>Littorina saxatilis</i>	3	1.7
<i>Trichotrophis borealis</i>	1	0.6
Pelecypods:		
<i>Astarte elliptica</i>	5	2.9
<i>Astarte (montagui) striata</i>	14	8.1
<i>Chlamys islandica</i>	55	31.8
<i>Crenella decussata</i>	2	1.2
<i>Lyonsia hyalina</i>	1	0.6
<i>Macoma balthica</i>	23	13.3
<i>Mya arenaria</i>	14	8.1
<i>Mytilus edulis</i>	84	48.6
<i>Nucula delphinodonta</i>	1	0.6
<i>Nucula tenuis</i>	3	1.7
<i>Zirphaea crispata</i>	2	1.2
Cirripeds:		
<i>Balanus balanoides</i>	3	1.7
<i>Balanus hameri</i>	5	2.9
B. Southeastern region - southern Labrador to Maine (88 samples)		
Gastropods:		
<i>Boreotrophon truncatus</i>	1	1.1
<i>Buccinum undatum</i>	4	4.5
<i>Buccinum totteni?</i>	1	1.1
<i>Haminoea solitaria</i>	1	1.1
<i>Neptunia despecta tornata</i>	1	1.1
<i>Plicifusus kroyeri</i>	2	2.3
<i>Trichotrophis borealis</i>	2	2.3
Pelecypods:		
<i>Astarte undata</i>	1	1.1
<i>Cerastoderma pinnulatum</i>	1	1.1
<i>Chlamys islandica</i>	8	9.1
<i>Cyclocardia borealis</i>	1	1.1
<i>Cyrtodaria siliqua</i>	3	3.4
<i>Macoma balthica</i>	38	43.2
<i>Mya arenaria</i>	6	18.2
<i>Mytilus edulis</i>	24	27.3
<i>Nucula tenuis</i>	1	1.1
<i>Panomya arctica</i>	1	1.1
<i>Panopea norvegia?</i>	1	1.1
<i>Spisula</i> sp.	2	2.3
<i>Thyasira</i> sp.	2	2.3
Cirripeds:		
<i>Balanus hameri</i>	6	6.8

commonly reported boreal species in this assemblage from the Atlantic are *Mytilus edulis* (in 69.2% of samples), *Macoma balthica* (46.2%), *Chlamys islandica* (35.9%), *Mya arenaria* (25.6%), and *Balanus hameri* (15.4%; Table IV). Compared to the arctic assemblage with boreal species, this assemblage is characterized by strong increases in the epifaunal *M. edulis* (to clear dominance), *M. balthica*, and *M. arenaria*. Although this small inter-grade assemblage could be considered fully boreal and the prominence of *M. edulis* distinguishes it from "colder" assemblages, the still-abundant *H. arctica* and *M. truncata* distinguish it from the group here classified as fully boreal. Only two samples of this assemblage are known from the Pacific.

BOREAL ASSEMBLAGE (B)

The boreal assemblage comprises 16.1% of the database, 396 samples (Table I). In the Atlantic, only five species occur in >5% of samples. In order of abundance, these are *Mytilus edulis* (37.9% of samples), *Macoma balthica* (21.5%), *Mya arenaria* (13.6%), *Balanus hameri* (7.8%), and *Chlamys islandica* (5.6%; Table V). This group of most abundant

TABLE IV

Boreal species in boreal assemblages with arctic elements in the Atlantic (39 samples)

Boreal species	No. of samples	%
Gastropods:		
<i>Acmaea testudinalis</i>	1	2.6
<i>Buccinum undatum</i>	2	5.1
<i>Lacuna vineta</i>	1	2.6
<i>Littorina obtusata</i>	1	2.6
<i>Nucella lapellis</i>	1	2.6
Pelecypods:		
<i>Astarte crenata subaequilatera</i>	4	10.3
<i>Astarte montagui</i>	5	12.8
<i>Astarte striata</i>	2	5.1
<i>Chlamys islandica</i>	14	35.9
<i>Cyclocardia borealis</i>	3	7.7
<i>Cyrtodaria siliqua</i>	4	10.3
<i>Ensis directus</i>	3	7.7
<i>Macoma balthica</i>	8	46.2
<i>Mesodesma arctatum</i>	4	10.3
<i>Mesodesma deauratum</i>	1	2.6
<i>Mya arenaria</i>	10	25.6
<i>Mysella planulata</i>	1	2.6
<i>Mytilus edulis</i>	27	69.2
<i>Panomya arctica</i>	2	5.1
<i>Spisula polynyma</i>	3	7.7
<i>Spisula solidissima</i>	1	2.6
<i>Thracia septentrionalis</i>	1	2.6
<i>Zirphaea crispata</i>	2	5.1
Cirripeds:		
<i>Balanus balanoides</i>	1	2.6
<i>Balanus hameri</i>	6	15.4
Brachiopods:		
<i>Hemithyris psittacea</i>	5	12.8

species is nearly identical to the group of most abundant boreal animals in the **boreal assemblage with arctic species**; the two most common animals are the same in both groups. However, in the boreal assemblage, *C. islandica*

TABLE V

Taxa in boreal assemblages (396 samples)

Species	No. of samples	%
Atlantic		
Gastropods:		
<i>Buccinum undatum</i>	7	1.8
<i>Littorina littorea</i>	1	0.2
<i>Littorina obtusata</i>	1	0.2
<i>Littorina saxatilis</i>	1	0.2
<i>Neptunea despecta tornata</i>	1	0.2
<i>Nucella lapillus</i>	6	1.5
<i>Thais lapillus</i>	3	0.8
Pelecypods:		
<i>Arctica islandica</i>	3	0.8
<i>Astarte crenata subaequilatera</i>	1	0.2
<i>Astarte montagui striata</i>	1	0.2
<i>Astarte undata</i>	3	0.8
<i>Chlamys islandica</i>	22	5.6
<i>Cyclocardia borealis</i>	2	0.5
<i>Ensis directus</i>	1	0.2
<i>Macoma balthica</i>	85	21.5
<i>Mercenaria mercenaria</i>	1	0.2
<i>Mesodesma arctatum</i>	10	2.5
<i>Modiolus modiolus</i>	1	0.2
<i>Mya arenaria</i>	54	13.6
<i>Mytilus edulis</i>	150	37.9
<i>Nucella delphinodonta</i>	1	0.2
<i>Nucula proxima</i>	1	0.2
<i>Nucula tenuis</i>	1	0.2
<i>Nuculana minuta</i>	1	0.2
<i>Panopea norvegica</i>	1	0.2
<i>Placopecten magellanicus</i>	1	0.2
<i>Spisula polynyma</i>	6	1.5
<i>Spisula solidissima</i>	1	0.2
<i>Zirphaea crispata</i>	2	0.5
Cirripeds:		
<i>Balanus hameri</i>	31	7.8
Brachiopod:		
<i>Hemithyris psittacea</i>	1	0.2
Pacific		
Gastropods:		
<i>Fusitron oregonensis</i>	1	0.2
<i>Thais lamellosa</i>	1	0.2
Pelecypods:		
<i>Chlamys rubida</i>	1	0.2
<i>Clinocardium nutalli</i>	6	1.5
<i>Macoma brota</i>	1	0.2
<i>Macoma inquinata</i>	1	0.2
<i>Macoma liparia</i>	2	0.5
<i>Macoma nasuta</i>	1	0.2
<i>Mytilus</i> sp.	2	0.5
<i>Ostrea lirida</i>	1	0.2
<i>Pododesmus macroschisma</i>	1	0.2
<i>Saxidomus gigantea</i>	20	5.1

declines in rank whereas *M. arenaria* and *B. hameri* increase. Many boreal species are represented in this fossil record by occurrence in one sample. *Saxidomus gigantea* is the most common boreal species reported from the Pacific.

VIRGINIAN ASSEMBLAGE (V)

The Virginian assemblage comprises only 1.2% of the database. In the Atlantic it consists most commonly of oyster, *Crassostrea virginica*, communities (75% of samples; Table VI). Virginian taxa today range into the Bay of Fundy and the southwestern Gulf of St. Lawrence. That region has submerged during the Holocene which militates against fossil recovery. The temperate assemblage in the Pacific is represented by only five samples, two of which contain the mussel *Mytilus californianus*.

REPRESENTATIVENESS OF FOSSIL ASSEMBLAGES

The Late Quaternary marine fossil record is clearly dominated by only 15 species, 14 of which are molluscs (Table VII; Plates I and II). Most of the other 155 recorded taxa, generally 70-80% of taxa, are reported in <5% of samples (Tables II-VI) and many are single occurrences. This raises the question of how representative this particular fossil record is of its contemporaneous environments.

One approach to addressing this question lies in examining the sharing of rare species among the various assemblages. Take "rare" to be species listed as single occurrences or very low percentages where sample size is large (Tables II-VI). The number of rare species is similar in each assemblage, and with one exception, well over half of these occur uniquely in their groups (Table VIII). In this view, even the rare species are "representative" of the environmental categories here erected. Except in the odd case where a rare species is the only one in a sample, they have not themselves determined the classifications of the samples.

TABLE VI

Species in Virginian (temperate) assemblages

Species	No. of Samples	%
A. Atlantic (24 samples)		
Gastropods:		
<i>Polinices heros</i>	1	4.2
Pelecypods:		
<i>Crassostrea virginica</i>	18	75.0
<i>Gukensia demissa</i>	2	8.3
<i>Mercenaria mercenaria</i>	1	4.2
<i>Pecten irradians</i>	1	4.2
<i>Spisula solidissima</i>	1	4.2
B. Pacific (5 samples)		
Pelecypods:		
<i>Hinnites multirugosus</i>	1	
<i>Mytilus californianus</i>	2	
<i>Protothaca tenerrima</i>	1	
<i>Solen sicarius</i>	1	

TABLE VII

The top 15 marine invertebrates - percentage reported occurrences in assemblages (see footnote for definitions)

	RA	DA	ABn	ABs	BA	B	V
<i>H. arctica</i>	64	43	81	74	62	0	0
<i>M. truncata</i>	50	45	77	50	46	0	0
<i>P. arctica</i>	7	7	2	16	3	0	0
<i>M. calcarea</i>	0	41	34	35	5	0	0
<i>C. ciliatum</i>	0	19	17	8	0	0	0
<i>S. groenlandicus</i>	0	14	15	11	3	0	0
<i>A. borealis</i>	0	13	6	2	3	0	0
<i>M. pseudoarenaria</i>	0	7	4	8	8	0	0
<i>M. edulis</i>	0	0	49	27	69	38	0
<i>C. islandica</i>	0	0	32	9	36	6	0
<i>M. balthica</i>	0	0	13	43	46	22	0
<i>A. striata</i>	0	0	8	0	5	0	0
<i>M. arenaria</i>	0	0	8	18	26	14	0
<i>B. hameri</i>	0	0	3	7	15	8	0
<i>C. virginica</i>	0	0	0	0	0	0	75

RA: restricted arctic; **DA:** diverse arctic; **ABn:** arctic with boreal elements, northern areas; **ABs:** arctic with boreal elements, southeastern areas (not an extant environment); **BA:** boreal with arctic elements; **B:** boreal; and **V:** Virginian.

Note: Other than the 15 species listed above, the only taxa prominently represented in the fossil record are the widespread barnacles, which occur in 66% of samples classified as "widespread" (115 samples) and are also common in all environmental groups other than RA. In the samples with widespread taxa only, 31% record *Balanus* sp., 22% *B. balanus*, and 13% *B. crenatus*.

TABLE VIII

Sharing of rare species of marine molluscs among assemblages

Assemblage	Rare Species	Shared 1 other	Shared >1 other	% Shared
Diverse arctic	16	0	1	6.3
Arctic-boreal, N	13	1	3	30.8
Arctic-boreal, SE	8	1	4	62.5
Boreal-arctic	12	1	3	33.3
Boreal	18	2	3	27.8
Virginian	5	1	1	40.0

Another approach is simply to measure "inclusiveness" by comparing regional lists of modern marine invertebrates with the list of fossils. Two major compilations cover most of our fossil sample sites. Bousfield (1960) described marine invertebrates occurring in the Atlantic Provinces region but most of these range well beyond there. He listed 51 gastropod species, 14 (27.5%) of which are represented in the fossil database; 32 of 55 pelecypod species (58.2%) are represented, 4 of 6 cirripeds, 2 of 5 echinoderms, and 1 of 2 brachiopods. About 50% of the missing gastropods and pelecypods range minimally into the region from the south, moreover into a region of Holocene submergence. This can largely account for their absence from the current fossil record, which is reasonably inclusive with respect to more wide ranging species. Still,

one suspects a more serious under-representation of gastropods than of pelecypods. Several species listed for Atlantic Canada but not represented in our list of fossils build thin, fragile, translucent shells (e.g. *Velutina laevigata*, *Skenea planorbis*, *Mitrella lunata*, *Margarites costalis*).

Lubinsky (1980) presented a comprehensive list of pelecypods in the Canadian Arctic Archipelago and mainland south to Strait of Belle Isle. Of the 64 species listed, 41 (64.1%) are reported as fossils. Of the 23 unrepresented species, 11 are described as rare in the Canadian Arctic, some have single, unconfirmed reports, some have depth ranges that make them unlikely fossil exposures in postglacial raised marine deposits, and others range marginally into the region of postglacial emergence from the Beaufort Sea. Thus, the current fossil list includes about 75% of more common nearshore species. The data of Valentine (1989) and Aitken (1990) discussed above, collected to assess the representativeness of the fossil record, suggest that the record that we use here is reasonably inclusive.

However, considerations of inclusiveness do not address the question of whether the relative abundances of fossils reasonably reflect abundances of animals in the former communities. In particular, it would be useful to know whether the 15 abundant species (Table VII) dominate the various nearshore environments in rough proportion to their reported fossil abundance. The paucity of quantitative inventories of molluscs in the wide range of Canadian cold-water environments makes this difficult to assess.

FOSSIL MOLLUSC ASSEMBLAGES AND MODERN FAUNISTIC ZONES

Our database is dominated by arctic and subarctic assemblages of molluscs, primarily bivalves, as would be expected from the general paleoenvironmental conditions. Therefore, we use here the terminology and definition of bivalve zones of Lubinsky (1980) who treats the arctic, subarctic, and adjoining boreal zones in sufficient detail for our purposes. She based her classification and zoogeographic subdivisions on bivalves particular to cold, primarily shallow, waters. As discussed above, no modern faunal zone corresponds to the restricted arctic assemblage consisting of *Hiatella arctica* and *Mya truncata* only. Such a zone existed in ice-proximal waters during deglaciation, but many samples classified here as restricted arctic would be reclassified if fossil inventories were more completely reported. Most would likely fall into the diverse arctic group.

The diverse arctic fossil assemblage corresponds in composition closely to most of Lubinsky's (1980, p. 57-62) **High Arctic Faunistic Subzone** (Arctic Zone). Specifically, it corresponds to her subdivisions I, II, and IV, which include most of the Arctic Archipelago south to Cape Dyer. This zone is dominated entirely by polar surface water from the Arctic Ocean; it lies north of the farthest penetration of subarctic waters. Sea-ice cover persists for 7-12 months a year, resulting in mostly negative water temperatures. The upper 50-100 m of water, corresponding to depths represented by most fossils, exhibits slight seasonal variability with summer water temperatures rising to 0-5°C (Lubinsky, 1980). This region

lacks vertical zonation of faunas because warming is insufficient for survival of the hardiest of more southern species.

Our fossil arctic assemblage with boreal species, as represented by samples from northern sites (Table IIIA), corresponds to Lubinsky's subdivision III of the High Arctic Faunistic Subzone (the southwestern archipelago and adjacent mainland coast), to her **Low-Arctic Faunistic Subzone** (Hudson and James bays) and to the northernmost subdivision of her **Subarctic Faunistic Zone** (Hudson Strait to Cape Dyer). In these areas of polar surface water, with minimal admixture of other waters, the littoral zone is warmed enough seasonally for subarctic-boreal species to survive. Hence, these are the northernmost areas that exhibit a vertical thermal and faunal zonation. Its northern boundary corresponds essentially to that of the marine subarctic of Dunbar (1968). Those subarctic-boreal species in the southwestern archipelago extend from the Pacific via the Beaufort Sea; Beaufort Shelf Water is warmer and less saline than Arctic Ocean Surface Water due to Mackenzie River discharge.

As mentioned above, that part of the arctic assemblage with boreal elements as represented by samples from southeastern sites (Table IIIB) lacks a strict modern analog. We infer that these probably reflect the extra seasonal warming of littoral waters to be expected in more southerly areas. Because of this, more thermophilous species were viable but warming did not proceed to the point that would have prevented arctic fauna from dominating in relatively shallow water.

The fossil boreal assemblage with arctic species resembles that found today in mixed polar and Atlantic waters between eastern Newfoundland and the north shore of the Gulf of St. Lawrence in the south and Hudson Strait in the north. It thus corresponds most closely to Lubinsky's **Subarctic Faunistic Zone**, particularly to southern Labrador (subdivision VII), which today shows the first marked increase southward in species diversity, and to her **Northern Acadian Faunistic Subzone**, which shows a further increase in diversity. These areas are influenced strongly by the Labrador Current but seasonal warming and advection of non-polar water yields a warm surface layer thick enough that boreal-subarctic species occupy littoral and sublittoral vertical zones. Summer surface water temperatures remain below 12°C. Arctic elements are restricted to species like *Hiatella arctica* and *Mya truncata* that have greater tolerances for relatively warm water. Lubinsky (1980) suggested that they acquired these tolerances during southward displacements at glacial maxima.

Our boreal assemblage resembles that found in the Gulf of St. Lawrence region, the **Acadian Faunistic Zone**. Summer sea surface temperatures in this region are 12-15°C. Bousfield (1960) classifies the constituent molluscs, which dominate the Atlantic Provinces fauna, as boreal or cold-temperate. Most member species range mainly between southern Labrador and North Carolina. Solar heating and incursion of warm Atlantic water resulted in exclusion of arctic species within sampled paleo-water depths (up to about 150 m). Arctic species need water below 10°C for reproduction and do not survive where summer temperatures exceed

20°C; optimum temperatures for reproduction of boreal species lie mostly between 5° and 15°C (Bousfield, 1960).

The Virginian fossil assemblage corresponds to the present temperate or **Virginian Faunistic Zone** where summer surface water temperatures exceed 18°C. However, Virginian species extend into the southern Acadian Faunistic Zone. In Atlantic Canada and adjacent USA, this zone is one of warm waters resulting either from exceptional seasonal warming or from incursion of Gulf Stream water. Virginian taxa today range from the Gulf of Mexico to the Bay of Fundy and south-western Gulf of St. Lawrence, although they are interrupted by a large cold-water gap in the Gulf of Maine. These animals require high temperatures for reproduction, 20°C in the case of the oyster, the most numerous fossil in this assemblage (Bousfield, 1960).

REGIONAL TIME SERIES OF MOLLUSC ASSEMBLAGES

In this section we examine frequency distributions of mollusc assemblages through time for sixteen regions (Fig. 2) that conform generally to (but extend) Lubinsky's (1980) faunistic provinces. The discussion proceeds generally from the warmest region to the coldest in the east and then to the Pacific after a discussion of the aggregate frequency distribution of radiocarbon dates.

AGGREGATE FREQUENCY DISTRIBUTION OF DATES

Several factors conspire to generate an uneven frequency distribution of dates on marine shells for northern North America (Fig. 3). An obvious one is the extent of glacier ice cover. The dates do not extend all the way back to the last glacial maximum at 18 ka BP. Fossils of that age can only be

found beyond the glacial limit and below the glacial maximum shorelines which are now generally submerged by 100-120 m. Few samples are older than 14 ka BP. The strong increase in number of samples dating 14-9 ka BP correlates with a progressive increase in extent of postglacial seas. However, these seas continued to increase until about 6 ka BP. For example, Hudson Bay and Foxe Basin were deglaciated 8-6.5 ka BP. Hence, the steady decline in number of samples dating <9 ka BP is not easy to explain. The relatively few samples dated <6 ka BP probably reflects lessened interest in dating late Holocene marine features and the progressive decrease in area occupied by younger raised marine sediments. But perhaps there are biological influences on the distribution of dates (Fig. 3); the dynamic deglacial environment 10-7 ka BP, with its high meltwater flux and water mass turnover, may have created a greater number and variety of habitats attractive to molluscs while high sedimentation rates enhanced preservation. The practical implication of the distribution in Figure 3 for the present analysis is that the different time intervals are unevenly rich in data. The impoverishment in late Holocene data is unfortunate in that this time provides the best means of linking the fossil record, particularly in terms of representativeness, with modern zoogeography.

GULF OF MAINE - GULF OF ST LAWRENCE

The Gulf of Maine - Gulf of St. Lawrence region as used here (#1 in Fig. 2) includes the former Champlain Sea. The region, roughly the modern Acadian Faunistic Zone, has richly dated Late Wisconsinan marine faunas but poorly dated Holocene faunas (Fig. 4). This primarily reflects regional sea level history (Grant, 1989). In most of the region, the shoreline regressed to present levels and lower by early Holocene; only the northern Gulf of St. Lawrence has an emerged and readily accessible Holocene marine record.

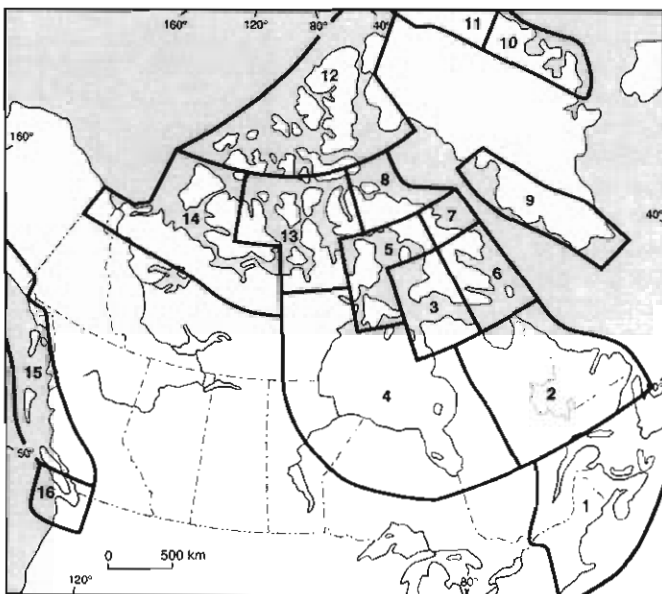


FIGURE 2. Regions for which histograms of mollusc assemblages are presented. Names are provided in the text.

Carte des régions pour lesquelles les histogrammes de fréquence des assemblages de mollusques ont été préparés. Les noms apparaissent dans le texte.

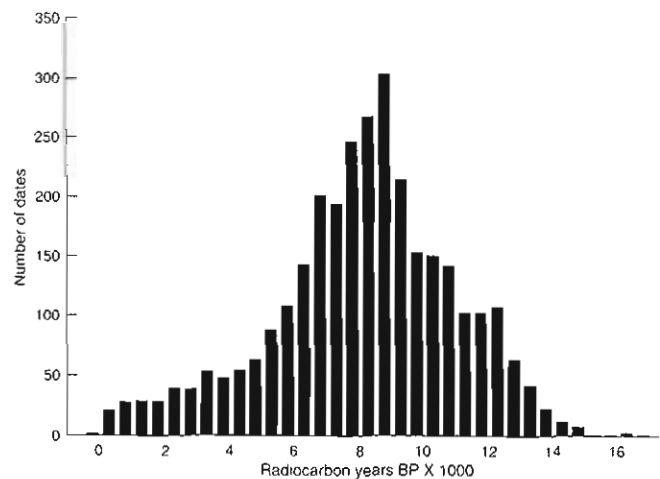


FIGURE 3. Frequency distribution of radiocarbon dates on marine shells north of 40°N in North America, including Greenland (n=3080).

Histogramme de fréquence des âges au radiocarbone des coquillages marins au nord du 40° lat. N en Amérique du Nord et au Groenland (n=3080).

This region is at the southeastern limit of glaciation where the ice sheet margin must have contacted the warmest waters along its entire eastern side. The earliest faunas, dating close to glacial maximum, were dominantly, but not exclusively, arctic in character. The oldest record (off scale on Fig. 4), is of *Portlandia arctica* dated 17 ka BP from the Scotian Shelf, but *Nucula proxima*, which presently ranges from Nova Scotia to Texas, was also present there at 16.3 ka BP. The entire record older than 14 ka BP consists of 6 samples of *P. arctica*, 3 of *Hiatella arctica*, 1 of *Macoma calcarea*, all arctic-subarctic species; single samples of the boreal species *N. proxima*, *N. tenuis*, *Mesodesma arctatum*, and *Balanus hameri*; and a sample of the widespread *Balanus crenatus*.

After ice retreat onshore, the restricted *Hiatella arctica* - *Mya truncata* assemblage was common throughout the remaining Late Wisconsinan. This assemblage is represented by only two samples after 8.5 ka BP, despite the fact that both molluscs range into the region today. In every 1 ka interval before 8 ka BP, *H. arctica* outnumbers *M. truncata* by a factor of 2-4, reflecting its greater substrate adaptability and possibly its more advantageous position at glacial maximum resulting from its greater depth range. The boreal elements noted above at glacial maximum remained the most common early in deglaciation. The ratio of boreal to arctic assemblages increased to boreal dominance about 8.5 ka BP when there was no longer any glacier ice left in the region. Boreal-Virginian taxa are sporadically recorded back to 13.5 ka BP and are relatively well represented between 11 ka and 3.5 ka BP, mainly by *Crassostrea virginica*. The late Holocene record is entirely boreal as expected for the Acadian Faunistic Zone.

LABRADOR

This region includes the lower Québec North Shore, both sides of the Strait of Belle Isle, the Labrador coast and Ungava Bay (#2 in Fig. 2). It thus consists mainly of the southern two provinces of Lubinsky's Subarctic Faunistic Zone. Most of it has experienced continuous postglacial emergence (Vincent, 1989). Its molluscan fauna is fairly well dated and spans the last 13 ka starting with deglaciation of the Strait of Belle Isle area (Fig. 5). The record shows dominantly arctic assemblages before 9 ka BP, a mosaic of boreal, boreal-arctic, and diverse arctic assemblages from 9 ka to 4 ka BP, and mostly boreal assemblages after 4 ka.

The lack of prominence of the restricted arctic assemblage here during deglaciation is interesting but may simply reflect better reporting of taxa by regional workers. Boreal species were among the first to enter, including *Mytilus edulis* by 12.6 ka BP. *Cyrtodaria siliqua*, *Chlamys islandica*, and *Buccinum undatum* followed shortly thereafter (>12 ka BP), the first and last of which reach their northern limits here today. The single record classified as Virginian is one of *Spisula solidissima* at St Anthony, northernmost Newfoundland; its modern range is Nova Scotia to South Carolina. Hence, this record represents a substantial range extension.

