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**The benthos zonation of the Disko Fjord,
West Greenland**

Michael K. Schmid and Dieter Piepenburg



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Whereas faunistic knowledge of the Greenland benthos is quite complete on the larger scale, more detailed community studies of the bottom fauna in the numerous Greenlandic fjords are relatively scarce. The benthos of the Disko Fjord on the west coast of Disko Island (West Greenland) was sampled using a van-Veen grab. Benthos communities were distinguished by cluster analysis and multidimensional scaling. The zonation pattern mainly reflects a bathymetrical gradient, but the spatial distribution of the fauna is also influenced by the strong aestival river runoff at the origin of the fjord. The resemblances between zones in terms of diversity, abundance, biomass, and faunistic composition were related to possible causes in terms of hydrography, sediment heterogeneity, and temporal patterns of ice cover and primary production. Aspects of zoogeography, trophic structure, and reproduction ecology were also considered in the discussion of community distribution and composition.

Key words:

benthos, Disko Fjord, community, zonation.

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Introduction

Our large scale faunistic knowledge of the coastal waters of West Greenland is almost completely due to the work of several Danish researchers. *Fauna Groenlandica* (Fabricius 1780) already contains the first benthos inventory, which was followed by several taxonomic and zoogeographic studies (e.g. Ditlevsen 1914, Wesenberg-Lund 1950).

Community studies based on quantitative sampling were introduced by Thorson (1933, 1934), Spärck (1933) and Bertelsen (1937) during studies in East Greenlandic fjords. Vibe (1939) described the composition of shallow water assemblages of the Thule district (Northwest Greenland). Ellis (1960) investigated bottom communities at selected sites in West Greenland, Baffin Island and Foxe Basin.

Fjords are typical morphological features of the Greenland coasts. According to the definition given by Gade (1986) they are extremely deep estuaries whose brackish water emissions originating from meltwater and fluvial input may influence the hydrography and current regime of the adjacent coastal waters. Some of the world's largest fjord complexes are found in Greenland, e.g. Kejsers Franz Josephs Fjord and Scoresby Sund in East Greenland. There are also large fjord areas in West Greenland, especially in the southern

part, e.g. Nordre Strømfjord and Bredefjord. The various fjords are distinguished by morphological and hydrographical characteristics which have been shown to have a significant impact on the distribution and composition of the benthos (Wesenberg-Lund 1950).

The Disko Fjord studied in this paper is situated in a region influenced by relatively warm Atlantic water. In terms of zoogeography, this area is characterized as "sub-arctic" (Dunbar 1968). Ecological investigations have not been conducted in the fjord until the recent past. Andersen (1981a, 1981b) described the hydrographic conditions and the composition of the phytoplankton. Curtis (1977) and Petersen (1978) took some benthos samples in the fjord for their studies of biology and life cycles of polychaetes and bivalves respectively. But hitherto there has been no analysis of the benthos communities of the Disko Fjord based on a comprehensive faunistic inventory as conducted in other Greenlandic fjords (Thorson 1933, 1934; Spärck 1933, Ellis 1960). In order to achieve this, benthos sampling with a van Veen grab was included in the scientific programme of an expedition sent by the Institut für Polarökologie to Disko Island in August 1987 (Petersen 1988). In detail, the various questions to be answered by this benthos study were:

– Which species occur in the Disko Fjord? The faunistic inventory enables a zoogeographic characterization

of the fjord benthos and forms the basis of the following community analysis.

- What structure can be identified in the spatial distribution pattern of the bottom fauna? By means of multivariate statistics station groups were distinguished, allowing us to describe the spatial distribution structure of the fauna.
- What are the characteristic features of the different benthos communities? The communities are described in terms of abundances, biomasses, diversities, character species and proportions of feeding and reproduction types.
- Which factors cause the zonation of the fjord fauna? The spatial distribution patterns as well as the faunistic and ecological structure of the fjord fauna are discussed with regard to sediments, temperature, salinity and food supply.

For the description of the benthos zonation the term “community” is used as described by Mills (1969):

“Community means a group of organisms occurring in a particular environment, presumably interacting with each other and with the environment, and separable by means of ecological survey from other groups.”

This pragmatic approach is based on methodology and avoids an ecological interpretation of the community concept which has been controversial (see Petersen 1989) at least since the formulation of the “parallel community” hypothesis by Thorson (1957). The differences between the various theories are mainly a matter of the degree of integration of communities and thus of whether the spatial distribution of species is mainly influenced by biological interactions or by the gradients of abiotic factors (Gray 1984). The present study follows the descriptive approach of Mills (1969) and does not contribute to the ongoing discussion of the community concept. This would require further study of autecological aspects.

Materials and methods

Study area

The Disko Fjord on the west coast of Disko Island (West Greenland), is situated approximately 200 km north of the Arctic Circle, at 69°N and 54°W (Fig. 1). Its length along its main branch is approximately 30 km, its maximum width is 8 km. The fjord is embedded in mountains with heights ranging from 400 m to more than 1000 m. On the southern coast at the fjord mouth, near Nipisat, there is a small wadden region with an area of approximately 10,000 m² (Becker *et al.* 1988).

The Disko Fjord is the largest “non-glacial fjord” of

Disko Island, i.e. there is no glacier flowing directly into the fjord, only several rivers of different sizes. Most of these fall into the southeastern fjord branch called Kangikerlak, forming an extensive river delta there. They carry the aestival fresh water discharge of the Steenstrup Glacier about 20 km further inland.

Little is known about the bathymetry of the Disko Fjord (Petersen 1964, Andersen 1981a). The greatest depths (approximately 200 m) are at the fjord mouth (Fig. 2). The Fjord lacks the mouth sill typical of many Greenlandic fjords. The sounding information available indicates the existence of an internal sill approximately 20 km west of Qivittut (Petersen 1964).

The large-scale hydrography of the waters around Disko Island is shaped by the mixing of the cold Baffin Current coming from the north and the relatively warm West Greenland Current coming from the south (Andersen 1981a). The sea ice cover lasts for eight months from October to May. Large icebergs originating from the huge glaciers of the mainland of Greenland occur throughout the year.

The hydrography of the Disko Fjord is shaped by (1) the superficial inflow of fluvial freshwater, especially during summer in the southeastern fjord branch, and (2) the inflow of relatively warm and salty deep water from the adjacent open sea (Andersen 1981a). In summer the temperatures of a shallow surface layer rise to 14°C. At a depth of approximately 5 m there is a sharp thermocline below which the temperature drops quickly to 5°C. At depths between 50 and 75 m there is a temperature minimum of approximately 1°C. Because of the aestival freshwater inflow the surface salinities are only 15 to 20 ppt. Below the halocline at a depth of less than 5 m the salinity values rise very rapidly to approximately 33 ppt.

Depending on the wind direction there is an outflow of turbid fjord surface water or an inflow of cold sea surface water carrying icebergs (Andersen 1981a). There are also occasional upwelling events (Andersen 1981a).

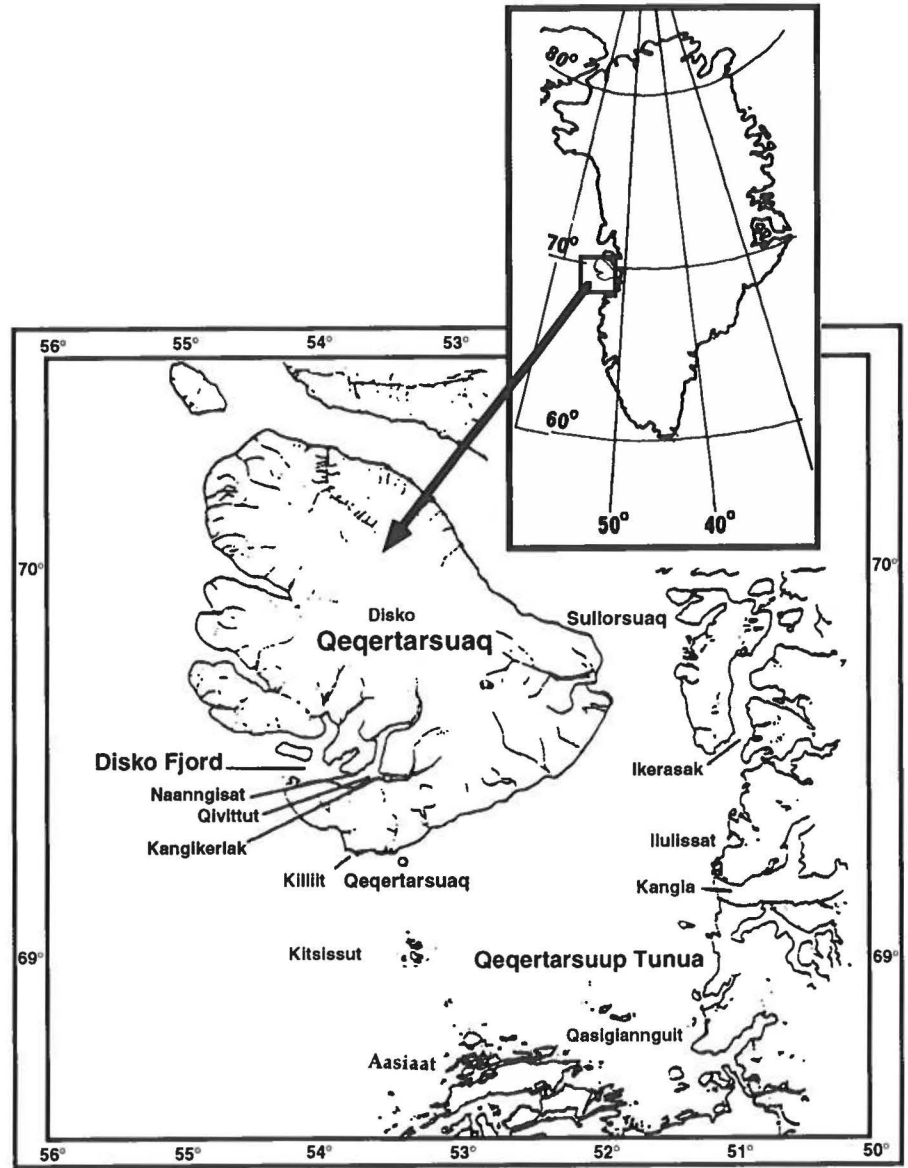
Tides follow a semi-diurnal rhythm. The maximum tidal surface variation at Nipisat is 2.5 m (Becker *et al.* 1988).

