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Marine Mollusca from Expedition Fiord, Western Axel Heiberg Island, Northwest Territories, Canada

ALEC E. AITKEN¹ and ROBERT GILBERT²

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ABSTRACT. Marine molluscs, including bivalves, gastropods and scaphopods, were recovered by dredging at depths of 3-82 m in Expedition Fiord, Axel Heiberg Island, Canada. Cluster analysis, based on presence/absence data at 27 stations, defined two mollusc associations within the fiord. A *Portlandia-Thyasira* association, characterized by the abundance of *Portlandia arctica* and *Thyasira gouldi*, inhabits silty clay substrates at depths of 32-82 m throughout the fiord. An *Astarte* association, characterized by the abundance of *Astarte borealis* and *Astarte warhami*, inhabits sandy mud substrates at depths of 3-32 m in the middle and outer fiord. The absence of this mollusc association at the fiord head suggests that the suspension-feeding molluscs that constitute this association, such as *Astarte*, *Hiatella*, *Mya* and *Trichotropis*, are intolerant of the lowered salinities and high suspended-sediment concentrations created by the discharge of Expedition River into the fiord-head environment. The Expedition Fiord molluscan fauna is compared to the molluscan fauna recorded in Jørgen Brønlund Fjord, Greenland. In the latter fiord, shallow-water (5-19 m) molluscan faunas are characterized by the abundance of *Thyasira dunbari*. Molluscs recovered live in both of these fiords are distributed widely in high-latitude fiord and continental shelf environments.

Key words: mollusca, fiords, Canadian Arctic, Axel Heiberg Island, Greenland, ecology, zoogeography

RÉSUMÉ. On a recueilli des mollusques marins — comprenant des bivalves, des gastéropodes et des scaphopodes — par dragages effectués à des profondeurs allant de 3 à 82 m dans le fjord Expedition, situé dans l'île Axel Heiberg au Canada. Des analyses typologiques, établies sur les données de présence ou d'absence à 27 stations, ont permis de définir deux associations de mollusques à l'intérieur du fjord. Une association *Portlandia-Thyasira*, caractérisée par l'abondance de *Portlandia arctica* et de *Thyasira gouldi*, habite les substratums d'argile limoneuse à des profondeurs allant de 32 à 82 m dans le fjord tout entier. Une association *Astarte*, caractérisée par l'abondance de *Astarte borealis* et de *Astarte warhami*, habite les substratums de vase sableuse à des profondeurs allant de 3 à 32 m dans le milieu ou en aval du fjord. L'absence de cette association de mollusques à l'extrémité amont du fjord suggère que les mollusques se nourrissant d'éléments en suspension qui forment cette association, comme *Astarte*, *Hiatella*, *Mya* et *Trichotropis*, ne tolèrent pas les faibles salinités et les fortes concentrations de sédiments en suspension que crée le déversement de la rivière Expedition dans l'extrémité amont du fjord. On compare la faune des mollusques du fjord Expedition à celle enregistrée dans le fjord Jørgen Brønlund du Groenland. Dans ce fjord, les faunes de mollusques en eau peu profonde (de 5 à 19 m) sont caractérisées par l'abondance de *Portlandia arctica* et de *Hiatella arctica*, tandis que les faunes situées en eau profonde (de 22 à 48 m) sont caractérisées par l'abondance de *Thyasira dunbari*. Les mollusques recueillis vivants dans ces deux fjords sont largement répandus dans les fjords et les plates-formes continentales des latitudes élevées.

Mots clés: mollusques, fjords, Arctique canadien, île Axel Heiberg, Groenland, écologie, zoogéographie

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INTRODUCTION

The biology of Canadian arctic fiords, specifically the fiords along the eastern coast of Baffin Island, has been the subject of several studies (Aitken et al., 1988; Dale et al., 1989; Syvitski et al., 1989; Aitken and Fournier, 1993). The biology of Canadian high arctic fiords, however, remains uninvestigated except for unpublished work by Fisheries and Oceans Canada (Hunter and Leach, 1983) and studies by Curtis (1972) and Dale (1985) on Ellesmere Island. Benthic macrofauna inhabiting Expedition Fiord, western Axel Heiberg Island, N.W.T. (Fig.1), were recovered from dredge samples taken in August 1990 as part of a collaborative research program investigating the terrestrial and marine Quaternary geology of the region (Gilbert et al., 1993; Lemmen et al., 1994). The material collected is the most complete record of the macrobenthos inhabiting a Canadian high arctic fiord: polychaetes, molluscs (gastropods, bivalves, scaphopods), crustaceans (amphipods, cumaceans, isopods, shrimp), pycnogonids, bryozoans, and echinoderms (echinoids, holothurians, ophiuroids) are represented in the collections. This paper examines the distribution of molluscs in Expedition Fiord and compares these macrofauna with the more thoroughly studied molluscan macrofaunas inhabiting

¹ Department of Geography, University of Saskatchewan, 9 Campus Drive, Saskatoon, Saskatchewan S7N 5A5, Canada

² Department of Geography, Queen's University, Kingston, Ontario K7L 3N6, Canada

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FIG. 1. Location in the Canadian Arctic Archipelago of Expedition Fiord, Axel Heiberg Island, and other places referred to in the text. The division of arctic and subarctic waters in Baffin Bay is according to Dunbar (1951).

the high-latitude fiords of eastern and northern Greenland and eastern Baffin Island.

METHODS AND MATERIALS

Working from an inflatable boat, the researchers determined the bathymetry (Fig. 2) of the fiord by surveying with an echo sounder and a subbottom profiling system (Gilbert et al., 1993). A Kolquitz dredge, fitted with a 1.0 mm mesh net, sampled the macrobenthos at depths of 3-82 m. Twentyseven dredge samples, each consisting of 5-15 L of sediment, were recovered from several sites within the fiord (Fig. 2). Each dredge sample was sieved on site through a 0.5 mm brass sieve in seawater. Material retained on the sieve was preserved in buffered formalin. In the laboratory, marine invertebrates were sorted manually under a binocular microscope at $10 \times$ to $25 \times$ magnification and identified to the level of species whenever possible. The binomial nomenclature used for mollusc species in this study conforms with Macpherson (1971) and Lubinsky (1980). Subsamples of sediment recovered in the dredge, each 40 to 60 g, were



FIG. 2A. (upper frame) The bathymetry of the inner and middle basins of Expedition Fiord showing the location of dredge sampling stations (after Gilbert et al., 1993). At sites A, D and F, dredge samples were taken at intervals along a transect line perpendicular to the shore. Dredge samples were taken at various locations within the inner basin; only those stations that yielded molluscs (B2, B3 and B6) are shown. Sample depths are given in Appendix 1. Informal place names are in quotation marks. FIG. 2B. (lower frame) The bathymetry of the outer basin of Expedition Fiord showing the location of dredge sampling stations (after Gilbert et al., 1993). At sites C and E, dredge samples were taken at intervals along a transect line perpendicular to the shore; sample depths are given in Appendix 2. Informal place names are in quotation marks.

retained for the determination of grain-size distribution by sieving and SediGraph analysis.