HUDSON STRAIT

This region includes central and western Hudson Strait and adjacent segments of Hudson Bay and Foxe Basin (#3 in

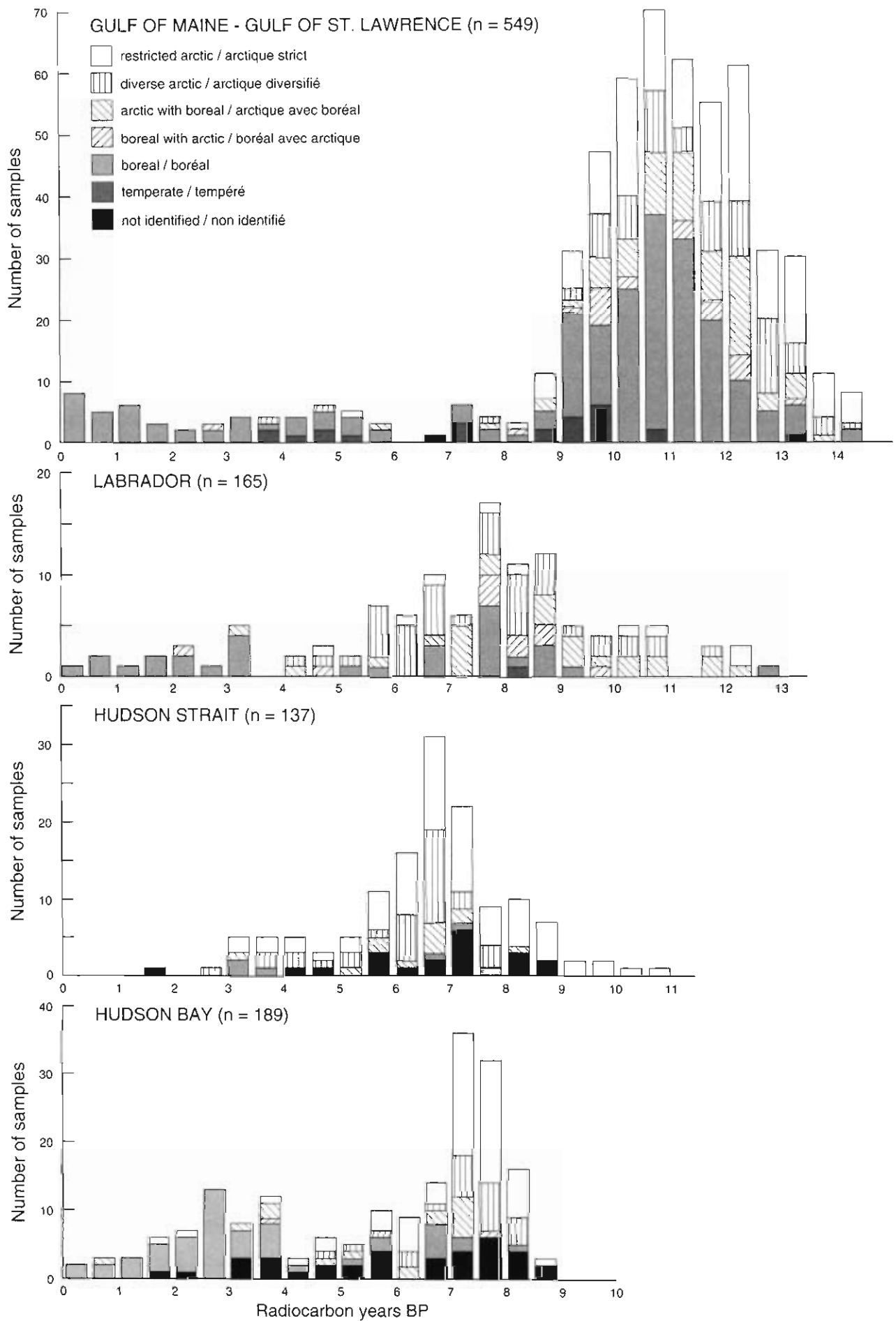
Fig. 2). It occupies the modern subarctic-arctic transition of Lubinsky (1980). Because this is entirely an area of continuing postglacial emergence, the decline in frequency of dated faunas after 7 ka BP (Fig. 6) reflects either decreasing faunal abundance, a decrease in deposition of sediments that can host marine fossils, or decreased interest in dating younger deposits. The dated faunal record extends securely back to about 9 ka BP and more tenuously to nearly 11 ka BP. The suite of dates older than 9 ka BP is mostly from a thin bed containing *Portlandia arctica* and *Yoldiella fraterna* in the bottomsets of a glaciomarine delta. Dates on this bed range from 10.675 ka to 8.51 ka BP (Gray *et al.*, 1993). The older dates were the basis for the proposed "early" deglaciation of Hudson Strait (*e.g.* Dyke and Prest, 1987), but the range of dates on this bed is problematic: if all are accepted as valid, it indicates a near zero accumulation rate and unvarying faunal composition in an ice-proximal, glaciomarine deltaic environment for >2 ka. This aside, the pre-8 ka BP faunas are dominated by the restricted arctic assemblage consisting of the species mentioned plus *Hiatella arctica* and *Mya truncata*.

The post-8 ka BP record demonstrates a dominant mixture of restricted and diverse arctic assemblages but boreal elements are present throughout. The first recorded boreal entry is of *Mytilus edulis* at 8.04 ka BP. This and four other recorded boreal species range through the region today. However, the barnacle *Balanus hameri* occurs in three samples dated between 7.83 ka and 7.08 ka BP but ranges today only north to Hamilton Inlet, thus indicating a range extension of 1100 km. *Mya arenaria* is reported in a sample dated 7.16 ka BP and also now has its northern limit at Hamilton Inlet.

HUDSON BAY

Hudson Bay (#4 in Fig. 2), which comprises Lubinsky's entire Low Arctic Subzone, is thought to have been deglaciated about 8 ka BP (Andrews and Falconer, 1969; Dyke and Prest, 1987). However, four radiocarbon dates on marine shells, two from Québec (QU-242, 8.55 ka; QU-244, 8.23 ka) and two from Manitoba (BGS-813, 8.2 ka; GX-1063, 8.01 ka), suggest that the 8 ka estimate may be conservative. Until 7 ka BP, the Tyrrell Sea (postglacial Hudson Bay) apparently had a low diversity marine molluscan fauna (Fig. 7) consisting of 7 species. Of 40 samples with identified species dating >7 ka BP, *Hiatella arctica* occurs in 70%, *Macoma calcarea* in 22.5%, *Mya truncata* in 20%, *Macoma* sp., *Chlamys islandica*, and *Clinocardium ciliatum*, each in 5%, and *Portlandia arctica* and *Mytilus edulis* in single samples (2.5%). This agrees with Wagner's (1969) high elevation *Hiatella*-dominated zone. The abundance of *M. calcarea* (especially adding *Macoma* sp.) relative to *M. truncata*, along with its prolonged presence when other common arctic molluscs were so rare, is not characteristic of any of the environmental groups in aggregate (Table VII).

The two recorded boreal species dating >7 ka BP range throughout the bay today and entered soon upon deglaciation (7.88 ka BP). The proportion of samples with boreal elements increased in the interval 7-6 ka BP but may have declined again; sparse dating of middle Holocene faunas leaves this unclear. The increase in boreal elements is due almost en-



FIGURES 4-7. Frequency distributions of marine mollusc assem- *Histogrammes de fréquence des assemblages de mollusques marins*

tirely to *Mytilus edulis*, which occurs in 33% of identified samples dating 6-7 ka BP and is the second most recorded species. The first recorded appearance of *Macoma balthica* is at 6.1 ka BP. *Mya pseudoarenaria* occurs first in the same sample. The taxa list for 7-6 ka BP increases to 20, mainly by addition of common arctic species. *Hiatella arctica* remains strongly dominant (71% of samples), but *Macoma calcarea* declines to 15.6%, whereas *Mya truncata* increases to 26.7%.

The late Holocene record is dominated by boreal assemblages, mainly by *Mytilus edulis*, which occurs in 83% of identified samples dating <4 ka BP. The taxa list for this interval contains only 14 species. This may reflect a focus on collecting *M. edulis* to date raised beaches because of its intertidal habitat, but it is not clear why this bias is not prevalent in older samples. Lubinsky (1980, p. 54) refers to the "pauperization" of the fauna of James Bay because of uplift (shallowing and freshening). Perhaps the record in Figure 7 reflects a similar process for Hudson basin in general, where deeper water species have become increasingly restricted to small parts of the bay. The only range extension recorded by the Hudson Bay faunal record is that of *Mya arenaria* in a sample (I-3907) from Cape Henrietta Maria on the south shore dated at 2.41 ka BP; the present limit is at Hamilton Inlet.

FOXES BASIN

The Foxe Basin region as defined here (#5 in Fig. 2) includes a part of southern Gulf of Boothia because data were sorted by geographic coordinates. The basin proper probably was not deglaciated until about 6.9 ka BP, the oldest shells dated from there; pre-7 ka samples on Figure 8 are from Gulf of Boothia. The region is within Lubinsky's High Arctic Subzone province 11b, which has the peculiarity of having the least number of mollusc species in the entire Arctic, partly because of shallowness and restricted currents flowing in from the open ocean. *Mytilus edulis*, *Macoma balthica*, and *Chlamys islandica*, common in Hudson Bay, are absent here. This large region of continuous emergence remains inadequately dated and more than half the ages are concentrated in the immediate postglacial interval (Fig. 8). The record may illustrate a postglacial succession from restricted to diverse arctic assemblages, but the poor dating of the middle and late Holocene leaves this uncertain.

Two samples record a boreal species in the basin. Both report *Mya arenaria* on the western side, the earlier at 6.26 ka BP (GSC-4798). In light of the large range extension implied and the absence of *Mytilus edulis* and *Chlamys islandica*, which are more north-ranging than *M. arenaria*, in both the present fauna and as fossils, these shells are probably *Mya pseudoarenaria*. The latter is reported from one site on the Baffin shore of the basin (GSC-5395).

The fossil record of Foxe Basin is impoverished with only 13 species, excluding *M. arenaria*. The 7-6 ka BP record, with 9 species, is dominated by *Hiatella arctica* (81.1% of samples), *Mya truncata* (40.5%), and *Macoma calcarea* (10.8%), the only species reported in more than one sample. The 6-4 ka BP record, with 12 species, is more balanced, with *H. arctica* (61.5%), *M. truncata* (42.3%), *M. calcarea* (30.8%), *Clinocardium ciliatum* (11.5%), and *Serripes groenlandicus*

(11.5%), again the only molluscs in more than one sample. The post-4 ka record has 9 species dominated by *M. truncata* (73.3%), *M. calcarea* (26.7%), *S. groenlandicus* (26.7%), *H. arctica* (20%), and *C. ciliatum* (13.3%).

There are interesting contrasts between the fossil records of Hudson Bay and Foxe Basin beyond the northward impoverishment in species. In Hudson Bay, *M. calcarea* was abundant - more so than *M. truncata* - in the first 1 ka after deglaciation, then decreased as the assemblage diversified. In Foxe Basin, *M. calcarea* was subordinate in the first 1 ka after deglaciation, then increased as the assemblage diversified.

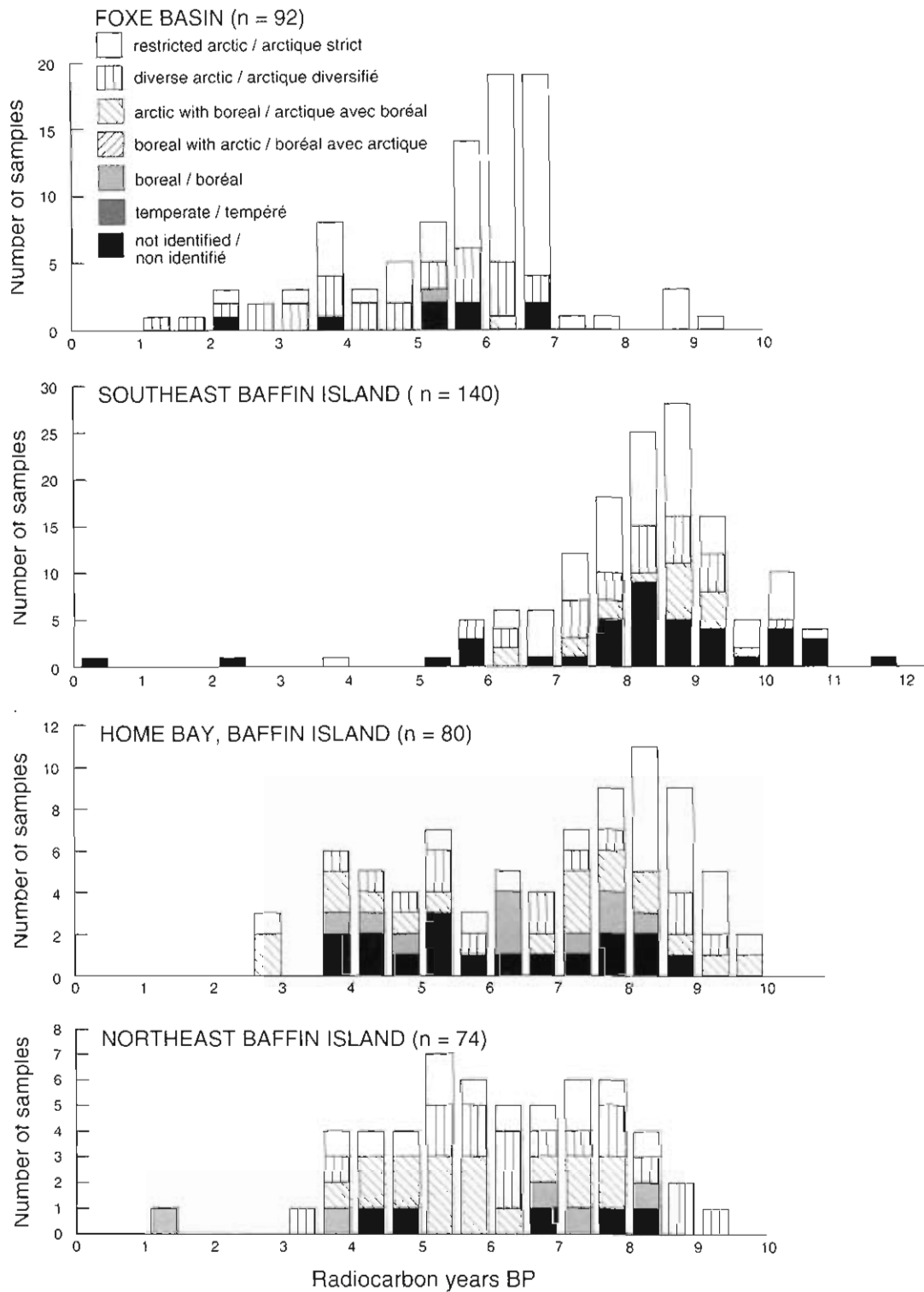
Lubinsky (1980, p. 60) pointed out that the subarctic species *Crenella faba* and *Yoldia hyperborea* occur in the northern part of Foxe Basin, probably as postglacial relicts. This implies that they extended their ranges into the basin under conditions more favourable than today. As yet these are missing from the fossil record.

SOUTHEAST BAFFIN ISLAND

This region extends from eastern Hudson Strait to the present northern limit of boreal-subarctic species just north of Cape Dyer (#6 in Fig. 2). It coincides with Lubinsky's northernmost subarctic province. The faunal record is well dated for the general interval of deglaciation but is almost blank thereafter (Fig. 9). The easternmost parts of the region have experienced middle to late Holocene submergence but the rest has undergone continuous emergence (Andrews, 1989). Hence, the near absence of records younger than 6 ka BP is not adequately explained by the sea-level history. There is little evidence of ecostratigraphic succession in this record. Thermophiles are present early in deglaciation and there is no evidence of a period when their range retracted south of the region. *Chlamys islandica* is the most common of these and makes the first recorded appearance (9.51 ka BP), followed by *Macoma balthica* (8.23 ka BP), *Mytilus edulis* (7.61 ka BP), *Balanus balanoides* (7.08 ka BP), and *Lyonsia hyalina* (6.4 ka BP). Excepting the last, which is a single, unconfirmed and dubious record of a Virginian species, none of these represent range extensions. However, species diversification may have occurred in that only 3 species (*Mya truncata*, *Hiatella arctica*, and *Balanus balanoides*) are recorded for the pre-10 ka BP interval, whereas successive 1 ka intervals record 11 species (10-9 ka), 18 species (9-8 ka), 13 species (8-7 ka), and 18 species (7-6 ka). There are no consistent trends in abundances of the dominant *H. arctica* and *M. truncata*.

HOME BAY

The Home Bay area of central eastern Baffin Island extends north from the present marine subarctic-arctic boundary (#7 in Fig. 2). Thus, it is sensitively located to record shifts of this boundary as indicated by range extensions. The dated faunal record extends from 10 to 2.7 ka BP. Boreal-subarctic species apparently extended throughout the Home Bay area for most of that time (Fig. 10). The first to appear was *Astarte striata* at 9.28 ka BP. It is probably the least warmth-demanding in that it occupies arctic outposts today, but it is



FIGURES 8-11. Frequency distributions of marine mollusc assemblages in the Foxe Basin region, the southeast Baffin Island region, the Home Bay region, and the northeast Baffin Island region.

Histogrammes de fréquence des assemblages de mollusques marins dans les régions du bassin de Foxe, du sud-est de l'île de Baffin, de la baie de Home, et du nord-est de l'île de Baffin.

considered a thermophile north of Cape Dyer (Andrews, 1972). *Chlamys islandica* appears in the record at 8.23 ka BP, *Mytilus edulis* at 8.19 ka BP, and *Macoma balthica* at 7.08 ka BP. The latter two are common in the interval 5-3 ka BP when *Astarte montagui* is also listed. *A. montagui* is similar to *A. striata* but has a more southerly range. Collectively these southern species seem to have been most abundant 8-7 ka BP, with 12 records, but *M. edulis* and *M. balthica* are most common from 7-3 ka BP. *Hiatella arctica* is not recorded in samples older than 9 ka and is subordinate to *Mya truncata* throughout. The dearth of samples dating younger than 2.7 ka BP leaves the retraction of ranges to present limits undated.

NORTHEAST BAFFIN ISLAND

This region (#8 in Fig. 2) coincides largely with Lubinsky's high arctic province IV, and although farther north, subarctic species that do not occur in Home Bay - including *Astarte striata* and *Mytilus edulis* - sporadically reappear here. The region may represent a westward extension of the relatively warm West Greenland faunal region (Lubinsky, 1980, p. 61), or the present outposts of subarctic species may be relicts of a general expansion of ranges up the Baffin coast. The outpost of *M. edulis* at Pond Inlet may have been reseeded from mussels attached to whaling ships in the last century (J.T. Andrews, personal communication, 1995).

The histogram for this region (Fig. 11) has the usual profile of well-dated earlier Holocene faunas and a nearly undated later Holocene. Much of the region has experienced late Holocene submergence, which partly accounts for this. This record does not display an early dominance of the restricted arctic assemblage. Instead, diverse arctic assemblages and arctic assemblages with boreal-subarctic elements comprise the bulk of the record. The earliest recorded boreal entries, both in the same sample, are *Mytilus edulis* and *Macoma balthica* at 8.25 ka BP. These two dominate occurrences of boreal taxa and jointly reach maximum percentile abundance in the interval 6-4 ka BP when each occurs in 27.3% of identified samples. *M. balthica* withdrew sometime after 4 ka BP to a limit about 1000 km to the south; *M. edulis* remains in isolated colonies but its main limit has retracted a comparable distance, assuming a southward rather than eastward retreat. Thus, there appears to have been greater influence of subarctic water masses or much greater solar warming of the littoral zone during the period 8.25-4 ka BP than after.

The other recorded boreal species are *Astarte striata*, *A. montagui*, and *Mya arenaria*, the latter two in single samples and the last indicating a range extension of 2300 km at 4.85 ka BP (GSC-4379). As with other extreme range extensions, the identification should be checked to guard against misidentification of *M. pseudoarenaria*.

Recent field work by Dyke (see McNeely and Jorgensen, 1993; McNeely, in press) has shown a difference between Holocene molluscs present on either side of the western boundary of this region. *Mytilus edulis* fossils were found at several sites along Navy Board and Milne inlets, just east of the boundary, but not along Admiralty Inlet, just west; earlier collections by B.G. Craig show the same pattern. We are

confident that the maximum range extension of the boreal taxa was not beyond the mouth of Navy Board Inlet.

The dominant species in this record, in order of apparent abundance, are *Hiatella arctica*, *Mya truncata*, *Macoma calcaria*, *Mytilus edulis*, and *Macoma balthica*. *M. calcaria* reaches peak abundance (54.5% of samples) at 6-4 ka BP as do the two boreal elements. *M. truncata* also is at peak percentile abundance then (86.4%), but *H. arctica* declines about 6 ka BP (from 80% to 59.1%).

SOUTHERN WEST GREENLAND

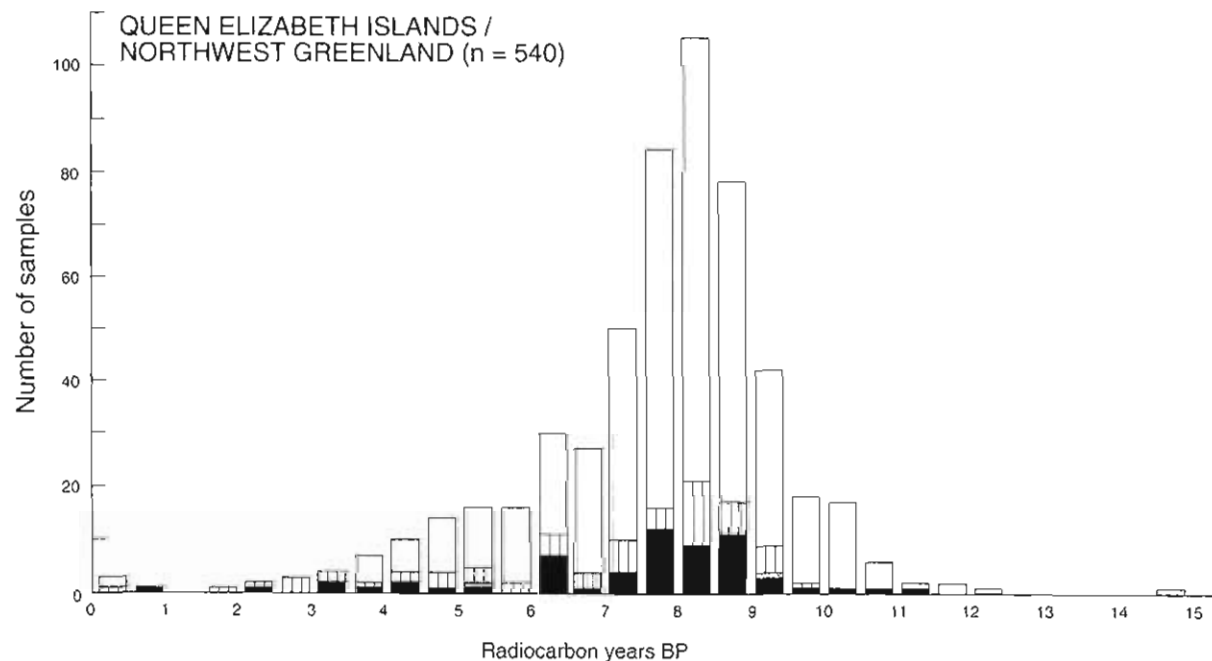
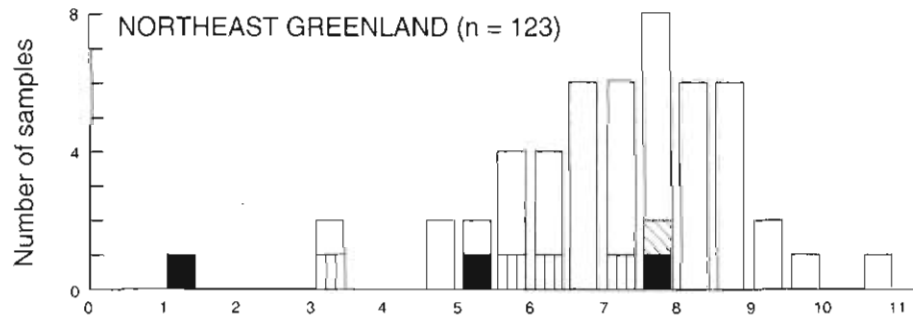
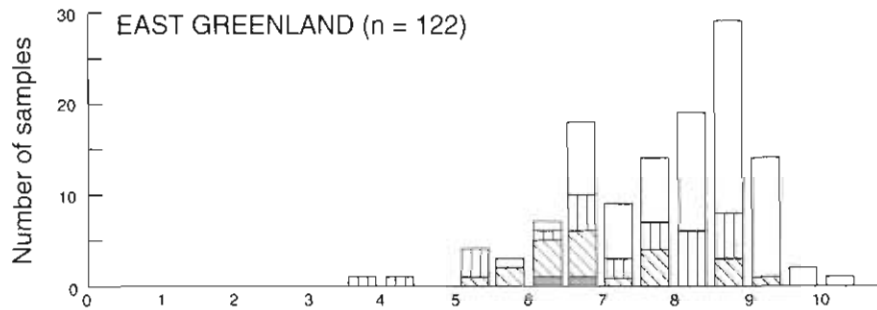
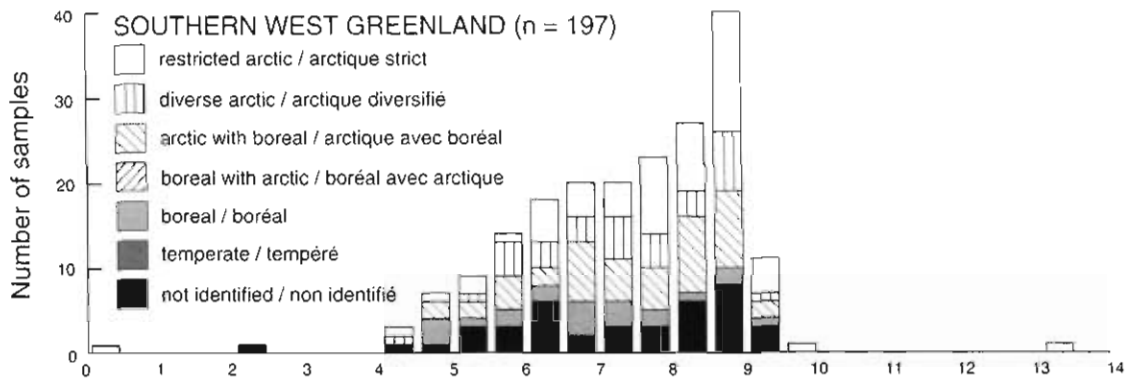
This subarctic region (#9 in Fig. 2) is warmed by the West Greenland Current. The dated faunal record extends back to 10 ka BP with an outlier (*Mya truncata*) at 13.5 ka BP. Much of the region has experienced late Holocene submergence (Kelly, 1973).