The aestival freshwater inflow carries large amounts of fine terrigenous particles which cause high turbidity in surface waters and finally sediment at sheltered fjord locations (Andersen 1981a).

Field sampling

In August 1987 bottom samples were taken from aboard the research vessel “Porsild” at 13 stations in the Disko Fjord by means of a van Veen grab with an aperture of 0.1 m² (Fig. 2). In order to get a representative picture of the bottom fauna the stations were arranged in four transects covering a depth range of 4 to 190 m (Table 1).

Fig. 1. Location of the study area (modified after Andersen 1981 and Thomsen 1982).



The first transect (“Saattut”) lies at the fjord mouth. The second (“Nipisat Havn”), situated two nautical miles to the east, begins at the wadden area of Nipisat. The third transect (“Disko Fjord”) lies approximately in the middle of the fjord, and the fourth (“Qivittut”) covers the area of the fjord origin. At each station two or three replicate samples were taken, i.e. a total of 32 grab samples were obtained.

Samples were washed through screens with 1 mm mesh size. The remainder was preserved in a borax-buffered 4% formalin-seawater solution.

Data analyses

In the lab of the Institut für Polarökologie the formalin-preserved animals were sorted out of the samples, determined to species level and counted. Only molluscs, polychaetes and echinoderms were considered in the following analyses since only abundances of these sessile or little mobile organisms can be estimated quantitatively by the van Veen grab (Eleftheriou & Holme 1984). There were very few specimens of amphipods, decapods or fish in the samples. Such catches are considered too random to be significant.

For species identifications the following literature was used:

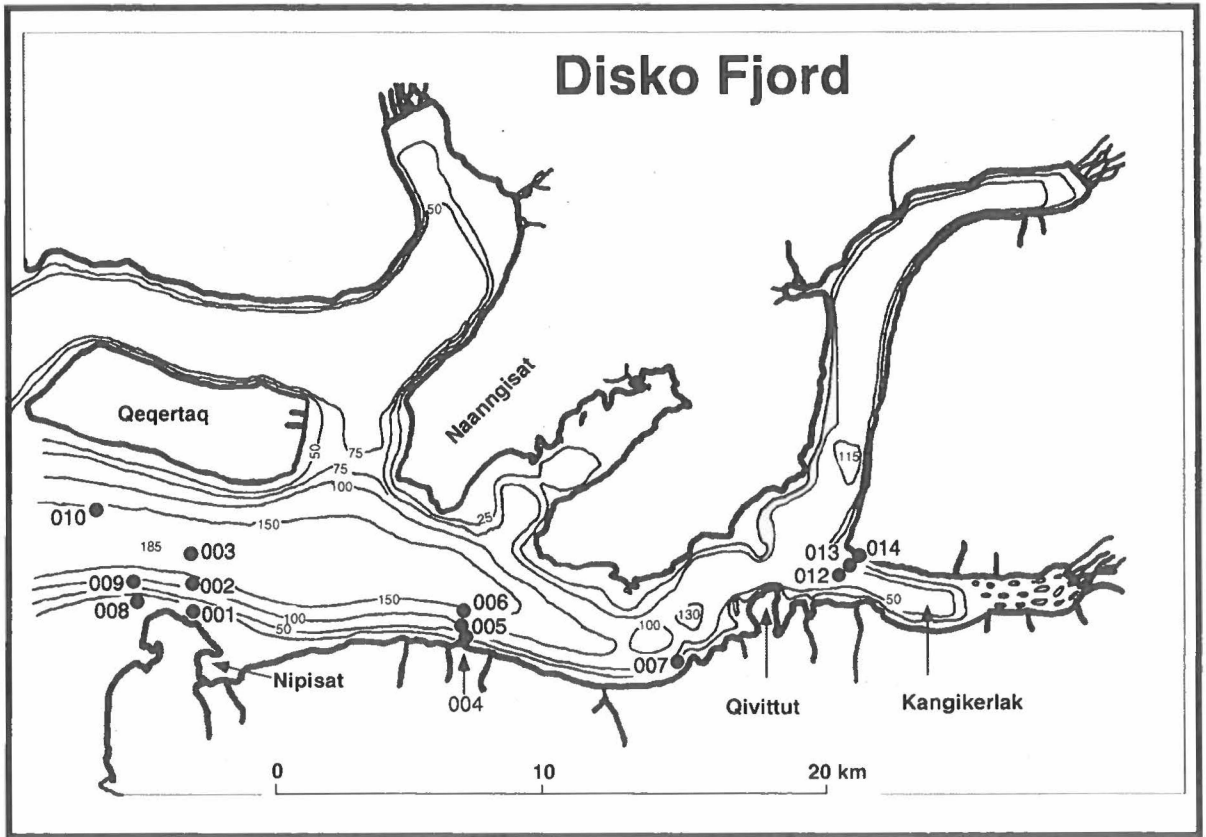


Fig. 2. Bathymetry of the Disko Fjord (Disko Island, West Greenland; after Petersen 1964, Andersen 1981 and O. Humlum (pers. comm.)), and location of the benthos stations sampled in August 1987.

- *Molluscs*: Bernard (1979), Gaevskaia (1948), Lemche (1941), Lubinsky (1980), Macpherson (1971), Schiøtte (1989), Thorson (1944) and Ziegelmeier (1957, 1966).
- *Polychaetes*: Blake (1971), Fauchald (1977), Fauvel (1923, 1927), Hartmann-Schröder (1971), Holthe (1986), Pettibone (1954, 1956, 1963), Rainer (1984), Ramberg & Schramm (1983), Reish (1965) and Wessenberg-Lund (1953).
- *Echinoderms*: Mortensen (1927) and D'Yakonov (1954).

For the most abundant species ash-free dry weight (AFDW) was determined as biomass parameter by multiplying the species-specific mean weights of individuals by abundance values. In order to estimate the mean weights of each species considered a certain number of undamaged specimens – if necessary of different sizes – were dried at 110°C for 24 hours, weighed, then burned at 520°C for 24 hours and finally weighed again. Sample biomass was estimated by summing up the biomass values of these species, which represented as much as 83% to 100% of the total abundance per sample.

The abundance and biomass values were then calculated for 1 m².

The species-station table for abundances forms the basis for the statistical analysis of the spatial distribution patterns of the fjord benthos, following the multi-step approach of Field *et al.* (1982). As data transformation method the “root-root” transform was used. This transformation of the raw data has the effect of reducing the influence of highly abundant species to following calculations.

$$Y_{ij} = \sqrt[4]{X_{ij}} = X_{ij}^{1/4}$$

where X_{ij} = raw abundance of the *i*th species in the *j*th sample and Y_{ij} = corresponding transformed abundance.

As the parameter of faunistic resemblance we used the Bray-Curtis-Index (Bray & Curtis 1957). The index was calculated for all possible sample pairs (*j*, *k*).

Table 1. Station list of van Veen grab samples taken in the Disko Fjord in August 1987.

Station	Sample	Date	Depth (m)	Sediment
Transect "Nipisat Havn"				
1	1a	10.8.87	6	sand, mud
	1b		8	sand, mud
	1c		8	sand, mud
2	2a	10.8.87	114	mud
	2b		104	mud
	2c		110	mud
3	3a	10.8.87	180	mud
	3b		190	mud
Transect "Disko Fjord"				
4	4a	10.8.87	6	sand, mud
	4b		6	sand, mud
	4c		6	sand, mud
5	5a	10.8.87	60	mud
	5b		60	many stones
	5c		60	shells
6	6a	10.8.87	130	-
	6b		130	many stones
"Naanngisat"				
7	7a	10.8.87	24	mud
	7b		32	mud
Transect "Saattut"				
8	8a	11.8.87	12	sand
	8b		12	sand
	8c		14	sand, shells
9	9a	11.8.87	55	sand, mud
	9b		56	sand, mud
	9c		58	sand, mud
10	10a	11.8.87	150	mud
	10b		180	mud
	10c		180	mud
Transect "Qivittut"				
12	12a	12.8.87	82	mud
	12b		87	mud
13	13a	12.8.87	40	mud
	13b		36	mud
14	14a	12.8.87	7	mud
	14b		11	mud

$$\delta_{jk} = \frac{\sum_{i=1}^s |Y_{ij} - Y_{ik}|}{\sum_{i=1}^s (Y_{ij} + Y_{ik})}$$

s: species
i: index of species
j, k: compared samples
Y: abundance values

The Bray-Curtis Index is not affected by joint absences and is therefore sufficiently robust for marine data. For classification of the stations (cluster analysis) there are several sorting strategies (Clifford & Stephenson 1975). The method used was the UPGMA (unweighted pair group method using arithmetic averages), which defines similarity between any two clusters as the arithmetic average of the similarities between the objects in the one cluster and the objects in the other (Romesburg 1984).

In ordination the resemblances between objects are

expressed in a simplified spatial model of few dimensions, e.g. by ordering the objects in a two-dimensional plot according to their resemblances.