Seawater temperature, salinity, and suspended sediment content were measured irregularly throughout the fiord during the open-water period of 1988 and 1990 (Gilbert, 1990; Gilbert et al., 1993). A compilation of the hydrographic data acquired in Expedition Fiord is available from the authors upon request.

At present, there is a dearth of information relating to the benthic marine ecology of the Canadian Arctic Archipelago. For comparison, we examined the distribution of molluscs recovered by dredging in Expedition Fiord and Jørgen Brønlund Fjord, northeastern Greenland (Fig. 3; Schiøtte, unpubl. data). The presence and abundance of molluscs in each dredge sample were recorded and entered in a data matrix; only those stations that yielded molluscs were included in the data matrix. Separate matrices were developed for Expedition Fiord and Jørgen Brønlund Fjord (Appendices 1-3). These data matrices were reduced to include only those

species present at two or more stations, then evaluated by cluster analysis using SAS/STAT Version 6 clustering procedures (SAS Institute Inc., 1989). The sampling methods employed in Expedition Fiord and Jørgen Brønlund Fjord preclude quantitative analysis of the benthic macrofauna. In this situation Jaccard's coefficient, which is based on the presence or absence of species within a sample, was employed to create similarity matrices. Clusters present within the similarity matrices were determined by Ward's method, as recommended by Jones (1988).

PHYSICAL ENVIRONMENT

Study Area

As discussed in detail by Gilbert et al. (1993) and Lemmen et al. (1994), Expedition Fiord leads from glaciated highlands



FIG. 3. The bathymetry of Jørgen Brønlund Fjord showing the location of dredge sampling stations (after Just, 1970). Only those stations that yielded molluscs are shown. Sample depths are given in Appendix 3.

in central Axel Heiberg Island into Strand Bay on the western coast of the island. Expedition Fiord is normally ice-covered 11 to 12 months of the year; sea ice more than 2 m thick was observed in the fiord. The fiord was virtually free of sea ice, however, throughout the period of study, 1-14 August 1990. In addition to sea ice, icebergs of various sizes, calved from a tidewater glacier in adjacent Iceberg Bay (Fig. 2B), were observed in the fiord. The fiord's major source of water and sediment is Expedition River, which drains an area covered extensively by glaciers. The rapid advance of the Expedition River delta, averaging 9 m a⁻¹ since 1959, reflects the input of large quantities of sediment at the fiord head (Gilbert, 1990; Gilbert et al., 1993).

A sill (at 70 m depth north of the "Middle Islands" and less than 60 m depth south of the "Middle Islands") separates several shallow basins (maximum depth 132 m) from the outer fiord (to the west of the "Middle Islands" and north of "Outer Island"), which deepens to more than 300 m near the mouth (Fig. 2B). This sill prevents icebergs with deep keels from entering the eastern portion of the fiord, although icebergs with shallow keels move freely throughout the fiord during periods of open water (Gilbert et al., 1993). Bottom sediments above 70 m depth east of the sill are scoured extensively by iceberg keels to produce a distinctly rough bottom topography. The fiord floor west of the "Middle Islands" is also scoured extensively by iceberg keels, suggesting that there is no sill between outer Expedition Fiord and Iceberg Bay at any depth shallower than 300 m (Gilbert et al., 1993).

Measurements of temperature and salinity in Expedition Fiord recorded in 1988 and 1990 indicate the presence of a well-defined overflowing cap. A sharp pycnocline at 6-6.5 m depth separates overflowing brackish water with temperatures from 1.8° to 6.9° C and salinities from 1.2‰ to 12.1‰ from seawater below, where temperature decreases gradually to -2° C at 50 m and salinity varies between 25‰ and 33.7‰ (Fig. 4). The overflow formed a strong cap everywhere in the fiord, thinning gradually to 4.5-5 m depth at the fiord mouth. Staff gauge readings at "Camp Fan" from 1-14August 1990 showed a semidiurnal tide with a mean range of 0.42 m; thus, tidal currents are probably ineffective as an agent of mixing across the pycnocline.

The upper 50 m of the water column is well-oxygenated throughout the fiord. Dissolved oxygen values range from 9.3 to 13.9 mL L⁻¹, with the greatest values occurring at depth. Gilbert (1990) reported values of 9.4 to 11.8 mL L⁻¹ at the fiord head in August, 1988.

Water Masses

The distribution of benthic molluscs at high latitudes is influenced strongly by the distribution of water masses. Along the coasts of the Canadian Arctic Archipelago and northern Greenland, the continental shelf extends to depths of 400–650 m (Johnson et al., 1990). Three distinct water masses occur at these depths in the Arctic Ocean basin; fiord water, polar water, and Atlantic water. Data relating to the physical properties of polar and Atlantic waters in the Arctic Ocean basin are presented by Coachman and Aagaard (1974) and Lewis (1989). A brief summary of these data follows.

Polar waters occupy the uppermost 200 m of the Arctic Ocean basin and exhibit varying physical characteristics that reflect the inflow and mixing of Pacific and Atlantic waters with fresh water derived from the land and the decay of sea



FIG. 4. Temperature and salinity in the upper water of Expedition Fiord on 18 August 1988 at stations from 0.9 to 16 km from the mouth of Expedition River at the fiord head (after Gilbert, 1990).

ice. Along the northern coast of the Canadian Arctic Archipelago and Greenland, polar waters exhibit summer temperatures of $1-2^{\circ}$ C and salinities of 30‰ to 32‰ at 50 m depth, increasing to 34.5‰ at 200 m. In winter, polar waters exhibit salinities of 32‰ to 34‰ and temperatures approaching the freezing point of seawater.