In that boreal and diverse arctic species are present at deglaciation, there is no obvious succession of postglacial environments (Fig. 12). The dominant species throughout are *Mya truncata* and *Hiatella arctica*, with the former consistently more numerous. However species diversity does change through time: 15 species are recorded for 10-8 ka BP, 31 for 8-6 ka, and 15 for 6-4 ka. The increased diversity at 8-6 ka is due mainly to addition of boreal elements, with 13 such species at that time compared to only 3 previously. The first appearances of boreal animals in the record are: *Chlamys islandica* at 9.4 ka, *Mytilus edulis* at 9.07 ka, *Balanus hameri* at 8.54 ka, *Astarte striata* at 7.98 ka, *Buccinum undatum* at 7.73 ka, *Lora nobilis* at 7.73 ka, *Lima subauriculata* at 7.55 ka, *Crenella decussata* at 7.34 ka, *Epitonium* sp. at 7.22 ka, *Macoma balthica* at 6.84 ka, *Littorina saxatilis* at 6.84 ka, and *Zirphaea crispata* at 5.19 ka. Funder and Weidick (1991) list additional taxa, now extinct in Greenland, that occupied the area 8.4-4.9 ka BP. Funder and Weidick (1991) pointed out that the extinct species occurred along a small part of the West Greenland coast where today the cold polar water is deflected westward across Davis Strait, leaving water from the Irminger Current to warm the coastal zone. They thus infer that this division of currents has been in place since at least 8.4 ka BP.

EAST GREENLAND

The faunal record of East Greenland (#10 in Fig. 2; Fig. 13) differs greatly from that of West Greenland. The East Greenland record has an arctic aspect in that it is dominated by the restricted arctic assemblage from deglaciation until 6.5 ka BP and species diversity is markedly reduced. The interval 10.3-8 ka has 10 species; 8-6 ka, 12 species; and 6-4 ka, 9 species. *Mya truncata* and *Hiatella arctica* are exceedingly abundant, the former somewhat more than the latter. Both decline in relative abundance through time, from 90.8% to 62.5% and from 70.8% to 50%, respectively. At the same time *Macoma calcaria* increases from 13.8% to 62.5% of records.

Species regarded here as thermophiles represent range extensions into the area. Their order of appearance in the record is: *Astarte elliptica* at 9.01 ka, *Nucula tenuis* and 8.67 ka, *Chlamys islandica* at 8.58 ka, *Mytilus edulis* at 7.87 ka, and *Mya arenaria* at 5.58 ka BP. Only *M. edulis* is



FIGURES 12-15. Frequency distributions of marine mollusc assemblages in the southwest Greenland region, the east Greenland region, the northeast Greenland region, and the Queen Elizabeth Islands / northwest Greenland region.

Histogrammes de fréquence des assemblages de mollusques marins du sud-ouest du Groenland, de l'est du Groenland, du nord-est du Groenland, ainsi que de l'archipel de la Reine Elizabeth et du nord-ouest du Groenland.

common; it occurs in about 25% of samples from 8 to 4 ka BP. Hjort and Funder (1974) suggested that *C. islandica* and *M. edulis* expanded into this area from Spitsbergen, rather than from south Greenland, and that this could have been caused by a shift in the balance between the cold East Greenland and the warm West Spitsbergen current.

NORTHEAST GREENLAND

The faunal record for northeast Greenland (#11 in Fig. 2; Fig. 14) is further impoverished with respect to central East Greenland. All but 5 samples with identified taxa fall in the restricted arctic assemblage. Only 5 species are listed from this region, all pelecypods. Bennike (1987) reports 10 species of subfossil pelecypods from the region but does not provide radiocarbon dates. Before 8 ka BP, *Hiatella arctica* is dominant; thereafter it and *Mya truncata* are equally abundant. The more diverse assemblage results from the additional presence of *Astarte borealis*. *Astarte elliptica* is the single boreal-subarctic species appearing at 7.73 ka BP (W-1088). It has a low arctic-boreal range today extending up the West Greenland coast to the head of Baffin Bay and northward to Cumberland Sound in the Canadian Arctic.

QUEEN ELIZABETH ISLANDS - NW GREENLAND

The faunal record of this high arctic region (#12 in Fig. 2; Fig. 15), which corresponds to Lubinsky's "endemic province of northern Canadian Arctic Archipelago", resembles that of northeast Greenland. The record is dominated by restricted arctic assemblages with diverse arctic assemblages making up most of the rest. The oldest date is on *Hiatella arctica* at 14.88 ka BP (TO-475) from northern Ellesmere Island (Evans, 1990). This important sample demonstrates that at least this species survived the last glacial maximum along the shores of the Arctic Ocean. Thus, postglacial recolonization by molluscs did not necessarily occur in the form of a front advancing from the south. Since completion of the database, a second record of this species from the region, dating 14.6 ka BP, has been published (Hodgson *et al.*, 1994), but further dating has shown this to be a blended age.

Boreal elements are recorded in only two samples. *Mytilus edulis* and *Chlamys islandica* occur in a sample dated 9.15 ka BP (K-4781) in the Thule area of northwest Greenland. This records early penetration of these thermophiles to the head of Baffin Bay and indicates that the West Greenland Current was functioning by then. The only record of a southern species in the Queen Elizabeth Islands is that of *C. islandica* on east-central Ellesmere Island at 5.35 ka BP (TO-390). This site is in the small part of the Queen Elizabeth Islands influenced by the West Greenland Current.

The faunal records illustrated by Figures 14 and 15 represent high arctic marine environments that have never warmed enough to allow a wider variety of molluscs to survive than are there today. Under these restricted conditions, a dramatic postglacial succession would not be expected. Yet a subtle succession seems to have occurred. Before 10 ka BP only 4 species are recorded. This increases to 17 species for the period 10-8 ka. The most common additions to the fauna after 10 ka are *Astarte* sp., *A. borealis*, and *Macoma calcaria*.

Astarte becomes the dominant taxon in the record for the last 4 ka (55.6% of samples, n=18). But unfortunately, this part of the record is too little dated to determine firmly whether an important shift in faunal composition occurred. *Hiatella arctica* and *Mya truncata* were strongly dominant, in that order, before 4 ka BP. Although *H. arctica* and *M. truncata* today range southward into the subarctic, we suggest that the closest analogue of fossil assemblages strongly dominated by - or limited to - these species in present boreal to low arctic areas is the postglacial records of the Queen Elizabeth Islands and northeast Greenland.

CENTRAL ARCTIC ISLANDS

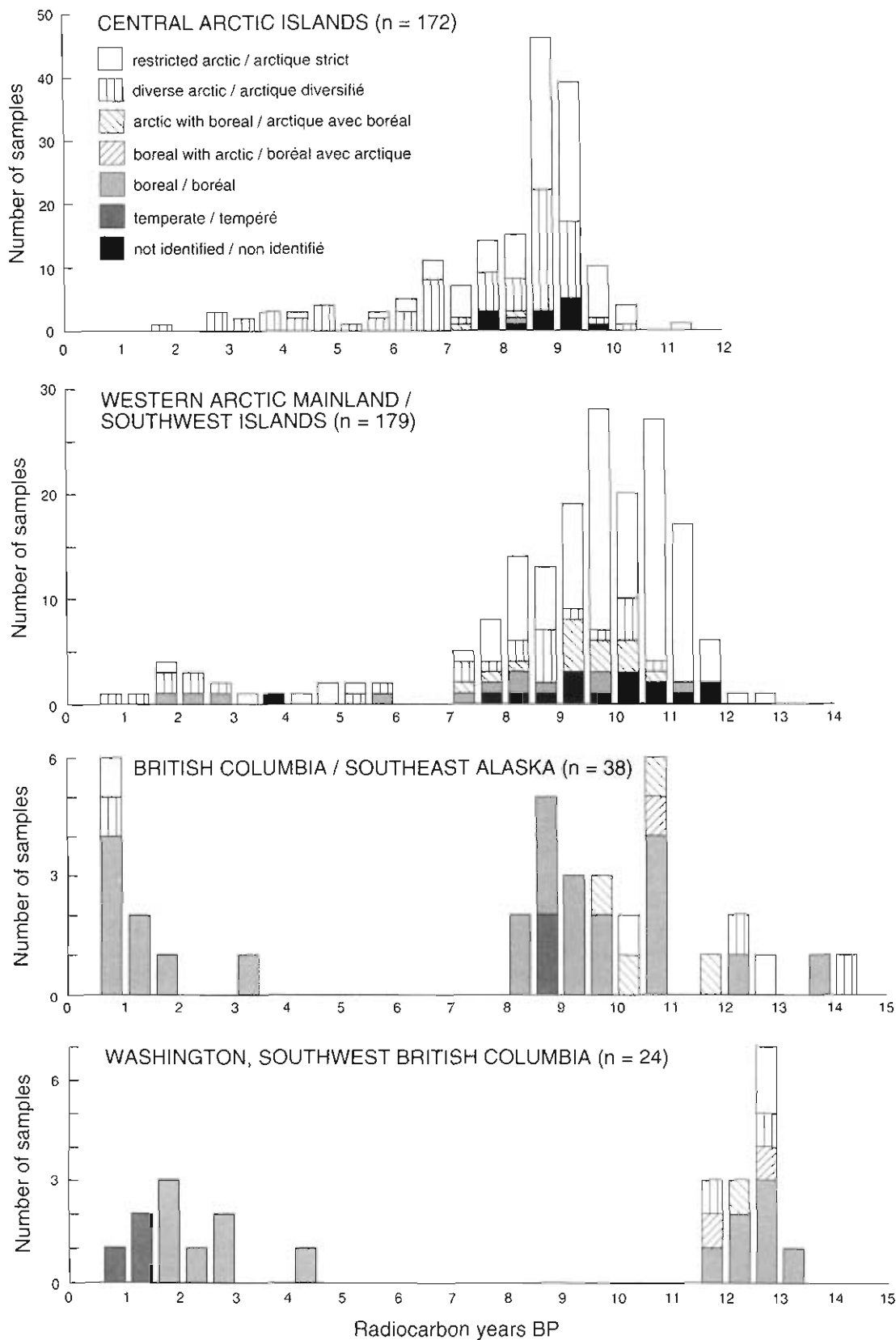
The central arctic islands region coincides with Lubinsky's central shallow-water province of the high arctic. It lies south of and contiguous with the Queen Elizabeth Islands (#13 in Fig. 2). Although not as intensively dated, its faunal record differs somewhat from that of the northernmost region in its greater diversity, *i.e.* a smaller proportion reporting *Hiatella arctica* and *Mya truncata* only (Fig. 16). The central region exhibits a similar diversification through time. Comparing the 11-8 ka BP interval with the post-6 ka BP interval, *H. arctica* declines from presence in 84% to 45% of samples; *M. truncata* declines from 68.9% to 45%; *Astarte borealis* increases from 8.5% to 60%; *Serripes groenlandicus* from 5.7% to 30%; and *Macoma calcaria* from 8.5% to 25%. As farther north, this middle Holocene diversification is not sufficiently well dated at present to be adequately characterized.

Three samples reportedly contain boreal species. *Mya arenaria* is reported from northeast Victoria Island at 8.37 ka BP (GSC-4650) and *Macoma balthica* from southern Victoria Island at 8.12 ka BP (GSC-4242). A single record of *Mytilus edulis* from the northern mainland is dated 7.16 ka BP (I(GSC)-212). *Mytilus* extends nearly to the southwestern boundary of the region today from the Beaufort Sea (see below) and this sample may represent a brief extension of that range. Neither of the other two occur in or near the region. In the Pacific, *M. arenaria* ranges north to the Aleutian Islands and *M. balthica* into the Bering Sea. The latter is thus poised to enter the Arctic Ocean through Bering Strait and is identified in several samples from the region discussed next.

The data from this region along with that from Foxe Basin and northeast Baffin Island do not support the conclusion of Andrews (1972) that *M. edulis* and *M. balthica* spread westward across the entire mainland coast during the period 8-2.5 ka BP. If such extensions occurred, they were very brief and have not yet been recorded. Apart from diversification following deglaciation, the regional faunal record indicates unwavering high arctic conditions.

WESTERN ARCTIC MAINLAND - SOUTHWESTERN ISLANDS

This region (#14 in Fig. 2) corresponds to Lubinsky's southwestern Canadian Archipelago province and differs from the rest of her high arctic faunistic zone in the presence here of Pacific species and subarctic elements, especially *Mytilus edulis*. The western third of the region has been submerging throughout the Late Wisconsinan and Holocene but the east-



FIGURES 16-19. Frequency distributions of marine mollusc assemblages in the central Arctic Islands region, the western arctic mainland / southwestern arctic islands region, the British Columbia/southeast Alaska region, and the Washington / southwest British Columbia region.

Histogrammes de fréquence des assemblages de mollusques marins dans les régions des îles centrales de l'Arctique, de l'Arctique de l'ouest continental et des îles du sud-ouest de l'Arctique, de la Colombie-Britannique et du sud-est de l'Alaska, ainsi que de l'état de Washington et du sud-ouest de la Colombie-Britannique.

ern part has been emerging since deglaciation (Dyke and Dredge, 1989).

There are two interesting features of the this faunal record. First, the greater importance of boreal elements than in neighbouring records is clear (Fig. 17) and is expected from the present fauna. Second, a strong shift in relative abundances of *Hiatella arctica* and *Mya truncata* occurred at 10-10.5 ka BP. This was not anticipated as a feature of this faunal record and has not been previously documented; it may be generally significant for the high arctic paleoenvironmental record. *H. arctica* occurs in 89.6% of samples (n=67) dated >10 ka BP (*Portlandia arctica* accounts for most of the rest); *M. truncata* occurs in 3%, in 2 samples dated 11.8 ka and 10.2 ka BP. This severe imbalance of the proportions of these two species is unique to this region and to this age group. The imbalance disappears about 10.3 ka BP (10.2-10.5 ka); in the 10-8 ka age group *H. arctica* occurs in 67.6% of samples (n=68) and *M. truncata* in 36.8%. We suggest below that the shift from imbalanced to balanced proportions coincides with submergence of Bering Strait, with influx of Pacific surface water to the Arctic Ocean, and with the entry of bowhead whales into the High Arctic (Dyke and Morris, 1989; Dyke *et al.*, in review). These correlations suggest that *H. arctica* colonized the Canadian Arctic Archipelago before 10.5 ka BP by dispersing from the Arctic Ocean or from the Atlantic via North Greenland very early in deglaciation. *Portlandia arctica* was also a very early arrival or survivor in the Arctic Ocean. *M. truncata*, in contrast, may have been eliminated from the Arctic Ocean by the last glacial maximum and unable to access the western arctic mainland until opening of Bering Strait.

This dramatic ecostratigraphic change in the record of the western Arctic stands out simply because of the large number of samples that date older than 10 ka BP. The paucity of dates in that range in the neighbouring regions to the east and north precludes as clear a recognition of this event. However, available data indicate that *M. truncata* was absent or exceedingly sparse there too before 10.5 ka BP. Its earliest records from the central arctic islands region are samples dated 10.1 and 10.07 ka, whereas the record of *Hiatella arctica* there extends back to 11.01 ka BP. *M. truncata* is dated at 12.2 ka BP on Saunders Island at the head of Baffin Bay, but this site was accessible directly from the Atlantic and the record does not imply presence of the species in the Arctic Ocean. Its only record in the entire Queen Elizabeth Islands before 10 ka BP is in a sample from Hot Weather Creek, west-central Ellesmere Island. *H. arctica* in that sample dated 10.6 ka BP. There are 25 records of *H. arctica* in the Queen Elizabeth Islands with dates >9.8 ka BP as compared to the one *M. truncata*.

The earliest recorded entry of a boreal species to the western arctic mainland region (Fig. 17) is a sample reporting *Macoma balthica* dating 11.4 ka BP (GSC-3840). If correctly identified, it indicates either migration into the region along the Eurasian coast from the Barents Sea or incursion of Pacific fauna into the Arctic Ocean by that time. In either case it surprisingly precedes *M. truncata*. Entry from the Pacific at 11.4 ka BP is problematic: it requires submergence of Bering Strait, with a sill depth of about 50 m, at a time when global

eustatic sea level was much lower (about -75 m; Fairbanks, 1989; Tushingham and Peltier, 1991). Migration from Barents Sea is thus more feasible. The significant implications for water temperatures along the Eurasian coastline require that this record be confirmed.

Subsequent boreal species records are about 1 ka younger: *M. balthica* at 10.5 ka (I(GSC)-25) and *Mytilus edulis* at 10.35 ka BP (UQ-722). These are essentially coincident with the arrival of *M. truncata*. The only other reported boreal species in this record is *Mya arenaria*, which is listed in five samples (GSC-4747, -4537, -4608, -4579, and AECV-948c), the oldest of which dates 9.64 ka BP. This represents a great range extension of the Pacific population which now ranges north to the Aleutian Islands. As with all high arctic records of this species, identifications should be confirmed.

This regional record lists only 13 species of pelecypods and cirripeds. None of the Pacific forms that are unique to this part of the Canadian High Arctic yet have a fossil record. The common arctic mollusc *Serripes groenlandicus* occurs in the area but is not reported in any fossil collection and *Clinocardium ciliatum* is poorly represented. The absence of *Chlamys islandica* is interesting because on the Atlantic side it extended its range in company with *M. edulis*, ahead of *M. balthica*, and much farther than *M. arenaria*. In the Pacific today it ranges north to Alaska. *M. edulis* still occupies the region and is the third most common species of record. It occurs in 17.6% of samples for the interval 10-8 ka, 8.3% for 8-6 ka, and 15.6% for <6 ka BP. It exceeds *Macoma calcarea*, the only other commonly reported pelecypod, in abundance and far exceeds *Astarte borealis*, which appears to be rare here. *M. balthica* has withdrawn to the Bering Sea; its youngest record is 2.51 ka BP (GSC-158).

BRITISH COLUMBIA - SE ALASKA

The entire coast from the Mackenzie Delta to southern Alaska lacks a fossil mollusc record for the last 18 ka. This coastline has been submerging throughout that time and its faunal record is not available. Some of the species that survived during the last glacial cycle south of Beringia are known from the list of early arrivals in the western Arctic discussed above.

Even the emergent, glaciated coastline of the Pacific is poorly sampled. We have found only 37 dated samples of identified marine shells for the British Columbia - SE Alaska region (#15 in Fig. 2; Fig. 18). About as many shell dates have no taxa reported. The database, however, points to a record of a different type than any discussed above. Although some arctic-subarctic molluscs are reported, boreal taxa dominate even at deglaciation, and there is some suggestion of a faunal succession. Before 12 ka BP there are records of only 4 species of pelecypods and *Balanus* sp. in 7 samples. These include the panarctic *Mya truncata* and *Macoma calcarea* but also two animals that have their northern limits in the area today - *Macoma nasuta* and *Macoma liparia*. The list for 12-10 ka BP (12 samples) includes 14 species of pelecypods and 3 gastropods, all of which occur in the region today. Only 6 species are recorded for the 13 samples dated 10-8 ka BP but 5 of these are additions to the previous fauna. One,

Protothaca tenerrima from Haines Creek at 53°56' N dating 8.85 ka BP (GSC-2534), may record a range extension from its present limit around Vancouver.

SW BRITISH COLUMBIA - WASHINGTON

This region (#16 in Fig. 2) is the counterpart of the Gulf of Maine in that the Cordilleran Ice Sheet advanced here into the warmest water at the last glacial maximum. Although mollusc assemblages here are not extensively dated (Fig. 19; no identifications found for 57 of 88 samples), the record differs from that of the Gulf of Maine in that arctic molluscs were not dominant during early stages of deglaciation. Considering the small data set, there is a diverse array of mostly boreal taxa - 22 in 16 samples (6 identified to genera only). The least thermophilous taxa for the interval >11 ka BP extend to Puget Sound today. On this evidence, the glacial maximum and early deglacial seas may not have been much colder than present. Hence, the southwestern and perhaps much of the western margin (Fig. 18) of the Cordilleran Ice Sheet terminated in warmer water than did the Laurentide Ice Sheet at its southeast extremity. In this light, it seems improbable that the periglacial zone of the Cordilleran Ice Sheet at the last glacial maximum served as a refugium of many arctic marine invertebrates. Those that retreated to the Pacific likely survived along the Beringian coast.

PALEOGEOGRAPHY

In this section, we examine the mollusc data in 1 ka steps in order to map shifting paleofaunistic zones as they relate to the shrinking ice sheets. We infer general surface water mass characteristics from mollusc assemblages and postulate causal mechanisms for changes. We assume that ocean circulation at the last glacial maximum involved a Gulf Stream transporting warm water northward and other currents transporting cold water southward in the North Atlantic. We also assume existence of a proto-Beaufort Gyre. This is supported by wind directions along the Beaufort coast during the glacial maximum (Carter, 1981), but the assumption does not constrain our data interpretations. We also consider constraints as well as supporting and conflicting interpretations arising from other marine paleoenvironmental data sets. However, it is not our intention to synthesize these latter data. Because there are no dated molluscs for the height of the last glacial maximum (18 ka BP) and sparse data immediately thereafter, we start the map series at 14 ka BP. Each map displays data for the preceding 1 ka interval but we interpret conditions for the end of each interval.

Outlines of ice sheets and shorelines, are simplified and modified from Dyke and Prest (1987) with the addition of Cordilleran Ice Sheet margins for 13, 12, and 11 ka BP from Ryder (unpublished contract report to GSC, 1993). There is a growing need to generally update the deglaciation history of Dyke and Prest (1987). However, this is well beyond the scope of this paper as it involves more than simply incorporating suggested revisions. The more substantive proposed revisions indicate later ice retreat than proposed by Dyke and Prest (1987). Those proposed by Macpherson (1988; personal communication, 1995) for the Avalon Peninsula of Newfound-

land and by Richard *et al.* (in review) for the Gaspé Peninsula of Québec are incorporated in the paleogeographic maps herein. Macpherson (1988) argued that the Avalon Peninsula of Newfoundland remained ice covered until about 10 ka BP based on basal lake sediment ages, 3 ka later than proposed by Dyke and Prest. Richard *et al.* (in review) showed by AMS dating of macrofossils that previous conventional radiocarbon dates from the plateau of Gaspé Peninsula are too old and that deglaciation finally occurred after 10 ka BP rather than about 12 ka BP. Payette (1993) and Gray *et al.* (1993) proposed that final deglaciation of the Ungava region of Québec occurred 5.5-5 ka BP, 1 ka later than the date suggested by Dyke and Prest (1987). The younger deglaciation proposal for that area is based on a few basal peat and gyttja dates that Dyke and Prest (1987) regarded as not closely constraining the dates of deglaciation and on a peculiarity in the present distribution of *Larix*. Similarly Lemmen *et al.* (1994b) took the sparse set of basal organic dates from the District of Mackenzie to more closely date deglaciation than did Dyke and Prest and thus decreased the date of deglaciation on average by about 0.5 ka.

MOLLUSCAN ZONES AT 14 ka BP

Sparsity of data makes any reconstruction of faunistic zones at this time tentative. Data from the Gulf of Alaska indicate a diverse arctic assemblage just before 14 ka BP. As discussed above, the waters at the southwestern margin of the Cordilleran Ice Sheet had mollusc assemblages warmer than those in the Gulf of Maine - Gulf of St. Lawrence region. Hence, we show a broad Pacific boreal zone with subarctic conditions only in the periglacial fringe where meltwater would have been influential. The Pacific boreal zone today extends south to 34°N; therefore, the area labelled "undefined" on Figure 20 was probably entirely boreal.

Boreal taxa in the Gulf of Maine and, at least as a minor element, on the Scotian Shelf indicate that a north-flowing Gulf Stream mitigated the effect of the melting ice sheet on the adjacent ocean (Fig. 20). However, the boreal zone may have been narrow for most of the southeastern periglacial region supported arctic taxa. Water temperatures would have been depressed by the large meltwater flow and by strong northwesterly winds (COHMAP Members, 1988; Mudie and McCarthy, 1994) and the effect of the Gulf Stream would have been further limited by its sharp eastward deflection by the emergent Georges Bank. The modern arctic faunal zone lacks vertical zonation due to insufficient seasonal heating. This was unlikely in the Gulf of St. Lawrence and on the shallow Scotian Shelf at 14 ka BP, where conditions were probably subarctic. However, summer meltwater flow through the inner gulf at 14 ka BP was enough to freshen the entire water column (deep water salinity <20 per mil; Rodrigues *et al.*, 1993).

Rahman and de Vernal (1994) concluded that the sea off eastern Newfoundland was cold and (or) seasonally ice covered between 23 and 13 ka BP on the basis of the nannofossil record in a well-dated sediment core. The Labrador Current at that time may have been a direct continuation of the East Greenland Current and neither was influenced by the Irminger Current. Therefore, arctic water probably occupied the entire

east coast to southeastern Newfoundland. Between 14 and 13 ka BP the Labrador Current was influenced by exceptional ice berg production that produced a distinct layer of ice-rafted detritus, a so-called Heinrich layer (event), across much of the North Atlantic (Dowdeswell *et al.*, 1995). Andrews *et al.* (1994) suggested that this berg calving was accompanied by major meltwater discharge from Hudson Strait and by rapid retreat of the eastern Laurentide Ice Sheet. The 14-13 ka BP Heinrich layer (H1) is also distinguished by a peak abundance of reworked pre-Quaternary microfossils of European provenance, which indicates that the Fennoscandian and (or) British ice sheets also released bursts of ice bergs at the same time, presumably in response to a common controlling mechanism (Rahman, 1995). The extensive oceanic ice front and ice berg production at 14 ka BP would have chilled surface water and retarded seasonal warming.

The sample of *Hiattella arctica* from the Arctic Ocean shore (Fig. 20) illustrates that this mollusc was able to survive glacial maximum conditions in the most polar sites. Its dominance of faunas south to the Bay of Fundy demonstrates an enormous range in shallow water at 14 ka BP. It must be one of the most robust animals in terms of adaptation to environmental change. The large latitudinal span of western North Atlantic arctic taxa is in striking contrast to that of its boreal taxa as is the span of the Pacific boreal zone. Habitats of obligate shallow-water boreal species at 18 ka BP in the Atlantic, when the Laurentide Ice Sheet extended to Long Island, must have been even more restricted than at 14 ka.

MOLLUSCAN ZONES AT 13 ka BP

Boreal molluscs extended north of Vancouver Island by 13 ka BP. We suggest an expanding marine boreal zone and shrinking subarctic zone there but the database is inadequate to define boundaries properly (Fig. 21). The Gulf of Maine - Gulf of St. Lawrence region, in contrast, is richly dated. Restricted arctic and diverse arctic assemblages dominate the regional fauna (74% of samples), particularly in the Gulf of St. Lawrence. However, a few boreal elements are present, possibly indicating vertical faunal zonation. The fauna grades to mostly boreal southward and the boreal zone seems to have expanded northward since 14 ka BP. This could be due to a decreased meltwater flux through the Gulf of Maine by 13 ka BP. The fauna in the more ice-proximal Bay of Fundy retained an arctic aspect. The single arctic site dated >13 ka BP (southwest Greenland) records the minimum northward extension of *Mya truncata*. Foraminiferal and diatom records from the continental shelf off Hudson Strait indicate moderate biological productivity and water seasonally cleared of sea ice by 13 ka BP (Andrews *et al.*, 1990).