Classification and ordination procedures (hierarchical cluster analysis (UPGMA) and multidimensional scaling (MDS) resp.) were employed to distinguish groups of stations with similar faunal composition. As pictorial representation of the similarity pattern, cluster analysis yields a dendrogram, MDS a scatterplot in two dimensions. For both statistical methods there are measures for the "goodness-of-fit": the "Cophenetic Index" (Clifford & Stephenson 1975) for cluster dendrogram and the "stress" of the configuration of the MDS plot (Kruskal 1977). The pattern recognition itself is a subjective process, i.e. this approach involves no statistical tests to verify the group delimitations made. The stations grouped together are characterized by similar faunas and can thus be regarded as locations with the same or at least similar habitats. The geographical distribution of the station groups exhibits a benthic zonation pattern.

The delimitation of faunistic zones was followed by determination and comparison of several indices of community structure to examine the between-habitat differences of the benthic fauna. Species number, diversity H' after Shannon & Weaver (1963), and evenness E after Heip (1974) were calculated to express the different aspects of species diversity. The H -test after Kruskal & Wallis (1952) was used for the statistical assessment of between-zone differences, the U -test after Mann-Whitney (1947) for the subsequent pairwise comparisons of zone characteristics. Non-parametric tests were used instead of ANOVA because our data do not *a-priori* fulfil the preconditions for applying parametric statistics.

As measures of the importance of any species within communities, frequency, dominance and the Biological Index BI after McCloskey (1970) were calculated. The BI combines information on the frequency and abundance of a species. Two indices of community fidelity were computed for each species: DAI (degree of association regarding individuals, i.e. the number of individuals of the species concerned within the association as a percentage of the number of individuals of that species found in the whole study area), and DAS (degree of association regarding stations, i.e. the number of stations with the association at which the species concerned occurred as the percentage of the total number of stations at which that species occurred) (Salzwedel *et al.* 1985). Criteria for the identification of characterizing species were:

- frequency within the association of at least 75%.
- dominance within the association of at least 5%.
- DAI or DAS at least 66%.

In order to characterize the bottom fauna under certain aspects, species were classified according to their zoogeo-

Table 2. List of benthic species in van Veen grab samples taken in the Disko Fjord (Disko Island, West Greenland) in August 1987. Species names given as in literature cited on page 6. Also given is information about the distribution and larval development of the species (a = arctic, ab = atlantoboreal, aba = atlantoboreal-arctic, c = cosmopolitan, - = no information available).

	Distribution	Larval development
MOLLUSCA		
Gastropoda		
<i>Acmea testudinalis</i> (O. F. MÜLLER, 1776)	aba	-
<i>Margarites helicinus</i> (PHIPPS, 1774)	ab	-
<i>Natica clausa</i> BRODERIP & SOWERBY, 1829	ab	-
<i>Oenopota turricula</i> MONTAGU	ab	-
<i>Oenopota spec.</i>	ab	-
<i>Retusa obtusa</i> (MONTAGU, 1803)	ab	-
<i>Retusa spec.</i>	ab	-
Bivalvia		
<i>Nucula belloti</i> (ADAMS 1956)	ab	lecithotrophic
<i>Nuculana minuta</i> (FABRICIUS, 1776)	ab	lecithotrophic
<i>Nuculana pernula</i> (MÜLLER, 1779)	aba	lecithotrophic
<i>Yoldia spec.</i>	a	lecithotrophic
<i>Crenella decussata</i> (MONTAGU, 1808)	ab	lecithotrophic
<i>Musculus niger</i> (GRAY, 1824)	ab	-
<i>Astarte elliptica</i> (BROWN, 1827)	ab	lecithotrophic
<i>Astarte montagui</i> (DILLWYN, 1817)	aba	lecithotrophic
<i>Thyasira gouldii</i> (PHILIPPI, 1845)	a	lecithotrophic
<i>Serripes groenlandicus</i> (BRUGUIERE, 1789)	a	planktotrophic
<i>Clinocardium ciliatum</i> (FABRICIUS, 1780)	a	lecithotrophic
<i>Clinocardium elegantulum</i> MØLLER (BECK)	a	brood care
<i>Macoma calcarea</i> (GMELIN, 1791)	ab	planktotrophic
<i>Hiatella byssifera</i> (FABRICIUS)	c	planktotrophic
<i>Mya truncata</i> LINNE, 1758	ab	-
<i>Mya pseudoarenaria</i> SCHLESCH, 1931	ab	planktotrophic
<i>Thracia myopsis</i> MØLLER (BECK MS), 1842	a	lecithotrophic
POLYCHAETA		
Errantia		
<i>Harmothoë impar</i> (JOHNSTON, 1839)	aba	planktotrophic
<i>Harmothoë longisetis</i> (GRUBE, 1863)	ab	planktotrophic
<i>Harmothoë nodosa</i> (M. SARS, 1860)	ab	planktotrophic
<i>Antinoëlla sarsi</i> (KINGBERG, 1865)	a	planktotrophic
<i>Gattyana cirrosa</i> PALLAS, 1766	aba	planktotrophic
<i>Pholoe minuta</i> (FABRICIUS, 1780)	aba	lecithotrophic
<i>Eteone flava</i> (FABRICIUS, 1780)	aba	planktotrophic
<i>Eteone longa</i> (FABRICIUS, 1780)	aba	planktotrophic
<i>Anaitides groenlandica</i> (ØRSTEDT, 1873)	aba	planktotrophic
<i>Anaitides maculata</i> (L.)	ab	planktotrophic
<i>Anaitides mucosa</i> (ØRSTEDT, 1843)	ab	planktotrophic
<i>Nereimyra punctata</i> MÜLLER, 1776	aba	planktotrophic
<i>Typosyllis armillaris</i> (O. F. MÜLLER, 1776)	a	planktotrophic
<i>Nereis zonata</i> MALMGREN, 1867	aba	planktotrophic
<i>Nephtys paradoxa</i> MALM, 1864	aba	planktotrophic
<i>Nephtys caeca</i> (FABRICIUS, 1780)	aba	planktotrophic
<i>Nephtys longosetosa</i> (ØRSTEDT, 1843)	c	planktotrophic
<i>Lumbrineris fragilis</i> (MÜLLER, 1776)	aba	direct
Sedentaria		
<i>Scoloplo sarmiger</i> (O.F. MÜLLER, 1776)	c	lecithotrophic
<i>Aricidea suecica</i> (ELIASON, 1920)	ab	direct
<i>Spio filicornis</i> (O.F. MÜLLER 1766)	aba	lecithotrophic
<i>Polydora caulleryi</i> MESNIL, 1897	aba	planktotrophic
<i>Polydora caeca</i> (ØRSTEDT, 1843)	c	-
<i>Polydora flava</i> CLAPARÈDE, 1870	c	-
<i>Pygospio elegans</i> CLAPARÈDE, 1863	aba	brood care
<i>Prionospio malmgreni</i> CLAPARÈDE, 1868	c	planktotrophic
<i>Tharyx spec.</i>	ab	-
<i>Cirratulus cirratus</i> MÜLLER, 1776	aba	direct
<i>Chaetozone setosa</i> (MALMGREN, 1867)	aba	direct
<i>Cossura longocirrata</i> WEBSTER & BENEDICT, 1887	aba	-
<i>Scalibregma inflatum</i> RATHKE, 1834	aba	lecithotrophic
<i>Ophelia limacina</i> (RATHKE, 1843)	aba	lecithotrophic
<i>Ophelina acuminata</i> ØRSTEDT, 1843	aba	-

Continued

	Distribution	Larval development
<i>Capitella capitata</i> (FABRICIUS, 1780)	aba	brood care
<i>Heteromastus filiformis</i> (CLAPARÈDE, 1864)	aba	lecithotrophic
<i>Maldane sarsi</i> MALMGREN, 1865	aba	—
<i>Euclymene praetermissa</i> (MALMGREN, 1865)	ab	—
<i>Owenia fusiformis</i> DELLE CHIAJE, 1841	aba	asexual
<i>Galathowenia oculata</i> (ZACHS, 1922)	aba	planktotrophic
<i>Pectinaria granulata</i> (L.)	aba	planktotrophic
<i>Pectinaria hyperborea</i> (MALMGREN, 1866)	aba	planktotrophic
<i>Melinna cristata</i> (M. SARS, 1851)	aba	lecithotrophic
<i>Lysippe labiata</i> MALMGREN, 1866	aba	brood care
<i>Ampharete acutifrons</i> (GRUBE, 1860)	aba	lecithotrophic
<i>Lanassa venusta</i> (MALM, 1874)	aba	lecithotrophic
<i>Amphitrite cirrata</i> MÜLLER, 1771	aba	lecithotrophic
<i>Terebellides stroemi</i> M. SARS, 1835	aba	lecithotrophic
<i>Euchone analis</i> (KRØYER, 1856)	aba	brood care
ECHINODERMATA		
Asteroidea		
<i>Ctenodiscus crispatus</i> (RETZIUS, 1805)	—	—
Ophiuroidea		
<i>Ophiura robusta</i> (AYRES, 1851)	—	—
<i>Stegophiura stuwützi</i> (LÜTKEN, 1857)	—	—

graphic distribution patterns, their feeding ecology, and their ontogenetic development. For each association species and abundance proportions of these species classes were computed.

The classification of species in terms of their zoogeographical distribution was done after Holthe (1978) and Bilyard & Carey (1980). An important prerequisite for this categorization is the definition of Arctic boundaries. The following regions at the periphery of the Arctic Ocean proper were considered as Arctic: the circum-polar shelf seas north of Alaska and Siberia, the Canadian Archipelago, the waters off North and East Greenland and off North and East Svalbard, the northern Barents Sea. Four zoogeographic species groups were distinguished:

- (1) Arctic: occurring only in Arctic regions.
- (2) Atlantoboreal-arctic: occurring both in Arctic and boreal regions of the Atlantic, but not in the Pacific.
- (3) Amphiboreal-arctic: occurring in Arctic regions, but also in boreal regions of both the Atlantic and the Pacific.
- (4) Cosmopolitan: occurring in all oceans.