The Atlantic layer lies beneath polar waters at depths of 200-500 m. The source of this water is the north Atlantic Ocean via the Norwegian and Greenland Seas. Over the Canadian continental shelf, Atlantic waters exhibit temperatures lower than 0.5° C and salinties of 34.92% to 34.99%.

Danish authors (see review by Ockelmann, 1958), working in the fiords of eastern Greenland, differentiate between polar waters and fiord waters, the latter representing relatively warm (> 0°C), low-salinity (< 20‰) water produced by the inflow of fresh water from rivers discharging into fiords and by the melting of sea ice (Ockelmann, 1958). We employ the term "fiord water" to represent the overflowing brackish-water layer described earlier in this paper.

The outflow of water from the Arctic Ocean basin into Baffin Bay, through the channels of the Canadian Arctic Archipelago, contributes to the Baffin Current. This ocean current is formed by cold, low-salinity water (-1.8 to 1.8° C, < 34.5%; Dunbar, 1951; Meunch, 1971) that flows southward at depths of 100–300 m across the continental shelf of eastern Baffin Island. This water mass is of Atlantic origin and enters Baffin Bay via Davis Strait, where it is modified by cooling and mixing with surface runoff in northeastern Baffin Bay; or it is modified by cooling and freshening within the Arctic Ocean prior to entering Baffin Bay via Smith, Jones, and Lancaster Sounds (Meunch, 1971).

The Greenland Current flows below the Baffin Current. It is a relatively warm, saline water mass (0° to 2.0°C, 34.2‰ to 35‰; Bailey, 1957; Meunch, 1971) that flows southward at depths of 300–1300 m across the outer continental shelf and slope of eastern Baffin Island. This water originates in the Atlantic Ocean and is advected north via Davis Strait into Baffin Bay by the West Greenland Current. Here the Greenland Current water mixes with Baffin Current water and loses heat as it flows southward along the Baffin Island coast.

Mixing of Baffin Current water and Greenland Current water occurs across a broad front extending from 67°N on eastern Baffin Island to 77°N on western Greenland (Fig. 1). This region, occupied by waters of mixed polar and Atlantic origin, is known as the subarctic marine zone (Dunbar, 1951).

RESULTS

The 26 species of marine molluscs recovered from Expedition Fiord, Axel Heiberg Island (17 bivalves, 8 gastropods and 1 scaphopod) cluster into two discrete mollusc associations (Table 1 and Fig. 5). A *Portlandia-Thyasira* association occurs on sandy mud substrates (Table 2) in the prodeltaic environment of Expedition River and on silty clay substrates (Table 2) at depths of 32–82 m elsewhere in the fiord. *Portlandia arctica* and *Thyasira gouldi* are common species in this mollusc association. Species diversity increases seawards from the prodeltaic environment (i.e., stations B2 and B3, Fig. 2A) through the addition of the bivalves *Yoldiella* spp. and *Delectopecten greenlandicus* and the scaphopod *Siphonodentalium lobatum* in the middle and outer fiord.

An Astarte association occurs throughout Expedition Fiord on silty clay substrates (Table 2) at depths of 3–32 m, except at the fiord head (i.e., stations B2 and B3; Fig. 2A). The bivalves Astarte borealis and Astarte warhami and the gastropod Trichotropis borealis are the most common and abundant species in this mollusc association. The bivalves Macoma calcarea, Macoma loveni and Hiatella arctica and the gastropod Cylichna occulta occur commonly and in low abundance at Sites A, D and F in the middle fiord (Fig. 2A). The diversity of this molluscan association increases in the outer fiord (i.e., Sites C and E; Fig. 2A,B), through the addition of the bivalves Clinocardium ciliatum and Cuspidaria arctica and the gastropod Oenopota novajasemliensis.

The molluscan fauna recorded at sampling stations C4, D4 and D5 marks a transition from the shallow-water *Astarte* association to the deep-water *Portlandia-Thyasira* association. This macrofauna consists of *Astarte borealis* and *Astarte warhami*, representing elements of the *Astarte* association, and *Yoldiella* spp. and *Siphonodentalium lobatum*, representing elements of the *Portlandia-Thyasira* association.

Two mollusc associations were identified by cluster analysis in Jørgen Brønlund Fjord (Table 1 and Fig. 6). A *Thyasira*



FIG. 5. Cross-plot of sampling stations (ordering based on R-mode analysis) versus species (ordering based on Q-mode analysis) from Expedition Fiord. Cluster analyses are based on presence/absence data from dredge samples. Both dendrograms are based on the Jaccard coefficient and Ward's method of clustering. The thick black lines define clusters described in Table 1. Numbers appearing in the cells of the grid record the abundance of molluscs at a sampling station. Depth is reported as the average water depth at which sampling occurred (see Appendices 1 and 2).

TABLE 1. Mollusc associations determined by cluster analysis of the presence or absence of species in dredge samples recovered from Expedition Fiord and Jørgen Brønlund Fjord.

	Association	Stations				
Expedition Fiord:	Portlandia-Thyasira (prodelta)	B2, B3				
	Portlandia-Thyasira (middle & outer Fiord)	A3, A4, B6, C5, E4, E5, F3, F4				
	Astarte	A6, C1, C2, C3, D1, D2, D3, E1, E2, F1				
Jørgen Brønlund Fjord:	Portlandia-Hiatella	H1, H4, H7, H9, H11, H12, H13, H14, H15				
	Thyasira	H2, H3, H5, H8				

association, consisting of *Thyasira dunbari*, *Thyasira pygmaea* and *Yoldiella intermedia* occurs on substrates consisting of clay and stones at depths of 22 to 48 m in the inner and outer basins of the fiord. Bottom water temperatures and salinities, recorded in May and June 1966, range from -1.33°C to -0.70°C and from 31.2‰ to 31.6‰, respectively (Just, 1970).