MOLLUSCAN ZONES AT 12 ka BP

Pacific boreal fauna extended north at least to Queen Charlotte Sound and was common in fairly ice-proximal sites in southwestern British Columbia (Fig. 22). The Cordilleran ice margin had largely retreated from the outer coast so that meltwater influence on the nearshore zone was less. Subarctic conditions may have persisted along the Gulf of Alaska, but lack of identified taxa among the four dated samples from the region leaves this uncertain.

The Gulf of Maine records mainly boreal assemblages, boreal assemblages with arctic elements, and arctic dominated assemblages with boreal elements during the period 12.9-12 ka BP (Fig. 22). Arctic influence diminished until by 12 ka BP boreal conditions apparently were established throughout the gulf. Boreal faunas also extended their range, diversity, and dominance in the Gulf of St. Lawrence to the point that the ice-distal part was boreal by 12 ka BP. Subarctic conditions continued to prevail along the north shore where the Laurentide margin approximated the present coastline. This zone remained cold not only because of its ice-proximal setting but also because the Strait of Belle Isle had opened: the Coriolis effect diverts a branch of the Labrador Current through the strait and along the north shore. The oldest dates on marine molluscs from the Champlain Sea exceed 12 ka BP (as much as 12.8 ka) and are plotted here incongruously in glacial Lake Iroquois (Lake St. Lawrence of Rodrigues and Vilks, 1994) and within the ice margin; these dates are considered to be 500-1000 years too old because of the "old water" (meltwater) effect in the Champlain Sea (Anderson, 1987). The samples illustrate, however, that even the earliest invaders here included boreal taxa.

In the Arctic, *Portlandia arctica* appears in the record on Victoria Island. Arctic Ocean conditions at this time were likely little different from those at 18 ka BP. Therefore, *P. arctica* probably survived through the last glacial maximum along with *Hiattella arctica*. Both *H. arctica* and *Mya truncata* extended to the head of Baffin Bay by 12 ka BP. Distal glaciomarine conditions are indicated by benthic foraminiferal assemblages along the Baffin Shelf by 12 ka BP, though dating of the sediment cores is insecure (Osterman and Nelson, 1989). Williams (1990) recognized diatom productivity in one of seven cores from western Baffin Bay, suggesting seasonal open water, starting about 12.5 ka BP but with a brief barren interval at 12 ka BP.

MOLLUSCAN ZONES AT 11 ka BP

There are only three classified marine mollusc samples from the Pacific for the interval 11.99-11 ka BP. The Cordilleran Ice Sheet and hence the periglacial subarctic zone had all but disappeared by 11 ka BP. Reconstructions for 11 ka BP and younger in the Pacific are depicted as shown in Figure 23 - boreal conditions extending to the Aleutian Islands.

Abundantly dated faunas from the early phase of the Champlain Sea do not indicate a dominance of arctic assemblages in spite of its periglacial setting and strong meltwater influence. Boreal taxa, notably *Macoma balthica*, are strongly represented along with *Hiattella arctica* and *Portlandia arctica*. *M. balthica* requires summer water temperatures of at least 10°C for survival of its pelagic larvae (Lammens, 1967). The distribution of faunal associations in the Champlain Sea appears to have been controlled mainly by salinity and grain-size of the bottom (Rodrigues and Richard, 1986). The sea was salinity stratified throughout its existence (Rodrigues, 1987). *P. arctica* here is associated with high-salinity waters, whereas elsewhere it is most commonly associated with meltwater-diluted, ice-proximal deltaic environments. It does occur

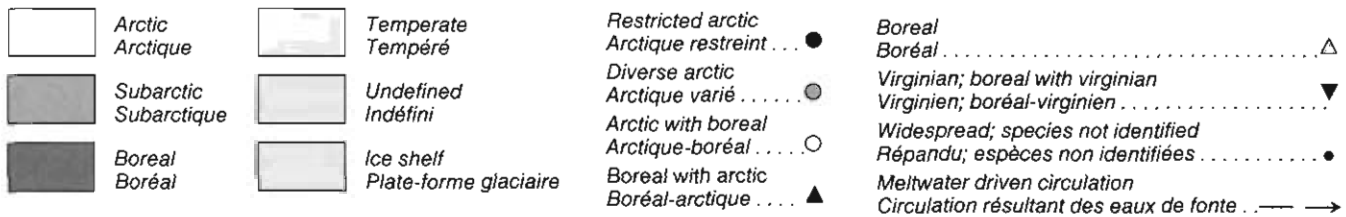


FIGURE 20. Molluscan faunistic zones at 14 ka BP. Plotted samples date 14-17.99 ka BP.

Zones fauniques des mollusques à 14 ka BP. Les âges des échantillons sont répartis de 14-17,99 ka BP.

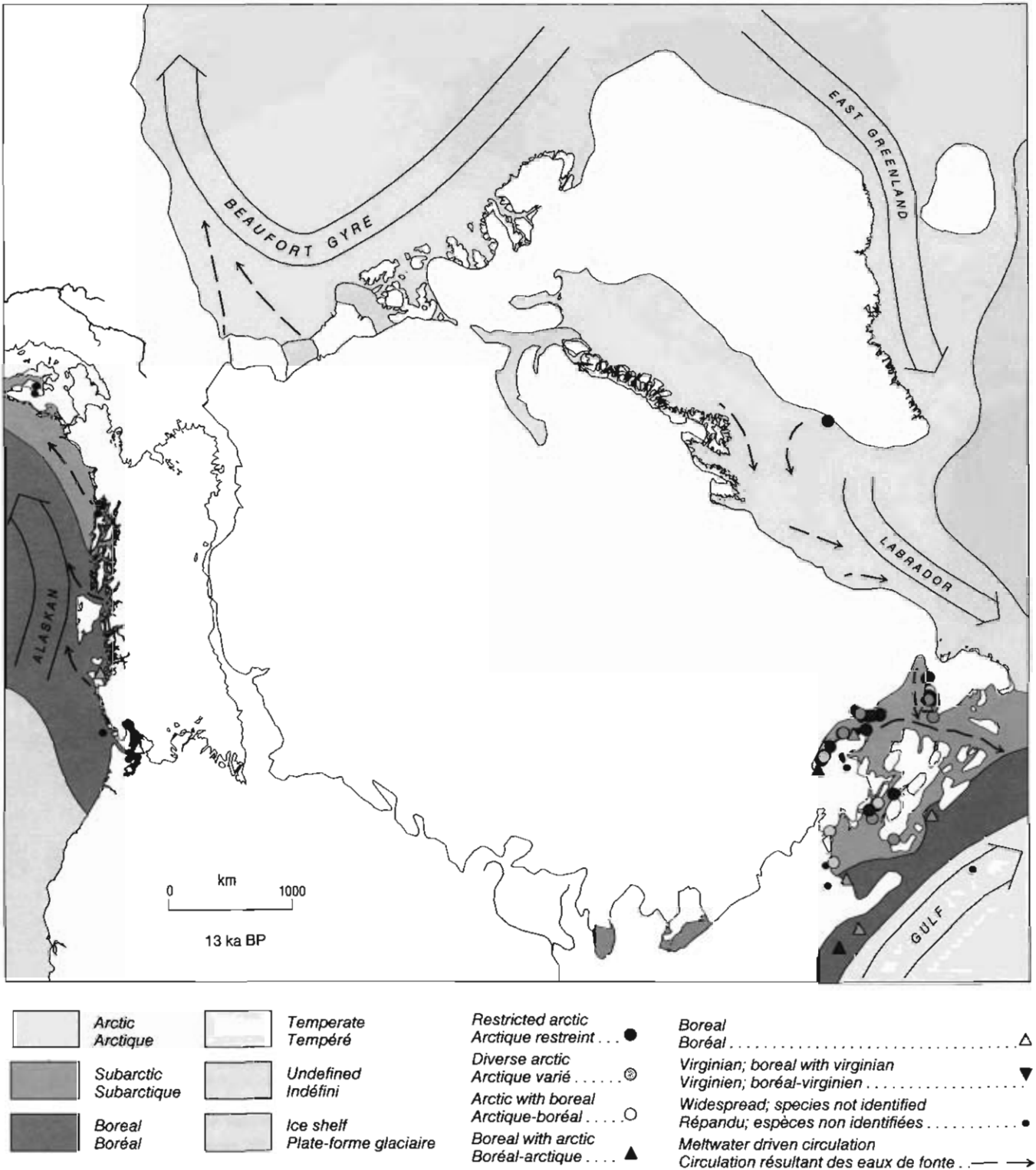


FIGURE 21. Molluscan faunistic zones at 13 ka BP. Plotted samples date 13-13.99 ka BP.

Zones fauniques des mollusques à 13 ka BP. Les âges des échantillons sont répartis de 13-13,99 ka BP.

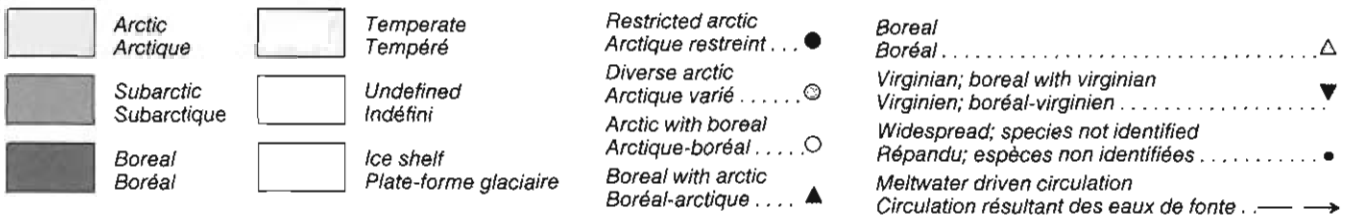
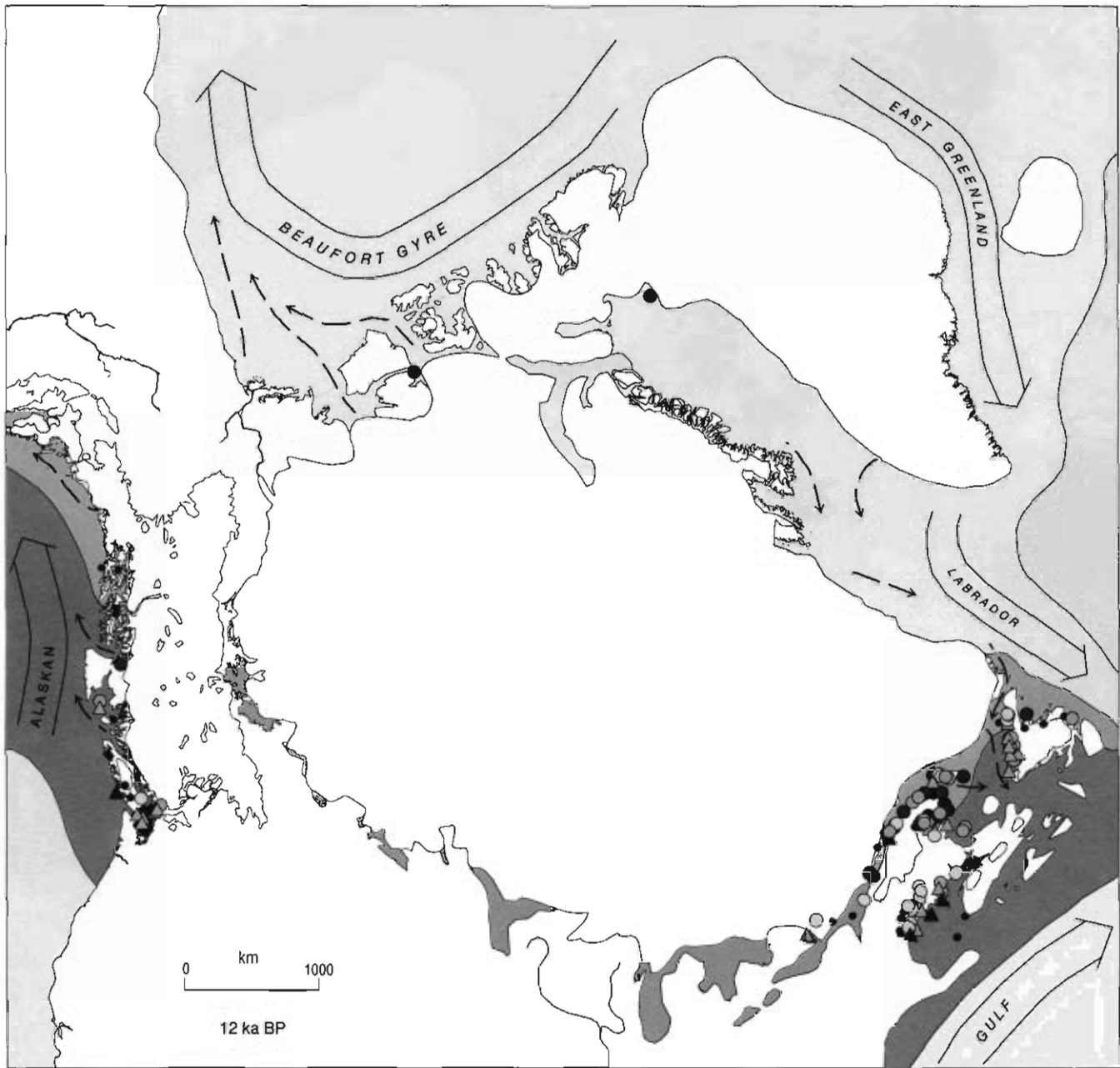


FIGURE 22. Molluscan faunistic zones at 12 ka BP. Plotted samples date 12-12.99 ka BP.

Zones fauniques des mollusques à 12 ka BP. Les âges des échantillons sont répartis de 12-12,99 ka BP.

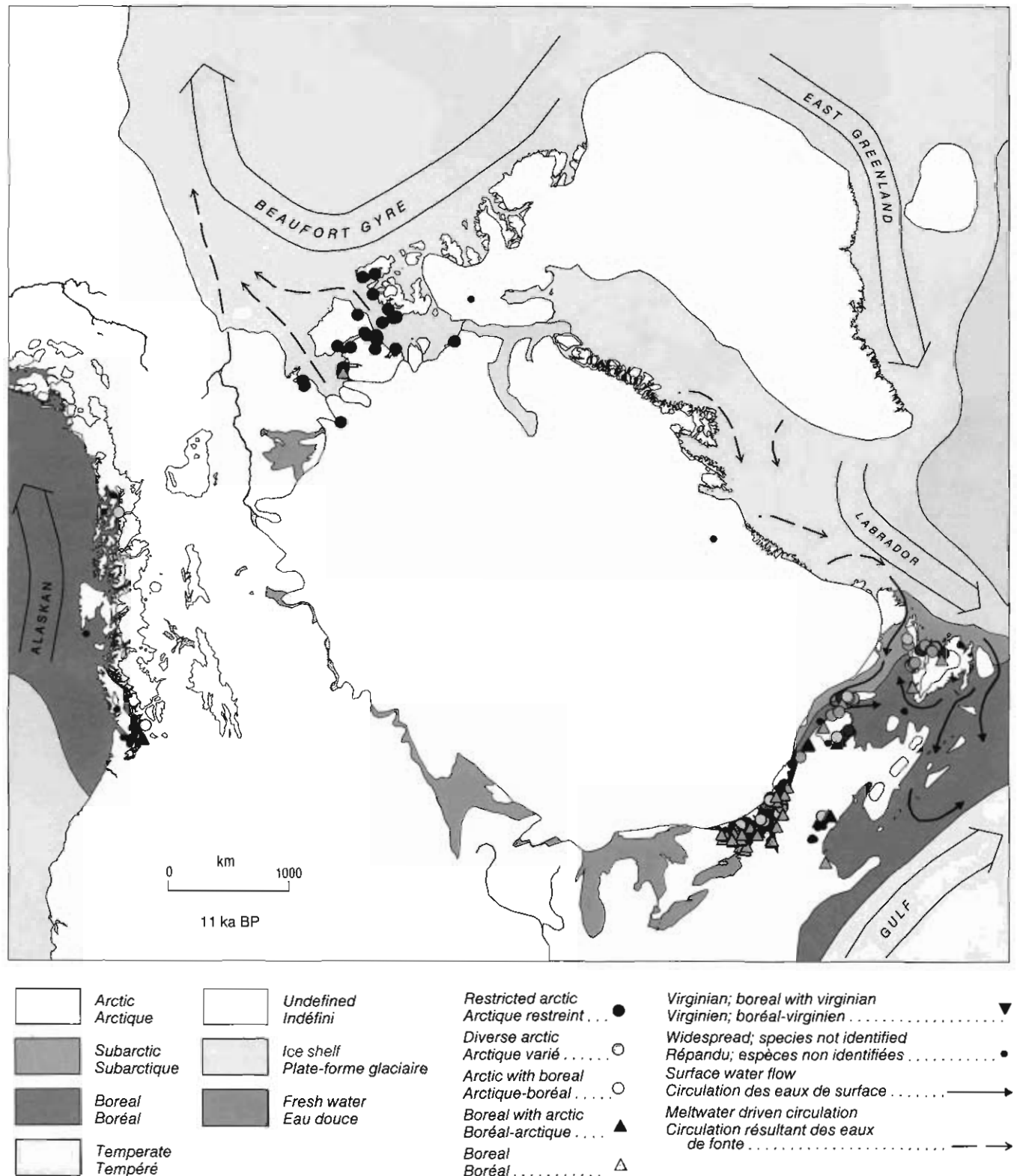


FIGURE 23. Molluscan faunistic zones at 11 ka BP. Plotted samples date 11-11.99 ka BP.

Zones fauniques des mollusques à 11 ka BP. Les âges des échantillons sont répartis de 11-11,99 ka BP.

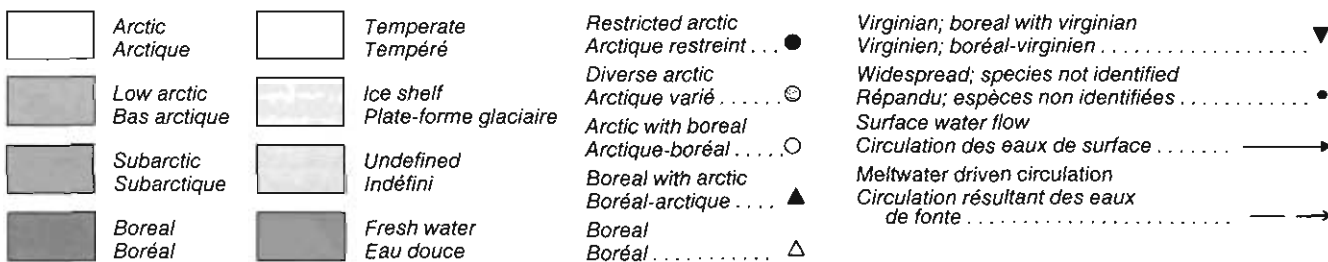
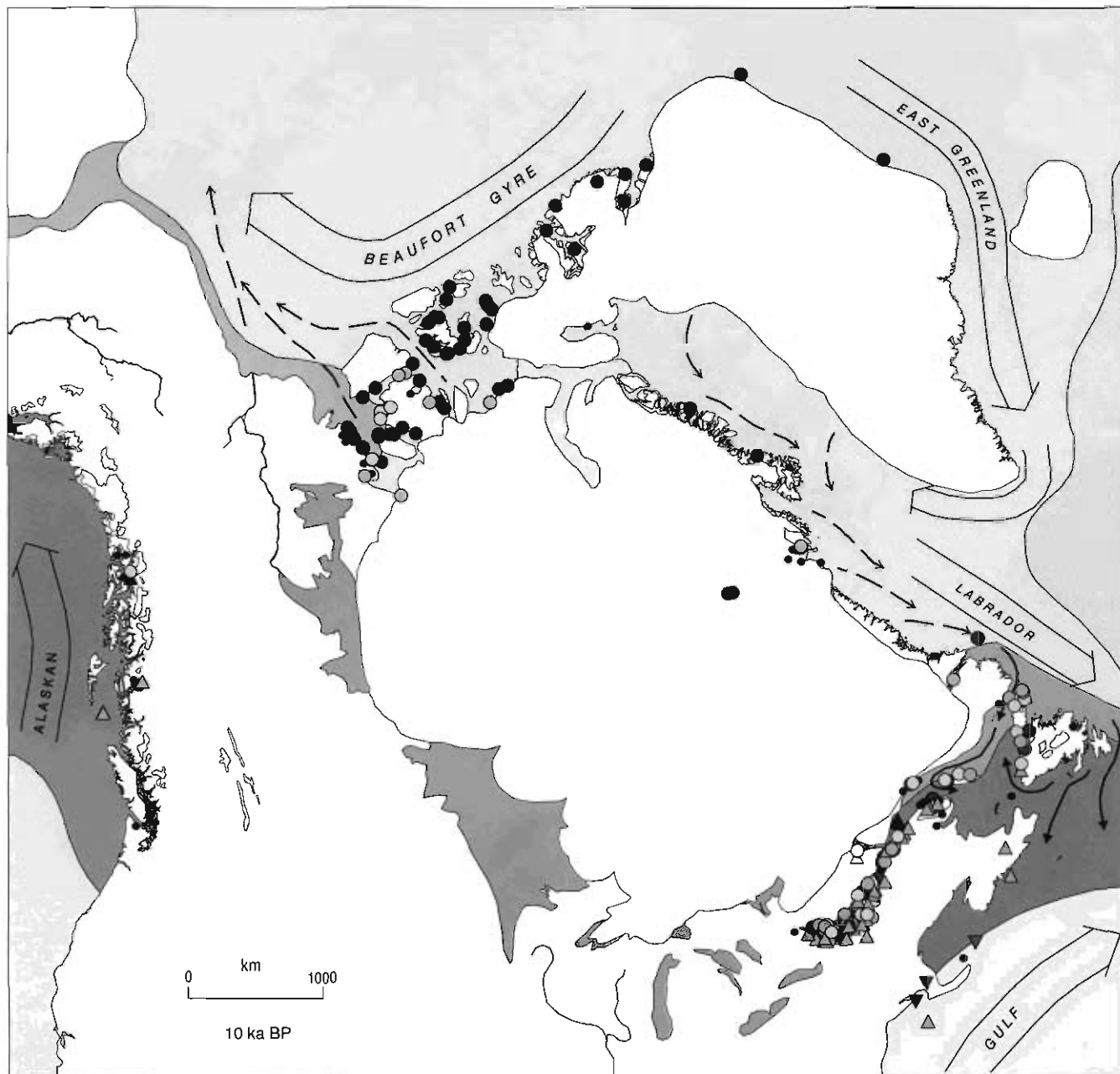


FIGURE 24. Molluscan faunistic zones at 10 ka BP. Plotted samples date 10-10.99 ka BP.

Zones fauniques des mollusques à 10 BP. Les âges des échantillons sont répartis de 10-10,99 ka BP.