With regard to their feeding ecology, species were roughly classified into (1) suspension feeders, (2) deposit feeders, and (3) predators.

For the classification of ontogenetic development strategies the terminology of Jablonski & Lutz (1983) has been employed. Two types were distinguished: (1) planktotrophic, i.e. species with free-swimming, feeding larvae, and (2) non-planktotrophic, i.e. species with free-swimming, but non-feeding (lecithotrophic) larvae or with direct development (offspring emerge as benthic juveniles).

Results

Species list

A total of 75 benthic species were found in the van Veen grab samples from Disko Fjord – 48 polychaete species, 24 mollusc species, and 3 echinoderm species (Table 2).

For further quantitative studies only the species of Mollusca and Polychaeta were considered. A total of 17,000 individuals of these species were sorted from 32 grab samples.

Zonation

The examination of multispecies distribution pattern by cluster analysis (Fig. 3) and multidimensional scaling (Fig. 4) showed four distinct station groups:

All six samples from the three stations of the transect Qivittut (Stns. 12, 13 and 14) formed a well defined group (QIVITTUT), independently of the depth range (7–87 m). The composition of the other station groups reflected a depth zonation of the fjord benthos: the five samples from Stns. 1, 4 and 8 (depth range: 6–14 m) were classified as the group SHALLOW. Five samples from depths of 24 to 58 m (Stns. 7 and 9) formed a transitional group (TRANS), and a station group called DEEP encompassed the 12 samples from Stns. 2, 3, 5, 6 and 10 (depths: 60–190 m).

The abscissa of the two-dimensional MDS-plot reflects very clearly a depth gradient whereas the ordinate reflects less distinctly a topographical gradient from the fjord origin to the mouth.

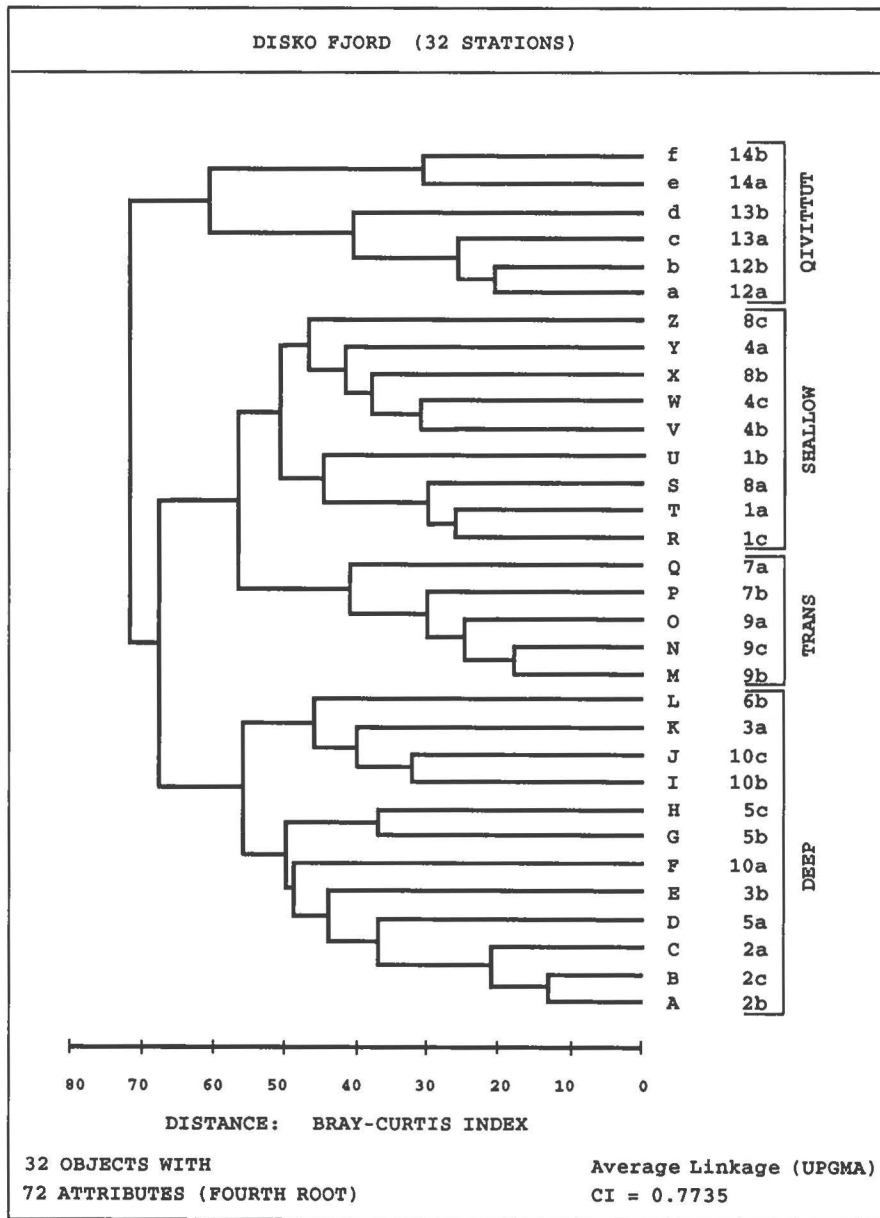


Fig. 3. Dendrogram from the cluster analysis of the van Veen grab samples taken in the Disko Fjord in August 1987 (root-root transformation of species abundances values, Bray-Curtis index as resemblance measure, UPGMA linkage strategy; Cophenetic index: 0.77).

Fig. 5 provides a map exhibiting the zonation pattern of the benthos in the Disko Fjord.

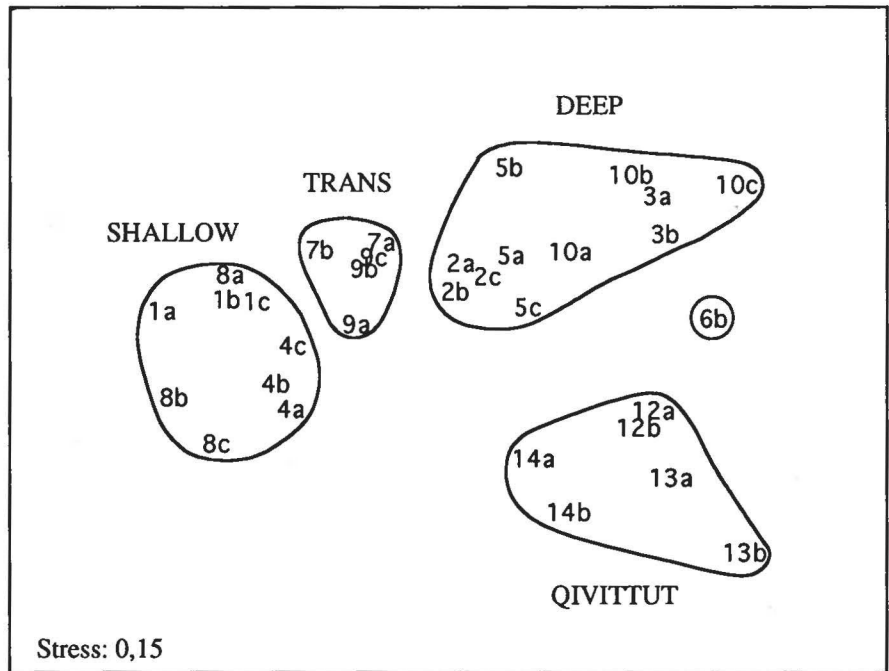
Abundance, biomass and diversity

Benthic abundances differed significantly between zones (Table 3, H-Test: $p = 0.002$). They were significantly higher at stations in the zones SHALLOW and TRANS than compared to those in DEEP and QIVITTUT (Table 3, U-test, $p < 0.05$). Median values were

3080 ind m^{-2} and 7390 ind m^{-2} for SHALLOW and TRANS respectively, and 995 ind m^{-2} and 1220 ind m^{-2} for DEEP and QIVITTUT respectively (Table 3). Highest abundances were found in SHALLOW (21,820 ind m^{-2}) and lowest in DEEP (310 ind m^{-2}).

Benthic biomass differed significantly between zones (Table 3, H-Test: $p = 0.001$). It did not vary significantly between stations in zones SHALLOW, TRANS, and QIVITTUT, but was significantly less in DEEP (Table 3, U-test, $p < 0.05$). Median values were 35.12 gAFDW m^{-2} , 31.58 gAFDW m^{-2} , and 18.14 gAFDW m^{-2} for SHALLOW, TRANS and QIVITTUT respectively,

Fig. 4. Plot of the multidimensional scaling (two dimensions) of the van Veen grab samples taken in the Disko Fjord in August 1987 (root-root transformation of species abundances values, Bray-Curtis index as resemblance measure, stress of MDS solution: 0.15).



and 2.76 gAFDW m^{-2} for DEEP (Table 3). Highest biomass was found in zone SHALLOW (89.34 gAFDW m^{-2}) and lowest in zone DEEP (0.37 gAFDW m^{-2}).