A *Portlandia-Hiatella* association occurs on heterogeneous substrates consisting of gravel, sand and clay at depths of 5–19 m throughout Jørgen Brønlund Fjord. Bottom water temperatures and salinities, recorded in May and June 1966, range from -0.23°C to -0.93°C and from 30.0‰ to 33.1‰, respectively (Just, 1970). This mollusc association is characterized by the presence and abundance of the bivalves *Portlandia arctica* and *Hiatella arctica*. The diversity of this



11.5 Water depth (m)

FIG. 6. Cross-plot of sampling stations (ordering based on R-mode analysis) versus species (ordering based on Q-mode analysis) from Jørgen Brønlund Fjord. Cluster analyses are based on presence/absence data from dredge samples. Both dendrograms are based on the Jaccard coefficient and Ward's method of clustering. The thick black lines define clusters described in Table 1. Numbers appearing in the cells of the grid record the abundance of molluscs at a station. Depth is reported as the average water depth at which sampling occurred (see Appendix 3).

 TABLE 2. Texture of bottom sediments recovered from Expedition Fiord.

	% Gravel & Sand	% Silt	% Clay
Astarte Association:			
Middle and outer fiord (1	0 samples; 3–32 m dep	oth)	
Mean	1.1	32.4	66.5
Standard Deviation	1.4	8.2	8.3
Portlandia-Thyasira Assoc	iation:		
Fiord head (3 samples; 15	5-57 m depth		
Fiord head (3 samples; 15 Mean	5–57 m depth) 9.3	43.7	47.2
Fiord head (3 samples; 15 Mean Standard Deviation	5–57 m depth) 9.3 6.1	43.7 15.3	47.2 19.9
Fiord head (3 samples; 15 Mean Standard Deviation Middle and outer fiord (1	5–57 m depth) 9.3 6.1 2 samples; 32–81 m de	43.7 15.3 epth)	47.2 19.9
Fiord head (3 samples; 15 Mean Standard Deviation Middle and outer fiord (1 Mean	5-57 m depth) 9.3 6.1 2 samples; 32-81 m de 1.1	43.7 15.3 epth) 37.9	47.2 19.9 61.9

mollusc association increases seawards from the fiord head. The bivalves *Astarte borealis*, *Macoma calcarea*, *Nucula belloti* and *Thyasira gouldi*, and the gastropod *Cylichna alba* occur commonly and in low abundance in the inner and middle fiord. In addition to these species, the bivalves *Astarte warhami* and *Musculus niger* occur commonly and in low abundance in the outer fiord.

DISCUSSION

Zoogeography

Lemche (1941), Thorson (1944), Ockelmann (1958), Macpherson (1971), and Lubinsky (1980) all have noted the similarity in species composition of mollusc faunas

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	Axel H	xel Heiberg Island Ellesmere Island		Gre	enland	Svalbard
	А	В	С	D	E	F
Bivalvia						
Astarte borealis	3 - 45			12-52	6-16	15-25
Astarte warhami	3 - 53				6-47	
Clinocardium ciliatum	9 - 20			12 - 52		15 - 18
Cuspidaria arctica	9 - 14				30 - 80	
Delectopecten greenlandicus	14 - 67	152,180			10 - 190	
Hiatella arctica	3 - 40		Intertidal	8-64	2 - 45	1 - 25
Macoma calcarea	4-16		Intertidal	8-64	2 - 16	
Macoma loveni	3 - 32				6-38	
Mya truncata	3 - 32		Intertidal	8-64	2 - 40	12-15
Portlandia arctica	4 - 81				3-18	
Nuculana pernula	9 - 40			40 - 54	30 - 80	
Thracia devexa	4 - 16				16 - 140	
Thyasira gouldi	5 - 82				8-16	
Thyasira dunbari 8-	-10,57				19 - 47	
Yoldiella fraterna	32 - 45	152				
Yoldiella intermedia	34-66	160, 425 - 604			45 - 190	
Yoldiella lenticula	9-82	180-604			30-50	
Scaphopoda						
Siphonodentalium lobatum	48-72	175, 487			50 - 80	
Gastropoda						
Cylichna alba	18 - 20		Intertidal		5 - 190	15 - 18
Cylichna occulta	4 - 32				3-80	15 - 18
Lepeta caeca	34 - 40			54	15-35	1 - 10
Oenopota cinerea	4 - 6					
Oenopota decussata	30-32					
Oenopota novajasemliensis	9-65				6-40	
Oenopota reticulata	8 - 10				3 - 50	
Trichotropis borealis	4-32			18 - 45	2, 68, 140	

TABLE 3. Depth distribution in metres (m) of molluscs recovered from high arctic fiord and continental shelf environments.

Sources of information: A – Expedition Fiord, Axel Heiberg Island, this study; B – Axel Heiberg Island continental shelf (Wagner, 1964) and unpublished (see Appendix 4); C – Cape Herschel and Alexandra Fiord, Ellesmere Island (Dale, 1985); D – continental shelf off Thule, Northwest Greenland (Vibe, 1939, 1950); E – Jørgen Brønlund Fjord, Greenland (Schiøtte, 1989); F – Van Keulen Fjord, Spitsbergen, Svalbard (Rózycki, 1984).

inhabiting high-latitude continental shelves in the Northern Hemisphere. Table 3 illustrates clearly that the marine molluscs inhabiting Expedition Fiord and Jørgen Brønlund Fjord are distributed widely in high arctic estuarine and continental shelf environments.

The arctic marine zone is defined by the distribution of polar waters on the continental shelves of the Canadian Arctic Archipelago (Fig. 1). Amongst the molluscs recorded from Expedition Fiord, the following species are associated with the arctic marine zone: Astarte warhami, Cuspidaria arctica, Delectopecten greenlandicus, Oenopota novajasemliensis, Portlandia arctica, Thracia devexa, Thyasira dunbari and Yoldiella intermedia. Lubinsky (1980:38) notes that Thyasira dunbari is a shallow water, high arctic species endemic to the northernmost islands of the Canadian Arctic Archipelago and northern Greenland. The remaining 18 species possess a broad tolerance to higher temperatures and salinities and inhabit the marine subarctic zone as well. This group of panarctic molluscs includes: Astarte borealis, Clinocardium ciliatum, Cylichna alba, Cylichna occulta, Hiatella arctica, Lepeta caeca, Macoma calcarea, Macoma loveni, Mya truncata, Nuculana pernula, Oenopota cinerea, Oenopota decussata, Oenopota reticulata, Siphonodentalium lobatum, Thyasira gouldi, Trichotropis borealis, Yoldiella fraterna

and *Yoldiella lenticula*. Note that *Siphonodentalium lobatum*, *Yoldiella fraterna* and *Yoldiella lenticula* inhabit water depths associated with the Atlantic layer in the Arctic Ocean basin (Table 3).