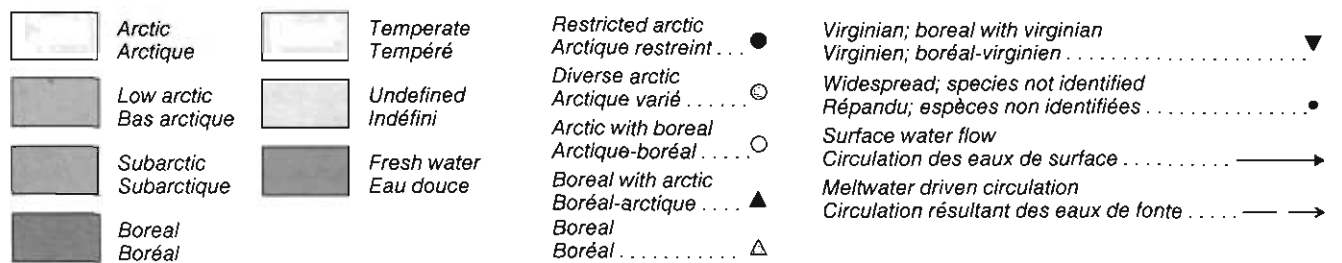
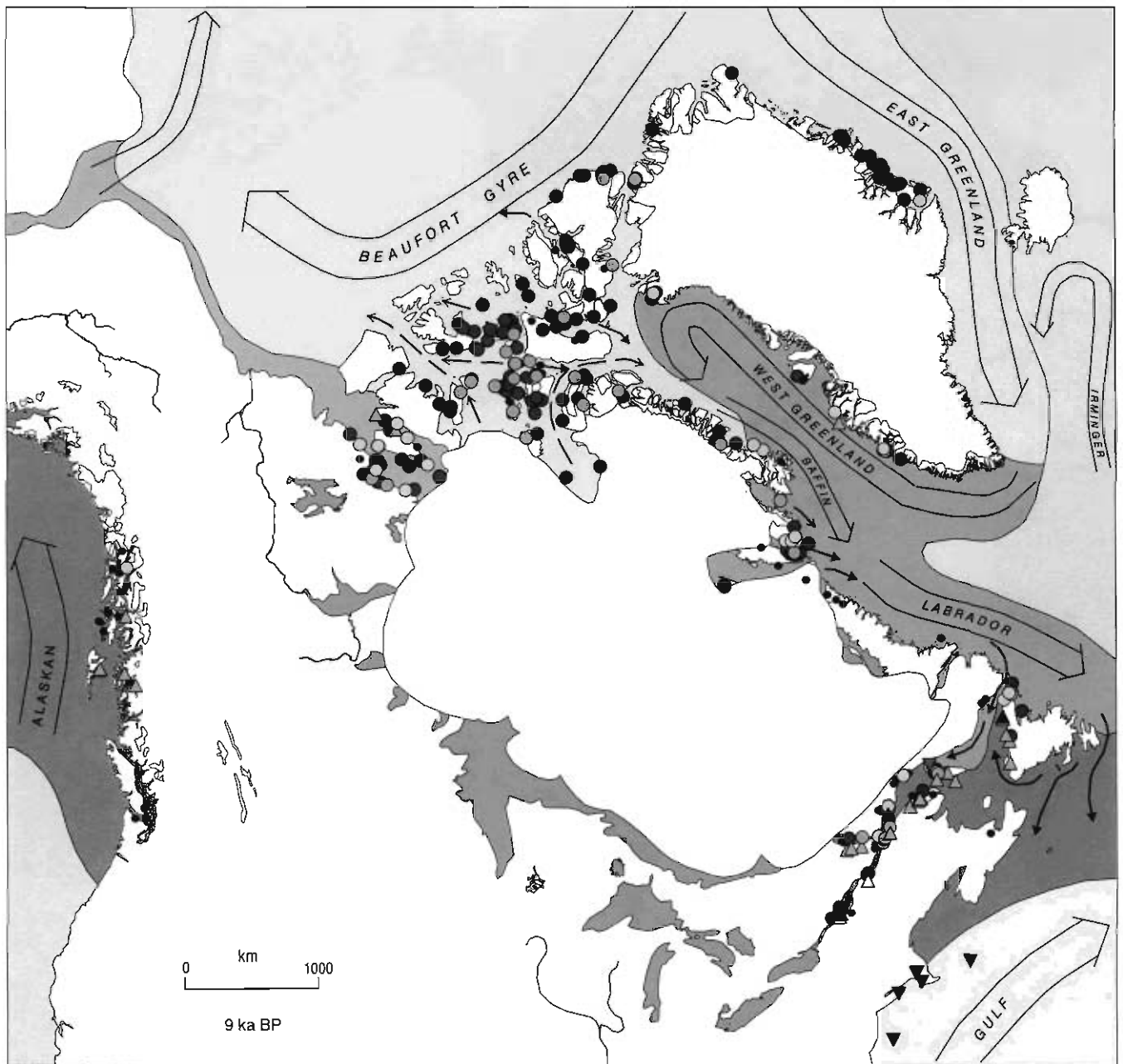
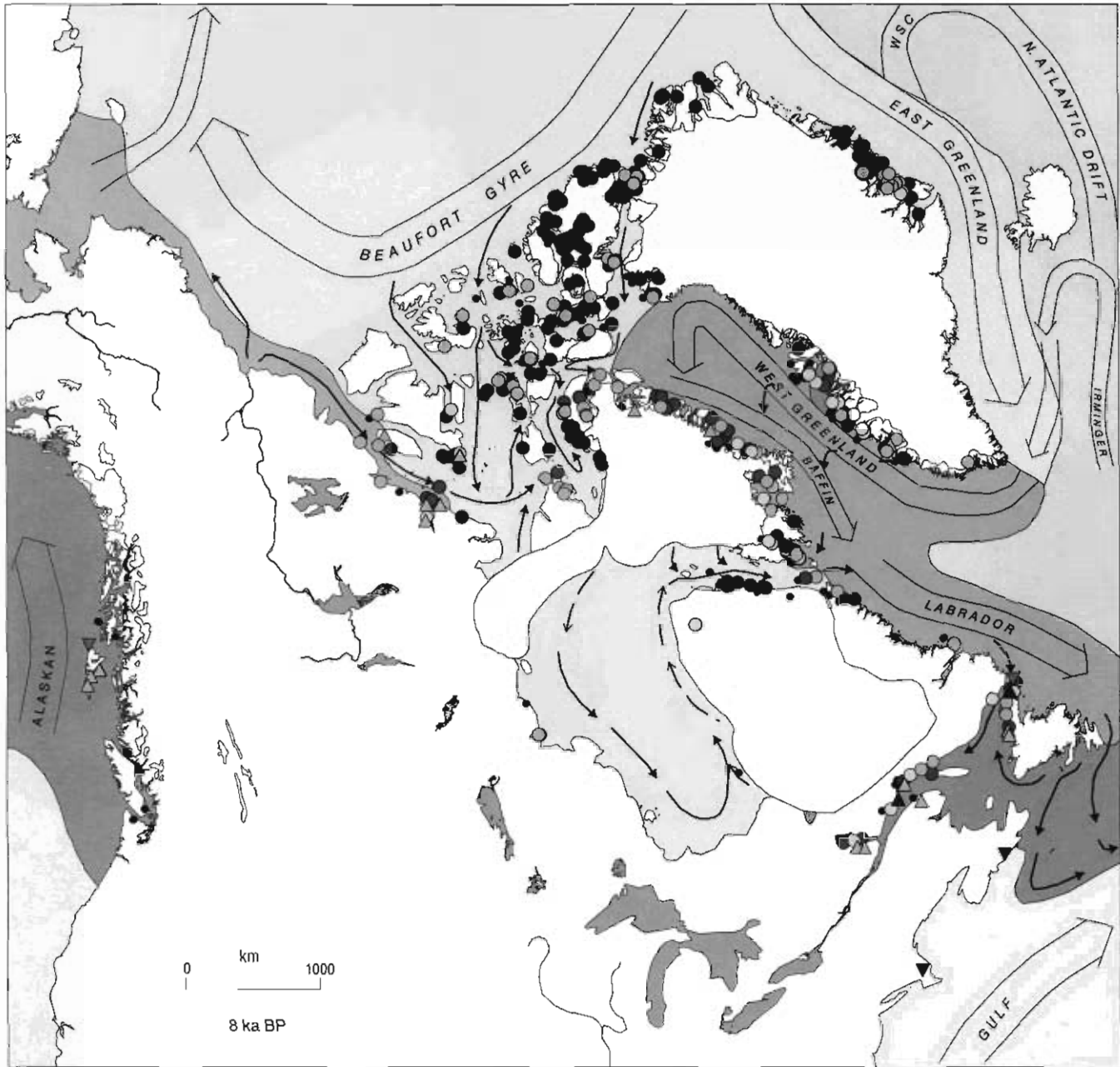


FIGURE 25. Molluscan faunistic zones at 9 ka BP. Plotted samples date 9-9.99 ka BP. Zones fauniques des mollusques à 9 ka BP. Les âges des échantillons sont répartis de 9-9,99 ka BP.



0 km 1000
8 ka BP

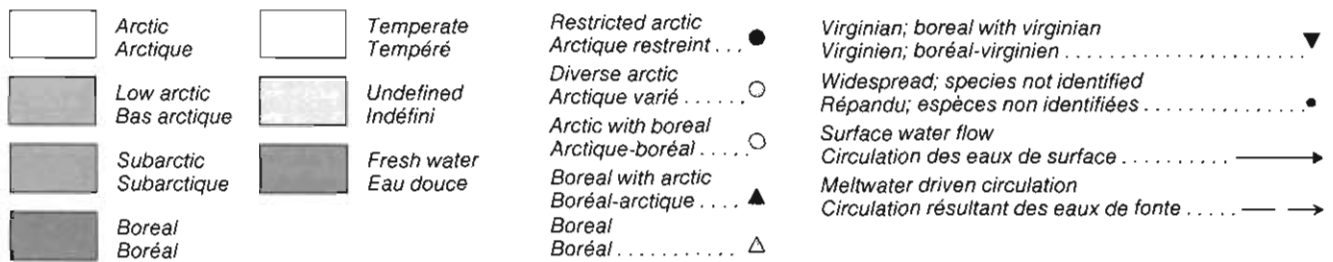


FIGURE 26. Molluscan faunistic zones at 8 ka BP. Plotted samples date 8-8.99 ka BP. Zones fauniques des mollusques à 8 ka BP. Les âges des échantillons sont répartis de 8-8,99 ka BP.

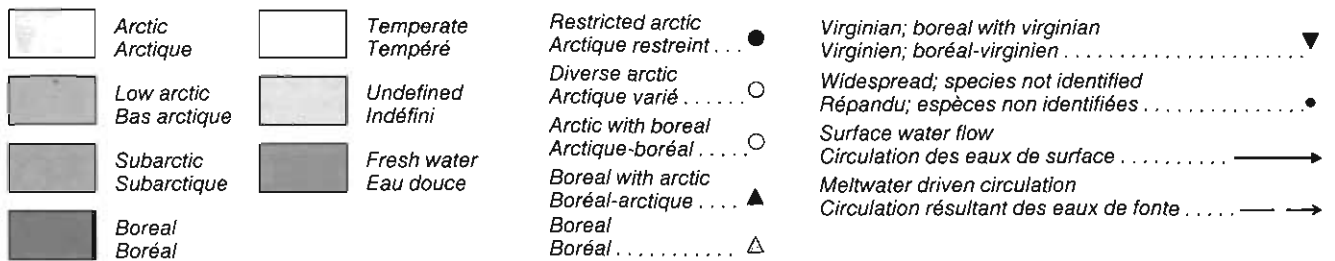
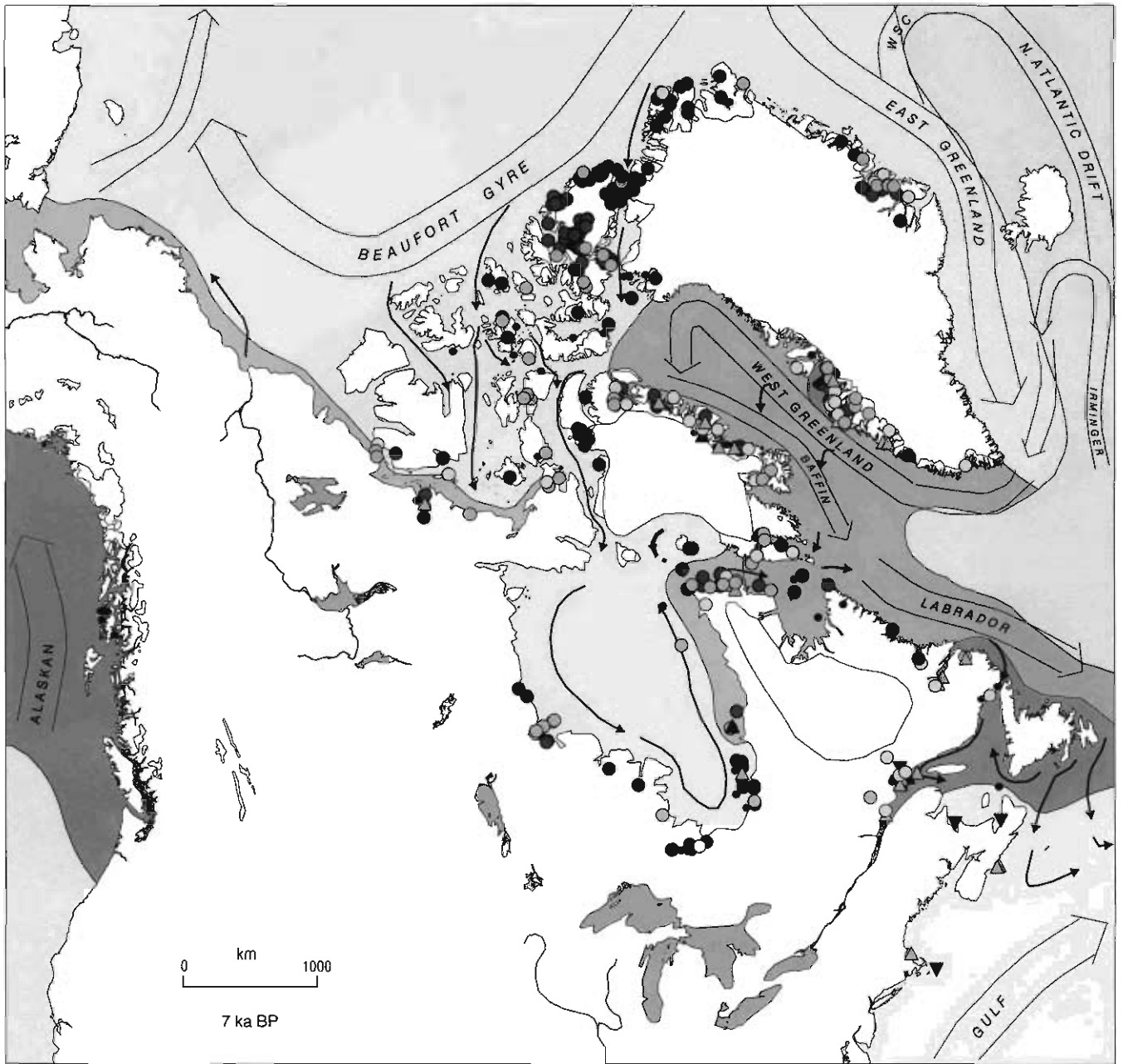


FIGURE 27. Molluscan faunistic zones at 7 ka BP. Plotted samples date 7-7.99 ka BP.

Zones fauniques des mollusques à 7 ka BP. Les âges des échantillons sont répartis de 7-7,99 ka BP.

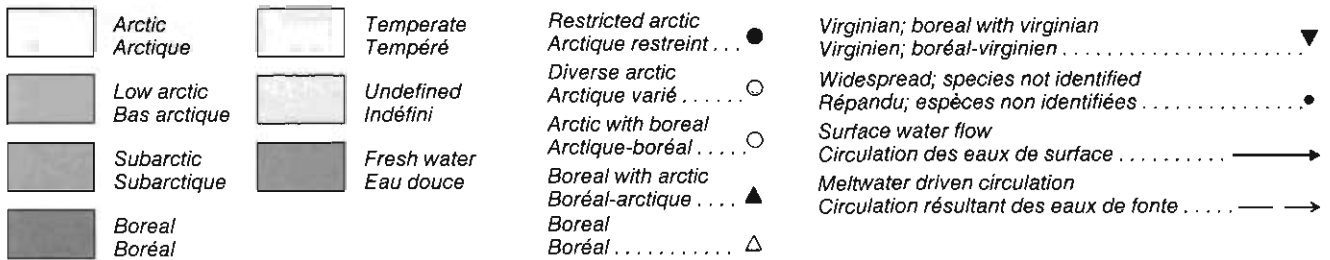


FIGURE 28. Molluscan faunistic zones at 6 ka BP. Plotted samples date 6-6.99 ka BP.

Zones fauniques des mollusques à 6 ka BP. Les âges des échantillons sont répartis de 6-6,99 ka BP.

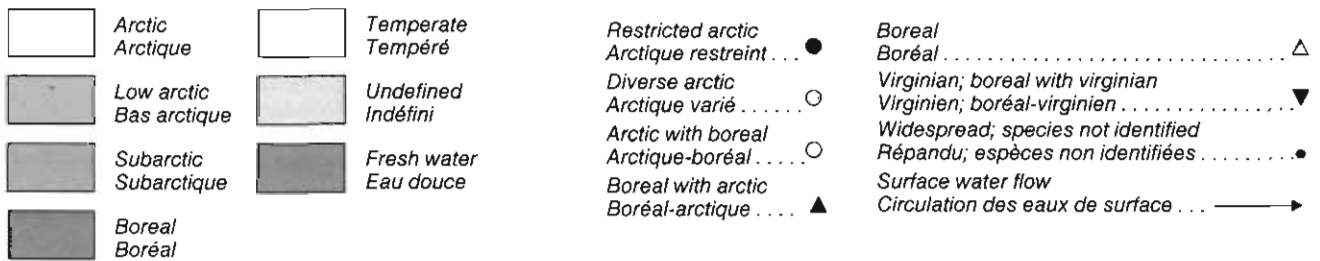
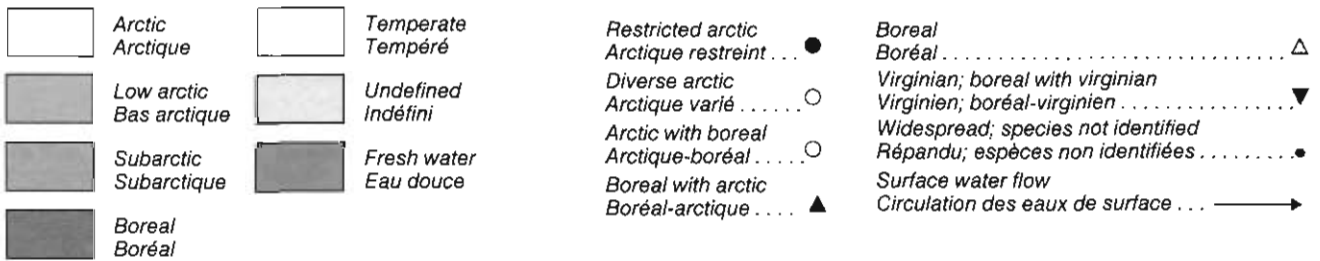


FIGURE 29. Molluscan faunistic zones at 5 ka BP. Plotted samples date 5-5.99 ka BP.

Zones fauniques des mollusques à 5 ka BP. Les âges des échantillons sont répartis de 5-5,99 ka BP.



FIGURES 30. Molluscan faunistic zones at 4 ka BP. Plotted samples date 4-4.99 ka BP.

Zones fauniques des mollusques à 4 ka BP. Les âges des échantillons sont répartis de 4-4,99 ka BP

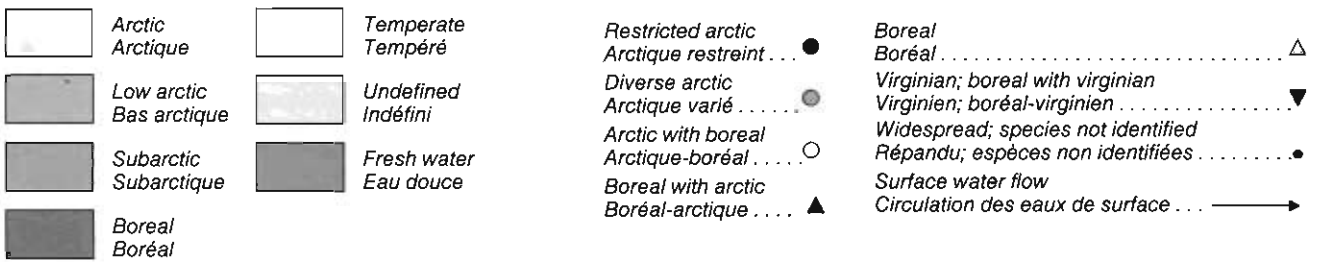
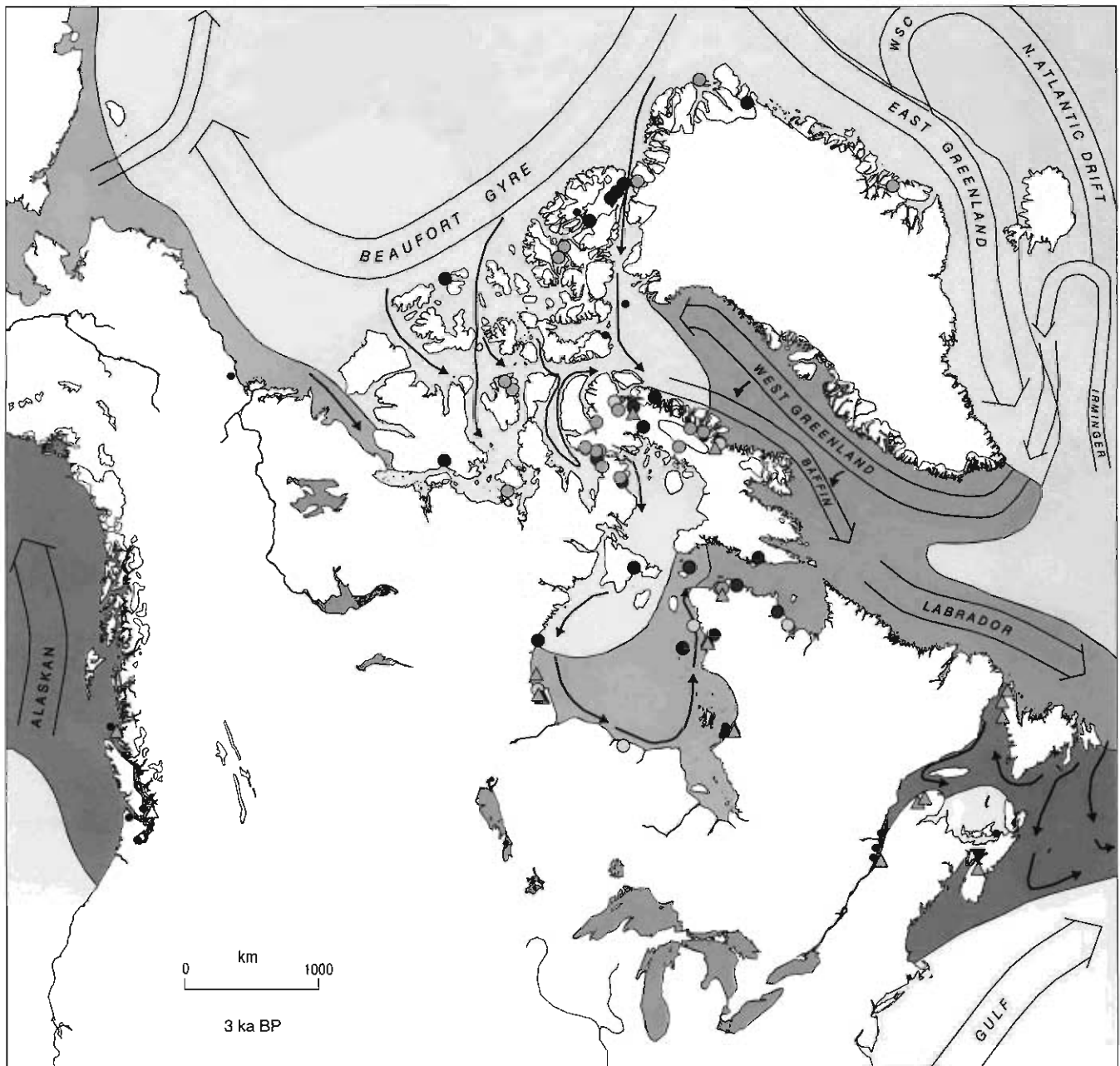


FIGURE 31. Molluscan faunistic zones at 3 ka BP. Plotted samples date 3-3.99 ka BP. Zones fauniques des mollusques à 3 ka BP. Les âges des échantillons sont répartis de 3-3,99 ka BP.

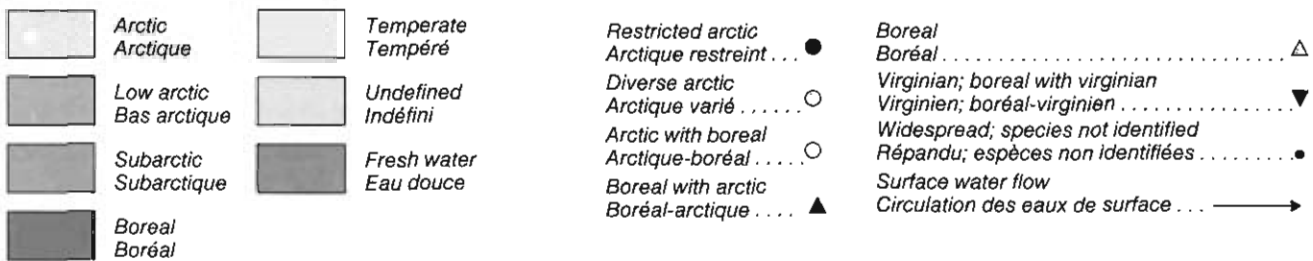
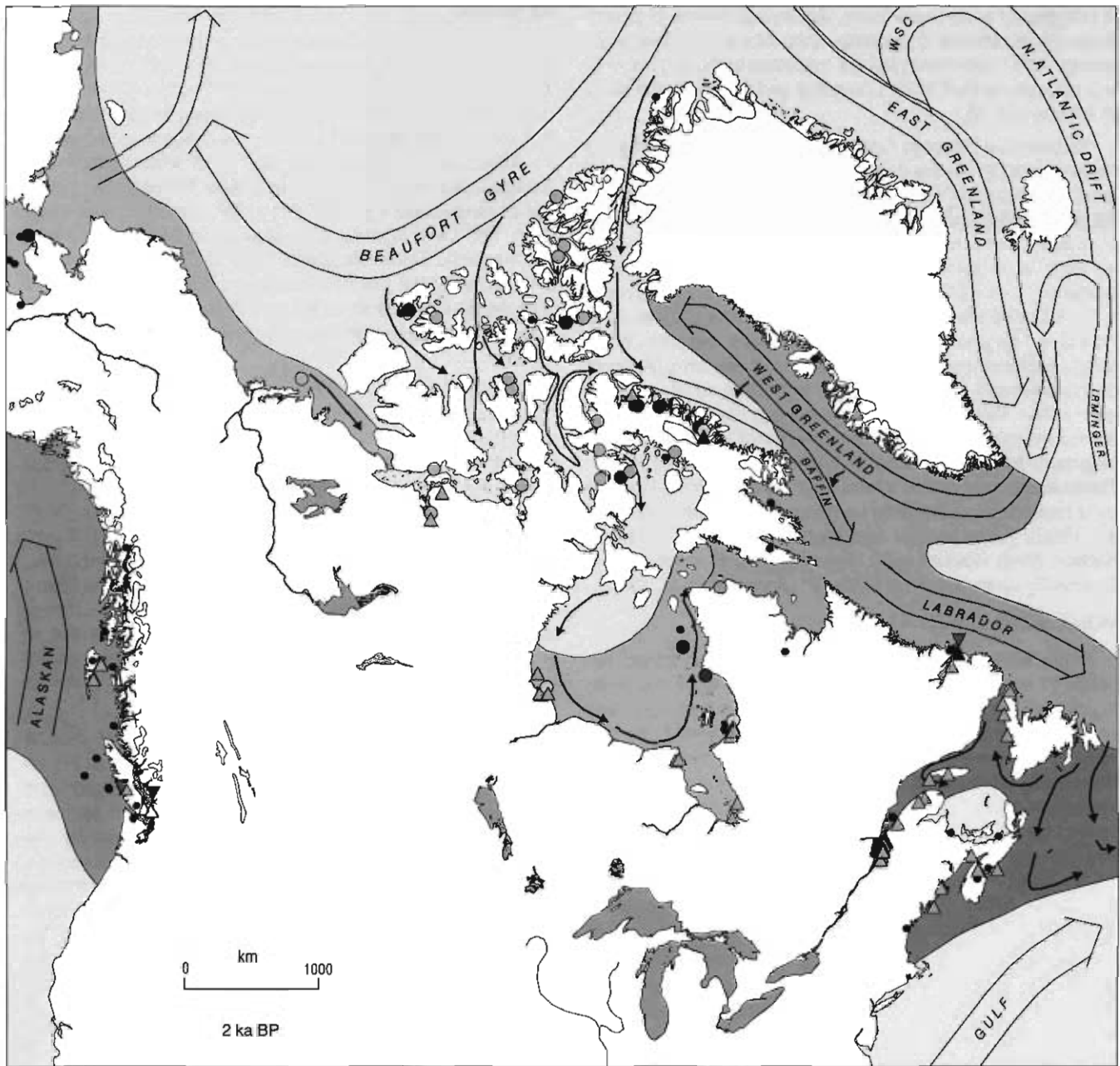


FIGURE 32. Molluscan faunistic zones at 2 ka BP. Plotted samples date 0-2.99 ka BP. Zones fauniques des mollusques à 2 ka BP. Les âges des échantillons sont répartis de 0-2,99 ka BP.

in non-diluted arctic fiords today (Aitken and Gilbert, in press). Subarctic conditions supporting arctic faunas with boreal elements and local boreal faunas prevailed along the ice contact zone of the Gulf of St. Lawrence and the northeast coast of Newfoundland.

Widespread molluscs first appear in the Arctic during this interval, most in the western arctic islands and adjacent mainland. As discussed in the section on regional mollusc assemblages, samples exclusively record *Hiatella arctica* with three exceptions; one each record *Portlandia arctica* and *Mya truncata*. More surprising is the record of the boreal *Macoma balthica* (11.4 ka BP) which at this time could only have come in from the Pacific or from the Atlantic via the Barents Sea. As this is 1 ka ahead of other Pacific arrivals and problematically early for submergence of Bering Strait, the sample should be re-examined to confirm that it is not the more common and similar *Macoma calcarea*. A sample placed well inside the ice margin in Hudson Strait consists of unidentified shell fragments from till on Akpatok Island dated at 11.97 ka BP. These apparently record a brief opening of the strait followed by a readvance of ice onto southern Baffin Island (Gray *et al.*, 1993). Foraminiferal and diatom records of cores off Hudson Strait indicate fairly high biological productivity and seasonally open water 12-11 ka BP (Andrews *et al.*, 1990).