The species numbers differed significantly between zones (Table 3, H-Test: $p = 0.0002$). The numbers per sample did not vary significantly between SHALLOW and DEEP (Table 3: medians 18 and 17 respectively), but were significantly highest in TRANS with a median of 28, and lowest in QIVITTUT with a median of 9 (Table 3, U-test, $p < 0.05$). In species diversity H' there was no significant difference between SHALLOW, TRANS and DEEP (Table 3: medians 1.83, 2.15 and 2.07 respectively), but the diversities in QIVITTUT (median 1.11) were significantly lower (Table 3, U-test, $p < 0.05$). Regarding the sample evenness QIVITTUT showed no significant difference from the other zones (Table 3: U-test, $p < 0.05$) given its the wide range of values (0.15 to 0.60). The evenness values in SHALLOW and TRANS were similar (medians 0.32 and 0.29 respectively), but in both zones the values were significantly lower than in DEEP (Table 3: median 0.46; U-test, $p < 0.05$).

Summarizing the results of the inter-zone comparisons (Table 3), the samples from SHALLOW were characterized by relatively high abundances and biomasses, high diversities, intermediate species numbers, and low evenness. Abundances and biomasses were also high in zone TRANS, and diversity and evenness values were also high and low respectively, but the species numbers in the samples were even significantly higher. The properties of the fauna of zone DEEP were low abundance and low biomass, but intermediate species

numbers, and high diversity and evenness values. Abundances in zone QIVITTUT were low like those in DEEP, but biomasses were significantly higher. Species numbers and diversities were both found to be lower than in all other zones, but evenness values were not.

Species composition

For each station group the most important species, i.e. those species having at least 5% dominance at any one station of the group, are listed in Tables 4–7. Character species were identified according to the criteria defined in "Material and methods".

Species characterizing the benthic fauna of SHALLOW were the polychaetes *Euchone analis*, *Owenia fusiformis*, *Polydora caulleryi* and *Pygospio elegans*, and the bivalve *Mya pseudoarenaria*, which also had the highest mean biomass (Table 4: 16.4 gAFTG m^{-2}).

The character species of TRANS were two polychaete species, *Spio filicornis* and *Ampharete acutifrons* (Table 5). Both species occurred at all stations of this station group. *Spio filicornis* had the highest mean abundance (2,006 ind m^{-2}) and the highest mean biomass (3.09 gAFDW m^{-2}). Other small polychaetes like *Prionospio malmgreni* and *Pygospio elegans* were also dominant in the samples from TRANS, but their association degree was not very high.

There was only one character species for DEEP, the polychaete *Scalibregma inflatum* (Table 6). The other

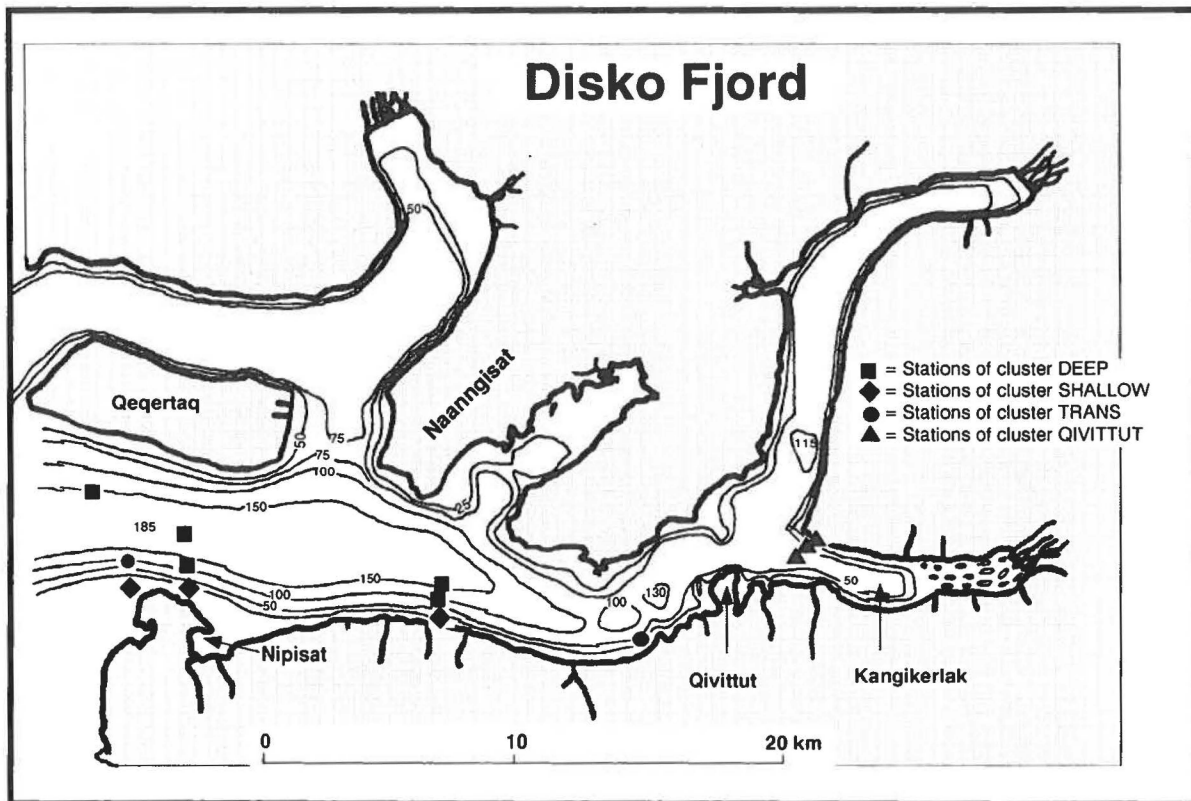


Fig. 5. Faunistic zonation of the benthos of the Disko Fjord.

dominant species in the rather poor samples from this zone (*Chaetozone setosa*, *Prionospio malmgreni*, *Scoloplos armiger*, *Nephtys paradoxa*) showed only low association degrees.

The bivalve *Nucula bellotii* was the character species of QIVITTUT (Table 7). It was the only species which occurred in all samples from this zone, and with a mean abundance of 712 ind m⁻² and a mean biomass of 7.54 gAFDW m⁻² it was by far the predominant species.

Zoogeography

With regard to the geographic distribution of the species four types were distinguished: arctic, atlantoboreal-arctic, amphiboreal-arctic, and cosmopolitan.

Arctic species were the minority in all four zones, both with regard to species proportions and to abundance proportions (Table 8). They only accounted for up to 10% of the species and 2% to 4% of the individuals. In all zones most of the species belonged to the amphiboreal-arctic distribution type. Their species percentages differed only little between station groups (54%, 55%, 60%, and 55% in SHALLOW, TRANS, DEEP, and QIVITTUT respectively). The same was the case with the distinctly smaller species percentages

of the other two distribution types. Atlantoboreal-arctic species accounted for 21% to 29% of the species, and cosmopolitan species for 6% to 14%.

The differences between station groups with regard to abundance proportions were much more pronounced because of the occasionally high abundances of certain species. Overall, amphiboreal-arctic species, mainly polychaetes, occurred with the highest abundances. In total, they accounted for about 3/4 of the sampled individuals. In SHALLOW, they accounted for 86% of the individuals, primarily because of the three amphiboreal-arctic species (*Euchone analis*, *Pygospio elegans*, and *Polydora caulleryi*). The high abundances of the polychaetes *Pholoe minuta* and *Chaetozone setosa* caused the 25% abundance of amphiboreal-arctic species in QIVITTUT.

The atlantoboreal-arctic bivalve *Nucula bellotii* was responsible for the distinct predominance (72%) of this distribution type in QIVITTUT. It was mainly the occurrence of the bivalves *Macoma calcarea* and *Mya pseudoarenaria* from the same distribution type that gave rise to the 9% atlantoboreal-arctic abundance in SHALLOW. *M. calcarea* and, once more, *N. bellotii* accounted for the major abundance share in DEEP.

Species with an extremely wide zoogeographical distribution, mainly cosmopolitans like the polychaete *Prionospio malmgreni*, were also found with consid-

Table 3. Abundances, biomass, species numbers, diversities (after Shannon & Weaver 1963), and evenness values (after Heip 1974) of the van Veen grab samples from the four faunistic zones (SHALLOW, TRANS, DEEP, QIVITTUT) distinguished in the Disko Fjord. For each zone minimum, median, and maximum values are given. Non-parametric H-tests (after Kruskal and Wallis 1952) were used to assess the significance of between-zone differences (p values are given). U-tests (after Mann & Whitney 1947) were used for subsequent pairwise zone comparisons (p < 0.05).

	Shallow (n = 9)	Trans (n = 5)	Deep (n = 12)	Qivittut (n = 6)	H-test (p-value)	Multiple comparisons (U-tests)
Depth (m)	6 8 14	24 55 58	60 122 190	7 38 87		D > T, Q > S
Abundance (ind m ⁻²)	1,080 3,080 21,820	2,850 7,390 10,070	310 995 3,010	620 1,120 1,530	0.002	S, T > D, Q
Biomass (gAFDW m ⁻²)	12.45 35.12 89.34	8.46 31.58 86.06	0.37 2.76 17.42	4.10 18.14 23.79	0.001	S, T, Q > D
Species number per sample	15 18 27	23 28 35	7 17 24	4 9 10	0.0002	T > S, D > Q
Diversity (H')	1.62 1.83 2.36	1.82 2.15 2.68	1.61 2.07 2.30	0.56 1.11 1.86	0.0145	S, T, D > Q
Evenness (E)	0.22 0.32 0.56	0.19 0.29 0.40	0.39 0.46 0.67	0.15 0.28 0.60	0.0159	D > S, T (Q = S, T, D)

erable densities in the Disko Fjord, mainly in the zones DEEP and TRANS (abundance shares of 34% and 22% respectively).

Trophic structure

For the description of the trophic structure of the benthic communities in Disko Fjord three feeding types were distinguished: filter feeders, deposit feeders, and predators.