Ice Action in the Sublittoral Environment of Expedition Fiord

The absence of invertebrate macrofauna at depths less than 3 m throughout Expedition Fiord can probably be attributed to the presence of a thick, landfast sea ice cover within Expedition Fiord. Numerous authors have observed a barren zone to depths as great as 5 m that apparently develops in association with landfast sea ice (Madsen, 1936, 1940; Ellis and Wilce, 1961; Bergeron and Bourget, 1984; Thomson et al., 1986). Mortality due to direct freezing of organisms during icefoot development, abrasion by drift ice during breakup in early summer, and physiological stress associated with lower salinities created by melting sea ice and icebergs in summer are believed to contribute to the absence of a shallow-water macrofauna in high arctic fiords. High mortality of shallow marine invertebrates has been observed on shorelines affected by ice abrasion (MacGinitie, 1955; George, 1977; Petersen, 1977; Gordon and Desplanque, 1983; Aitken et al., 1988). Active abrasion of shorelines by first-year and multiyear ice floes was observed in Expedition Fiord during the summer of 1991.

At all sampling sites within Expedition Fiord, with the exception of stations B2 and B3 (Fig. 2A), iceberg scouring has also disturbed the seafloor (Gilbert et al., 1993). The effects of iceberg scouring on the physical properties of marine sediments have received considerable attention in the literature (Reimnitz et al., 1978; Pereira et al., 1988; Bass and Lever, 1989; Woodworth-Lynas et al., 1989); however, less is known about the effects of iceberg scouring on sublittoral benthic community structure. Petersen (1977) has observed that shorelines in southern Greenland exposed to scouring by drifting ice floes and icebergs are devoid of macrofauna to depths of 5 to 10 m. On the inner continental shelf of the Beaufort Sea, the low abundance and biomass of macrofaunal organisms observed at depths of 15 to 25 m is attributed in part to direct destruction of organisms by ice scouring (Carey and Ruff, 1977; Carey, 1991).

Both epifaunal and infaunal organisms may also be frozen directly into developing landfast sea ice and then removed subsequently from their original habitat by drifting ice floes during ice breakup (Medcof and Thomas, 1974; Aitken et al., 1988; Reimnitz et al., 1992). Reimnitz et al. (1992) observed carcasses of shallow marine invertebrates, including the bivalves Astarte borealis, Hiatella arctica and Mya truncata, on the surface of drifting ice floes in channels of the Canadian Arctic Archipelago. These organisms are believed to have been frozen into the ice through the combined action of anchor ice growth and suspension freezing during frazil formation. Both of these processes operate at water depths as great as 20-30 m (Reimnitz and Kempema, 1987; Reimnitz et al., 1987). Although the organisms observed by Reimnitz et al. (1992) are common in the Astarte association inhabiting Expedition Fiord, no marine invertebrates were observed incorporated into sea ice.

Comparison with Other High-Latitude Fiords

The *Portlandia-Thyasira* association inhabiting the prodeltaic environment of Expedition Fiord is characterized by the low diversity and abundance of molluscs. This molluscan association shares these characteristics with *Portlandia* associations recorded from prodeltaic environments in Coronation and Itirbilung Fiords (Syvitski et al., 1989; Aitken and Fournier, 1993) and Scott Inlet (Thomson et al., 1986) along the eastern coast of Baffin Island. Species represented in the *Portlandia-Thyasira* association include *Portlandia arctica*, *Thyasira gouldi* and *Thyasira dunbari* (Table 4).

Water samples recovered from 20 m depth in inner Expedition Fiord indicate that suspended sediment concentrations vary from 6 to 10 mgL⁻¹, temperatures are less than -1.0°C, and salinity is greater than 25‰ (cf. data at 0.9 km, Fig. 4). The three-orders-of-magnitude decrease in suspended sediment concentration between the mouth of Expedition River (i.e., 2-6 gL⁻¹; Maag, 1969; Gilbert, 1990) and the prodeltaic environment indicates high rates of sedimentation (Gilbert et al., 1993).

As was the case in Expedition Fiord, there is a significant input of fresh water and suspended sediment to the fiord-head environment of Coronation and Itirbilung Fiords (Syvitski et al., 1989, 1990; Syvitski and Hein, 1991). In both of these fiords, suspended sediment concentrations in surface waters decrease rapidly seaward from the fiord head. For example, suspended sediment concentrations decrease from 88-153 mgL^{-1} at the mouth of the Itirbilung River to $1-4 mgL^{-1}$ within the prodeltaic environment of Itirbilung Fiord, indicating high rates of sedimentation (Syvitski and Hein, 1991). Water samples recovered at 20 m depth in the prodeltaic environment of Coronation and Itirbilung Fiords indicate that temperature varies from 0°C to -1°C and salinity varies from 30‰ to 32.5‰ (Asprey et al., 1983; Trites et al., 1983; Dale et al., 1989). It is apparent that the organisms constituting the Portlandia-Thyasira association in prodeltaic environments tolerate high suspended-sediment concentrations, rapid sedimentation rates, cold temperatures and variable salinity.

In contrast to the prodeltaic environment, the habitat of the Portlandia-Thyasira association observed in the middle and outer basins of Expedition Fiord is characterized by low sedimentation rates (about 0.5 mm a⁻¹; Gilbert et al., 1993) and salinities greater than 30%. The presence of Delectopecten greenlandicus, Yoldiella spp. and Siphonodentalium lobatum differentiates this mollusc association from the Portlandia-Thyasira association inhabiting the prodeltaic environment. Mollusc faunas inhabiting depths greater than 30 m in Baffin Island fiords and greater than 45 m in Greenland fiords are characterized by species also found in the Portlandia-Thyasira association of Expedition Fiord. Delectopecten greenlandicus, Thyasira gouldi and Yoldiella spp. are common in the Astarte crenata-Bathyarca glacialis association that occurs on muddy substrates at depths of 45 to 200 m in Greenland fiords (Spärck, 1933; Thorson, 1934). In Baffin Island fiords Delectopecten greenlandicus has been observed on muddy substrates at depths of 30-150 m, although it is most abundant on coarse substrates associated with fiord-mouth sills (Dale et al., 1989). Portlandia arctica, Thyasira gouldi and Yoldiella spp. are present within the Onuphid and Maldanid (= Astarte crenata-Bathyarca glacialis) associations that occur on mixed substrates of gravel, sand and mud at depths of 125 to 750 m in Baffin Island fiords (Syvitski et al., 1989; Aitken and Fournier, 1993).