MOLLUSCAN ZONES AT 10 ka BP

There were important changes in molluscan zones between 11 and 10 ka BP (Fig. 24). We discuss them in a south to north sequence¹. The first dated Virginian taxa appeared on the submerging New England shelf between 11 ka and 10 ka BP, where only boreal species were reported previously. Hence, the warming effect of the Gulf Stream extended farther north and coastward than before, perhaps simply because of progressive inundation of the outer shelf or perhaps because of enhanced warming during the summer insolation maximum of the late Pleistocene - early Holocene (Berger, 1978). The oyster (*Crassostrea virginica*) requires minimum summer temperatures of 20°C for spawning.

The faunal record of the outer Gulf of St. Lawrence is impoverished by 10 ka BP because of ongoing submergence. This precludes examination of the molluscan response to the Younger Dryas cooling recorded in pollen assemblages in the Maritimes (Mott *et al.*, 1986) and in foraminiferal assemblages in the central North Atlantic (Ruddiman, 1987). However, the western extension of the gulf, the Champlain Sea, has well-dated molluscan faunas. These can still be characterized as boreal, but a relatively larger proportion of samples record arctic faunas between 10.9 and 10 ka BP than before. This is surprising in light of the early concept of a *Hiatella arctica* phase succeeded by a *Mya arenaria* phase (Elson, 1969b). Yet a general cooling of the sea may be expected in light of

1. The two samples placed far inside the ice margin in Hudson Strait are regionally anomalous. One is a date on shell fragments from the till surface and may, therefore, be on shells of mixed ages. The other is one of several dates on a thin bed of shells in a delta that have yielded ages with a variance of about 2000 years that remains unexplained (Gray *et al.*, 1993).

the changing discharge into it from the west: from 11-10 ka BP, the entire proglacial lake sequence west to Lake Agassiz drained into the sea via Lake Ontario and the Ottawa Valley (Clayton and Moran, 1982; Teller and Clayton, 1983; Teller, 1985, 1987; Dyke and Prest, 1987; Teller, 1990; Rodrigues and Vilks, 1994). Before 11 ka BP, Lake Agassiz drained via the Mississippi River into the Gulf of Mexico. It had been thought that flow returned to the Gulf of Mexico after blockage of eastern outlets about 9.9 ka BP. However, it now appears that Lake Agassiz discharged northward at that time into the Arctic Ocean via glacial Lake McConnell (Fisher and Smith, 1995), that this flow continued until re-establishment of eastward drainage about 9.5 ka BP, and that meltwater flow never resumed down the Mississippi River (Marchitto and Wei, 1995).

Because the eastward diversion of Agassiz waters into the Champlain Sea correlates with the Younger Dryas cooling recorded in pollen records on both sides of the North Atlantic and with a 15° latitude southward shift of the marine polar front in the North Atlantic, the diversion has been invoked as the causal mechanism of the cooling (Broecker *et al.*, 1989). The Agassiz meltwater, in this view, produced a cold, "fresh" water lid on the North Atlantic which dampened thermohaline circulation (bottom water production in the northern North Atlantic) and consequently northward advection of subtropical surface waters. If the freshening effect was so strong in the open ocean, there should have been a strong response in the relatively small Champlain Sea itself, through which all the water passed.

The suggestion of a more "arctic" fauna at 10-11 than at 11-12 ka BP in the Champlain Sea (*cf.* Fig. 23 and 24) invites a closer comparison of data for pre-Younger Dryas and Younger Dryas intervals (Table IX). Both are well dated, with 75 and 94 samples, respectively, and with essentially the same suite of taxa. The boreal *Mya arenaria* increases strongly from the older interval to the Younger Dryas (as expected from Elson's biostratigraphy) whereas other boreal species, *Macoma balthica* and *Balanus hameri*, decrease. The largest change is the marked increase during the Younger Dryas in the proportion of samples reporting *Hiatella arctica*, especially those reporting that species only.

TABLE IX

Abundances of common marine invertebrates of the Champlain Sea as percentage presence in samples from the Younger Dryas cold interval and the preceding interval

Species	11-11.99 ka BP (n=75 samples)	10-10.99 ka BP (n=94 samples)
<i>Macoma balthica</i>	47.0	29.8
<i>Hiatella arctica</i> total	24.0	44.7
<i>Hiatella arctica</i> alone	6.7	22.3
<i>Balanus hameri</i>	22.7	11.8
<i>Portlandia arctica</i>	12.0	11.8
<i>Mytilus edulis</i>	6.7	8.5
<i>Mya arenaria</i>	2.7	18.1
<i>Mya truncata</i>	4.0	6.4
<i>Macoma calcarea</i>	1.3	7.4

These faunal changes are not likely artefacts of sampling, given the attention that Champlain Sea faunas have received. In that Rodrigues and Richard (1986) linked *M. balthica* and *B. hameri* in this sea to high salinity bottom waters, their decrease can be seen as compatible with Agassiz-induced freshening, although the former is euryhaline. Similarly, *M. arenaria* prefers brackish conditions (Wagner, 1959). *H. arctica* could tolerate both water mass cooling and seasonally changing salinities. Thus the faunal changes broadly suggested on Figure 24 and outlined more fully in Table IX are compatible with the history of discharge into the Champlain Sea although they are not necessarily diagnostic of it. However, Rodrigues and Vilks (1994) provided a different analysis of the effects of Agassiz discharge on the Champlain Sea and Gulf of St. Lawrence. They recognized freshening of the Champlain Sea, but only after 10.5 ka BP, and suggested that this could also be explained by shallowing as uplift progressed. Agassiz runoff through the Gulf of St. Lawrence during the Younger Dryas occurred during a broader interval (12.1-8.7 ka BP) of low salinity bottom waters there. The Agassiz outflow apparently did not mix with bottom water. In their assessment, Agassiz outflow did not trigger Younger Dryas cooling.

The Arctic faunal record by 10 ka BP is more widely distributed than previously. The restricted arctic assemblage still dominates on both Baffin Bay and Arctic Ocean sides. However, in the southwestern arctic islands, we define a low arctic molluscan zone due to the presence in several samples of *Mytilus edulis* and *Macoma balthica* and reportedly *Mya arenaria*. Although we regard the latter as dubious, the presence of the other species requires that Bering Strait was open, as discussed earlier, and that these waters were warmer than present despite meltwater effects (Andrews *et al.*, 1993), including the considerable discharges of lakes Agassiz and McConnell. Because there are no extra-regional currents to import warm water to this region (even with Bering Strait open), we infer greater seasonal warming than occurs today. This is not problematic in that a woodland existed north of present treeline in the Mackenzie Delta area by 11 ka BP and Northern Hemisphere summer insolation was at a maximum at 10 ka BP (Ritchie *et al.*, 1983; Ritchie, 1989).

The molluscan chronology of the Canadian Arctic places the opening of Bering Strait at 10.5-10.3 ka BP (dates corrected for reservoir age of 400 years). Submergence of the strait is not well dated directly and the molluscs may provide the best age control available. The deepest part of the sill is shallower than 50 m and Fairbanks' (1989) eustatic curve for Barbados would place the sea rising to that level about 9.5 ka BP. However, hydro-isostatic deformation imparts a variable eustatic sea level history to extra-glacial regions (Walcott, 1972; Tushingham and Peltier, 1991) which makes it unlikely that the Barbados curve would precisely apply to Bering Strait. Furthermore, it is improbable that thermophilous molluscs arrived in the western Canadian Arctic at 10.3 ka BP from the Atlantic via North Greenland without leaving any record of this passage. Therefore, we suggest they provide a minimum age on the opening of Bering Strait. This opening is important to the history of the Arctic Ocean because it marks the first postglacial inflow of Pacific water to the head of the

Transpolar Drift and contribution to formation of Arctic Ocean surface water as today.

Although *M. edulis* remains in this area today, Lubinsky (1980) includes the southwest Canadian Arctic in her High Arctic Faunistic Zone (region III). However, the region bears strong similarity to the Low Arctic Faunistic Zone in its greater seasonal warming of littoral waters due to continental runoff and to higher summer temperatures as evidenced by the proximity of the region to treeline. In the Atlantic the northern limit of *M. edulis* marks the boundary between arctic and subarctic, and in Hudson Bay between high arctic and low arctic. For consistency in interpreting the fossil record, we exclude *Mytilus*-bearing regions from the high arctic zone.

The only diverse arctic assemblages recorded for this interval in the western Arctic occur in the belt adjoining the low arctic zone. This suggests a coherent spatial pattern of high arctic species diversification, the equivalent of the temporal diversification suggested by the regional arctic records. If so, the postglacial arctic diversification wave, including the spread of *M. truncata*, may have originated in the Pacific. Elsewhere in arctic Canada and Greenland, only *Hiatella arctica* and *Mya truncata* occur, with the former being strongly dominant. Feyling-Hanssen and Olsson (1960) reported that raised marine terraces of Billefjorden, Spitsbergen older than 10 ka BP likewise contain *H. arctica* and *M. truncata* only. Thus, the restricted arctic assemblage may have dominated much of the Arctic Ocean until about 10 ka BP.

Because of interest in the Younger Dryas cool interval, particularly its hemispheric or even global occurrence, we have examined all the molluscan data for this interval. We recognize credible evidence of freshening and probably cooling in the Champlain Sea, a strong suggestion of warming off New England in the advance of Virginian taxa, and clear evidence of warmer than present marine conditions along the western arctic mainland despite its ice-proximal setting. This is not supportive of a hemispheric Younger Dryas event. Our interpretations clearly do not challenge the proposal of a meltwater trigger via the Champlain Sea for the Younger Dryas cooling. However, Andrews *et al.* (1990) regarded that as an insufficient mechanism. They recognized diatom- and foraminifera-barren zones of Younger Dryas age in cores off Hudson Strait and postulated a major correlative glacial readvance into seas with either an ice shelf or with summer-persistent sea ice. They speculated, along with Miller and Kaufman (1990), that enhanced calving of ice bergs off Hudson Strait during the glacial advance triggered the Younger Dryas cooling. However, that cooling does not then explain the Laurentide advance (11.5-10.5 ka BP) which may invoke cooling by another mechanism.

MOLLUSCAN ZONES AT 9 ka BP

Important changes in oceanographic conditions occurred between 10 and 9 ka BP, mainly in arctic areas (Fig. 25). At 9 ka BP, warm temperate (Virginian) faunas appear to have held their previous distribution off New England. However, the sparse record suggests a farther northward advance, as might be expected from continuing submergence of the continental shelf.

Arctic elements, mostly *Hiattella arctica*, occurred in the late phase Champlain Sea. This may be due to continued salinity and temperature effects of discharge from glacial lakes. *Portlandia arctica*, which today ranges south to Hamilton Inlet, was present in proglacial Lac Saint-Jean basin. Other than these local effects, the Gulf of St. Lawrence faunal record appears similar to today and probably warmer than at 10 ka BP, perhaps due to continued ice sheet retreat inland. The local faunas of the west coast of Newfoundland and the St. Lawrence estuary present a more boreal aspect than previously. No range extensions are involved except for an oyster *Crassostrea virginica* reported from the north shore of the gulf. But this shell is not directly dated and occurs in odd association with the dated *Mya truncata* (UQ-1375).

The eastern arctic record is highly informative by 9 ka BP. Funder and Weidick (1991) showed that the extension of *Mytilus edulis* and *Chlamys islandica* to the Thule area of northwest Greenland requires that the West Greenland Current was established by 9.1 ka BP. The occurrence of *C. islandica* in southwest Greenland at 9.4 ka BP indicates that the current extended at least into Davis Strait by then. *M. edulis* also extended farther up the Baffin coast by 9 ka BP than it does today.

A warm West Greenland Current requires presence of the Irminger Current, the branch of the North Atlantic Drift that provides warm water to it (Fig. 25). The Irminger Current probably started to influence the northeastern Labrador Sea about 10 ka BP when warm-water dinoflagellates increased (De Vernal and Hillaire-Marcel, 1987). Similarly establishment of a suite of boreal molluscs in Svalbard after 10 ka BP, including *M. edulis* and *C. islandica*, (Feyling-Hanssen and Olssen, 1960) signals establishment of the North Atlantic Drift and the warm West Spitsbergen Current. The oldest radiocarbon dates on *M. edulis* from Svalbard are 9375 ± 80 BP (DIC-3076; Forman, 1990) and 9360 ± 110 BP (T-3098; Salvigsen and Österholm, 1982); a sample containing *C. islandica* dated 9535 ± 90 BP (DIC-3055; Forman, 1990). These dates suggest that these animals entered central East Greenland from Svalbard, as inferred by Hjort and Funder (1974). West Greenland and the eastern Canadian Arctic may have been settled by boreal mollusc larvae arriving broadly from Spitsbergen and Iceland via the West Spitsbergen, Irminger, and West Greenland currents. Although both *M. edulis* and *C. islandica* were present in the Gulf of St. Lawrence well before 10 ka BP, the Labrador Current would have hampered northward dispersion.

A southward flow along the Baffin Island shore, a Baffin Current, must also have formed as the West Greenland Current became established. But the chilling effect of this current along the north coast of Cumberland Peninsula was less severe than it is today. It possibly was mitigated by greater admixture of water from the West Greenland Current or greater seasonal warming of the littoral zone during a longer summer ice-free period (Fig. 25). Melt rates on the Devon and Agassiz ice caps in the Canadian high arctic were at a maximum in the early Holocene (Koerner, 1989; Koerner and Fisher, 1990; Fisher *et al.*, 1995) and the greater summer heating implied can probably explain the range extension

(relative to present) of *Astarte striata* and *M. edulis* along Cumberland Peninsula. Dinoflagellate and foraminiferal records from southern Baffin Bay also indicate warmer conditions, possibly because of little Arctic water flow into northern Baffin Bay to form Baffin Bay Bottom Water (Aksu and Mudie, 1985).

Because eastern Baffin Island has an important record of molluscan range extensions and retractions, we summarize regional oceanographic variability at this point. A number of factors can influence the temperature of coastal waters along eastern Baffin Island: (1) the thickness of the cold, low-salinity, surface water flow in the Baffin Current, largely derived now from outflow of surface water from the Arctic Ocean, (2) the sea-ice load of that current, (3) the relative contribution of warm water from the West Greenland Current to the inner Baffin shelf and its depth of flow, and (4) the relative contribution of warm bottom water of Atlantic origin flowing out at depth from the Arctic Ocean via the Queen Elizabeth Islands. Williams *et al.* (1995) pointed out that postglacial uplift of the Queen Elizabeth Islands has led to a steadily diminishing flow of deep Atlantic water from the Arctic Ocean into Baffin Bay. The inflow of Pacific water through Bering Strait would also have affected the character of outflowing Arctic Ocean water in the upper 200 m. The sea-ice load carried by the Baffin Current is dictated partly by the pattern of summer ice clearance in the arctic islands.

Dyke and Morris (1990) and Dyke *et al.* (in review a, b) concluded for several reasons that surface water flow from the Arctic Ocean to Baffin Bay started at 8.6-8.5 ka BP. It was not until then that driftwood was carried into the Canadian Arctic Islands from the Arctic Ocean. Before then driftwood entry was prevented in spite of widespread bowhead whale penetration. Furthermore, driftwood was arriving at Svalbard via the Arctic Ocean before 8.5 ka BP. They concluded that a meltwater-driven surface water outflow from the islands exported sea ice, allowing access by whales, while deflecting driftwood before 8.5 ka BP.

Considering these constraints and the factors listed above, we can suggest some likely oceanographic conditions, in addition to greater solar heating, that could have made coastal waters of western Baffin Bay warmer than present during the early Holocene. The Baffin Current probably comprised only a thin meltwater-derived surface layer that flowed above warmer water derived from the West Greenland Current, from Atlantic water exiting the Arctic Ocean, or from both. The meltwater-derived layer was sufficiently thin that the warmer water below was able to affect the nearshore zone, thus its molluscs. The mollusc record seems at odds with William's (1990) conclusion of severe summer sea-ice conditions in western Baffin Bay during the early Holocene. However, this may arise in part from uncertain core chronologies.

Conditions in the western Arctic at 9 ka were similar to those at 10 ka BP. The low arctic zone was dominated by restricted and diverse arctic local faunas but *Mytilus edulis* occurred in its maximum postglacial abundance, even in the periglacial zone. Thus, coastal waters were probably warmer than during the preceding interval and than at present.

Molluscs were very widespread throughout the Canadian Arctic Islands and along North and East Greenland by 9 ka BP. *Hiatella arctica* was regionally dominant, *Mya truncata* was common, and diverse arctic assemblages were widespread, though perhaps not in the Sverdrup Islands region. That region apparently never cleared of sea ice in the summers sufficiently to allow reliable entry of bowhead whales at any time during the Holocene (Dyke *et al.*, in review b) and panarctic molluscs have a restricted distribution there today (Lubinsky, 1980).

MOLLUSCAN ZONES AT 8 ka BP

Molluscan zones shifted significantly between 9 and 8 ka BP (Fig. 26). These shifts can not be explained simply by deglaciation so we seek oceanographic explanations. The largest and best documented changes were in the Arctic but zones also appear to have shifted along the Atlantic. We argue in this section that 8.5 ka BP was a time of profound change in polar regions with repercussions in middle latitudes.

The record of shifting zones off the Atlantic Provinces is tentative but suggests a further northward expansion of temperate molluscs by 8 ka BP. The gastropod *Polinices heros* is recorded off Nova Scotia at 8.83 ka BP, the earliest Virginian recorded so far north. However, it ranges into southwestern Gulf of St. Lawrence today and thus does not represent a range extension with respect to present. A probable range extension is recorded by the pelecypod *Mysella planulata* in a sample dating 8.28 ka BP from the north shore of the St. Lawrence estuary (Bigras et Dubois, 1987). It ranges today from southwestern Gulf of St. Lawrence to Texas. A larger range extension is recorded by *Spisula solidissima* in a sample from St. Anthony, northernmost Newfoundland dated at 8.17 ka BP (Robertson, 1987). This bivalve today ranges from South Carolina to Nova Scotia. Its occurrence at a site now strongly affected by the Labrador Current is highly significant though additional records of this extension should be sought.

Bearing in mind that the regional record for this interval is difficult to sample due to submergence, we take the foregoing as evidence that the temperate zone by 8 ka BP had expanded well up the shallowly submerged Scotian Shelf; the boreal environment of the Gulf of St. Lawrence had expanded and warmed enough for entry of a few temperate taxa. This suggests that the cooling influence of the Labrador Current on the north shore of the gulf was lessened. We can reasonably invoke diminished inflow of water from the Labrador Current due to shallowing of the Strait of Belle Isle, increased inflow and upwelling of Atlantic bottom water into the deepening southern gulf (Grant, 1989), or warming of the Labrador Current itself as suggested by the arctic data.

In order to explore possible feedbacks from region to region, we next discuss the eastern arctic molluscan record in a down-current sequence starting in East Greenland. Two thermophiles appeared in East Greenland by 8 ka BP, one extinct in the area now. However, the regional faunal record is so dominantly arctic that at 8 ka BP perhaps the subarctic faunas were able to establish only in restricted enclaves. Yet initial colonization by *C. islandica* at 8.58 ka BP is important. Boreal molluscs now extend to highest latitudes in the east-

ern North Atlantic due to warming by the North Atlantic Drift (Fig. 26). Some of these had reached Spitsbergen by 9.4 ka BP (Forman, 1990). Thus a reasonable mechanism for these animals reaching central East Greenland, well north of Iceland and the Irminger Current, is transport of their larvae in the warm West Spitsbergen Current (Hjort and Funder, 1974). This requires that the West Spitsbergen Current had a greater influence on coastal northeast Greenland than previously and than it does today. Occupation of central East Greenland by *Mytilus edulis* indicates that this condition lasted till 5.5 ka BP (Hjort and Funder, 1974). In that the West Spitsbergen Current along East Greenland today flows outside of and below the East Greenland Current at about 150 m depth, the East Greenland Current may formerly have been thinner.

Increased influence of the West Spitsbergen Current on East Greenland may indicate its strengthening or a weakening flow of the Transpolar Drift to the East Greenland Current. A stronger West Spitsbergen Current could arise from generally increased transport of North Atlantic Drift waters. Abrupt nanofossil changes in a core off south Greenland are thought to indicate strengthening of the Irminger Current and North Atlantic Drift at 8.4 ka BP (Rahman and De Vernal, 1994). However, the Transpolar Drift may have shifted at the same time. Because the Transpolar Drift crosses the central Arctic Ocean and approaches the apex of northeast Greenland, a small lateral shift can divert much of it into the Beaufort Gyre, on the one hand, or into the East Greenland Current, on the other. Dyke *et al.* (in review a) suggested that shifts of the Transpolar Drift, which carries most driftwood across the Arctic Ocean, account for changing patterns of wood delivery to the Canadian Arctic and Svalbard. When the distal Transpolar Drift takes a more westward route both the East and West Greenland currents, and possibly the Baffin and Labrador currents will be warmer. The widespread onset of driftwood stranding in the Canadian Arctic Archipelago at 8.6-8.5 ka BP correlates with the initial arrival of thermophilous molluscs in East Greenland and may have a common cause.

Another, more remote, change at about 8.5 ka BP may have profoundly affected the Transpolar Drift and systems down current. Until about 8.5 ka BP much of the western Laurentide Ice Sheet discharged meltwater into the Arctic Ocean via the Mackenzie River. At about 8.5 ka BP, the ice margin withdrew from that watershed (Dyke and Prest, 1987). Mackenzie discharge apparently now affects sea ice and related conditions in the region from the Beaufort Sea to the Labrador Sea (Mysak and Manak, 1989; Mysak *et al.*, 1990; Mysak and Power, 1991; 1992) so it probably also affected conditions in the past. Seasons of heavy discharge lead to increased sea ice production on the Beaufort Shelf because freshened surface water freezes at a higher temperature than shelf water. High Mackenzie discharges today result in increased sea ice discharge through Fram Strait 3-5 years later. This produces "Great Ice and Salinity Anomalies" (GISAs) in the Greenland-Iceland Sea that migrate through the Labrador Sea south to Newfoundland. As the Mackenzie switched from a glacial to a nonglacial river at 8.5 ka BP reduction of discharge must have been orders of magnitude greater than any historic fluctuation. Hence, at 8.5 ka BP there must have

been a great reduction in sea ice discharge through Fram Strait. This alone could have led to an increase in temperatures of currents downstream to the North Atlantic Drift.

Mackenzie-regulated ice discharge through Fram Strait has further feedbacks on climate (Mysak and Power, 1992). Great ice discharge into the Greenland-Iceland Sea freshens surface water on melting. This reduces convective overturning of water, heat transfer from the water, cyclogenesis in the North Atlantic, and precipitation in polar regions including the Canadian Arctic Islands. These feedbacks in the modern climate system strongly suggest that retreat of the Laurentide ice margin from the Mackenzie watershed, complemented by a reduction in glacial meltwater entering the adjacent archipelago (Andrews *et al.*, 1993), could have triggered a general change in North Atlantic climate. We postulate a "Truly Great Ice and Salinity Anomaly" before 8.5 ka BP followed by the modern regime when the Greenland-Iceland Sea became warmer, more saline, and more convective and cyclogenesis became stronger and more frequent.

By 8 ka BP subarctic West Greenland was populated by *Chlamys islandica* and *Mytilus edulis*. Funder and Weidick (1991) also report the occurrence in part of southwest Greenland at this time of more thermophilous *Panopea norvegica* and *Arctica islandica*, now extinct there. The area of occurrence is related to regional submarine topography. The West Greenland Current carries both cold water from the East Greenland Current (running on the coastal side in southernmost West Greenland; Funder and Weidick, 1991) and warm water from the Irminger Current (Fig. 26). Shallow banks at 65°N now deflect the colder water and its sea-ice load westward into Davis Strait creating warmer conditions over the banks than farther south. The fossil mollusc record suggests that this pattern of separation of water masses by the banks started by 8.4 ka BP, probably as postglacial sea level change established the critical water depths (Funder and Weidick, 1991). Thus, transport of cold water northward into Baffin Bay then decreased further by this effect.

Boreal molluscs extended along the entire east coast of Baffin Island by 8.2 ka BP, almost 1000 km north of their present limit on that coast. The record is not detailed enough to reveal whether these animals extended their ranges northward between 9 and 8 ka BP or settled the area from Greenland. Because of their zoogeographic significance, any collection containing these range-extension indicators is almost certain to be radiocarbon dated. Thus, they are not under-represented in the record. These boreal species may never have been able to exploit more than restricted niches along the northeast Baffin coast so the portrayal of general subarctic conditions in all of Baffin Bay at 8 ka BP (Fig. 26) is perhaps too broad. Nevertheless, coastal marine conditions were certainly warmer than today or than they were at 9 ka BP.

Conditions inferred for the Canadian Arctic Archipelago at 8 ka BP (Fig. 26; Dyke *et al.*, in review b) may, at first glance, appear contradictory of those in Baffin Bay. By 8 ka BP flow through the archipelago of surface water from the Arctic Ocean was established, replacing the previous meltwater-dominated outflow. A consequence of this change was that the inter-island channels became congested with sea ice

which between 8 ka and 6 ka BP cleared only minimally in the summers, severely restricting the range of the bowhead whale. Although these "bad-ice summers" in the archipelago may appear to contradict warm conditions in Baffin Bay, we suggest that retention of sea ice in the archipelago would have reduced the ice load of the Baffin and Labrador currents. This would have allowed longer ice-free summers from eastern Baffin Island to southeastern Newfoundland and diminished chilling of the Gulf of St. Lawrence and the Gulf Stream. Furthermore, as pointed out by Williams *et al.* (1995), the outflow of warm bottom water of Atlantic origin through the archipelago was then larger than now, allowing it to more strongly affect the then-deeper Baffin Shelf and fiords.

The mollusc record of the archipelago at 8 ka BP was similar to that at 9 ka. Both restricted and diverse arctic assemblages were widespread, the latter perhaps more than before. *Mytilus edulis* extended along the mainland coast to Bathurst Inlet, defining a shallow coastal zone of enhanced solar warming as today. The record of *Mya arenaria* from northeast Victoria Island is dubious as is perhaps that of *Macoma balthica* farther south.

Just formed and expanding, Hudson Bay (Tyrrell Sea) was probably fully arctic due to a large meltwater and ice berg flux. An occurrence of *Mytilus edulis* along with *Hiattella arctica* dating 8.04 ka BP (UQ-761) from the northeastern part of the bay is plotted inside the ice margin (Fig. 26). Data from the Ottawa Islands suggest that the *Mytilus* site was not deglaciated so early (Andrews and Falconer, 1969), and attempts to replicate the date from that site have failed (cf GSC-4332).