Overall, deposit feeders were most important in the samples from Disko Fjord (Table 9). In total, they accounted for 47% of the species and about 75% of the individuals. Their species percentages did not differ very much between zones, ranging from 46% in SHALLOW to 58% in DEEP. Variation in abundance proportions between station groups was considerably more pronounced. The percentages ranged from 65% in SHALLOW to 86% in TRANS. Among the most abundant deposit feeders were the polychaetes *Spio filicornis* and *Prionospio malmgreni* in TRANS, the polychaetes *Polydora caulleryi* and *Pygospio elegans* in SHALLOW, and the bivalve *Nucula bellotii* in QIVITTUT.

Filter feeders were evidently of less numerical importance in the benthos of the Disko Fjord. They accounted for 18% of both species and individuals. The relatively highest abundance proportion for filter feeders was found in SHALLOW (28%), mainly because of the occurrence of the polychaete *Euchone analis*. This species and the bivalve *Thyasira gouldii* (as a facultative

filter feeder) were the most abundant filter feeders in DEEP, the latter also in TRANS. In QIVITTUT only three filter feeding species, the bivalves *Clinocardium ciliatum*, *Mya pseudoarenaria*, and *T. gouldii*, were found.

Predators accounted in total for more than a quarter (28%) of the species, but for only 8% of the individuals. Their relatively highest importance was in QIVITTUT (31% and 16% of the species and the individuals respectively), mainly because of the occurrence of the carnivorous polychaetes *Pholoe minuta* and *Lumbrineris fragilis*. Other abundant predators were the polychaete *Nephtys paradoxa* in the zones TRANS and DEEP, and the polychaetes *Eteone flava* and *P. minuta* in SHALLOW.

Early life ecology

In the Disko Fjord most of the benthic organisms (45% of the species and 67% of the individuals) exhibit no pelagic planktotrophic phase in their ontogeny (Table 10). The species proportions of this reproduction type did not differ much between station groups, ranging from 50% in both SHALLOW and DEEP to 56% in QIVITTUT. The abundance percentage of species without planktotrophic offspring was also highest in QIVITTUT (83%), mainly because of the predominance of the bivalve *Nucula bellotii*, which propagates with lecithotrophic larvae. The most abundant species with this reproduction ecology were the polychaetes

Table 4. Station group SHALLOW: List of the numerically most important species. All species showing at least a 5% dominance at any one station of the station group are listed (here: 15 of a total of 48 species). For each species values of the Biological Index (BI, after McCloskey 1970), percentage frequency (Freq), percentage dominance (Dom), mean abundance (Abun: ind m⁻²), mean biomass (Biom: gAFDWm⁻²), and percentage group association degrees (Degree of Association regarding Individuals (DAI) and Degree of Association regarding stations (DAS)) are given. Species are ranked according to BI values. Character species are underlined.

Species	BI	Freq %	Dom %	Abun ind m ⁻²	Biom gAFDW m ⁻²	DAI %	DAS %
<i>Spio filicornis</i>	57	100	4.4	300	0.46	21	47
<i>Macoma calcarea</i>	54	100	3.1	211	12.92	50	33
<u><i>Euchone analis</i></u>	54	89	20.0	1367	2.89	95	40
<u><i>Mya pseudoarenaria</i></u>	53	100	5.4	372	16.37	86	53
<i>Pholoe minuta</i>	43	89	4.4	302	0.36	74	42
<i>Pectinaria granulata</i>	43	89	3.4	234	2.32	94	80
<u><i>Owenia fusiformis</i></u>	36	78	9.3	637	0.61	99	70
<i>Scoloplos armiger</i>	34	89	2.2	153	0.13	43	38
<i>Chaetozone setosa</i>	34	100	7.1	487	0.20	44	29
<i>Thyasira gouldii</i>	33	89	2.1	146	2.20	49	40
<u><i>Pygospio elegans</i></u>	31	78	15.9	1087	0.12	74	54
<u><i>Polydora caulleryi</i></u>	29	89	19.6	341	0.70	99	80
<i>Eteone flava</i>	22	56	2.0	137	0.29	85	42
<i>Amphitrite cirrata</i>	12	44	0.5	33	/	46	44
<i>Capitella capitata</i>	11	44	0.6	40	0.02	50	31

Table 5. Station group TRANS: List of the numerically most important species. All species showing at least a 5% dominance at any one station of the station group are listed (here: 7 of a total of 45 species). For each species values of the Biological Index (BI, after McCloskey 1970), percentage frequency (Freq), percentage dominance (Dom), mean abundance (Abun: ind m⁻²), mean biomass (Biom: gAFDW m⁻²), and percentage group association degrees (Degree of Association regarding Individuals (DAI) and Degree of Association regarding stations (DAS)) are given. Species are ranked according to BI values. Character species are underlined.

Species	BI	Freq %	Dom %	Abun ind m ⁻²	Biom gAFDW m ⁻²	DAI %	DAS %
<u><i>Spio filicornis</i></u>	90	100	38.9	2006	3.09	77	26
<i>Prionospio malmgreni</i>	88	100	24.2	1246	0.75	63	21
<i>Pygospio elegans</i>	72	100	13.4	690	0.07	26	39
<i>Nephtys paradoxa</i>	58	100	4.4	226	0.09	48	23
<i>Chaetozone setosa</i>	50	100	3.1	162	0.06	8	16
<u><i>Ampharete acutifrons</i></u>	46	100	12.2	630	0.19	94	50
<i>Thyasira gouldii</i>	24	80	3.8	194	2.92	37	20

Table 6. Station group DEEP: List of the numerically most important species. All species showing at least a 5% dominance at any one station of the station group are listed (here: 14 of a total of 47 species). For each species values of the Biological Index (BI, after McCloskey 1970), percentage frequency (Freq), percentage dominance (Dom), mean abundance (Abun: ind m⁻²), mean biomass (Abun: gAFDWm⁻²), and percentage group association degrees (Degree of Association regarding Individuals (DAI) and Degree of Association regarding stations (DAS)) are given. Species are ranked according to BI values. Character species are underlined.

Species	BI	Freq %	Dom %	Abun ind m ⁻²	Biom gAFDW m ⁻²	DAI %	DAS %
<i>Chaetozone setosa</i>	95	100	29.1	365	0.149	44	39
<i>Prionospio malmgreni</i>	89	100	23.3	292	0.175	35	50
<i>Nephtys paradoxa</i>	61	92	6.3	78	0.031	40	50
<u><i>Scalibregma inflatum</i></u>	60	92	5.5	69	0.088	82	69
<i>Scoloplos armiger</i>	54	75	9.9	124	0.111	46	43
<i>Macoma calcarea</i>	31	67	3.2	40	2.448	13	30
<i>Nucula bellotii</i>	22	50	1.9	24	0.256	6	35
<i>Lysippe labiata</i>	21	58	3.2	40	0.107	65	47
<i>Euchone analis</i>	20	67	1.4	18	0.037	2	40
<i>Eteone flava</i>	17	50	1.3	17	0.035	14	50
<i>Terebellides stroemi</i>	15	50	0.6	8	0.013	39	50
<i>Lumbrineris fragilis</i>	13	33	1.6	18	/	40	36
<i>Heteromastus filiformis</i>	13	25	0.5	6	/	15	38
<i>Lanassa venusta</i>	11	33	0.6	8	0.057	100	100

Table 7. Station group QIVITTUT: List of the numerically most important species. All species showing at least a 5% dominance at any one station of the station group are listed (here: 9 of a total of 16 species). For each species values of the Biological Index (BI, after McCloskey 1970), percentage frequency (Freq), percentage dominance (Dom), mean abundance (Abun: ind m⁻²), mean biomass (Biom: g AFDW m⁻²), and percentage group association degrees (Degree of Association regarding Individuals (DAI) and Degree of Association regarding stations (DAS)) are given. Species are ranked according to BI values. Character species are underlined.

Species	BI	Freq %	Dom %	Abun ind m ⁻²	Biom gAFDW m ⁻²	DAI %	DAS %
<u>Nucula bellotii</u>	85	100	64.8	712	7.54	89	35
Macoma calcarea	68	83	8.0	88	5.41	14	19
Chaetozone setosa	67	83	6.4	70	0.03	4	16
Nephtys paradoxa	53	83	4.1	45	0.02	12	23
Lumbrineris fragilis	45	67	4.1	45	0.07	51	36
Pholoe minuta	33	33	7.0	77	0.09	13	11
Thyasira gouldii	32	50	1.8	20	0.30	5	15
Terebellides stroemi	28	50	1.4	15	0.49	39	25
Mya pseudoarenaria	20	33	2.4	27	1.17	4	12

Euchone analis and *Pygospio elegans* in SHALLOW, *Spio filicornis* in TRANS, and *Chaetozone setosa* in DEEP.

A total of 39% of the species and 32% of the individuals propagate with pelagic planktotrophous larvae. The variation between station groups was significantly more pronounced in terms of abundance percentages, ranging from 17% in QIVITTUT to 37% in DEEP, than in terms of species percentages, ranging from 40% in DEEP to 44% in QIVITTUT. The most abundant species with this reproduction strategy were the polychaete *Prionospio malmgreni* in DEEP and TRANS, the polychaete *Polydora caulleryi* in SHALLOW, and the bivalve *Macoma calcarea* in QIVITTUT.

For 16% of the species no information on their reproduction biology was available. The abundances of these species were, however, very low, accounting only for a total of 0.7% of all individuals.

Discussion

Zoogeography

The Arctic Ocean as a cold water system is rather young in terms of geological history. Contrary to the Antarctic

a specially adapted fauna could not evolve because of the recurrent immigration of species from adjacent areas, the young age as a cold water system, and the variation of abiotic factors (Clarke & Crame 1989). Many authors have characterized the Arctic littoral fauna as "immature" (Zenkevitch 1963, Bernard 1979).