The *Thyasira* association observed in Jørgen Brønlund Fjord is impoverished in terms of both the diversity and abundance of molluscs—characteristics it shares with the prodeltaic *Portlandia-Thyasira* association observed in Expedition Fiord (Table 4). The distribution of the *Thyasira* association on clay substrates at depths greater than 20 m seaward of the fiord-head prodeltaic environment, however, is similar to that of the deep-water *Portlandia-Thyasira* association observed in Expedition Fiord. As in Expedition Fiord, deep-water environments in Jørgen Brønlund Fjord are characterized by the deposition of clay from suspension in brackish surface waters and salinities greater than 30‰ (Just, 1970).

The species composition of the *Portlandia-Hiatella* association inhabiting Jørgen Brønlund Fjord (Table 4) resembles

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TABLE 4. Comparison of the species composition of marine mollusc associations occurring in high-latitude fiords.

Portlandia-Thyasira association recorded in Expedition Fiord and Jørgen Brønlund Fjord:

		Expe Fic Axel H Isl	dition ord, Ieiberg and	Jørgen Brønlund Fjord, Greenland	Itirbilung and Coronation Fiords, Baffin Island
Species	Depth (m):	$15 - 57^{1}$	$5-57^1$ $32-82^2$ $22-$		$55 - 148^4$
Bivalvia					
Delectopecter	n greenlandicus		Х		
Portlandia ar	ctica	Х	Х		Х
Thyasira dun	bari	Х		Х	
Thyasira gou	ldi	Х	Х		
Thyasira pyg	maea			Х	
Yoldiella inte	rmedia		Х	Х	
Yoldiella lent	icula		Х		
Gastropoda					
Buccinum sp.					Х
Naticidae			Х		
Scaphopoda					
Siphonodenta	lium lobatum		Х		

Astarte association recorded in Expedition Fiord:

	Exped	lition	Franz Joseph	Scoresby
	Fio	rd,	Fjord,	Sund,
	Axel H	leiberg	Greenland	Greenland
	Isla	ınd	_	
	Middle	Outer		
	Fiord	Fiord		
Species Depth (m)	: 3-20	4-32	3-455	$5 - 50^{5}$
Bivalvia				
Astarte borealis	Х	Х	Х	Х
Astarte elliptica			Х	Х
Astarte montagui			Х	Х
Astarte warhami	Х	Х		
Bathyarca glacialis				Х
Clinocardium ciliatum		Х	Х	Х
Cuspidaria arctica	Х	Х		Х
Dacridium vitreum				Х
Delectopecten greenlandicus		Х	Х	
Hiatella arctica	Х		Х	
Lyonsia arenosa			Х	Х
Macoma calcarea	Х	Х	Х	Х
Macoma loveni	Х		Х	
Macoma moesta				Х
Musculus discors			Х	Х
Musculus niger			Х	Х
Mya truncata	Х	Х	Х	Х
Nucula tenuis			Х	Х
Nuculana pernula		Х	Х	Х
Pandora glacialis			Х	Х
Portlandia arctica	Х		Х	Х
Thracia devexa	Х	Х		
Thyasira gouldi	Х		Х	Х
Serripes groenlandicus			Х	
Yoldiella frigida				Х
Yoldiella intermedia			Х	
Yoldiella lenticula		Х		Х
Gastropoda				
Alvania janmayeni			Х	Х
Buccinum hydrophanum			Х	
Colus sp.			Х	
Cylichna alba			Х	
Cylichna occulta	Х	Х		
Lepeta caeca			Х	
Lunatia pallida			Х	Х
Margarites groenlandicus			Х	Х

Astarte association recorded in Expedition Fiord continued:

		Expec Fio Axel H Isla	lition rd, leiberg ınd	Franz Joseph Fjord, Greenland	Scoresby Sund, Greenland
Species	Fiord: Depth (m):	Middle 3-20	Outer 4-32	3-455	5-505
Gastropoda c Oenopota bicc Oenopota nov Oenopota pyr Oenopota tenu Trichotropis b	ontinued: arinata ajasemliensis amidalis uiscostata porealis	x	Х	X X X X X	X X

Portlandia-Hiatella association recorded in Jørgen Brønlund Fjord:

		Jør Brør Fjo Gree	gen ilund ord, nland	McBeth Fiord, Baffin Island	Scoresby Sund, Greenland
	Fiord:	Inner/ Middle	Middle/ Outer		
Species	Depth (m):	5 - 19	5 - 19	$5 - 40^{6}$	10-60
Bivalvia					
Astarte borealis		Х	Х		
Astarte warhami			Х		
Axinopsida orbio	culata			Х	
Clinocardium ci	liatum				Х
Delectopecten gr	reenlandicus				Х
Hiatella arctica		Х	Х	Х	Х
Macoma calcare	ea	Х	Х	Х	Х
Musculus discor.	\$			Х	
Musculus niger			Х		
Mya truncata			Х	Х	Х
Nucula belloti		Х	Х	Х	
Periploma abyss	orum			Х	
Portlandia arctic	ca	Х	Х	Х	Х
<i>Thracia</i> sp.				Х	
Thracia devexa		Х			
Thracia truncata	ı				Х
Thyasira gouldi		Х	Х	Х	Х
Gastropoda					
Cylichna alba		Х	Х		
Cylichna occulta	ı		Х	Х	
<i>Cylichna</i> sp.					Х
Diaphana minut	а	Х	Х		
Entocolax ludwi	gi		Х		
Oenopota bicari	nata		Х		
Philine sp.					Х
Retusa obtusa					Х
Trichotropis bor	realis	Х			

¹ *Portlandia-Thyasira* association inhabiting the prodeltaic environment as described in this study

² *Portlandia-Thyasira* association inhabiting the middle and outer fiord as described in this study