MOLLUSCAN ZONES AT 7 ka BP

The most prominent change in molluscan zones between 8 and 7 ka BP (Fig. 27) was a northward expansion of the temperate mollusc zone. The earliest records of the oyster *Crassostrea virginica* in the Gulf of St. Lawrence date just before 7 ka BP. Its apparent absence earlier may be due to the near intractability of the submerged molluscan record; the earlier occurrence of *Spisula solidissima* at St. Anthony (8.17 ka) may better indicate expansion of warm-temperate fauna into the gulf. Nevertheless, by 7 ka BP at least the southwestern part of the gulf hosted warm-temperate fauna, likely in broad shallow waters that heated to >20°C.

Expansion of the temperate zone into the gulf, although still meagrely recorded, is a pivotal event in explaining modern molluscan distributions (Bousfield and Thomas, 1975). Warm-water taxa comprise 35% of marine invertebrate species in the southwestern Gulf of St. Lawrence. They probably settled the area during the regional marine thermal optimum but are now separated from the main range to the south by a cold-water gap of 1300 km. Bousfield and Thomas (1975), without reference to the mollusc fossil record, placed the maximum range extension of warm-temperate fauna in the gulf at about 7 ka BP based on the hypsithermal pollen record. Current data do not refute this, but that date should be considered a minimum. They attributed the subsequent breach of the temperate zone to growing tidal amplitude in the Gulf of Maine - Bay of Fundy, brought on by submergence.

The more vigorous tides destroyed summer thermal stratification of nearshore waters and eliminated the warm-water faunas. The Gulf of Maine was then re-invaded by its present boreal fauna.

The mollusc assemblages in Hudson Bay at 7 ka BP resembled those of the High Arctic, dominated by *Hiattella arctica* as Wagner (1969) proposed. Throughout the interval 8-7 ka BP Hudson Bay would have been strongly affected by melt-water and ice berg production, particularly from ice over Foxe Basin. A sparse record of boreal-subarctic species along the east coast and in western Hudson Strait indicates an incipient low arctic zone there. The low arctic faunal zone of the western Arctic possibly extended as a coastal strip as far as Boothia Peninsula. However, this relies on a single report of *Mytilus edulis* from there and on another from Bathurst Inlet (Fig. 27). Two additional reports of the full-boreal *Mya arenaria* are dubious.

MOLLUSCAN ZONES AT 6 ka BP

Faunal zones at 6 ka BP (Fig. 28) were not greatly different from those earlier. The most important changes involved the following: probable disjunction of the temperate zone in the Gulf of St. Lawrence; a well-documented expansion and diversification of the boreal-subarctic molluscan component in Hudson Bay indicating evolution toward present low arctic conditions; and expansion of a low arctic zone along a segment of the East Greenland coast, indicating the maximum effect of the West Spitsbergen Current. In contrast, there is suggestion of a small range retraction of boreal-subarctic molluscs along the northeast Baffin Island coast. There is a change from 16 thermophiles north of present limits dated 8-7 ka BP to 7 for the interval 7-6 ka BP and the area of occurrence is more restricted. Evidence for persistence of a low arctic fauna along the arctic mainland is limited to a single sample of *Mytilus edulis* south of Chantrey Inlet. Summer sea ice conditions in the archipelago were at their postglacial worst 7-6 ka BP (Dyke *et al.*, in review b) and possibly the low arctic zone shrank to runoff-dominated inlets where disjunct communities survived for a while.

MOLLUSCAN ZONES AT 5 ka BP

There is little evidence of shifting of zones from 6 to 5 ka BP (Fig. 29). However, the boreal-subarctic fauna along the northeast Baffin Island coast may have re-extended its range to Navy Board Inlet between 6 and 5 ka BP. During this interval *Chlamys islandica* reached its northernmost recorded position at Cape Herschel on east-central Ellesmere Island. Although boreal elements are less numerous represented in the West Greenland record by 5 ka BP, continued presence of *Zirphaea crispata* indicates local coastal niches warmer than present (Funder and Weidick, 1991). The low arctic zone of East Greenland had either shrunk to niche environments or disappeared by 5 ka BP.

The faunal record from Hudson Bay for this interval is puzzling. *Mytilus edulis* occurs in only 1 sample dating 6-5 ka BP compared to 15 samples dating 7-6 ka BP and is not replaced by other boreal-subarctic elements. Nothing in the history of the region reasonably explains this.

MOLLUSCAN ZONES AT 4 ka BP AND LATER

Only the Baffin Bay and high arctic regions have well distributed local faunas dated to the interval 5-4 ka BP (Fig. 30). Molluscan zones elsewhere are based on an assumption of conservative differences from present and previous conditions. By 4 ka BP the low arctic zone had disappeared from East Greenland and the boreal zone from West Greenland. However, boreal-subarctic species still extended fully up the northeast Baffin coast until shortly after 4 ka BP, though their record is less numerous for the interval 5-4 ka BP than before.

The faunal database is increasingly impoverished through time in the late Holocene for various reasons discussed earlier. This unfortunately limits our ability to examine the response of molluscs to the hemispheric climate changes documented for the Neoglacial period (3-0 ka BP). However, data for the interval 4-3 ka BP show the start of a large shift in molluscan zones: retraction of the subarctic boundary in Baffin Bay (Fig. 31). By 3 ka BP the boundary had retreated to the middle Baffin coast. *Mytilus edulis* and *Macoma balthica* north of there date 3.6 ka BP or older; *M. edulis* remained in the vicinity of that boundary until about 2.8 ka BP after which it has no record north of its present limit other than at its relict outpost at Pond Inlet (Fig. 32).

Williams *et al.* (1995) invoked diminished outflow of warm bottom water of Atlantic origin from the Arctic Ocean due to rebound of the Queen Elizabeth Islands, combined with shallowing of the inner northeastern Baffin Shelf and fiords, to account for this retreat of molluscs. This mechanism may have played an influential role but two others should also be considered. First, the fact that the molluscs retreated during the Neoglacial suggests that reduced solar heating may have been responsible. Second, the Neoglacial period in the high arctic islands was characterized by a sharp increase in arrival of driftwood. Dyke *et al.* (in review a) implicate a westward diversion of much of the Transpolar Drift to explain this. Because that water filtered through the islands to the Baffin Current, it may also have lowered its temperature.

NORTHWEST ATLANTIC REFUGIUM AND ROLE OF THE LABRADOR CURRENT

To what extent can the present fossil mollusc database address the issue in our opening quote from Franz and Merrill (1980): "Little is known of the fate of boreal species, and to a lesser extent arctic-boreal species in the northwest Atlantic during the last glacial maximum?" The question here is essentially which species survived in full glacial refugia along the shoreline on the outer continental shelf in the western North Atlantic south of the Laurentide Ice Sheet and which species settled North America from Europe via Iceland and Greenland during the postglacial marine thermal optimum? Any settling from Europe before establishment of the West Greenland Current about 9.4-9.1 ka BP seem improbable. However, starting about 9 ka BP many of the subarctic molluscs of eastern Canada may have arrived from Europe via Svalbard, Iceland, and Greenland.

Dated species occupying the southern Labrador to Gulf of Maine region before 9.5 ka BP are listed in Table XA in order

TABLE X

Species from southern Labrador to Gulf of Maine listed in order of oldest radiocarbon date (ka BP). Those present before 9.5 ka BP likely extended northward from the full-glacial refugium. Western North Atlantic endemic and temperate species that have younger limiting radiocarbon dates are listed at the end of section A

A. Dated species	Time interval (ka BP)					
	>14	>13	>12	>11	>10	>9.5
<i>Portlandia arctica</i> (16.98)	x	x	x	x	x	
<i>Nucula proxima</i> (16.29)	x					
<i>Mesodesma arctatum</i> (14.85)	x	x	x		x	x
<i>Nucula tenuis</i> (14.47)	x		x	x	x	
<i>Balanus hameri</i> (14.42)	x	x		x	x	x
<i>Hiatella arctica</i> (14.4)	x	x	x	x	x	x
<i>Balanus crenatus</i> (14.25)	x		x	x	x	x
<i>Macoma calcarea</i> (14.03)	x	x	x	x	x	x
<i>Mya truncata</i> (13.9)	x	x	x	x	x	
<i>Serripes groenlandicus</i> (13.8)		x	x		x	x
<i>Mya arenaria</i> (13.7)		x	x	x	x	x
<i>Mya pseudoarenaria</i> (13.5)		x	x	x	x	x
<i>Macoma balthica</i> (13.39)		x	x	x	x	x
<i>Nucula delphinodonta</i> (13.34)		x				
<i>Placopecten magellanicus</i> (13.2)		x				
<i>Neptunea despecta tornata</i> (13.2)		x	x			
<i>Buccinum tenuis</i> (13.2)		x	x	x	x	x
<i>Clinocardium ciliatum</i> (13.1)		x				x
<i>Portlandia arctica siliqua</i> (13.0)		x				
<i>Astarte crenata subaequilatera</i> (12.8)			x	x		
<i>Nuculana pemula</i> (12.79)			x	x	x	
<i>Mytilus edulis</i> (12.6)			x	x	x	x
<i>Natica clausa</i> (12.6)			x	x		x
<i>Chlamys islandica</i> (12.45)			x	x	x	x
<i>Trichotrophis borealis</i> (12.32)			x			
<i>Buccinum plectrum</i> (12.26)			x			
<i>Buccinum terranova</i> (12.2)			x	x		
<i>Hemithyris pssittacea</i> (12.1)			x		x	x
<i>Cyrtodaria siliqua</i> (12.0)			x	x	x	
<i>Spisula</i> sp. (12.0)			x			
<i>Panomya arctica</i> (11.95)				x		
<i>Balanus balanoides</i> (11.95)				x		
<i>Astarte montagui</i> (11.9)				x	x	x
<i>Ensis directus</i> (11.5)				x		
<i>Astarte undata</i> (11.34)				x	x	
<i>Thyasira</i> sp. (11.3)				x		
<i>Haminoea solitaria</i> (11.1)				x		
<i>Buccinum totteni?</i> (11.1)				x		
<i>Lunatia pallida</i> (11.1)				x	x	
<i>Buccinum undatum</i> (11.0)				x		x
<i>Spisula polynyma</i> (10.98)					x	x
<i>Crassostrea virginica</i> (10.85)				x	x	
<i>Echinorachnius</i> sp. (10.85)					x	
<i>Boreotrophon truncatus</i> (10.8)					x	
<i>Astarte crenata</i> (10.7)					x	x
<i>Buccinum hancocki</i> (10.7)					x	x
<i>Lepeta caeca</i> (10.6)					x	
<i>Arctica islandica</i> (10.59)					x	
<i>Musculus niger</i> (10.51)					x	
<i>Portlandia intermedia</i> (10.23)					x	
<i>Plicifusus kroyeri</i> (10.1)					x	
<i>Astarte borealis</i> (10.0)					x	
<i>Balanus balanus</i> (9.97)						x
<i>Astarte montagui striata</i> (9.97)						x

TABLE X (continued)

A. Dated species	Time interval (ka BP)					
	>14	>13	>12	>11	>10	>9.5
<i>Zirphaea crispata</i> (9.85)						x
<i>Astarte elliptica</i> (9.62)						x
<i>Cyclocardia borealis</i> (9.62)						x
<i>Macoma moesta</i> (9.62)						x
<i>Nuculana minuta</i> (9.62)						x
<i>Nuculana tenuisulcata</i> (9.62)						x
<i>Yoldia thraciaiformis</i> (9.62)						x
<i>Colus</i> sp. (9.62)						x

Amphiatlantic species (A), but not western North Atlantic endemic (E) or temperate species (T), appearing after 9.5 ka could possibly have migrated from Europe via Iceland and Greenland. Earliest appearances in the radiocarbon record (ka BP) of taxa not listed above are: *Polinices* (= *Lunatia*) *heros* (8.85, E), *Mercenaria mercenaria* (8.62, T), *Mesodesma deauratum* (8.28, E), *Thracia septentrionalis* (8.28, E), *Mysella planulata* (8.28, T), *Panopea norvegia* (7.69, A), *Cerastoderma pinnulatum* (5.8), *Nucella lapillus* (4.69, A), *Pecten irradians* (4.6, T), *Littorina obtusata* (4.33, A), *Acmaea testudinalis* (4.33, A), *Gukensia demissa* (3.8, T), *Littorina saxatilis* (3.25, A), *Pyramidella fusca* (2.54, A), *Lacuna vincta* (2.31, A), *Modiolus modiolus* (1.79, A), and *Littorina littorea* (0.65, A).

B. Regionally undated species from localities known to be >9.5 ka old.

Axinopsida orbiculata, *Cerastoderma pinnulatum*, *Cylichna alba*, *Epitonium greenlandicum*, *Lyonsia arenosa*, *Lyonsia hyalina*, *Margarites*, *Mysella planulata*, *Neptunea lyrata decemcostata*, *Polinices heros*, *Retusa obtusa*, *Serpula vermicularis*, *Spisula solidissima*, *Tachyrhynchus erosum*, *Yoldia limatula*

of oldest radiocarbon age determination. We suggest that these species expanded northward from the full-glacial refugium south of Long Island and along the continental shelf to the northeast. In addition to the 61 species listed in Table XA, Bloom (1963) and Wagner (1970) report an additional 15 species that have no regional radiocarbon record but must be older than 9.5 ka BP (Table XB). The dated list expands the known membership of the western North Atlantic refugium (Franz and Merrill, 1980) by about 25 species. Listed elements are about 4% arctic, 25% arctic-boreal, 20% boreal-subarctic, 33% boreal, 9% temperate, and 7% widespread. In Franz and Merrill's (1980) listings of "numerically and ecologically prominent" molluscs, their appearance in the regional fossil record of the southeastern glaciated region before (after) 9.5 ka BP are: arctic-boreal gastropods, 19% (7%); arctic-boreal pelecypods 53% (6%); boreal gastropods, 14% (18%); boreal pelecypods, 45% (3%); transhatteran gastropods, 0% (0%); and transhatteran bivalves, 14% (3%).

From the above we postulate that the Labrador Current may operate both as a biogeographic barrier and as a valve on glacial-interglacial time scales. It seems probable from the chronostratigraphic records that two groups of boreal-subarctic molluscs migrate into eastern Canada during interglaciations - one into the high subarctic of Baffin Bay and Hudson Bay from Europe, the other into the Atlantic Provinces region from the glacial refugium to the south. Each

glaciation forces a southward displacement of "European" molluscs to the full-glacial refugium in the western North Atlantic. Thus, just as the Atlantic received a flood of Pacific taxa during the transarctic migrations of the Late Tertiary, while the Pacific taxa diversified little and remained largely endemic, the western North Atlantic received migrants from the eastern North Atlantic, thus keeping degree of endemism on the American side low (Franz and Merrill, 1980). The central arctic islands during interglaciations that resemble the present one present a barrier to transarctic migrations of boreal-subarctic species, at least via the western half of the Arctic Ocean.

PROGRESSIVE EXTINCTION OF *MYA PSEUDOARENARIA*

Mya pseudoarenaria Schlesch (Plate II) is the only mollusc in Canadian waters that appears to be approaching global extinction. It is reported in some radiocarbon samples as *M. truncata* forma *ovata* Jensen. Laursen (1966) supported Jensen's placement of it as "at most an infrasubspecies" but MacNeil (1965) and Lubinsky (1980) firmly considered it a separate species. Jensen (1900; see summary in English by Laursen, 1966) re-examined hundreds of collections reporting *Mya arenaria* from arctic regions and pointed out that they were all misidentifications of a form of *Mya truncata* that lacks the abrupt truncation of the shell. Laursen (1966) re-examined postglacial fossils reported as *M. arenaria* from Hudson Bay and Baffin Island and determined that they too are *M. truncata* forma *ovata*. He also pointed out that some shells identified as *M. arenaria* from the postglacial of Maine are actually *M. truncata* forma *ovata*. This suggests the need to re-evaluate dated samples of *M. arenaria* from the Gulf of St. Lawrence. Likewise, Lubinsky (1980) determined that earlier collections of *M. arenaria* from Hudson Bay were Holocene fossils of *M. pseudoarenaria*. Dall (1924) reported *Mya intermedia* Dall (= *M. pseudoarenaria* Schlesch (Lubinsky, 1980)) in two postglacial fossil collections from Dolphin and Union Strait but no *M. arenaria* in any collection from the western Arctic. Samples identified as *M. arenaria* are still submitted for dating from arctic Canada and are treated here as probable *M. pseudoarenaria*.

Although widespread in early postglacial time, Lubinsky (1980) considered *Mya pseudoarenaria* to be nearly restricted to southeastern Hudson Bay and eastern James Bay. In James Bay it is dwarfed to about 25% of normal size due to depressed salinities. It also lives in outposts in Dolphin and Union Strait and off Point Barrow, Alaska (Dall, 1919; MacGinitie, 1959; MacNeil, 1965; map in Lubinsky, 1980, p. 91). More recent reports on Alaska suggest that it is more widespread than previously thought (Foster, 1991) but no indications are given of its abundance. Lubinsky (1980, p. 45) states: "There is no doubt that this species is close to extinction in its present relict area in the Canadian eastern Arctic. Schlesch (1931), MacNeil (1965), and Strauch (1972) showed that *M. pseudoarenaria* has retreated from the entire north-west Atlantic area." MacNeil identified it as present in the eastern North Atlantic (England) by Late Pliocene, apparently ahead of *Mya truncata*. It was among the earliest Pacific taxa

to arrive at Iceland about 3 Ma ago (Einarsson *et al.*, 1967). It occurs in the second oldest aminozone reported by Mode (1985) on eastern Baffin Island, which is of early Pleistocene or Pliocene age (Miller, 1985; Feyling-Hanssen, 1985). Thus it has a long record of withstanding the stresses of Quaternary glaciations and interglaciations. It appears to have maintained a circumpolar distribution until the Late Pleistocene to early Holocene for it occurs in beds of that age in northern Russia, eastern Siberia, northern Alaska, West Greenland and Spitsbergen. Although of Pacific derivation, it may have been extinct there by Late Tertiary (MacNeil, 1965), though we suspect that it occupied the last glacial maximum refugium south of Beringia (see below), which may explain its present Alaskan distribution (Foster, 1991).

Our database has 50 dated postglacial records of *M. pseudoarenaria* and 11 dubious records of *M. arenaria* from arctic sites are probably its similar arctic relative (Plate II). *M. pseudoarenaria* fossils range in age from 13.5 ka (GSC-4685) to about 3.5 ka BP. The dubious *M. arenaria* occupy the same age range, except for one sample from southern Hudson Bay that dated 2.41 ka BP (I-3907; Fig. 33). The remarkable features of its frequency distribution are its increasing representation until 3.5 ka BP and sudden decline. The decline may represent withdrawal of the animal into Hudson Bay. Laursen (1966) identified it in early (pre-radiocarbon dating) collections from Hudson and James bays. Further attention to its history in Hudson Bay (and elsewhere) could illuminate the processes involved in its apparent ongoing extinction.

Its early record, nine occurrences before 10.78 ka BP, is entirely from the Gulf of St. Lawrence area. Only one dated occurrence is from the Champlain Sea, where Wagner (1970) also reported a single (different) occurrence. It apparently thrived in areas there with a subarctic marine environment and declined as boreal conditions spread. It was largely extinct in the gulf by 7 ka but survived in places until 4 ka BP (GSC-1403, Port au Choix, NF; UQ-862, Bic, QC; Beta-13854, Rivière-Madeleine, QC).

The animal appears to have spread into the western and central arctic by 10.07-9.64 ka BP (S-2683; GSC-4747). This implies that it either entered the region at the earliest possible(?) time from Baffin Bay, that it entered from the Pacific, or that it spread into the region along the Eurasian coast from the Barents Sea. Of these possibilities, entry from Baffin Bay seems improbable in that there is no record of it in there before 8.5 ka BP. Entry from the Pacific seems most probable in that its appearance coincides with the arrival in the region of other animals from the Pacific - the molluscs, *Mytilus edulis* and *Macoma balthica*, and the bowhead whale, *Balaena mysticetus*. MacNeil (1965) emphasized that he had found no record of the species in the present Bering Sea or elsewhere in the Pacific Ocean, though he does report it on the north coast of Alaska and in Dolphin and Union Strait based collections of the Canadian Arctic Expedition identified as *Mya intermedia* Dall by Dall (1919). Its present low arctic distribution suggests that it did not survive in the Arctic Ocean through the last glacial maximum; thus survival along the south coast of Beringia is suggested. Its apparent decline in the western Arctic at 7 ka BP, with one outlier at about 5 ka BP, coincides

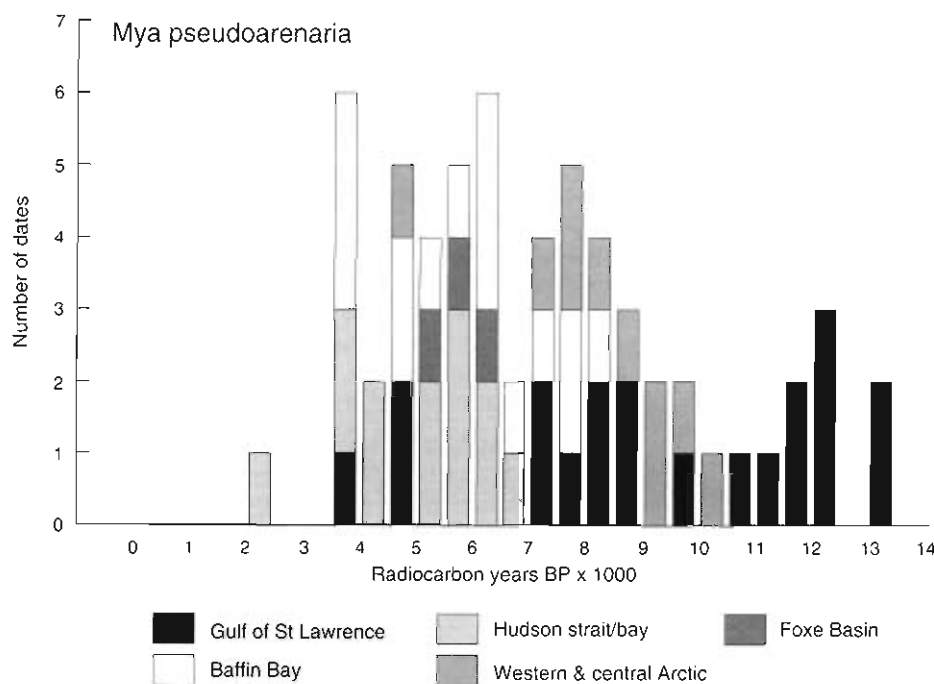


FIGURE 33. Radiocarbon dates on *Mya pseudoarenaria* (n=50) and on *Mya arenaria* that are probably *M. pseudoarenaria* (n=11).

Datations au radiocarbone de Mya pseudoarenaria (n=50) et de Mya arenaria lesquels sont probablement Mya pseudoarenaria (n=11).

with worsening sea-ice conditions there (Dyke *et al.*, in review b). It may have shrunk to a small relict in Dolphin and Union Strait thereafter.

Mya pseudoarenaria was present along the Baffin Bay coast from 8.5-3.5 ka BP. This is the interval when subarctic conditions spread to the head of Baffin Bay on the Canadian side. Its retreat from there coincides with the retreat of boreal molluscs. It thus appears that in the Arctic Holocene record the species can be regarded as a thermophile. Presuming the reported Foxe Basin *M. arenaria* to be *M. pseudoarenaria*, it was present there 6.5-5 ka BP, essentially starting with regional deglaciation.

M. pseudoarenaria is not a prominent member of any regional fauna recorded here. Of all regions, it appears to have thrived best in the Gulf of St. Lawrence during its subarctic phase. In decline there by 10 ka BP as the subarctic zone shrank from most of the gulf, it may have been unsuccessful at penetrating arctic waters along the Labrador coast and unable to maintain its range area and continuity. Northward dispersion of its pelagic larvae up the Labrador coast at 10 ka BP would have been prevented by the Labrador Current. Also, at 10 ka BP there may have been little Labrador coast available as staging sites. The Gulf of St. Lawrence population seems to have shrunk to extinction in the middle Holocene. Its apparent absence from the subarctic Labrador coast may be explained by such a history.

The penetration of *Mya pseudoarenaria* into Baffin Bay and ultimately into Hudson Bay, therefore, probably occurred via Greenland. Although we have only two radiocarbon records of it from Greenland (K-1558, 6.5 ka BP; I-5588; 6.03 ka BP), Laursen (1950) collected it from 16 raised marine sediment localities in West Greenland and the holotype specimen of the species is from Jensen's collection of "Pleistocene fossils" (presumably Holocene) from West Greenland (MacNeil,

1965, p. 37). According to Laursen's descriptions, it most commonly occurs in association with subarctic and boreal fossils. Feyling-Hanssen (1955) reported that "some of the numerous valves of *Mya truncata* from the Late-Pleistocene of Billefjorden were of form *ovata* Jensen..."; otherwise its postglacial occurrence in Spitsbergen is undated. As yet there is no evidence that it ever established large regional populations in either Baffin Bay or along the western Arctic mainland; it seems to have been confined to small, likely shifting niches.

With the Neoglacial retreat of the subarctic zone in the eastern Canadian Arctic and cooling of the subarctic zone in West Greenland, its range became restricted to Hudson Bay (Lubinsky, 1980). Why it failed to disperse southward along the Labrador coast is unclear. Its relict area apparently continues to shrink due to shoaling and lowering salinities in shallow inshore zones as shown by its dwarfism in James Bay. The process of extinction of this animal, therefore, may be one of habitat elimination of a now relatively intolerant species. In the Pliocene and Early Pleistocene it may have exploited a wider range of habitats.

SUMMARY AND DISCUSSION

We have attempted a synthesis of the marine mollusc record of the last 18 000 years for glaciated North America and Greenland. The database is rich and varied and representative of contemporaneous regional faunal assemblages. We have kept our view above the community level, where variations are governed by local controls of substrate type, water depth, and small scale salinity effects. Instead, we examined regional postglacial successions and gross shifts in molluscan zones in response to deglaciation and to oceanographic changes. Enough is known of molluscan zoogeography to place analysis at this level on a firm ecological basis.