For the purposes of the zoogeographical classification of species it is important to define the boundaries of the Arctic region. There are several definitions (Ekman 1953, Zenkevitch 1963, Dunbar 1968, Holthe 1978, Sakshaug & Holm-Hansen 1984). The Arctic s.s. encompasses the deep Arctic Ocean proper and its peripheral shelf seas north of America and Eurasia. This mediterranean sea is characterized by ice cover, mostly meridional sea currents and strong aestival river runoff.

Zenkevitch (1963) delimits and subdivides the "Arctic" on the basis of the zoogeographical distribution patterns of the benthic fauna.

The species and abundance proportions of the zoogeographical distribution types give hints of the colonization history of the Disko Fjord.

A total of 24 species of Mollusca have been identified, 7 snails and 17 bivalves accounting respectively for 8% of a total of 92 and 25% of a total of 62 species known to occur in West Greenland as a whole. Each of these 24 species has also been sampled in East Greenland (Ockelmann 1958, Thorson 1944). Abundances and biomass of snails were low in our samples. In terms

Table 8. Species percentages (S) and abundance percentages (A) of the species of four zoogeographical distribution types (Arctic, Atlantoboreal-arctic, Amphiboreal-arctic, and Cosmopolitan) in the Disko Fjord (as a whole) and in the four faunistic zones (SHALLOW, TRANS, DEEP, and QIVITTUT) of the Disko Fjord.

Distribution type	Disko Fjord		Shallow		Trans		Deep		Qivittut	
	%S	%A	%S	%A	%S	%A	%S	%A	%S	%A
Arctic	9	3	10	3	9	4	10	2	9	2
Atlantoboreal-arctic	28	12	29	9	21	7	22	7	21	72
Amphiboreal-arctic	53	73	54	86	55	67	60	57	55	25
Cosmopolitan	9	12	6	2	14	22	8	34	14	1

Table 9. Species percentages (S) and abundance percentages (A) of the species of four feeding types (filter feeders, deposit feeders, predators, and unknown) in the Disko Fjord (as a whole) and in the four faunistic zones (SHALLOW, TRANS, DEEP, and QIVITTUT) of the Disko Fjord respectively. – (= percentages < 1%, / (= absent).

Feeding type	Disko Fjord		Shallow		Trans		Deep		Qivittut	
	%S	%A	%S	%A	%S	%A	%S	%A	%S	%A
Deposit feeders	47	74	46	65	51	86	58	84	50	79
Filter feeders	18	18	23	28	19	6	16	4	19	4
Predators	28	8	29	7	26	8	26	12	31	16
Unknown	4	–	2	–	4	–	/	/	/	/

of zoogeographical distribution six species are atlantoboreal-arctic, one amphiboreal-arctic. Six of 17 bivalve species (35%) can be called Arctic. For the Canadian Arctic 70% of a total of 64 species are reported as Arctic (Lubinsky 1980). Ten of 17 bivalves (59%) have an atlantoboreal-arctic distribution such as *Nucula bellotii*, the character species of the station group QIVITTUT.

The similarity to the bivalve assemblages of the Canadian Arctic (Lubinsky 1980), the western Fram Strait (Piepenburg 1988), and the high-arctic Jørgen Brønlund Fjord in North Greenland (Schiøtte 1989) is low. Only one, four and six species respectively of a total of 64, 21 and 29 species were found in the Disko Fjord. Of those species only *Thyasira gouldii* is an Arctic species; the others all exhibit atlantoboreal-arctic distribution. A bivalve fauna dominated by amphiboreal-arctic species (50%) and atlantoboreal-arctic species (32%) has been reported from the Beaufort Sea north of Alaska (Bernard 1979). Thirteen species of a total of 53 species found in the Beaufort Sea also occur in the Disko Fjord.

A total of 50 polychaete species have been sampled in the Disko Fjord. These species represent a fifth of the 227 species known from West Greenland and a sixth of the 282 species known from Greenland as a whole (Curtis 1979). Curtis (1979) reported 53 benthic polychaete species from the Disko Bay area. 19 species found in the Disko Fjord are not included in his species list.

The polychaete fauna of the Disko Fjord is dominated by amphiboreal-arctic and cosmopolitan species with species and abundance percentages of 62% and 85% respectively. The species proportion of atlantoboreal-arctic species (8 species = 16%) is distinctly less than in case of the bivalves. Only one species, the rare

Typosyllis armillaris, exhibits an Arctic distribution. There is some evidence that some boreal polychaetes have recently extended their geographic distribution off the coast of West Greenland northwards into the Disko area (Kirkegaard pers. comm).

According to Ditlevsen (1937) up to three quarters of the polychaetes found in West Greenland are boreal immigrants. Arctic or atlantoboreal-arctic species account for only 28% of the fauna (Ekman 1953). Polychaete assemblages predominantly composed of amphiboreal-arctic species (77% of the fauna) have been reported from the Beaufort Sea (Bilyard & Carey 1980).

Low proportions of endemic species and a predominance of species with geographic distributions extending into the Atlantic and/or Pacific Ocean have also been reported for other locations and other taxa, e.g. isopod crustaceans (Menzies *et al.* 1973) and sea stars (Grainger 1966), as well as for mixed collections of benthic invertebrates (Piepenburg 1988). There is evidence, however, that Arctic endemism may vary over different taxa: fish exhibit the highest proportions of Arctic species, polychaetes the lowest (Piepenburg 1988).

The general boreal character of the fauna of arctic and sub-arctic shelves and the absence of a strong endemic component have been cited as evidence that the geographical distributions of benthic invertebrates in the North Atlantic, North Pacific and Arctic Ocean are not in equilibrium (Zenkevitch 1963, Knox & Lowry 1977). Fostered by meridional current regimes the zoogeographic isolation of the Arctic is poor and there is still a considerable exchange of species. This hypothesis is further supported by our results.

Table 10. Species percentages (S) and abundance percentages (A) of the species of three ontogenetic development types (planktotrophic, non-planktotrophic, and unknown) in the Disko Fjord (as a whole) and in the four faunistic zones (SHALLOW, TRANS, DEEP, and QIVITTUT) of the Disko Fjord. – (= percentages < 1%), / (= absent).

Distribution type	Disko Fjord		Shallow		Trans		Deep		Qivittut	
	%S	%A	%S	%A	%S	%A	%S	%A	%S	%A
Planktotrophic	39	32	40	34	43	30	40	37	44	17
Non-planktotrophic	45	67	50	66	51	68	50	62	56	83
Unknown	16	–	10	–	6	2	10	1	/	/

Zonation

The spatial distribution of the four faunistic zones in the Disko Fjord (SHALLOW, TRANS, DEEP, and QIVITTUT) reflects gradients of depth and terrestrial influence. The zones are inhabited by characteristic species assemblages which may be interpreted as benthos communities with typical composition. Since the work of Petersen (1913) many quantitative benthic collections from a variety of locations were analysed on the basis of the community concept (e.g. Spärck 1933, Thorson 1934, Zenkevitch 1963). On the basis of his investigations in arctic and boreal regions, Thorson (1951, 1957) developed a global system of "parallel animal communities" which are dominated by certain abundant characterizing species.

Only the species assemblage of the zone SHALLOW in the Disko Fjord fits the Thorson classification (1957). It can be called a modified *Macoma calcaria* community although *M. calcaria* is strictly speaking not a character species but is the most abundant bivalve of this zone. Two other dominant and characterizing species of SHALLOW, the bivalve *Mya pseudoarenaria* and the polychaete *Owenia fusiformis*, belong to the set of characterizing species of the *M. calcaria* community according to the Thorson classification (1957). Communities with a similar composition have been reported from fjords in East Greenland (Spärck 1933, Thorson 1933) and North America (Ellis 1960).

The faunistic composition of the other zones in the Disko Fjord is distinct from that of the communities defined by Thorson (1957). This result supports the findings of other recent community studies in northern regions (Carey & Ruff 1977, Piepenburg 1988). The inadequacy of the system of "parallel communities" is even more evident for boreal and especially for tropical waters (Petersen 1989). The community concept of Thorson (1957) has therefore been abandoned by most authors, and the concept in general is at present interpreted in various ways, especially as regards the degree of community integration and the role of biological self-regulation compared to abiotic factors (Gray 1984).

A variety of factors may cause the zonation of the benthos of Disko Fjord. Considering the narrow depth range of the fjord (0 to 200 m) the obvious depth zonation is certainly not due to depth *per se* (i.e. pressure effects) but to factors which are correlated with depth. Stoker (1981) listed four factors which are thought to have a strong influence on the distribution and structure of benthic communities: rate of primary production, inflow of terrestrial organic matter, bottom current patterns and predation pressure. Benthic biomass in the Bering Sea has been found to be mainly dependent on the quality and quantity of pelagic organic matter (Grebmeier *et al.* 1989). Temperature and sediment type are further prominent factors controlling benthos community structures (Long & Lewis 1987, Grebmeier

et al. 1989). In polar latitudes, the ice cover during winter can have very drastic effects on shallow-water benthos (Petersen 1977, Reimnitz & Barnes 1975).

For the Disko Fjord, unfortunately, little information is available on the factors mentioned above. There is, however, some evidence that it is mainly a depth-correlated gradient of amount and pattern of food supply that shapes the benthos zonation; other factors appear to be of minor importance.

In the Disko Fjord the primary production is very low ($32 \text{ gCm}^{-2}\text{y}^{-1}$) and in most years there is no vernal plankton bloom, only a short bloom during summer (Andersen 1981b). Until the end of August phytoplankton net production is confined to the upper 5 m because of the strong turbidity of the surface layer. Later the euphotic zone reaches a depth of 20 m (Andersen 1981b). The food supply of the benthos originating from pelagic primary production is therefore rather low. Near the shore benthic primary production and the input of terrestrial detritus are additional sources of organic matter. Abundances and biomasses in the zones SHALLOW and TRANS are significantly higher than at deeper stations. Large bivalves with high biomasses only occur in the upper littoral but are completely lacking in the deeper parts of the fjord.