- ³ Thyasira association as described in this study
- ⁴ Pioneering *Portlandia* association as described by Syvitski et al. (1989)
- ⁵ Macoma calcarea association as described by Thorson (1933, 1934)
- ⁶ Mature *Portlandia* association as described by Syvitski et al. (1989), Aitken and Fournier (1993)

that of Portlandia associations recorded in McBeth Fiord, Baffin Island (Syvitski et al., 1989; Aitken and Fournier, 1993) and in Scoresby Sund, Greenland (Thorson, 1934). P. arctica is generally considered to occur in greatest abundance on soft clay substrates close to river mouths and active glacier margins, environments characterized by rapid sedimentation and markedly reduced salinities (Ockelmann, 1958; Lubinsky, 1980). At McBeth Fiord and Scoresby Sund, P. arctica is abundant at depths of 5-60 m in fiord-head prodeltaic environments, and is found in association with Hiatella arctica, Astarte borealis, Macoma calcarea, Mya truncata, Thyasira gouldi and Delectopecten greenlandicus. In contrast to the situation in McBeth Fiord and Scoresby Sund, the Portlandia-Hiatella association occurs throughout the length of Jørgen Brønlund Fjord (Schiøtte, 1989). In McBeth Fiord, sediment-laden meltwater derived from hinterland glaciers passes over an extensive outwash plain. Sediment deposition within braided stream channels traversing the outwash plain surface reduces the input of clastic sediment to the fiord-head environment. In this situation organic carbon, derived from phytoplankton and benthic macroalgae, represents a greater fraction of the suspended sediment delivered to the benthos (Syvitski et al., 1989, 1990). This, in turn, may facilitate the shift from a macrofauna dominated by molluscs that are tolerant of food-limited environments, such as Portlandia arctica and Thyasira spp. (Yonge and Thompson, 1976), to a more diverse fauna of suspension-feeding molluscs characterized by the presence of Astarte, Hiatella and Mya.

The Astarte association inhabiting shallow waters in Expedition Fiord corresponds to the arctic Macoma association described by Thorson (1933, 1934) from Greenland fiords (Table 4) and the Astarte association on the inner continental shelf of eastern Baffin Island described by Thomson et al. (1986). The Macoma-Astarte association is characterized by the presence and abundance of Astarte borealis, Macoma calcarea, Mya truncata, and Hiatella arctica. This macrobenthos association inhabits mixed substrates of sand and mud at depths of 5–50 m throughout its range of distribution. The absence of the Astarte association in the inner basin of Expedition Fiord most probably relates to the intolerance of suspension-feeding molluscs such as Astarte, Hiatella, Mya and Trichotropis for the elevated suspended sediment concentrations encountered in this environment.

CONCLUSIONS

The molluscs recovered from Expedition Fiord, Axel Heiberg Island, and Jørgen Brønlund Fjord, Greenland are distributed widely within high-latitude estuaries and across the continental shelves bordering the Arctic Ocean. On the basis of their presence or absence in dredge samples, the 26 species of marine molluscs recovered from Expedition Fiord (17 bivalves, 8 gastropods, and 1 scaphopod) cluster into two discrete mollusc associations. In shallow water (3-32 m), an *Astarte* association is characterized by the presence and abundance of *Astarte borealis* and *Astarte warhami*. In deep

water (> 32 m), a *Portlandia-Thyasira* association is characterized by the presence and abundance of *Portlandia arctica* and *Thyasira gouldi*. In contrast to Expedition Fiord, the shallow-water (5–19 m) *Portlandia-Hiatella* association recorded in Jørgen Brønlund Fjord is characterized by the presence and abundance of *Portlandia arctica* and *Hiatella arctica*. The deep-water (22–48 m) *Thyasira* association recorded in Jørgen Brønlund Fjord is characterized by the presence and abundance of *Thyasira* dunbari and *Yoldiella intermedia*.

The prodeltaic environment of Expedition River is inhabited by an impoverished *Portlandia-Thyasira* association consisting only of *Portlandia arctica* and *Thyasira* spp. These molluscs apparently tolerate the high sedimentation rates, low salinities (< 30‰) and low temperatures (< 0°C) that characterize the prodeltaic environment. The *Portlandia-Thyasira* association observed in middle and outer Expedition Fiord inhabits an environment characterized by low sedimentation rates and salinities greater than 30‰. This mollusc association is differentiated from the fiord-head *Portlandia-Thyasira* association by the presence of the bivalves *Delectopecten greenlandicus* and *Yoldiella* spp. and the scaphopod *Siphonodentalium lobatum*.

The shallow-water *Astarte* association is not present at the fiord head. High suspended-sediment concentrations in inner Expedition Fiord preclude the presence of suspension-feeding molluscs such as *Astarte*, *Hiatella*, and *Macoma*: hence the absence of the *Astarte* association in this environment. The presence of sea ice also restricts the distribution of this mollusc association in Expedition Fiord. The absence of benthic macrofauna at depths of less than 3 m may be attributed to mortality due to direct freezing of organisms during icefoot development, abrasion by drift ice during breakup in early summer, and physiological stress associated with lower salinities created by melting sea ice and icebergs in summer. The processes contributing to the development and persistence of a barren zone to a depth of 3 m in Expedition Fiord remain to be investigated.

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			Inner Fior	d					Middle	e Fiord				
St Deptl	ation h (m)	B2 57	B3 15-20	B5 79-81	B6 34-39	A1 22-40	A2 35-44	A3 55-67	A4 79-81	A6 10-15	F1 3.4-8.8	F2 16-24	F3 32-45	F4 55-65
Bivalvia														
Astarte borealis										Х	Х	Х	Х	
Astarte warhami										Х	Х			
Delectopecten greenlandicus								Х						
Hiatella arctica											Х			
Macoma loveni											Х			
Mya truncata											Х			
Portlandia arctica		Х	Х		Х			Х	Х				Х	Х
Thyasira dunbari		Х												
Thyasira gouldi					Х				Х				Х	Х
Yoldiella fraterna													Х	
Yoldiella lenticula								Х	Х			Х		Х
Gastropoda														
Naticidae (egg cases)					Х				Х					
Cylichna occulta										Х				
Oenopota sp.														Х
Trichotropis borealis										Х				

APPENDIX 1. Living molluscs recovered in dredge samples from Expedition Fiord, Axel Heiberg Island. Stations from Sites A, B and F.

APPENDIX 2. Living molluscs recovered in dredge samples from Expedition Fiord, Axel Heiberg Island. Stations from Sites C, D and E.