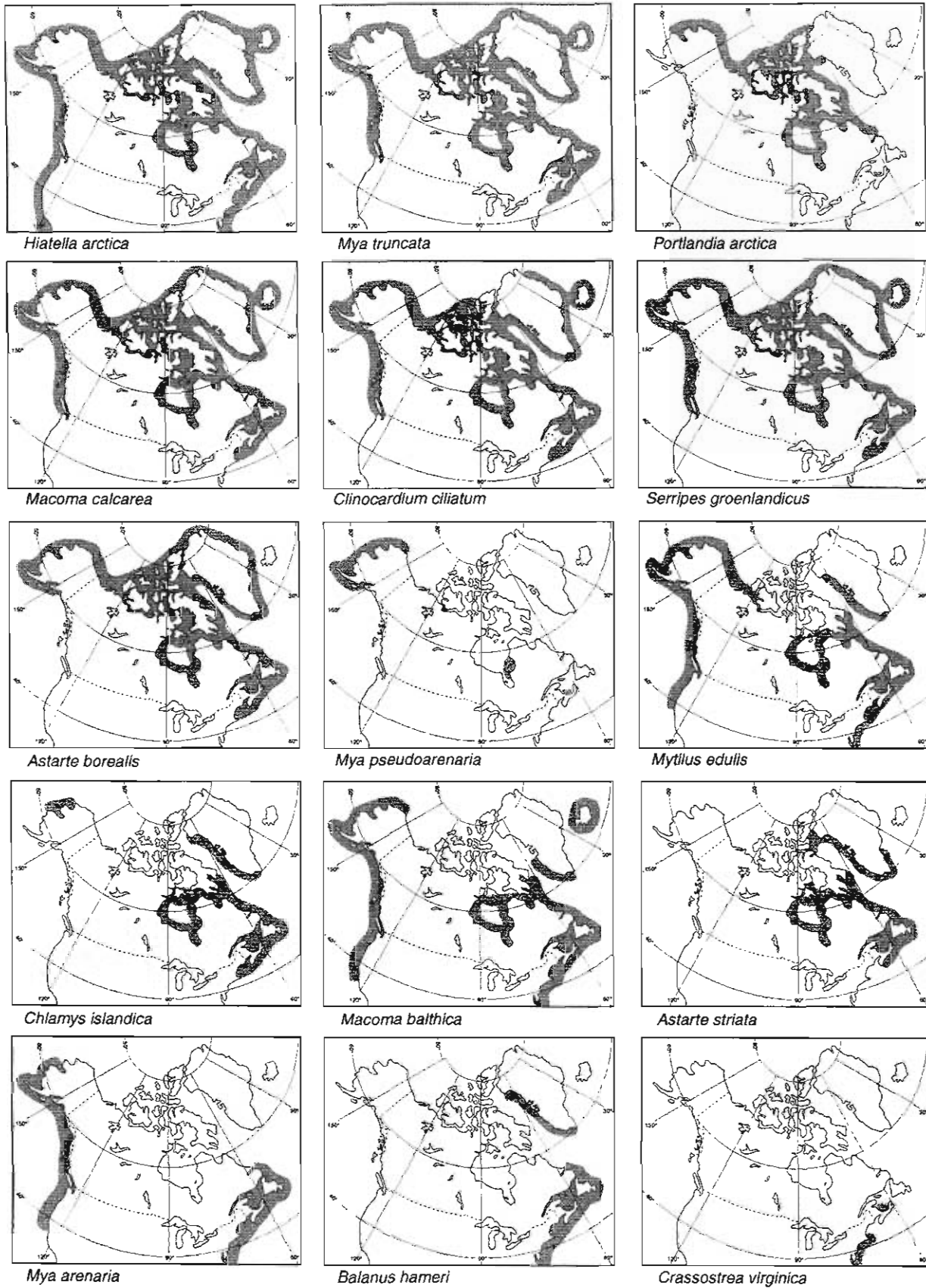


FIGURE 34. Distributions of the 15 marine invertebrates illustrated in Plates I and II. *Distribution des 15 Invertébrés marins illustrés aux planches I et II.*

The counterparts of the present arctic, low arctic, subarctic, boreal, and temperate molluscan zones with their well-defined ranges of thermal conditions can be recognized in the fossil record and mapped with reasonable confidence (Fig. 34).

The database (3084 samples in 1993; 2465 classified) records 170 taxa but is dominated by arctic assemblages, with *Hiattella arctica* and *Mya truncata* singly or together accounting for 47.4% of classified records. Wholly arctic assemblages account for 70.1%. Proceeding southward, the first boreal species added prominently to the record are *Astarte striata*, *Mytilus edulis*, *Chlamys islandica*, *Macoma balthica*, and *Mya arenaria*. The boreal assemblage comprises 16.1% of classified records. The oyster *Crassostrea virginica* represents the most thermophilous species. Only 15 species dominate the records.

There are strong suggestions of postglacial successions in many regional time series. In arctic regions that remained beyond the range of boreal taxa, the typical succession is *Hiattella arctica* followed by a *Hiattella arctica* - *Mya truncata* restricted assemblage, both of periglacial environments. This diversified through time by addition of *Astarte borealis*, *Macoma calcarea*, *Serripes groenlandicus*, and *Clinocardium ciliatum*, with order of appearance varying geographically in ill-defined ways. These regional successions remain inadequately defined and may be more complex and more informative than presently appears. The restricted assemblage has no modern analog but appears to be a valid paleontological entity even beyond present arctic regions. Extreme dominance of the early postglacial record in the high Arctic by *H. arctica* may indicate that it was the most populous survivor in the Arctic Ocean at the last glacial maximum. As yet the only other firm candidate for survival in the Arctic Ocean is *Portlandia arctica*.

At 14 ka BP the combined arctic-subarctic molluscan zone was vast, extending from the Arctic Ocean to the Gulf of Maine. The boreal zone in the western Atlantic was highly compressed but was extensive in the eastern Pacific where the subarctic-arctic zone was compressed. These zones advanced northward as deglaciation progressed; the boreal zone occupied the Gulf of St. Lawrence by 12 ka BP and all of the Gulf of Alaska by 11 ka.

Molluscs expanded greatly along the Arctic Ocean margin in the interval 12-11 ka BP from full-glacial polar refugia dominated by *Hiattella arctica*. Western arctic communities diversified about 10.5-10.3 ka BP when Bering Strait gave entry to other arctic species, including *Mya truncata* and probably *Mya pseudoarenaria*, as well as boreal-subarctic species from refugia in the north Pacific. Western arctic waters were warmer than present at that time. Meanwhile temperate species also advanced northward to the New England Shelf. Boreal species remained dominant in the Gulf of St. Lawrence 11-10 ka BP, but the Champlain Sea showed a reversion to faunas of more arctic aspect, possibly due to increased meltwater flow from proglacial lakes.

Important changes of molluscan zones between 10 and 9 ka BP reflect postglacial establishment of the West Greenland, Irminger, and Baffin currents or their migration to near-

present positions. The North Atlantic Drift affected Svalbard by 9.4 ka BP. The Baffin Current was not as chilling as today at 9 ka BP when boreal-subarctic molluscs exceeded present limits. Between 9 and 8 ka BP boreal-subarctic molluscs extended to the head of Baffin Bay on both coasts and full-boreal conditions were established in part of southern West Greenland. The first thermophiles also occurred in East Greenland due to increased influence of the warm West Spitsbergen Current. At the same time the Labrador Current seems to have had a less chilling influence on the Gulf of St. Lawrence where temperate faunas appeared. A brief interval around 8.5 ka BP seems to have been one of more intensive change than for the rest of postglacial time. We postulate that much of this may have been in response to withdrawal of the western Laurentide Ice Sheet margin from the Mackenzie watershed and its downstream effects on the oceanography and climatology of the North Atlantic. Concurrently, the distal part of the Transpolar Drift may have assumed a more westward flow and the North Atlantic Drift strengthened.

From 8-3 ka BP boreal molluscs exceeded present limits in the eastern Arctic. Virginian species also expanded into the Gulf of St. Lawrence 8-7 ka BP, if not earlier, but became separated from their main range shortly after as increasing tidal mixing in the Gulf of Maine - Bay of Fundy region created summer-cold water conditions. Shortly after 3 ka BP the subarctic molluscan zone retreated 1000 km in western Baffin Bay to its present position. This probably reflects cooling of the Baffin and Labrador currents downstream to the Grand Banks.

Shifting of molluscan habitats and zones continues today. The greatest changes may be those due to relative sea level change. Hudson Bay and Foxe basin are shallowing at a rate of about 1 m per century while much of Atlantic Canada is submerging at about 0.3 m per century. In Hudson Bay, pressure on the relict oceanic fauna in its relatively small eastern trench will continue (Lubinsky, 1980), and in the Gulf of St. Lawrence, deepening waters will increase pressure on disjunct populations of temperate faunas. Bousfield and Thomas (1975) predicted that some of the latter, including commercially important species, will likely become extinct in Canadian waters.

Other future changes may result from sustained regional changes in precipitation and atmospheric circulation such as are predicted to accompany global warming. For example, it seems well established that historic changes in discharge of the Mackenzie River affected oceanic and atmospheric conditions broadly in the North Atlantic. And well-documented changes in North Atlantic circulation during the present century between Canada and Greenland led to shifts of complex marine ecosystems, involving many economically important species of fish (e.g. Atlantic cod, *Gadus morhua*; Atlantic salmon, *Salmo salar*) and marine mammals (e.g. pilot whale, *Globicephala ventricosa*; Dunbar, 1976; Harington, 1980).

The paleogeographic reconstructions are a fairly detailed record of how a complex molluscan ecosystem responded to vast, externally imposed environmental changes of the sort that create ecological bottlenecks and opportunities. The last glaciation did not result in extinction of any marine molluscan

species other than *Atractodon stonei*, last known from the Sangamonian or Middle Wisconsinan (Clarke *et al.*, 1972; Wagner, 1977). The marine record thus stands in stark contrast to the great depletion of terrestrial mammals at the close of the last glaciation (Martin and Klein, 1984). The lack of extinction of molluscs arising from the last glaciation may simply reflect the fact that only highly adaptive species had survived the many earlier Pleistocene glaciations. This is indicated by elimination in the North Atlantic of more than half of the transarctic migrants from the Pacific in the earlier Pleistocene (Franz and Merrill, 1980). The only mollusc apparently now threatened with global extinction, *Mya pseudoarenaria*, seems more affected by habitat elimination and migrational restrictions during and following deglaciation than by the extreme displacements of glaciation itself. But what was uniquely disadvantageous for this animal in the last deglaciation is entirely unclear.

Despite lack of extinctions, both the boreal zone in the western Atlantic and the arctic zone in the north Pacific were severely constricted to an extent that may have approached critical, especially for shallow water forms. On the other hand the arctic zone in the Atlantic was extended so vastly that arctic animals were long exposed to conditions of greater variety than they would have otherwise experienced.

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APPENDIX

INDEX AND GEOGRAPHIC RANGES OF DATED MARINE INVERTEBRATE FAUNAS

PHYLUM MOLLUSCA

CLASS GASTROPODA

- Acmaea testudinalis* Müller, arctic-boreal, Arctic Islands to Connecticut, Bering Sea
- Boreotrophon clathratus* Linné, boreal-subarctic, southern Arctic to Maine
- Boreotrophon truncatus* Strom, boreal-subarctic, southern Arctic to Georges Bank, north coast of Alaska
- Buccinum (hancocki) glaciale* Linné, arctic-subarctic south to Gulf of St. Lawrence and Washington State
- Buccinum physematum* Dall, arctic, Arctic coast from Bernard Harbour to Pt Barrow, south to Bristol Bay
- Buccinum plectrum* Stimpson, arctic-subarctic, Arctic Ocean to Gulf of St. Lawrence and Puget Sound
- Buccinum (terranovae) polare* Gray, subarctic, Greenland to Newfoundland, Arctic Ocean to Alaska Peninsula
- Buccinum (tenuis) scaliforme* Möller, arctic-boreal south to Maine and Washington State
- Buccinum totteni* Stimpson, boreal-subarctic, Labrador to Gulf of St. Lawrence
- Buccinum undatum* Linné, boreal, Labrador to New Jersey
- Colus halli* Dall, boreal, Bering Sea to California
- Colus pubescens* Verrill, boreal, subarctic to South Carolina
- Colus togatus* Morch, arctic, northern Ellesmere south to?
- Cryptonatica clausa* Broderip and Sowerby, Arctic Ocean to North Carolina, = *Natica clausa* Broderip and Sowerby
- Epitonium* sp., many species, temperate to tropical waters
- Fusitron oregonensis* Redfield, boreal, Bering Sea to California
- Haminoea solitaria* Say, Virginian, southwestern Gulf of St. Lawrence to Georgia
- Lacuna vincta* Montagu, arctic-boreal, Labrador to New Jersey; Alaska to Puget Sound
- Lepeta caeca* Müller, arctic-boreal, central and eastern Arctic south to Cape Cod; Alaska to Vancouver Island
- Littorina littorea* Linné, boreal, southern Labrador to New Jersey
- Littorina obtusata* Linné, boreal, Labrador to New Jersey; Alaska to Puget Sound
- Littorina saxatilis* Olivi, subarctic-boreal, Baffin Island to New Jersey
- Lora nobilis* Möller, boreal, Greenland to Gulf of Maine; Bering Sea (= *Propebela nobilis* Möller; = *Oenopota turricula* Montagu in Canadian Arctic)
- Lunatia (Euspira) pallida* Broderip and Sowerby, widespread, panarctic south to North Carolina and California
- Moelleria* sp. Jeffreys, three species in North America, all cold water; Arctic seas to New England; Alaska to Queen Charlotte Islands
- Natica clausa* Broderip and Sowerby, arctic-boreal, Arctic Ocean to North Carolina and California

- Natica pallida* Broderip and Sowerby = *Lunatia pallida* Broderip and Sowerby
- Neptunea despecta tornata* Gould, boreal, Gulf of St. Lawrence to Cape Cod
- Notacmea testudinalis* Müller, (= *Acmaea testudinalis testudinalis* Müller), Arctic to New York
- Nucella delphinodonta* Mighels, boreal, southern Labrador to New Jersey
- Nucella (Thais) lamellosa* Gmelin, boreal, Bering Strait to California
- Nucella lapillus* Linné, boreal, southern Labrador to New York
- Oenopota* sp., many species, dominantly an arctic and boreal genus
- Plicifusus kroyeri* Möller, circumpolar, Greenland, Bering Sea
- Polinices heros* Say, (= *Lunatia heros*), Virginian, Gulf of St. Lawrence to North Carolina
- Polinices pallidus* = ? *Lunatia pallida* Broderip and Sowerby
- Puncturella noachina* Linné, circumpolar, south to Cape Cod and Aleutian Islands
- Pyramidella fusca* C.B. Adams, Virginian, southwestern Gulf of St. Lawrence to Florida (= *Sayella fusca* C.B. Adams)
- Solariella* sp. Wood, tropical to arctic waters
- Tachyrhynchus erosus* Couthouy, boreal, Greenland to Massachusetts; Alaska to British Columbia
- Thais lamellosa* = *Nucella lamellosa* Gmelin
- Thais lapillus* Linné = *Nucella lapillus* Linné
- Trichotropis borealis* Broderip and Sowerby, arctic-boreal south to Maine and British Columbia
- Turbonilla interrupta* Totten, Virginian, Gulf of St. Lawrence to West Indies
- Turritella* sp., temperate to tropical waters
- Vermetus* sp., reported only in sample SI-725, Ellesmere Island; there are no true *Vermitus* in the United States (Abbott, 1974), nor probably in Canada; probably a member of family Vermetidae

CLASS PELECYPODA

- Aequipecten irradians sablensis* Lamarck = *Argopecten irradians sablensis* Clarke
- Arctica islandica* Linné, Newfoundland to Cape Hatteras, mainly boreal-Virginian range
- Arctinula greenlandica* Sowerby = *Delectopecten greenlandicus* Sowerby
- Argopecten irradians sablensis* Clarke, Sable Island to Florida, extinct subspecies
- Astarte alaskensis* Dall, Pacific endemic, subarctic-boreal, Bering Sea to Washington
- Astarte banksii* Leach = *A. montagui* Dillwyn
- Astarte (Tridonta) borealis* Schumacher, arctic-subarctic, boreal east coast, south to Massachusetts; Alaska
- Astarte crenata* Gray, arctic-subarctic, south to Massachusetts

- Astarte crenata subaequilatera* Sowerby, subarctic, warmer waters than other forms of *A. crenata*, Labrador to Florida
- Astarte elliptica* Brown, low arctic to boreal Atlantic, south to Massachusetts
- Astarte montagui* Dillwyn (= *A. banksii* Leach), boreal with subarctic outposts, south to Massachusetts and Aleutian Islands
- Astarte striata* Leach, boreal-subarctic with high arctic outposts, south to Gulf of St. Lawrence
- Astarte undata* Gould, boreal, Labrador to Chesapeake Bay
- Axinopsida orbiculata* Sars, arctic-subarctic, south to Massachusetts
- Batharca (Arca) glacialis* Gray, arctic-subarctic, boreal in Atlantic, south to Gulf of St. Lawrence
- Batharca raridentata* Wood, Pacific endemic in southwestern Canadian Arctic Archipelago
- Cardium ciliatum*, reported in sample W-996 from Washington; (= *Clinocardium ciliatum*)
- Cerastoderma pinnulatum* Conrad, boreal, Labrador to North Carolina
- Chirona evermanni*
- Chlamys* sp.
- Chlamys hastata hericia* Gould
- Chlamys hericius* = *C. hastata hericia* Gould
- Chlamys (Pecten) islandica* Müller, boreal-subarctic, Cumberland Peninsula and Greenland to Massachusetts; Alaska to Washington
- Chlamys jordani* Arnold, boreal, Queen Charlotte Islands to Washington
- Chlamys rubida* Hinds, boreal, Alaska to southern California
- Clinocardium ciliatum* Fabricius, arctic-subarctic with boreal outposts, south to Cape Cod and Puget Sound; rare in Arctic Archipelago, abundant in eastern Arctic
- Clinocardium echinatum*, reported in sample I-6430, SW Greenland
- Clinocardium nuttallii* Conrad, boreal Pacific, Bering Sea to southern California (see QU-450 for *C. nuttallii*, incorrectly identified at Sept-Isle)
- Compsomyx subdiaphana* Carpenter, boreal northeast Pacific, Alaska to California
- Crassostrea virginica* Gmelin, Virginian species, southwestern Gulf of St. Lawrence to Gulf of Mexico
- Crenella decussata* Montagu, boreal, Hudson Strait to Cape Hatteras, Bering Sea to San Pedro, California
- Cyclocardia (Venericardia) borealis* Conrad, boreal, Hudson Strait to North Carolina
- Cyclocardia ventricosa* Gould, boreal, Alaska to Santa Barbara, California
- Cyrtodaria kurriana* Dunker, high arctic, south to Alaska and Labrador
- Cyrtodaria siliqua* Spengler, boreal, Labrador to Rhode Island
- Delectopecten (Pecten) greenlandicus* Sowerby, high arctic, south to Newfoundland in deep waters, = *Arctinula greenlandica* Sowerby
- Ensis directus* Conrad, boreal-subarctic, southern Labrador to South Carolina
- Ensis ensis* reported in I-2475, US Shelf; probably = *E. directus*
- Gastrana irus* Hanley = *Macoma inquinata* Deshayes
- Gukensia* sp. = *VolSELLA* sp.?
- Gukensia demissa* Dillwyn, Virginian, Gulf of St. Lawrence to Florida
- Hiatella arctica* Linné, arctic-subarctic, Arctic Ocean to West Indies and Panama in Pacific (southern occurrences in deep water)
- Hinnites multirugosus* Gale, temperate Pacific, British Columbia to Baja California
- Limatula (Lima) subauriculata* Montagu, boreal, Greenland to Puerto Rico, Alaska to Mexico
- Limatula hyperborea* = *Yoldia hyperborea* (Loven) Torell
- Lyonsia hyalina* Conrad, Virginian, southwestern Gulf of St. Lawrence to South Carolina
- Macoma balthica* Linné, boreal with subarctic outposts; Hudson Bay, north to Cumberland Sound, south to Massachusetts; Bering Sea to California; tolerant of low salinity
- Macoma brota* Dall, subarctic-boreal, Arctic Ocean to Puget Sound
- Macoma calcarea* Gmelin, arctic-subarctic, south to New York; Bering Sea to Washington
- Macoma incongrua* = *M. obliqua* Sowerby
- Macoma inconspicua* Broderip and Sowerby, Pacific, boreal-low arctic, east to Bathurst Inlet, south to southern California
- Macoma inquinata* (= *Gastrana irus* Hanley), boreal, Bering Sea to California
- Macoma liparea* Dall, boreal, Aleutian Islands to northern California
- Macoma moesta* Deshayes, high arctic south probably to Ungava Bay
- Macoma nasuta* Conrad, boreal-temperate, Alaska to Baja California
- Macoma obliqua* Sowerby, subarctic-boreal, Pt Barrow to Washington
- Macoma torelli* (Steenstrup) Jensen, high arctic
- Megayoldia thraciaeformis* Storer = *Yoldia thraciaeformis* Storer
- Mercenaria mercenaria* Linné, Virginian, southwestern Gulf of St. Lawrence to Gulf of Mexico
- Mesodesma arctatum* Conrad, boreal, Greenland to Chesapeake Bay
- Mesodesma (arctatum) deauratum* Conrad, boreal-subarctic, Greenland to Chesapeake Bay
- Modiolus modiolus* Linné = *VolSELLA modiolus*, southernmost arctic to Florida and to California
- Musculus discors* Linné, arctic with boreal outposts south to Cape Cod and Puget Sound
- Musculus discors (Modiolaria) laevigata* Gray, arctic-boreal, south to Cape Cod
- Musculus niger* Gray, arctic-boreal, Ellesmere Island and Greenland to Cape Hatteras, Alaska to Puget Sound
- Mya arenaria* Linné, boreal, Hamilton Inlet to Florida; Aleutian Islands to northern California; arctic occurrences referred to *M. arenaria* probably *M. pseudoarenaria*
- Mya pseudoarenaria* Schlessch (= *M. truncata forma ovata* Jensen), low arctic-subarctic, now nearly restricted to eastern Hudson Bay
- Mya truncata* Linné, arctic-subarctic, south to Massachusetts, common in northern Gulf of St. Lawrence; Arctic Ocean to Washington State
- Mya truncata uddevalensis* Forbes, most arctic occurrences probably uddevalensis
- Mysella planulata* Stimpson, Virginian, southwestern Gulf of St. Lawrence to Texas
- Mytilus californianus* Conrad, temperate, Aleutian Islands to Mexico
- Mytilus edulis* Linné, boreal-subarctic, Padloping Island and Greenland to Cape Hatteras (northern outpost at Pond Inlet); Pacific north and east to Bathurst Inlet in the west
- Nucula bellotii* Adams, arctic, replaced by *N. tenuis* in subarctic and boreal zones; Alaska north of Aleutian Islands
- Nucula delphinodonta* Mighels and Adams, boreal-subarctic, Hudson Strait to New England; outpost at Pond Inlet
- Nucula expansa* Reeve = *N. bellotii* Adams in cold waters; *N. tenuis* in Atlantic
- Nucula proxima* Say, Virginian, Nova Scotia to Texas
- Nucula suicata*, reported in sample K-994 from SW Greenland
- Nucula tenuis* Montagu, subarctic-boreal, Labrador to North Carolina; *N. tenuis* in cold water probably *N. belloti*
- Nuculana fossa* Baird, subarctic-boreal, Alaska to Puget Sound
- Nuculana minuta* Fabricius, boreal-subarctic, rare in high arctic, south to Massachusetts and Chatham Sound, British Columbia
- Nuculana (Leda) pemula* Müller, arctic with boreal outposts south to Massachusetts and Queen Charlotte Islands

Nuculana tenuisulcata Couthouy, arctic-boreal, Arctic Ocean south to Cape Cod
Ostrea lirida Carpenter, boreal-temperate, Alaska to Baja California
Palliolum imbrifer Lovén, arctic-boreal, arctic seas to New Jersey
Palliolum greenlandicum Sowerby, high arctic
Pandora glacialis Leach, high arctic circumpolar, south to subarctic
Panomya arctica Lamarck, boreal-subarctic, Aleutian Islands to Pt Barrow, Arctic seas to Chesapeake Bay
Panopea norvegica Spengler, boreal, Gulf of St Lawrence to Cape Cod
Pecten (Patinopecten) caurinus Gould, temperate, Aleutian Islands to Pt Reys, California
Pecten irradians, Virginian, Nova Scotia to North Carolina, = *Argopecten irradians* Lamarck
Placopecten magellanicus Gmelin, boreal, Labrador to North Carolina
Pododesmus macroschisma Deshayes, Alaska to California
Portlandia arctica Gray, arctic, south to Hamilton Inlet; deeper waters only in the subarctic
Portlandia arctica siliqua Reeve, shores of Baffin Bay and Foxe Basin to Labrador Shelf, northern Alaska; more southerly than *P. arctica*
Portlandia frigida = *Yoldiella frigida* Torell
Portlandia intermedia (= *Yoldiella intermedia* Sars), high arctic; relict in eastern trench of Hudson Bay
Portlandia lenticula (= *Yoldiella lenticula* Möller, arctic-subarctic, south to Maine
Protothaca staminea Conrad boreal-temperate, Aleutian Islands to Baja California
Protothaca tenerima Carpenter, temperate, Vancouver to Baja California
Saxidomus gigantea Deshayes, boreal, Aleutian Islands to California
Serripes sp., reported from Pacific; presumably *S. groenlandicus*
Serripes groenlandicus Bruguière, arctic-subarctic, south to Cape Cod; not abundant in archipelago; abundant in eastern Arctic
Solen sicarius Gould, temperate, British Columbia to Baja California
Spisula polynyma Stimpson, boreal-subarctic, Labrador to Rhode Island, Arctic seas to Puget Sound
Spisula solidissima Dillwyn, Virginian, Nova Scotia to South Carolina
Thracia septentrionalis Jeffreys, Greenland to Long Island; rare in Canadian Arctic

Thyasira gouldi Philippi, arctic-subarctic south probably to Massachusetts
Tresus capax Gould, boreal-temperate, Kodiak Island to Monterey, California
Yoldia arctica Messewitsch = *P. arctica* Gray
Yoldia glacialis = *P. a. siliqua* Reeve
Yoldia (Limatula) hyperborea (Loven) Torrell, arctic-subarctic, south to Newfoundland
Yoldia thraciaeformis Storer, boreal, Greenland to Cape Hatteras, Alaska to Puget Sound
Yoldiella fraterna Verrill and Bush, arctic, abyssal deep waters south to Georgia
Yoldiella frigida Torell, high arctic circumpolar
Yoldiella lenticula Möller, arctic-subarctic, south to Maine
Zirphaea crispata Linné, boreal, southern Labrador to South Carolina

PHYLUM ARTHROPODA

CLASS CIRRIPIEDIA

Balanus sp.
Balanus balanoides, subarctic-boreal, Baffin Island to New Jersey
Balanus balanus Linné, widespread, Arctic Ocean to Long Island
Balanus crenatus Bruguière, widespread, Arctic to New Jersey; Alaska to Santa Barbara, California
Balanus evermanni
Balanus hameri Ascanius, boreal-subarctic, West Greenland and Hamilton Inlet to North Carolina

PHYLUM BRACHIOPODA

Hemithyris psittacea Gmelin, arctic-boreal, Arctic Ocean to Gulf of St. Lawrence

PHYLUM ECHINODERMATA

CLASS ASTEROIDEA

Asterias vulgaris Verrill, southern Labrador to North Carolina

CLASS ECHINOIDEA

Echinorachinus sp., only species in Atlantic Canada is *E. parma* Lamarck, Arctic Ocean to Long Island
Strongylocentrotus dröbachiensis Müller, widespread, Arctic Ocean to New Jersey