The significance of sediment parameters for the distribution, composition and abundance of the benthic fauna has been shown by many surveys (e.g. Thorson 1957, Sanders 1960, Lie & Kelly 1970, Bilyard & Carey 1979). In the Disko Fjord, however, the benthos zonation is probably not primarily due to bottom heterogeneity. According to the rough substrate classification, soft-bottom sediments occurred at all but one station in Disko Fjord, in other words the between-station variation in sediment composition is rather low. Gravel and pebbles occurred only at one station near a river mouth.

A within-fjord heterogeneity of temperature and salinity may partly explain certain aspects of the benthic zonation pattern. During summer a pronounced pycnocline develops at a depth of approximately 5 m because of warming due to solar radiation and dilution due to meltwater inflow (Andersen 1981a). Temperatures of the thin surface layer can rise to about 10°C and more, and salinities can drop to 15–20 ppt. Within the thermocline and halocline water temperatures drop quickly to less than 1°C , and salinities rise to 33 ppt. Beneath the surface layer the water column is nearly homogenous. The distinct seasonal variation in temperatures and salinities in surface waters as well as ice effects during winter may be responsible for the significantly fewer species numbers in zone SHALLOW. Relatively few adapted species may be able to cope with these conditions. However, ice scour does not completely prevent benthic life in the upper littoral, as high biomasses of slow-growing, long-aged bivalves in this zone indicate. The ice foot may, on the contrary, have a protective effect for the organisms dwelling near the shoreline (Petersen 1977).

Unlike many other fjords in West Greenland the Disko Fjord lacks a threshold sill hindering the inflow of relatively warm Atlantic bottom water. The temperatures of fjord bottom water are therefore above 0°C even during winter (Andersen 1981a). From the few existing echo soundings there is evidence, however, that a sill exists in the eastern part of the fjord near Qivittut (Petersen 1964) causing bottom water temperatures to remain permanently below 0°C in this part of the fjord, which corresponds to the zone QIVITTUT. In addition to the temperature anomaly the conditions in this zone are mainly shaped by aestival river runoffs causing high inflow rates of freshwater and terrigenous particles, high water turbidity and high sedimentation rates.

Trophic structure

The benthic species were very roughly classified into three feeding types: deposit feeders, suspension feeders, and predators. The group of deposit feeders, which was the most important one in the grab samples from the Disko Fjord both with regard to species and abundance percentages actually includes species with rather different feeding modes. It includes, for instance, unselective deposit feeders like the polychaete *Capitella capitata* and selective deposit feeders like *Polydora* spp. In the latter case even subgroups called “suckers”, “fumlbers” or “pipetters” can be distinguished (Hempel 1957, Ott 1988). Deposit feeders rely on organic material which has accumulated on the sea bottom, i.e. the sea floor itself serves as a food store for the deposit feeders (Thayer 1979, Petersen 1978). Sedimentation and accumulation of particulate matter is promoted by low bottom current velocities which typically occur at sheltered, normally deep locations. This may be an explanation of the particularly great predominance of deposit feeders in the zones DEEP and QIVITTUT.

Suspension feeders showed significantly lower percentages than deposit feeders in the samples from the Disko Fjord, both with regard to species numbers and abundances. They reached their proportionally greatest importance in zone SHALLOW where each of the five character species is either an obligatory (*Euchone analis*, *Mya pseudoarenaria*, *Owenia fusiformis*) or facultative suspension feeder (*Pygospio elegans*, *Polydora caulleryi*).

Organisms of this type feed on the organic particulate matter which drifts in the near-bottom water layer after being imported to the benthos by sedimentation processes and/or lateral advection from the locations of production (pelagic realm, littoral-benthic habitats, terrestrial ecosystems). Generally, they cannot use the food source of the deposit feeders, the organic material which has accumulated in or on the sea floor after its final deposition. Suspension feeders are therefore particularly dependent on the amount and temporal var-

iation of the food import to the benthic system, i.e. on the conditions influencing the production of organic matter and the processes of sedimentation and/or resuspension.

The degradation of organic matter is generally less advanced for drifting particles than for finally deposited material, i.e. the nutritive quality of the food of suspension feeders is generally higher than that of deposit feeders. The suspension of particulate matter in water requires certain minimum bottom current velocities. Especially favourable conditions for suspension feeders are therefore generally found at exposed and shallow sites which are not too far apart from the locations of primary production and where current velocities are normally sufficiently high (Petersen 1978).

Pelagic primary production is known to be rather low – approximately 30 gCm⁻²y⁻¹ in the Disko Fjord (Andersen 1981b). The organic matter produced may to a great extent circulate within the pelagic system and, thus very little if any of it, may be exported to benthic systems. Most of the food for the benthic organisms probably comes from littoral sources and is preferably partitioned to the shallow water habitats. There, tidal currents and waves favour a (re)suspension of particulate material on which suspension feeders then can feed. On the other hand, very high sedimentation or resuspension rates may have a negative influence on suspension feeders because their filtering apparatus may be clogged (Carey & Ruff 1977). This may be the case in zone QIVITTUT where a lot of material – especially of terrigenous origin – is imported by the freshwater inflow, causing a very high water turbidity. At shallow sites too, the benthic fauna is characterized by the deposit-feeding bivalve *Nucula bellonii*.

To the predators found in the grab samples from the Disko Fjord belong species of limited mobility like the snail *Natica clausa* which feeds on sessile or hemi-sessile bivalves, but there were also errant polychaetes like *Gattyana* spp., *Harmothoe* spp. or *Anaitides* spp. which feed on mobile prey. The species percentages of predators are relatively high, perhaps indicating a high degree of specialization in a particular kind of prey and/or the lack of a food limitation for predators. The low abundances and biomasses of predators may be interpreted as an indication of low predation pressure in the benthos, a phenomenon which Thorson (1957) regarded as characteristic of arctic regions. According to Ellis (1960) the low abundances of predators are primarily caused by the low infaunal production in arctic waters.

Early life ecology

According to Thorson (1936, 1950) the reproduction of arctic as well as deep-sea species is generally characterized by features like direct development, brood care or a relatively short, lecithotrophic larval stage. On the

contrary, many species in warmer waters propagate by means of planktotrophic larvae. Mileikowski (1971) introduced the term "Thorson's rule" for the obvious tendency for species with planktotrophic larvae to decrease with increasing depth and latitude.

Ockelmann (1958) reported that only 15% of the bivalve species of East Greenland propagate by means of planktotrophic larvae. Piepenburg (1988) found that only 11% of the macrobenthic species in the western Fram Strait belong to this reproduction type. Compared to these data, in the Disko Fjord the species percentage of bottom species with planktotrophic larvae is quite high (about 40%). But this might be an overestimation. The classification of the species into reproduction types was carried out according to information taken from the literature (e.g. Hartmann-Schröder 1971, Pettibone 1963). This information is most often based on studies of populations in boreal areas and may not always apply to populations of the same species in arctic waters. It is known that polychaete species with a wide geographical distribution in particular can be very variable in their reproduction (Wesenberg-Lund 1950). For instance, there is evidence that the populations of the polychaete species *Pholoe minuta*, *Eteone longa* and *Capitella capitata* in the Disko Bugt differ in their reproduction ecology from those in boreal waters (Curtis 1977). This may also be true of other species in the Disko Fjord, and this implies that the percentage of the species with a non-planktotrophic reproduction may be greater than has been estimated in the present study.

In arctic regions species with planktotrophic larvae are generally in the minority with regard to species numbers, but quite often these very species dominate the benthic fauna with regard to abundance and/or biomass, as was found e.g. by Curtis (1977) and Petersen (1978) at littoral sites near Disko Island and by Piepenburg (1988) in the western Fram Strait. This pattern was not observed in the Disko Fjord, where species without planktotrophic larvae accounted for the highest abundance percentages in all zones (62% – 86%). The predominance of species with planktotrophic larvae in certain arctic areas may be attributed to a high pelagic production- at least temporarily and locally caused by favourable hydrographic conditions (e.g. polynyas, gyres etc.) and at least occasionally leads to high survival rates and subsequently to a high settlement success of meroplanktonic larvae. The special conditions assumed to promote pelagic production may be lacking in the Disko Fjord, where no pronounced spring bloom was observed by Andersen (1981b).

The preconditions for the stability of any population in a given arctic area are that a sufficiently high proportion of the offspring recruits to it each year and that any developmental stage (egg, larvae, adultus) is able to overwinter recurrently. In the waters near Disko Island Curtis (1977) found larvae in the tubes of the polychaetes *Capitella capitata*, *Euchone analis* and *Polydora*

caulleryi. Brood care adaptation increases the chance of survival of the individual larvae considerably and causes a retention of the offspring in the area. *E. analis* and *P. caulleryi* spawn in autumn, and their lecithotrophic larvae overwinter on or just above the sea floor (Curtis 1977).

In accordance with the results of Curtis (1977) and Petersen (1978) several of the benthic species in the shallow habitats of the Disko Fjord, both polychaetes (e.g. *Terebellides stroemi*, *Amphitrite cirrata*, *Polydora spp.*, *Euchone analis*) and bivalves (e.g. *Serripes groenlandica*, *Hiatella byssifera*), occurred with two or more size classes, indicating that the populations consisted of various cohorts. There is thus evidence that these species are able to overwinter as adults, even at littoral sites where there may be freezing, at least temporarily, during winter.

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Tarling, D. H. 1967. The palaeomagnetic properties of some Tertiary lavas from East Greenland. – Earth and Planetary Science Letters 3: 81–88.

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