			М	iddle Fio	rd					Οι	iter Fic	ord			
Dep	Station oth (m)	D1 4-4.6	D2 9-13.8	D3 18-20	D4 34-40	D5 57-66	E1 4-6	E2 8-10	E4 32-44	E5 55-65	C1 5	C2 14–16.2	C3 30-32	C4 48-53	C5 77-82
Bivalvia															
Astarte borealis		Х	Х	Х			Х	Х	Х			Х			
Astarte warhami			Х	Х	Х	Х	Х	Х		Х	Х	Х	Х	Х	
Clinocardium ciliatum			Х	Х											
Cuspidaria arctica			Х										Х		
Delectopecten greenla	ndicus				Х							Х			
Hiatella arctica		Х			Х		Х				Х		Х		
Macoma calcarea		Х	Х									Х			
Macoma loveni				Х			Х				Х		Х		
Mva truncata							Х						Х		
Nuculana pernula cost	igera		Х		Х										
Portlandia arctica		Х					х	Х		Х					
Thracia devexa			х				X								
Thyasira gouldi									x	x	x				x
Thyasira dunhari								x							
Yoldiella intermedia					x	x								x	
Yoldiella lenticula			Х		X	X								24	Х
Scaphopoda															
Siphonodentalium loba	itum													Х	Х
Gastropoda															
Cvlichna alba				Х											
Cvlichna occulta		Х					Х	Х			Х	Х	Х		
Lepeta caeca					Х										
Oenopota cinerea							Х								
Oenopota decussata													х		
Oenopota novajasemli	ensis		х	х					х	х		х			
Oenopota reticulata	0.0000							х							
Trichotropis borealis		Х					Х	2 x			Х		Х		

						Inner	Fiord	1							Mic	idle F	iord					Outer	Fiord	1
	Station	H1	H1	H2	H2	H3	H8	H9	H9	H11	H11	-	H4	H4	H12	H13	H13	H14	H14	H15	H5	H5	H7	H7
	Depth (m)	10	10	48	48	28	22	16	16	5	5		12	12	12	5	5	19	19	19	25	25	7	7
Bivalvia																								
Astarte borealis		Х	Х					Х	Х						Х	Х	Х						Х	Х
Astarte montagi	ıi													Х										
Astarte warham	i				Х			Х							Х	Х	Х		Х	Х				Х
Axinopsida orbi	culata														Х									
Bathvarca glaci	alis			Х																				
Hiatella arctica								Х	Х	Х	Х		Х	Х	Х	Х	Х						Х	Х
Macoma calcar	ea	Х						Х	Х	Х	Х			Х		Х							Х	Х
Macoma loveni															Х		Х		Х	Х				
Musculus niger															Х				Х	Х				
Mya truncata								Х												Х			Х	
Nucula belloti		Х	Х								Х		Х	Х	Х	Х	Х		Х				Х	Х
Nucula tenuis																				Х				
Portlandia arcti	ca							Х		Х	Х			Х	Х	Х	Х						Х	Х
Thracia devexa									Х										Х					
Thvasira dunba	ri			Х	Х	Х	Х													Х	Х	Х		
Thyasira gouldi		Х	Х					Х	Х					Х		Х							Х	Х
Thyasira pygma	ea			Х	Х																			
Yoldiella interm	edia			Х	Х																			
Gastropoda																								
Chaetoderma pr	roductum							Х																
Cvlichna alba		Х	Х						Х				Х	Х				Х						Х
Cylichna occult	а							Х								Х								
Diaphana minut	ta								Х						Х									
Entocolax ludwi	igi												Х		Х									
Oenopota bicar	inata												Х			Х								
Oenopota novai	asemliensis																Х							
Retusa obtusa													Х	Х	Х									
Trichotropis bon	realis	Х																						

APPENDIX 3. Living molluscs recovered in dredge samples from Jørgen Brønlund Fjord, Greenland.

APPENDIX 4. Marine molluscs dredged on the continental shelf of Axel Heiberg Island during cruises 85200 and 86200 of the Atlantic Geoscience Centre, Natural Resources Canada, Bedford Institute of Oceanography; (B) bivalve, (G) gastropod, (S) scaphopod.

Cruise	Station	°N Lat.	°W Long	Depth . (m)	Species	Cruise	Station	n °N Lat.	°W Long.	Depth (m)	Species
86200	17	80°59	′97°18	3′294	Oenopota declivis (Lovén) (G)	85200	28	81°05	′ 96°51	' 152	- continued:
					Totalella fraterna venni & Busii (G)						Dacridium vitreum (Möller) (B)
	23	81°03	′ 97°07	' 160	<i>Margarites vahli</i> (Möller) (G)						Delectopecten greenlandicus
					Trichotronis horealis						(Sowerby) (B) Hydrobia ventrosa Montagu (G)
					Broderip & Sowerby (G)						Limatula hyperborea Jensen (B)
					Yoldiella intermedia (M. Sars) (B)						Lyonsiella abyssicola (G. Sars) (B)
											Natica clausa Broderip & Sowerby (G)
	88	81°03	' 97°02	2' 150	Malletia abyssopolaris (Clarke) (B)						Neptunea despecta (L.) (G)
											Scissurrella lamellata (A. Adams) (G)
85200	24	81°08	' 96°20	175	Colus togatus (Mörch) (G)						<i>Solariella obscura</i> (Couthouy) (G)
85200	24	01 00	90 20	175	Siphonodentalium lobatum (Sowerby) (S)						<i>Turritellopsis acicula</i> (Stimpson) (G)
											<i>Velutina velutina</i> (Müller) (G)
	28	81°05	′ 96°51	' 152	Acmaea rubella (Fabricius) (G)						Yoldiella fraterna (Verrill & Bush) (B)
					Astarte crenata acuticostata Jeffrey (B)						Yoldiella frigida (Torell) (B)
					Bathyarca raridentata (Wood) (B)						
					Beringius beringi (Middendorff) (G)		44	81°02	96°31	' 102	Cyclopecten graui Knudsen (B)
					<i>Cerithiopsis costulata</i> Moller (G)		50	81°02	' 06°28	115	Baringius haringi (Middendorff) (G)
					Cusnidaria glacialis (Sars) (B)		50	01 02	70 20	115	bernigius bernigi (Middelidofff) (d)
					Cyclopecten graui Knudsen (B)		70	81°04	′ 96°23	' 125	Plicifusus kroyeri (Möller) (G)

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